THE ROLE OF

NITROGEN AVAILABILITY, HYDROPERIOD AND LITTER QUALITY

IN ROOT DECOMPOSITION

ALONG A BARRIER ISLAND CHRONOSEQUENCE

by

Christine Elizabeth Conn
B.S. Biology 1989, Towson State University
M.S. Biology 1991, Old Dominion University

A Dissertation submitted to the Faculty
of Old Dominion University in Partial Fulfillment
of the Requirement for the Degree of

DOCTOR OF PHILOSOPHY

ECOLOGICAL SCIENCES

OLD DOMINION UNIVERSITY
December 1994

Approved by:

Frank P. Day, Jr. (Director)

ACKNOWLEDGEMENTS

My thanks and appreciation are extended to the members of my dissertation committee, Professors Frank P. Day (Chairperson), Andrew Gordon and Richard Whittecar, for their thoughtful review and assistance during the completion of this research. Additionally, I appreciate the support and guidance provided by these members and my other candidacy committee members, Professors Mark Butler and Gerald Levy, throughout my doctoral program. I give special thanks to my advisor, Professor Frank P. Day, who gave invaluable encouragement and exemplary mentorship throughout my course of study at Old Dominion University.

The project was funded through National Science Foundation grant BSR-9007899. Additional financial assistance was provided by a Special Doctoral Research Assistantship from Old Dominion University. The University of Virginia provided the infrastructure making research possible at the Virginia Coast Reserve Long Term Ecological Research Site.

I thank all those who participated in the project. These efforts not only contributed to successful research but also forged bonds of mutual encouragement, support and friendship.

The unwavering belief in my success held by my mother and father, Barbara and David Conn, sister Elisa and brother Andy have been sources of strength. Thank you for being there. Finally, to my husband Doug: thank you for your patience, love and conviction. Your daily support has been an important part of my success and, together, we will reap the rewards.

TABLE OF CONTENTS

APPENDICES

LIST OF TABLES

TABLE

LIST OF FIGURES

FIGURE

CHAPTER I

INTRODUCTION

OVERVIEW OF THE RESEARCH PROBLEM

The decay of organic matter is a universal property of all ecosystems. However, the dynamics of decay differ widely among ecosystems and ultimately control ecosystem structure and function through influences upon soil fertility and nutrient cycling. The process of decomposition transfers organic matter to long-term soil organic pools (Parton et al. 1987) and controls the rate of nutrient release for plant uptake and production (Vitousek and Sanford 1986).

In the face of global climate change associated with rising carbon dioxide levels, the carbon and nutrient dynamics of decomposition are receiving increasingly more attention (Aber et al. 1990). A number of models, such as CENTURY and GEM, have been developed and refined in order to understand the carbon:nutrient interactions during decay that ultimately regulate production, mineralization of carbon and nutrients and long-term carbon and nutrient storage (Parton et al. 1987, Rastetter et al. 1991). Several important factors have emerged. Climate, particularly temperature and moisture, and litter substrate quality are considered the most important, at least on a regional to global scale (Meetenmeyer 1978, Donnelly et al. 1990, Vitousek et al. 1994). Substrate quality, referring to the chemical composition and physical structure of the litter type (Swift et al. 1979), is influenced by plant nutrient status and carbon allocation patterns (Vitousek. 1982, Chapin 1980). Nitrogen and phosphorus litter content have been linked to decay rates as a function of the nutritional requirements of decomposer communities (Bargali et al. 1993, Melillo et al. 1982, Enríquez et al. 1993). The types of carbon available in the litter substrate, such as lignin and cellulose, which vary in quantity and degradability, also regulate decay rates (Berendse et al. 1987, Day 1982).

On a more localized level, additional site-specific factors, such as soil texture, soil moisture, oxygen availability, pH, and the types of decomposer communities can influence decay dynamics (Cornejo et al. 1994, Howarth and Hobbie 1982, Smith 1982, Howard and Howard 1974). Soil nitrogen and phosphorus availability may also influence decay dynamics directly by supplementing microbial nutrition, or indirectly through influences on substrate quality (Hunt et al. 1988, Melillo et al. 1982, Shaver and Melillo 1984).

Factors that influence decay rates also influence the behavior of nutrients during the decay sequence (Melillo and Aber 1984, Berg and McClaugherty 1989). As an example, litter initially low in nitrogen decays more slowly and immobilizes more nitrogen, a process by which absolute amounts of nitrogen are accumulated over initial amounts (Cuevas and Medina 1988, Berendse et al. 1987). Not only is nitrogen immobilization influenced by microbial responses to nitrogen limitation, but lignin content of the substrate has been positively correlated to immobilization via a physicochemical complexing mechanism (Aber and Melillo 1982, Berg et al. 1984, Berendse et al. 1987). Similar dynamics have been proposed for phosphorus (Berg and McClaugherty 1989, Borie and Zunino 1983).

The bulk of research accumulated on this topic has focused on aboveground litter dynamics (Day and Megonigal 1993, Vogt et al. 1986, Parker et al. 1984). However, contribution to soil organic matter and nutrient pools by root turnover can equal or exceed aboveground litter inputs (Hendrick and Pregitzer 1993, Megonigal and Day 1988) and, as such, it is recognized that belowground processes play an important role in ecosystem dynamics (McClaugherty et al. 1982, Nadelhoffer et al. 1985, McKane et al. 1990). However, the breadth of our knowledge concerning ecological processes in the belowground environment lags far behind the advances made in understanding aboveground dynamics (Vogt et al. 1986). The technical difficulties encountered in the study of belowground systems and the time consuming nature of the work contribute to this disparity (Symbula and Day 1988, Montague and Day 1980).

In spite of the obstacles, a few studies have been conducted on root decomposition dynamics. Some studies suggest the burial of both aboveground and belowground litter increases decay and mineralization rates (McLachlan and van der Merwe 1991, Seastedt 1988, Seastedt et al. 1992). In contrast, other studies indicate belowground material decomposes more slowly and tends to immobilize more nitrogen and phosphorus during decay than aboveground litter (Aber et al. 1990, McClaugherty et al. 1982). More research needs to be conducted in order to tease apart controls on belowground processes and to assess differences between aboveground and belowground ecosystem level processes.

STUDY OBJECTIVES

This study sought to evaluate controls on belowground decomposition in light of generally held paradigms constructed for aboveground decomposition models. The following questions were addressed: Do belowground decomposition dynamics behave in ways similar to aboveground dynamics? Do influences of environment and substrate quality operate in similar ways? How is this behavior regulated by nutrient limitations or excesses? Answers to these questions were approached by studying the carbon, nitrogen and phosphorus dynamics of decomposing roots. The study was conducted on a nutrient-limited barrier island ecosystem which provided further insight concerning the influences of ecosystem nutrient status on these processes. Additionally, the research was conducted along an upland dune and wetland swale chronosequence. This arrangement provided the opportunity to evaluate environmental influences associated with landscape position and the unique physical, chemical and biological influences associated with site age on the decay dynamics of roots.

The following chapters present the research findings in detail. Chapter II addresses the environmental and substrate quality controls on the carbon, nitrogen and phosphorus dynamics of root decay. How these dynamics differ in response to differences associated with site age and topographic position (dune vs. swale) within same-aged sites were evaluated. Chapter III presents the results of a nitrogen fertilization study conducted along the dune chronosequence in order to determine whether decay process are nitrogen limited and how this affects ecosystem nutrient cycling. Chapter IV summarizes the research results. Chapter I contains a study site description and presentation of methods which are general to both studies.

INTRODUCTION TO THE STUDY AREA

The barrier island ecosystem

The barrier island ecosystem is regarded as a nutrient limited environment (Kachi and Hirose 1983, Willis and Yemm 1961, Ernst 1983), primarily due to the nature of the soils (van der Valk 1974). Sandy soils have very low cation exchange capacity, low water holding capacity, are well drained and generally do not accumulate large quantities of organic matter due to rapid carbon mineralization (Ehrenfeld 1990, Brady 1990, Parton et al. 1987). Leaching potentials are high and nutrient retention is low (Brady 1990, Willis et al. 1959). The majority of nutrients are stored in the live biomass component (Ehrenfeld 1990, van der Valk 1974).

A variety of fertilization experiments in coastal environments demonstrated that the major limiting nutrients to production are nitrogen, phosphorus and, to a slight degree, potassium (Willis 1963, Atkinson 1973, Kachi and Hirose 1983). Most nutrient inputs are in the form of salt spray which contributes potassium, magnesium, sodium and calcium (Clayton 1972, Etherington 1967) and has been identified as a possible source of nitrogen (Wilson 1959). A significant source of nitrogen input is nitrogen-fixing symbionts associated with dune plants such as *Lathyrus japonicus* L. and *Strophostyles helvola* (L.) Ell. and interdunal depression shrubs, *Myrica pennsylvanica* Loisel. and *M. cerifera* L. (Tiffney and Eveleigh 1983, Tyndall and Levy 1978). Nutrient losses are primarily in the form of groundwater export of leachates (Ehrenfeld 1990, van der Valk 1974) although denitrification losses can be significant in anaerobic environments (Vitousek and Howarth 1991).

The few studies that have investigated decomposition processes and nutrient dynamics in coastal environments have suggested turnover of organic matter and nutrients is rapid (van der Valk 1974, Atkinson 1973), especially belowground (McLachlan and van der Merwe 1991). The introduction of litter into the belowground system may be an important factor regulating coastal nutrient cycling and organic turnover.

The study site

Hog Island is one of thirteen islands that extend from Chincoteague inlet to the mouth of the Chesapeake Bay (Figure 1). These islands are part of the Nature Conservancy's Virginia Coast Reserve (VCR). The VCR is a National Science Foundation Long Term Ecological Research (LTER) site. VCR LTER research is administered by the University of Virginia.

Hog Island is a narrow low-lying barrier island 11.3 km in length, averaging 0.8 km in width and lying 14 km off the Virginia coastline of the Delmarva peninsula (Dueser et al. 1976, Figure 2). Mean daily temperatures for this region range from -1 to 10E C in January and 18 to 30E C in July. Records of mean annual total precipitation range from 81 to 122 cm.

Sandy soils of the Newhan, Corolla and Duckston series occur across the chronosequence (Dueser et al. 1976). The Newhan series (mixed, thermic typic udipsamments) are loose, excessively drained soils forming the frontal and interior dunes. Corolla soils (mixed, thermic aquic udipsamments) co-occur with Newhan soils, forming the Newhan-Corolla complex, and occupy lower areas of interior dunes. These soils are poorly to moderately well drained and possess a seasonally high water table. Interior

Figure 1. Location of Hog Island within the Virginia Coast Reserve.

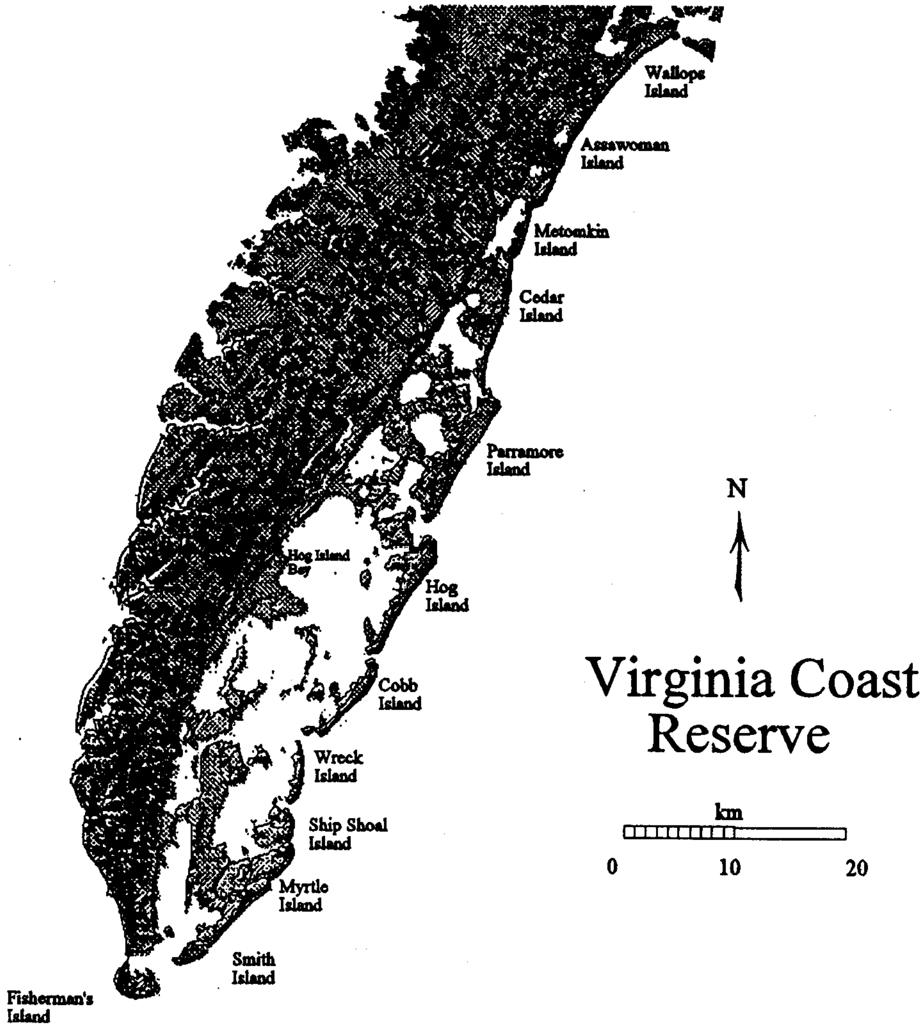
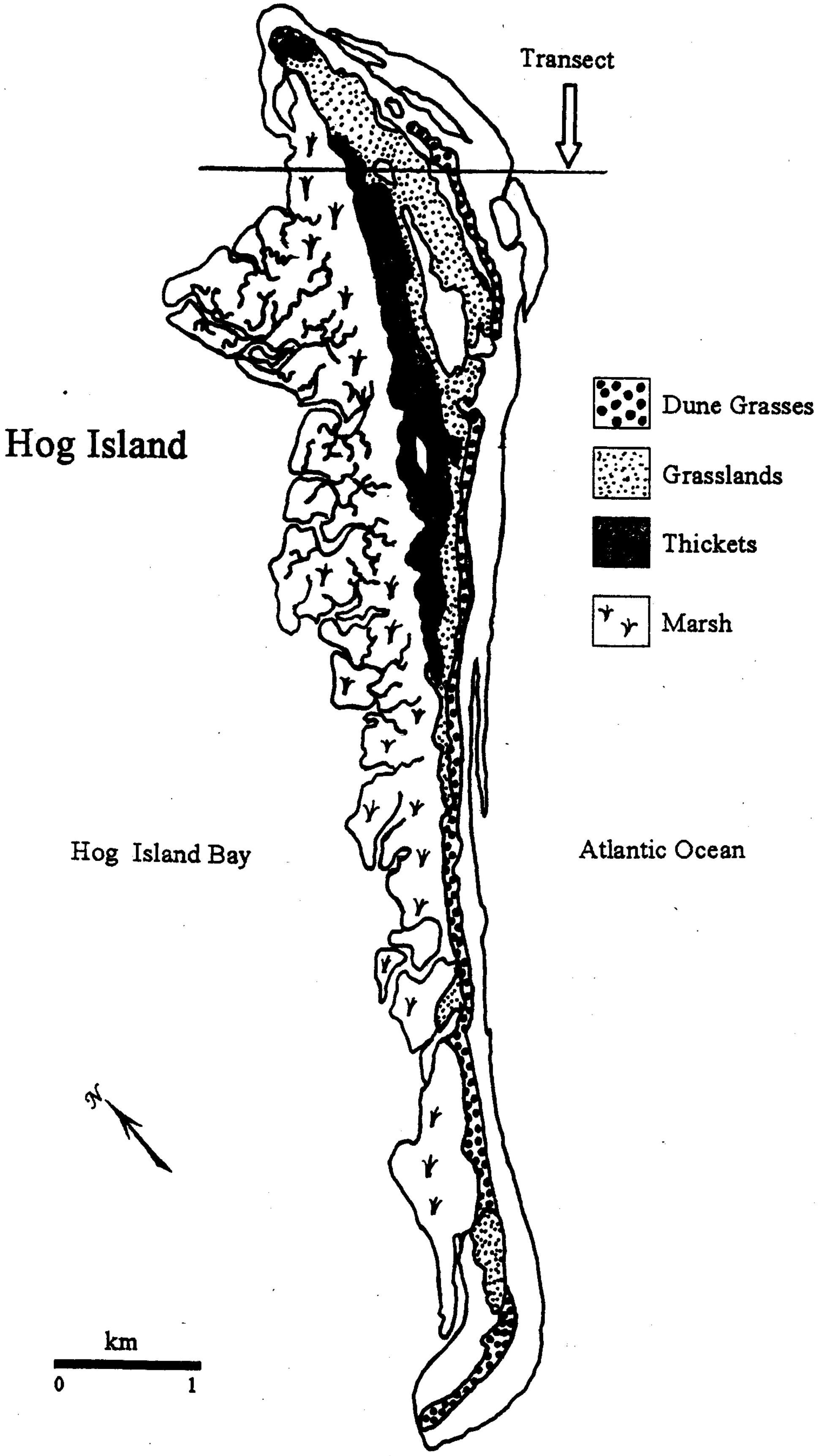

Wallops Island
Assawoman Island
Metomkin Island
Cedar Island
Parramore Island
N
Hog Island Bay
Hog Island
Virginia Coast Reserve
Cobb Island
Wreck Island
km
Ship Shoal Island
0
10
20
Myrtle Island
Smith Island
Fisherman's Island

Figure 2. Location of transect across Hog Island chronosequence.


Transect
Dune Grasses
Grasslands
Thickets
Marsh
Hog Island
Hog Island Bay
Atlantic Ocean
N
km
0
1

swales exhibit Duckston soils (mixed, thermic typic psammaquents). Duckston series generally have a permanent high water table, are nearly level, and may receive groundwater discharge from adjacent dunes.

Land use activity, first documented in the 1600s, began with Accomac and Accohannock Indian use of the islands and lagoons for fishing and hunting (Dueser et al. 1976). English settlers displaced the Indians during the early 1700s to acquire pasture lands for livestock. Continued use of the island culminated in the settlement of the village of Broadwater by the early 1900s. In 1933, a violent storm persuaded most villagers to abandon the island. The most significant land use since has been the presence of grazing cattle and sheep. The last feral cows were removed from Hog Island in the early 1980s (Hayden et al. 1991). Today, Hog Island is a protected wildlife refuge.

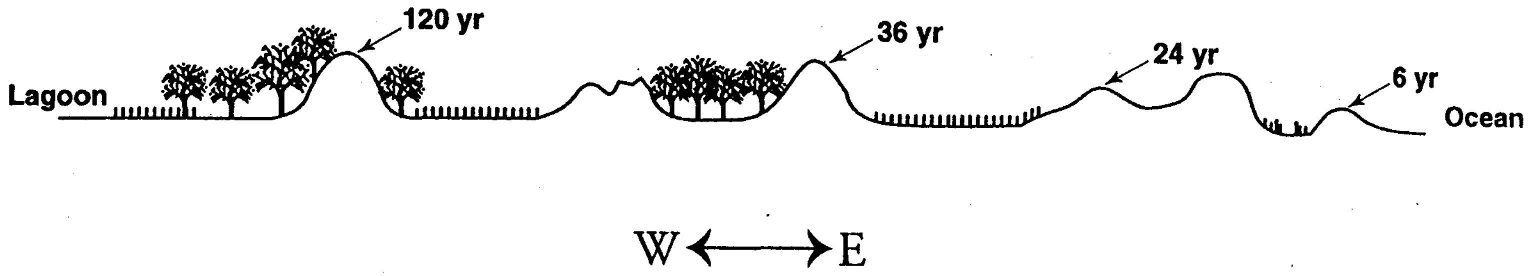
The Chronosequence

Historical surveys of Hog Island reveal remarkable shifts in shoreline position (Deuser et al. 1976). Prior to 1871, Hog Island had a broad accreting southern tip, typical of regressive island segments, which supported woodland communities comprised of loblolly pine (*Pinus taeda* L.), red cedar (*Juniperus virginiana* L.) and various oak species. Accretion rates were approximately 20 m/year. The slender northern two thirds of the island was undergoing a transgressive period, retreating at a rate of 11 m/year. The years following 1871 exhibited a reversal in accretion/erosion trends, producing a broadening northern end and retreating southern end. Currently, the northern end regresses at a rate of 5 m yr^{-1} while the southern end erodes 5 m yr^{-1} (Hayden et al. 1991). The north end regression produced a series of dune lines, lying parallel to the shoreline. These formations mark historic shoreline positions (Oertel 1974).

Four sites were identified along the chronosequence (Figure 3). Each area consisted of a dune formation with its associated swale. Dune lines were dated through historical records consisting of aerial photographs, disturbance events, such as fire and storms, and geologic markers associated with these disturbances (Hayden pers. comm., Hayden et al. 1991). The 6 year dune represents the current day primary dune line. The frontal dune is broken up by low flats and primarily supports *Ammophila breviligulata* Fernald. and *Spartina patens* (Aiton) Muhl.. Both are clonal perennial grasses and recognized dune building species (Cleary and Hosier 1974, Godfrey et al. 1974). The adjacent 6 year swale primarily supports *Spartina patens*. The three older dunes, aged 24, 36 and 120 years, also support these dune grasses. *Panicum amarum* Ell., another perennial and rhizomatous species, is present on both the 24 and 36 year dunes and, to a lesser degree, on the oldest dune. A variety of annual grasses, such as *Triplasis purpurea* (Walter) Chapman and *Aristida tuberculosa* Nutall., and other herbaceous species also occur in these dune environments. Both the 24 and 36 year old dune sites are located on fairly continuous and broad ridges. The ridge line of the 120 year dune has broken up but has fairly large dune islands surrounded by low *Myrica cerifera* L. (wax myrtle) thickets and *Spartina patens* marshes. Swale sites lie behind (west) of the dune sites. The 24 year swale supports a broad *Spartina patens* marsh. Dense thickets of *Myrica cerifera* dominate the 36 and 120 year swales.

Distinct zones of herbaceous vegetation nearest the beach, grading into shrubby thickets found along the Hog Island chronosequence, represent a typical gradational

Figure 3. Hog Island Chronosequence.


120 yr
36 yr
24 yr
6 yr
Lagoon
Ocean
W
E

change in vegetation seen in numerous regressive coastal environments (Wells 1942, Oosting 1945, Tyndall and Levy 1978, Ehrenfeld 1990). These zones, once considered seral stages of coastal primary succession (Wells 1942, Martin 1959), are now believed to be maintained by abiotic variables, such as salt spray, moisture levels and sand movement (Oosting 1945, van der Valk. 1974, Tyndall and Levy 1978). However, autogenic forces modify the coastal environment considerably. The increase of vegetation cover and patterns of species replacement along the chronosequence stabilizes shifting sands and increases soil fertility (Hawk and Sharp 1967, Willis et al. 1959). Biotic interactions, such as herbivory and competition, are also receiving more attention as important controls on barrier island vegetation structure (Ehrenfeld 1990). As a result of weathering and stabilization by vegetation, edaphic factors also exhibit gradients in space. Across coastal chronosequences, organic matter, total Kjeldahl nitrogen, phosphorus and cation exchange capacity increase and bulk density decreases (Willis et al. 1959, Etherington 1967). Similar gradients should exist along the Hog Island chronosequence and influence belowground carbon, nitrogen and phosphorus dynamics during decay.

METHODS

The environmental/substrate quality study and the nitrogen fertilization study were conducted at the same sites. Data could then be conveniently shared between both studies. The following methods section presents the study design, sampling regime and measurement techniques common to both studies. Methodologies used to address specific hypotheses are reserved for later chapters.

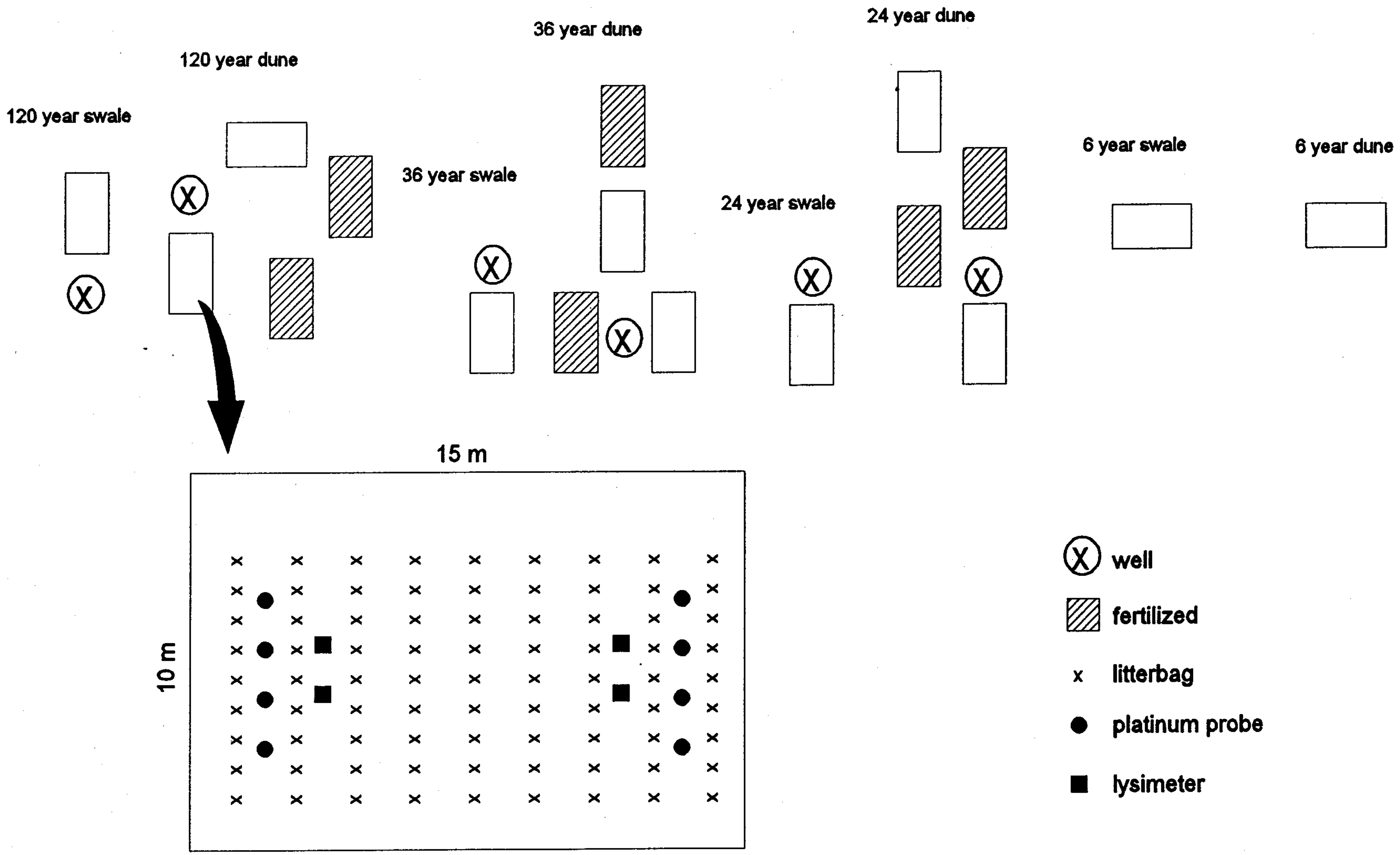
Field study design

At each site, sampling areas, approximately 150 m^2, were identified for intensive belowground process and microenvironmental measurements. Due to a fertilization experiment conducted at the three older dune sites, the sampling areas were expanded to a total of four areas of which two received a fertilization treatment. Swale sites and the youngest dune site had one intensive sampling area each. These localized study areas provided tight coupling between microenvironmental monitoring and process measurements that would have otherwise been impossible due to time and equipment constraints. Figure 4 illustrates the layout of sampling areas.

Within each of the sampling areas, litter bags containing roots were inserted into the soil profile during February 1991. Following Tupacz and Day (1989), the litter bags were constructed to integrate decay processes over a vertical soil profile. The bags were 40 cm long, divided into four 10 cm sections and inserted lengthwise into a vertical slit in the soil. The top of the litterbag was positioned at the top of the soil-atmosphere interface. Once inserted, the opened slit was closed, allowing full soil contact with the buried litterbag. The litterbags were systematically placed in each sampling area in a row formation. A 1 m gap between rows allowed one to walk down rows for sampling purposes while minimizing impacts upon specific burial sites (Figure 4).

Sampling began in March of 1991 and continued on a regular basis through March of 1992 for a total of 11 separate sampling events. Litterbags were retrieved after 30, 78, 111, 150, 187, 218, 255, 280, 306, 336 and 371 days. Three more sampling periods followed at 469, 622 and 833 days to account for longer term but less frequent analysis.

Figure 4. Map view of sampling areas.


120 year swale
120 year dune
36 year swale
36 year dune
24 year swale
24 year dune
6 year swale
6 year dune
15 m
10 m
well
fertilized
litterbag
platinum probe
lysimeter

The youngest dune and swale sites were sampled after 111, 187, 280, 371 and 622 days.

Decay measurements

Belowground plant material (roots and rhizomes, where applicable), collected during the fall and winter of 1990 from each dune and swale site, was representative of dominant communities at each site. A heterogenous assortment of litter more closely approximates the decay dynamics of the entire community (Day 1982, Dwyer and Merriam 1983). Only *Spartina patens* root and rhizome material was gathered from the 6 and 24 year swales while roots from the 36 and 120 year swales originated from *Myrica cerifera*. Root and rhizome material collected from dunes represented the dominant grasses present at each site. Upon harvesting, the root material was washed free of sand, air dried and placed in 1 mm nylon mesh litter bags. Air dry weights were recorded and converted to oven dry weights using conversion factors obtained from subsamples of the original belowground material. The air-dried substrate approach was used to avoid any chemical alterations of the material that might have occurred by oven drying (Hackney and de la Cruz 1980).

Five litter bags were randomly selected from each sampling area during each sampling period. The bags were rinsed with tap water to remove adhering sand, and roots growing into bags were plucked out and quantified by number and weight. The decomposing substrate was oven dried and weighed to determine mass loss. During the first 8 sampling periods (30 to 280 days) and on the 11th (371 days) and 13th (622 days) sampling period, three bags from each sample set were randomly chosen for chemical analyses. Individual samples were bulked by depth, ground in a Wiley mill (40 mesh) and digested by a sulfuric acid-hydrogen peroxide method (Technicon Instruments 1977). The digestate was analyzed colorimetrically on a Scientific Instruments AP-200 autoanalyzer using the modified Total Kjeldahl method for total Kjeldahl nitrogen and the molybdate blue method for phosphorus (Technicon Instruments 1977). From each site and treatment combination, the ground replicates from 111, 187, 280 and 371 day samples were bulked and analyzed for lignin-like constituents. This approach sacrificed statistical testing but significantly reduced the time required for analysis. Carbon quality was analyzed by an acid detergent fiber fractionation method resulting in an acid-insoluble residue classified as lignin (James and Theander 1981). This fraction also contains non-lignin acid-insoluble substances, but collectively will be referred to as lignin due to similarities in decomposability (Berg and McClaugherty 1989).

Environmental measurements

Throughout the first year of the study, hydroperiod, soil Eh, soil pH, and soil temperature were measured. Soil water and soil were collected for nutrient analyses and soil organic matter determinations. Monitoring microenvironmental variation over depth allowed tight coupling between biological process measurements and the corresponding microenvironmental influences.

Continuous records of groundwater fluctuations were generated by wells installed at each site that were equipped with Stevens model 68 type F water level recorders (Figure 4). Platinum probes, permanently buried at four different depths (5, 15, 25 and 35 cm, Figure 4), used in conjunction with an Orion specific ion meter and a calomel reference electrode provided soil redox potential measurements (Faulkner et al. 1989). Adding 244 millivolts to the recorded value standardized soil redox potential to a hydrogen electrode. Two sets of probes were permanently installed within each study area. Soil pH was measured in the field using a Photovolt portable pH meter and combination glass and reference electrode immersed in a 50:50 soil:deionized water slurry. Four depths in the soil profile were sampled (0-10 cm, 10-20 cm, 20-30 cm and 30-40 cm). Two sets of soil pH readings were taken in each area adjacent to regions where litterbags had been removed. Soil temperature was measured at two depths of the soil profile (10 and 30 cm) at two locations within each area situated by the permanently installed platinum probes. Soil water, collected by tension porous cup lysimeters permanently installed at 15 cm below ground level, was analyzed for salinity, ammonium, nitrate, total Kjeldahl nitrogen (TKN), total phosphorus, and orthophosphate levels (Figure 4). This paper provides an overview of nutrient and organic matter data. Full treatment of the data is presented elsewhere (Day and Lakshmi unpublished). Additionally, soil samples from the top 10 cm were collected for a soil nitrogen mineralization study which provided data on extractable soil nitrogen (ammonia and nitrite-nitrate) across the chronosequence.

Soil pH, Eh and temperature were gathered approximately every two weeks throughout the first year (February 1991 to February 1992). Soil water and soil collections coincided with sample bag collections. Ground water levels were not monitored at the 6 year old dune and swale site. However, one set of pH, Eh, and temperature measurements were collected from these sites during the same sampling periods for the older sites.

CHAPTER II

THE INFLUENCE OF ENVIRONMENT AND LITTER QUALITY ON ROOT DECOMPOSITION DYNAMICS

INTRODUCTION

As organic matter moves through fresh litter pools to the formation of stable organic matter, decomposition processes produce marked changes in carbon and nutrient chemistry as mass is lost. Initially, the influence of environment and initial litter quality assume critical roles in the chemical transformation and disappearance of organic matter (Melillo et al. 1989).

Environmental factors, such as low pH, low oxygen tension and low temperature can influence the rates and kinds of decomposer activities, generally resulting in an inhibition of decay (Anderson 1981, Atlas and Bartha 1987). In many wetland systems, hydroperiod exerts significant control on rates of organic matter decay through these abiotic factors and operates on both horizontal (soil surface) scales and vertical (soil profile) scales (Brinson et al. 1971, Day and Megonigal 1993). In continuously flooded systems, anoxic conditions can reduce decay belowground while high moisture availabilities, coupled with atmospheric oxygen flux, may increase aboveground decay (Neckles and Neill 1994). A vertical transect through saturated soils often shows a gradient of decreasing decay with increasing depth associated with increasing durations of soil anoxia (Tupacz and Day 1990, Hackney and de la Cruz 1980). A seasonal drawdown of water often increases decay rates, both aboveground and belowground, relative to continuously flooded and even non-flooded environments (Day and Megonigal 1993, Mitsch and Ewel 1979). Litter quality also regulates rates of decay (Day 1982, Taylor et al. 1989, Berg and McClaugherty 1989). Litter low in nitrogen and/or phosphorus and high in recalcitrant carbon fractions, such as lignin, makes a poor substrate for decomposers.

Melillo et al. (1989) proposed a paradigm, based on many aboveground decay studies, for nitrogen dynamics within the decaying litter, which can be tentatively extended to phosphorus dynamics. Typically, a phase of leaching occurs, followed by a period of nutrient accumulation, and terminates with a phase of net release (mineralization). Accumulation of nitrogen greater than initial amounts commonly occurs (net nitrogen immobilization). Increases to twice initial amounts are possible (Melillo and Aber 1984). Net nitrogen mineralization is triggered by carbon limitations imposed on microbial decomposers as C:N ratios drop to a critical threshold (Berendse et al. 1987) and is also correlated with the onset of lignin degradation. Decomposers are forced to attack more resistant forms of carbon and are no longer nitrogen limited (Berg and McClaugherty 1989, McClaugherty et al. 1985).

The potential for net nitrogen immobilization is controlled by a number of factors: 1) material initially low in nitrogen will immobilize more nitrogen due to microbial nutrient limitations (Vitousek et al. 1982), 2) material high in lignin is correlated with high nitrogen immobilization due to physicochemical reactions that bind nitrogenous compounds to polyphenolic compounds (Fauci and Dick 1994, Aber and Melillo 1982), and 3) high nitrogen levels coupled with high lignin levels intensify lignin-nitrogen interactions and can cause increased net nitrogen immobilization (Berg and Theander 1984) and suppression of decay rates due to the production of a highly refractory residue (Aber et al. 1990, Camiré et al. 1991). Rapidly decaying litter may proceed directly to the mineralization phase (Cornejo et al. 1994, Vogt et al. 1986, McClaugherty et al. 1984).

Environmental factors can influence nutrient dynamics directly through modification of decay rates and indirectly through modifications on carbon chemistry. Lignin concentrations typically increase during initial stages of decay as more easily degraded non-structural carbohydrates and structural carbohydrates are attacked (Berg et al. 1984, Smith 1982). Absolute amounts can increase by humification of secondary metabolites (Schlesinger 1985, Fogel and Cromack 1977). Under anoxic conditions, selective degradation of non-lignified organic material is enhanced since aerobic decay is required for polyphenolic degradation

(Wilson et al. 1986, Howarth and Hobbie 1982).

This study used the environmental, vegetational and nutritional differences associated with site age and topographic position (dunes and swales) to evaluate environmental and substrate quality controls on root decomposition dynamics.

METHODS

Study design

Roots from the 24 year swale (*Spartina patens*) buried at all sites, except for the 6 year old dune and swale, acted as a standard substrate for environmental/site effects. Within sites, comparison of *Spartina patens* root decay with native root decay demonstrated litter quality influences under similar environmental conditions. Thirtysix year swale roots (*Myrica cerifera*) buried in the 24 year swale allowed litter quality comparisons under 24 year swale environmental conditions. Combined site and substrate quality effects were assessed across the chronosequence by comparing native root dynamics. This *in situ* approach provided unique insights concerning gradients associated with landscape position and their influence upon the belowground nutrient cycles of a barrier island ecosystem.

Statistical analyses

Differences in soil temperature, soil pH and soil Eh (reduction-oxidation potential) between sites and between depths within a site were tested for significance using a split-plot ANOVA where site was the main plot and depth was the subplot. Residuals were used as the dependent variable following a regression based adjustment to remove temporal variation. Data lacking a depth factor (soil water salinity, soil nutrients and soil organic matter) were analyzed for site effects by one way ANOVA. Day and Lakshmi (unpublished) provided soil nutrient and organic matter analyses.

Differences in percent mass remaining of *Spartina patens* roots and native roots were evaluated using a three way analysis of variance where the depth factor was treated as a split-plot of both site and time. Two way ANOVA (site x time) tested for differences in percent nitrogen and phosphorus remaining in the litter. Assumptions of normality and homogeneity of variance were evaluated and transformations were performed, if needed. Tukey's Honestly Significant Difference (alpha = .05) test, adjusted for the actual number of comparisons using Ciccheti's approximation method (Ciccheti 1972), was used for multiple comparison tests on interaction effects.

Stepwise multiple regression tested for environmental influences on *Spartina patens* root decay across all sites. Annual means of soil Eh, soil pH, soil temperature, soil water salinity and total available soil nitrogen (NO_2-NO_3 and NH_4) at each depth measured were regressed against percent mass remaining for each depth x site combination after one year. A hydrologic variable, adjusted to depth by quantifying mean distance to the water table relative to a particular depth interval, was also included. Large positive values reflected well-drained dune soils, while negative values represented mean water table position either within or above a particular soil depth.

Relative decomposition rates (k) were derived from a fixed-intercept negative exponential model (Wieder and Lang 1982) according to the following formula:

$$X = e^{-kt}$$

$$\text{where } X = \frac{X_t}{X_0} \text{ proportion of initial mass } (X_0) \text{ remaining at time } t$$

Using the derived k values, time required to reach 1 percent mass remaining was extrapolated.

Initial litter quality characteristics were tested for relationships with decay and nitrogen immobilization through correlation analysis. Split plot ANOVA evaluated the effects of site and depth on average root ingrowth mass and density data gathered from native root litterbags. Correlation analysis evaluated relationships between decay and root production indices.

RESULTS

Environmental gradients

Hydrographs (February 1991-1992) demonstrated marked differences between dunes and swales and suggested the presence of a moisture gradient within each topographic class (Figure 5). Among swales and among dunes, mean water table position relative to the soil surface dropped from younger to older sites (Tables 1 and 2). All sites experienced a seasonal drop in water table position during June to July 1991 and, except for the 24 year swale, wells dried out for variable lengths of time. Saturated to flooded soils occurred frequently in swales. During this one year period, percent time surface flooding occurred was 75.6 %, 32.1 % and 27.9 % for the 24 year, 36 year and 120 year swales respectively.

Throughout one year of monitoring, dune soils, at all depths, had redox potentials above 300 mV (Figure 6), which, for most soils, approximates the shift from anoxic to oxic soil conditions (Gambrell and Patrick 1978). Between dune sites, annual mean (combined depths) redox potentials were significantly greater in the two older sites and generally decreased with depth (Table 1). Swale soil redox potentials frequently fell below the oxic-anoxic boundary and varied within and between sites in a manner reflective of hydroperiod (Figure 6). The 24 year swale always had soil redox potentials in the anoxic range. Soil redox potentials in other swales broached the oxic boundary, predominately during water table drawdown. Between swales, annual mean soil redox potential (depth combined) reflected the degree of soil saturation. Soil Eh of the 120 year swale was significantly higher in contrast to younger, wetter swales (Table 2). Annual mean soil redox potential showed a significant decrease with increased depth in the 6 year swale. In the three older swales, trends over depth differed seasonally resulting in greater similarities between annual means by depth within a site. The most obvious seasonal

Figure 5. Annual hydrographs (February 1991 to February 1992) for 24, 36 and 120 year dunes and swales based on two week averages. Missing data reflects periods when wells were dry.

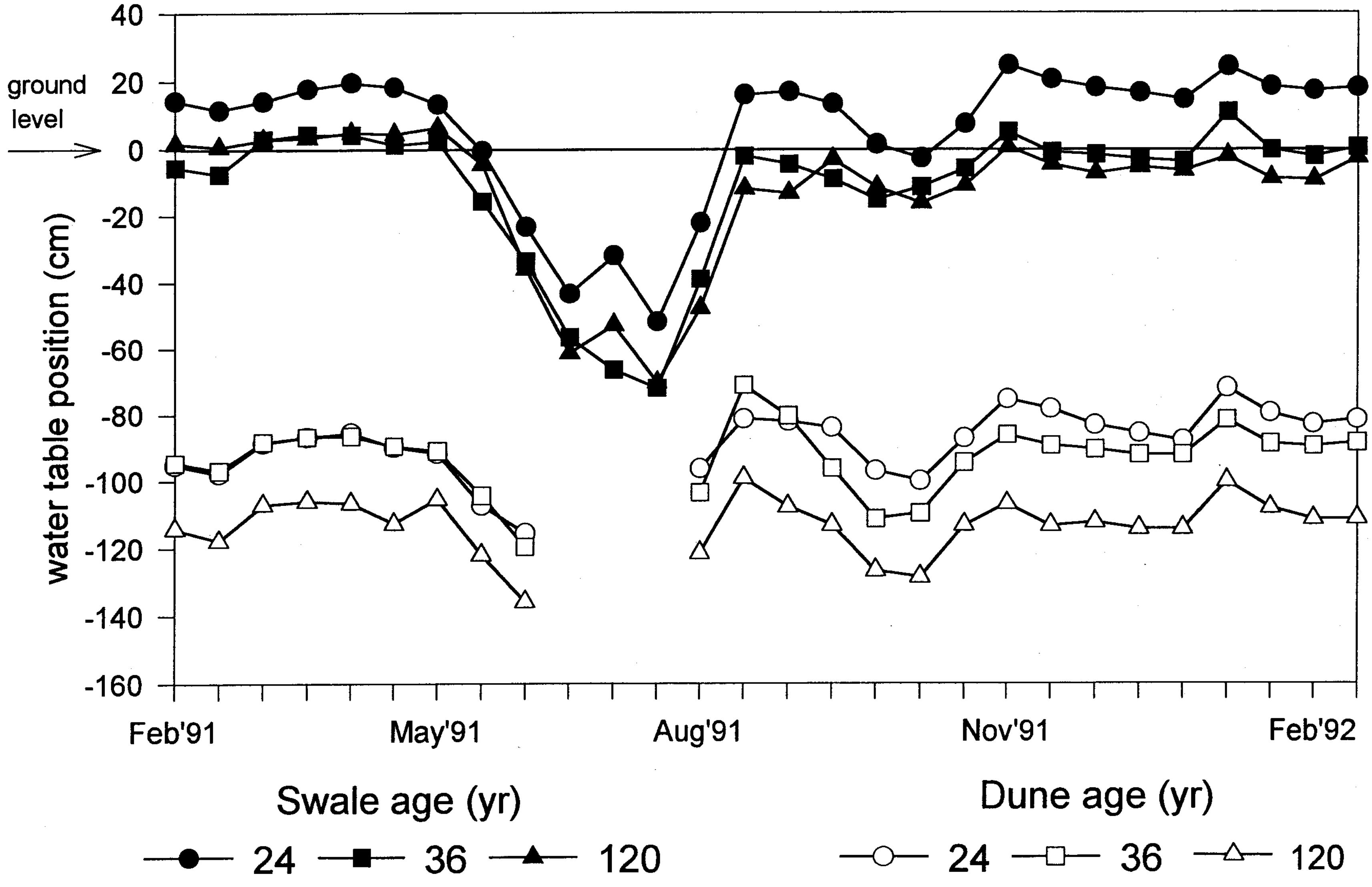

water table position (cm)
ground level
40
20
0
-20
-40
-60
-80
-100
-120
-140
-160
Feb'91
May'91
Aug'91
Nov'91
Feb'92
Swale age (yr)
24
36
120
Dune age (yr)
24
36
120

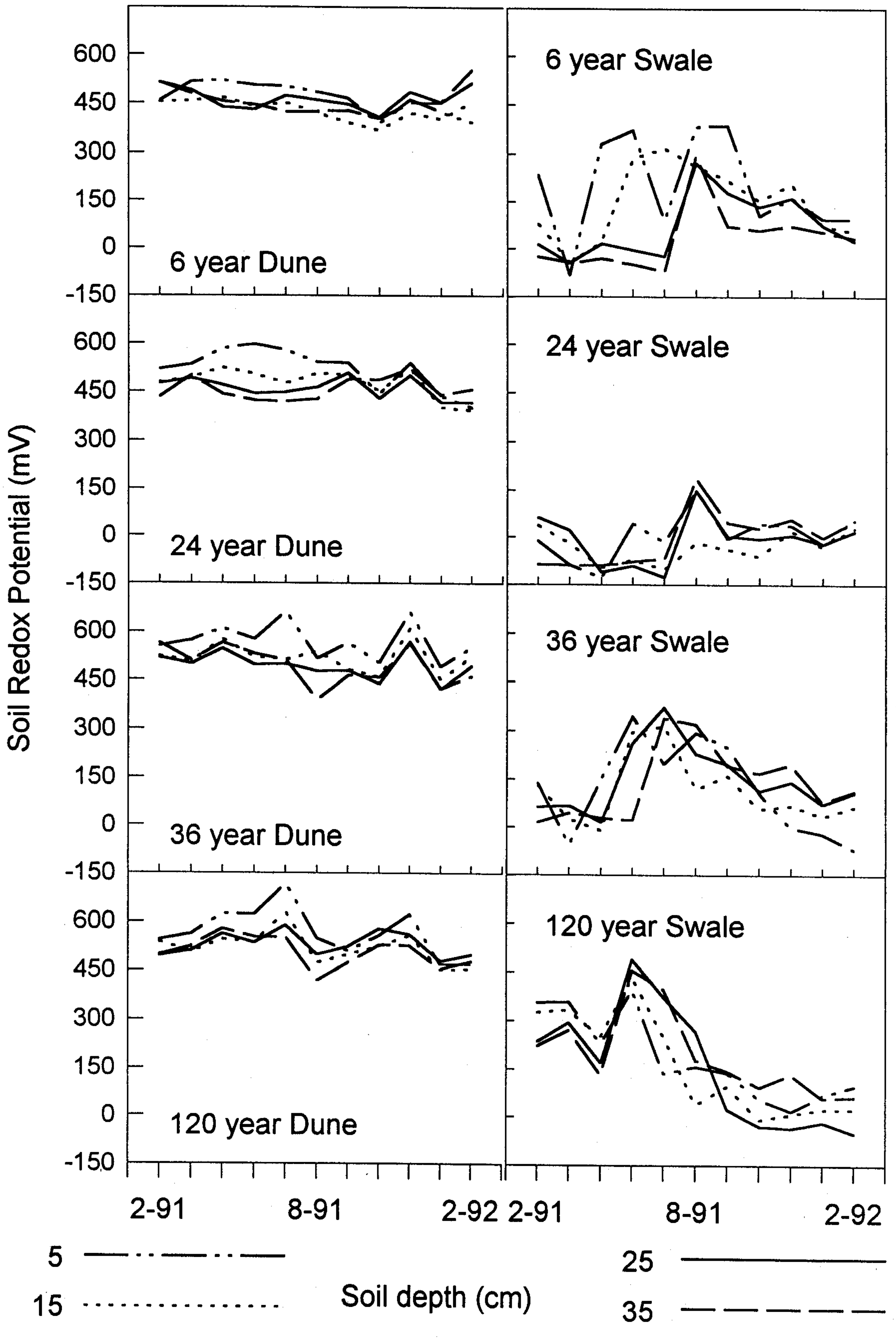
Table 1. Annual means for soil redox potential (Eh), soil pH, soil temperature, soil water salinity and groundwater level across dunes. One standard error in parentheses. Different uppercase superscripts indicate significant differences (p=.05) between sites (average of depth). Different lowercase superscripts indicate significant differences (p=.05) between depths. n = 19 (6 year) and 72-76 (24, 36 and 120 year) for each depth interval for soil Eh, soil pH and soil temperature measurements. n = 11 (6 year) and 41-44 (24, 36 and 120 year) for soil water salinity measurements.

	Dune Age			
	6 year	24 year	36 year	120 year
Soil Eh (mV)	449(8)^{B}	488(5)^{B}	529(5)^{A}	541(5)^{A}
5 cm	462(23)^{a}	538(10)^{a}	582(12)^{a}	584(14)^{a}
15 cm	432(10)^{a}	489(10)^{ab}	524(9)^{ab}	528(7)^{a}
25 cm	462(8)^{a}	466(6)^{ab}	502(8)^{b}	535(9)^{a}
35 cm	441(21)^{a}	461(9)^{b}	507(9)^{b}	519(8)^{a}
Soil pH	7.3(0.1)^{A}	6.2(0.1)^{B}	5.9(0.1)^{BC}	5.7(0.1)^{C}
0-10 cm	7.2(0.3)^{a}	6.1(0.1)^{a}	5.8(0.1)^{a}	5.7(0.1)^{a}
10-20 cm	7.3(0.3)^{a}	6.3(0.1)^{a}	6.0(0.1)^{a}	5.7(0.1)^{a}
20-30 cm	7.3(0.3)^{a}	6.2(0.1)^{a}	5.9(0.1)^{a}	5.6(0.1)^{a}
30-40 cm	7.5(0.3)a	6.3(0.1)^{a}	6.1(0.1)^{a}	5.8(0.1)^{a}
Soil temp. (EC)	22.3(1.8)^{AB}	22.1(0.9)^{B}	23.5(0.9)^{A}	23.3(0.8)^{A}
10 cm	24.7(3.0)^{a}	25.1(1.5)^{a}	27.3(1.4)^{a}	26.2(1.4)^{a}
range	6 to 50	5 to 53	7 to 48	8 to 54
30 cm	19.8(1.9)^{a}	19.2(0.9)^{b}	19.8(0.9)^{b}	20.4(0.8)^{b}
range	6 to 32	6 to 32	6 to 32	8 to 32
Salinity (ppt)	0.4(0.2)^{A}	0.4(0.1)^{A}	0.5(0.1)^{A}	0.3(0.1)^{A}
range	0 to 2	0 to 2	0 to 2	0 to 2
Groundwater level (cm) relative to soil surface		-92	-97	-116
range		-116 to -48	-134 to -39	-137 to -78

Table 2. Annual means for soil redox potential (Eh), soil pH, soil temperature, soil water salinity and groundwater level across swales. One standard error in parentheses. Different uppercase superscripts indicate significant differences (p=.05) between sites (average of depth). Different lowercase superscripts indicate significant differences (p=.05) between depths. n = 19 (6 year) and 36-38 (24, 36 and 120 year) for each depth interval for soil Eh, soil pH and soil temperature measurements. n = 11 (6 year) and 21-22 (24, 36 and 120 year) for soil water salinity measurements.

	Swale Age			
	6 year	24 year	36 year	120 year
Soil Eh (mV)	104(17)^{B}	-22(9)^{C}	136(14)^{B}	231(16)^{A}
5 cm	196(42)^{a}	-9(23)^{a}	131(30)^{a}	213(34)^{a}
15 cm	152(33)^{a}	-35(13)^{a}	130(27)^{a}	206(34)^{a}
25 cm	53(23)^{b}	-23(17)^{a}	158(26)^{a}	202(35)^{a}
35 cm	14(21)^{b}	-21(14)^{a}	124(27)^{a}	233(28)^{a}
Soil pH	7.2(0.1)^{A}	6.4(0.1)^{B}	5.6(0.1)^{C}	6.3(0.1)^{B}
0-10 cm	7.1(0.2)^{a}	6.3(0.1)^{a}	5.1(0.2)^{a}	6.1(0.1)^{a}
10-20 cm	7.2(0.2)^{a}	6.4(0.1)^{a}	5.6(0.1)^{b}	6.3(0.1)^{a}
20-30 cm	7.2(0.1)^{a}	6.5(0.1)^{a}	5.6(0.1)^{b}	6.4(0.1)^{a}
30-40 cm	7.1(0.1)^{a}	6.5(0.1)^{a}	5.9(0.1)^{b}	6.5(0.1)^{a}
Soil temp. (EC)	20.2(1.5)^{A}	18.2(0.9)^{AB}	15.3(0.6)^{B}	16.6(0.6)^{AB}
10 cm	22.1(2.4)^{a}	19.1(1.5)^{a}	15.8(1.0)^{a}	17.0(0.9)^{a}
range	7 to 40	6 to 40	5 to 26	7 to 26
30 cm	18.3(1.8)^{b}	17.3(1.1)^{a}	14.7(0.8)^{a}	16.1(0.8)^{a}
range	4 to 30	6 to 29	5 to 22	8 to 24
Salinity (ppt)	4.1(0.7)^{AB}	6.5(0.4)^{A}	2.6(0.4)^{B}	1.0(0.2)^{B}
range	0 to 16	2 to 22	0 to 14	0 to 4
Groundwater level (cm) relative to soil surface		5	-12	-14
range		-64 to 46	-72 to 25	-72 to 16

Figure 6. Soil redox potential measured over depth from February 1991 to February 1992.


Soil Redox Potential (mV)
600
450
300
150
0
-150
6 year Dune
24 year Dune
36 year Dune
120 year Dune
6 year Swale
24 year Swale
36 year Swale
120 year Swale
2-91
8-91
2-92
2-91
8-91
2-92
5
15
Soil depth (cm)
25
35

variation in depth profiles occurred during the mid-summer water table drawdown. Shallower soil depths exhibited lower soil redox potentials (Figure 3). In general, swale soils always exhibited significantly lower soil redox potentials than adjacent dunes based on annual means.

Few consistent trends in soil pH levels were evident throughout the study except for 1) a tendency for higher pH at oceanside (younger) sites and 2) an increase in pH with an increase in soil depth (Tables 1 and 2). On an annual basis, the most seaward sites (6 year dune and swale) exhibited significantly higher mean soil pH levels (depth combined) than all other sites. The interception of salt spray and the likelihood of greater calcareous particle density in the soils of these younger sites may have produced these patterns.

Significantly greater mean annual soil temperature (depth combined) occurred in the 36 and 120 year dune than in the 24 year dune (Table 1). Exposure to oceanic breezes at the 24 year old site may have reduced soil temperature through convective heat loss. In most dune sites, mean annual soil temperatures significantly decreased with increased depth. Among swales, significantly higher mean annual soil temperature occurred in younger sites (Table 2). Shading effects by *Myrica cerifera* thickets likely influenced this pattern. Soil temperature tended to decrease with increased depth, but was only significant for the 6 year swale. Although minimum soil temperatures were similar between dunes and swales, maximum soil temperatures, particularly at 10 cm belowground, differed widely due to greater insolation of bare dune soils. Except for the 6 year dune and swale, mean annual soil temperature was significantly greater in dunes than in adjacent swales.

Soil water salinity decreased across the swale chronosequence (Table 2). Great salinity fluctuations occurred in the 6 to 36 year sites. Higher soil water salinity occurred in the 24 year swale, but, on a mean annual basis, was only significantly greater than the 120 year swale. Among dunes, mean annual soil water salinity ranged from 0.2 to 0.3 parts per thousand (ppt) and never exceeded 2 ppt (Table 1).

Soil fertility parameters measured by Day and Lakshmi (unpublished, Tables 3 and 4) indicated nitrogen and soil organic matter gradients occurred across the chronosequence within each topographic class. Among swales, significantly greater soil NH_4, soil NO_2-NO_3 and soil organic matter levels occurred in the two older sites. Both these sites are dominated by *Myrica cerifera* which is symbiotically associated with a nitrogen fixing actinomycete. Across dunes, soil NH_4 and soil organic matter increased significantly. Similar trends occurred for soil NO_2-NO_3 and soil water NO_2-NO_3. Among all dune and swale sites, orthophosphate and total phosphate in soil water were similar except for higher orthophosphate and total phosphorus in the 6 year dune and higher total phosphorus in the 36 year swale. Available soil nitrogen was always significantly greater in swales than in adjacent dunes. Significantly greater soil organic matter occurred in swales than in adjacent dunes except for the 6 year dune and swale.

Environmental influences on decay dynamics

Analysis of variance on percent mass remaining of *Spartina patens* roots demonstrated significant ($p < .0001$) main effects (site, time, depth), first order interactions (site x time, site x depth, depth x time) and second order interaction (site x time x depth). Site effects ($F = 123.39$, $p < .0001$) indicated significant differences

Table 3. Nutrient and organic matter gradients across dune chronosequence. One standard error in parentheses. Different uppercase superscripts indicate significant differences (p=.05) between sites.

	Dune Age			
	6 year	24 year	36 year	120 year
Soil nutrients(% dry wt)				
	n=33	n=106	n=106	n=106
NH_4	$0.75(0.04)^B$	$2.11(0.17)^A$	$2.54(0.22)^A$	$2.46(0.25)^A$
NO_2-NO_3	$0.26(0.03)^{BC}$	$0.17(0.01)^C$	$0.28(0.01)^B$	$0.44(0.03)^A$
Soil water nutrients (mg/l)				
	n=10	n=46	n=44	n=44
NH_4	$0.04(0.01)^A$	$0.10(0.02)^A$	$0.08(0.02)^A$	$0.11(0.03)^A$
NO_2-NO_3	$0.03(0.02)^A$	$0.14(0.03)^A$	$0.29(0.06)^A$	$0.26(0.08)^A$
TKN	$0.87(0.31)^A$	$1.01(0.34)^A$	$0.79(0.13)^A$	$0.81(0.12)^A$
O-PO_4	$0.29(0.05)^A$	$0.02(0.003)^B$	$0.02(0.004)^B$	$0.02(0.006)^B$
T	$0.25(0.02)^A$	$0.07(0.01)^B$	$0.07(0.01)^B$	$0.09(0.02)^B$
% Soil organic matter				
	n=5	n=5	n=5	n=5
	$0.30(0.03)^B$	$0.51(0.05)^B$	$0.42(0.01)^B$	$0.60(0.08)^A$

Table 4. Nutrient and organic matter gradients across swale chronosequence. One standard error in parentheses. Different uppercase superscripts indicate significant differences (p=.05) between sites.

	Swale Age			
	6 year	24 year	36 year	120 year
Soil nutrients(% dry wt)				
	n=33	n=52	n=53	n=53
NH_4	$1.01(0.09)^{B}$	$1.01(0.08)^{B}$	$5.16(0.56)^{A}$	$4.75(0.44)^{A}$
NO_2-NO_3	$0.11(0.04)^{B}$	$0.05(0.003)^{B}$	$0.78(0.20)^{AB}$	$1.25(0.33)^{A}$
Soil water nutrients (mg/l)				
	n=14	n=27	n=27	n=28
NH_4	$0.05(0.01)^{A}$	$0.18(0.03)^{A}$	$2.56(0.30)^{B}$	$0.17(0.03)^{A}$
NO_2-NO_3	$0.02(0.003)^{A}$	$0.01(0.001)^{A}$	$1.14(0.44)^{B}$	$0.17(0.06)^{A}$
TKN	$0.57(0.12)^{A}$	$1.90(0.13)^{A}$	$6.69(0.54)^{B}$	$1.12(0.17)^{A}$
O-PO_4	$0.07(0.02)^{A}$	$0.02(0.003)^{B}$	$0.06(0.01)^{A}$	$0.02(0.003)^{B}$
TP	$0.10(0.02)^{AB}$	$0.04(0.01)^{B}$	$0.50(0.18)^{A}$	$0.04(0.01)^{B}$
% Soil organic matter				
	n=5	n=5	n=5	n=5
	$0.38(0.01)^{C}$	$1.80(0.35)^{BC}$	$5.04(0.80)^{AB}$	$6.03(1.36)^{A}$

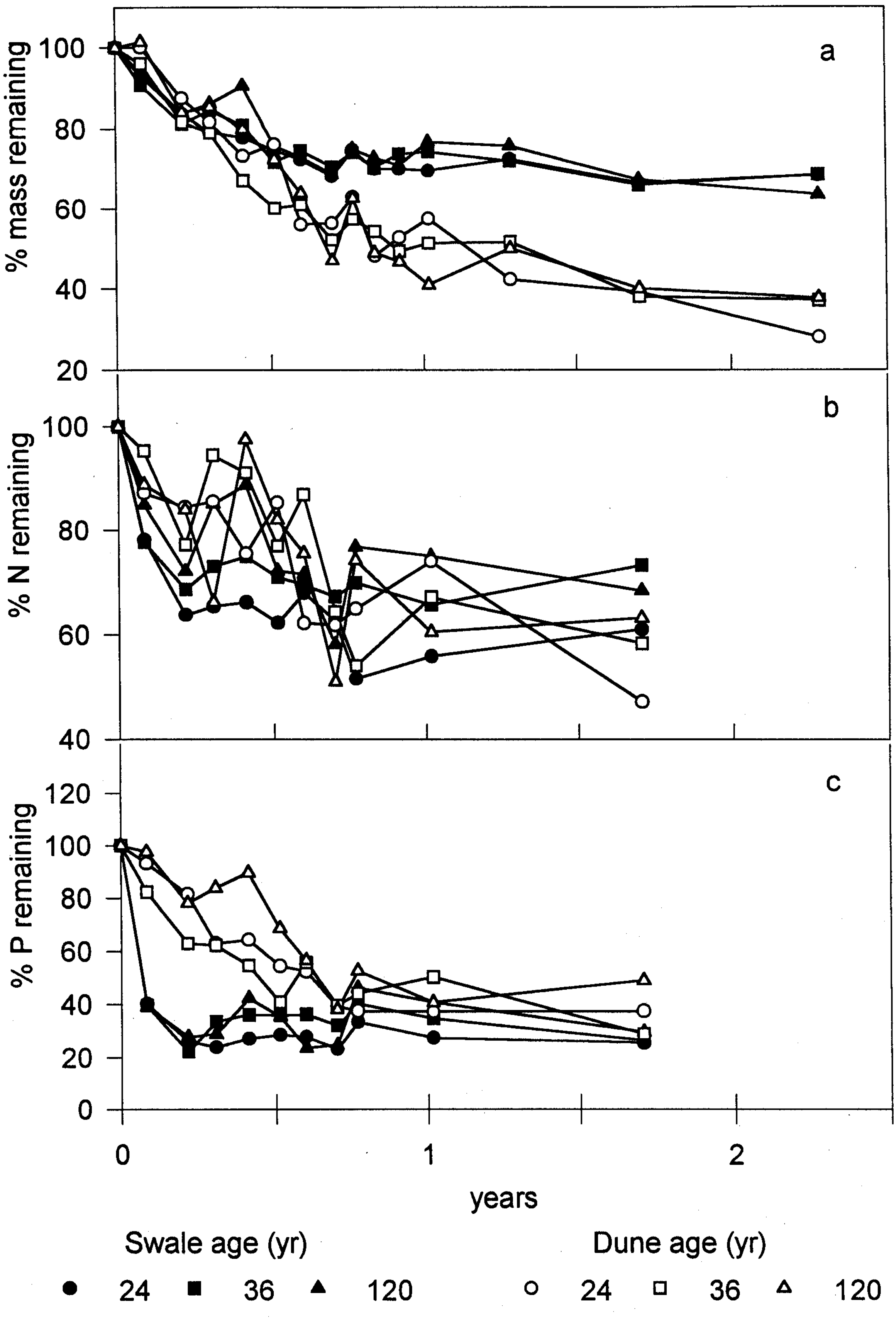
between each dune and swale of like age while no differences occurred between different aged sites within topographic classes. Decay constants reflect these differences (Table 5). Lower decay rates occurred in swales, which require approximately 17 years to reach 1 percent mass remaining compared to 7 years required in dune sites (Table 5). Site x time interactions ($F = 7.41$, $p < .0001$) demonstrate similar rates of decay in dunes and swales for the first 0.5 years of decay (Figure 7 a). Thereafter, dunes experienced greater rates of mass loss than swales. Site x depth interactions ($F = 14.69$, $p < .0001$) and site x depth x time interactions ($F = 1.32$, $p < .0001$) resulted in different patterns of decay over depth in swales vs. dunes. Among dunes, decay was greatest between 10 and 30 cm deep and slowest in the 0-10 cm depth (Table 6). After 2.25 years of decay, no differences in percent mass remaining over depth occurred in dune sites. In swales, patterns of decay over depth not only differed from dunes, but also differed between swales. Faster decay took place in the 24 year swale at the 10-20 cm depth in contrast to the faster decay at the 0-10 cm depth in the 36 and 120 year swales.

Relationships between decay and environmental influences resulted in strong correlations with hydrology ($r = 0.807$, $p < .0001$), soil Eh ($r = -0.727$, $p < .0001$) and soil temperature ($r = -0.645$, $p < .0001$) and weaker correlations with soil water salinity ($r = 0.453$, $p = .013$) and available soil nitrogen ($r = 0.469$, $p = .01$). With the inclusion of all independent variables, multiple regression explained 74 % of the variation in decomposition of *Spartina patens* roots ($F = 10.30$, $r^2 = 0.74$, $p < .0001$). As the first variable selected, hydrology accounted for most of the explained variance ($F = 41.22$, $r^2 = 0.65$, $p < .0001$). Additions of subsequent variables did not result in substantial

Table 5. Decay rates [-k (yr^{-1})], coefficient of determination (r^2) and time (yr) to reach 1 % mass remaining ($t_{.01}$) for *Spartina patens* roots incubated across dune and swale chronosequences. One standard error in parentheses. All regressions are significant at p<.0001.

	k	r^2	n	$t_{.01}$ (yr)
Dune Age				
24 year	.64 (.01)	.87	280	7.20
36 year	.59 (.01)	.87	280	7.81
120 year	.63 (.02)	.78	280	7.31
Swale Age				
24 year	.28 (.01)	.75	280	16.45
36 year	.28 (.01)	.76	280	16.45
120 year	.27 (.01)	.80	280	17.06

Figure 7. *Spartina patens* decay dynamics across the 24, 36 and 120 year dune and swale chronosequence: a) percent mass remaining, b) percent nitrogen remaining, c) percent phosphorus remaining.



a
b
c
% mass remaining
% N remaining
% P remaining
20
40
60
80
100
120
0
0
1
2
years
Swale age (yr)
● 24 ■ 36 ▲ 120
Dune age (yr)
○ 24 □ 36 △ 120

Table 6. Decay rates [-k (yr^{-1})], coefficient of determination (r^2) and percent mass remaining after 2.25 years of decay (% M) for *Spartina patens* decay at each depth interval. All regressions are significant at p=.0001. One standard error in parentheses. Different lowercase superscripts indicate significant differences (p=.05) between depths. n=70.

	Dunes			Swales		
	k	r^2	% M	k	r^2	% M
Site age						
24 year						
0-10	.59 (.03)	.82	27.62(4.19)^{a}	.29 (.02)	.75	68.26(4.56)^{ab}
10-20	.72 (.03)	.91	22.74(2.43)^{a}	.33 (.02)	.78	62.62(3.03)^{b}
20-30	.69 (.03)	.89	26.62(2.67)^{a}	.30 (.02)	.77	65.02(3.14)^{ab}
30-40	.57 (.02)	.91	35.64(0.95)^{a}	.21 (.01)	.74	77.65(1.43)^{a}
36 year						
0-10	.52 (.02)	.90	39.88(3.90)^{a}	.32 (.02)	.83	60.66(4.96)^{a}
10-20	.63 (.03)	.86	35.72(6.92)^{a}	.24 (.02)	.77	71.53(5.83)^{a}
20-30	.64 (.03)	.86	35.21(3.84)^{a}	.26 (.02)	.75	70.97(2.51)^{a}
30-40	.59 (.03)	.87	37.84(2.88)^{a}	.28 (.02)	.73	71.12(3.03)^{a}
120 year						
0-10	.54 (.02)	.88	37.33(3.35)^{a}	.32 (.01)	.86	51.88(2.52)^{b}
10-20	.70 (.05)	.71	36.87(5.45)^{a}	.26 (.02)	.80	66.55(2.20)^{a}
20-30	.68 (.04)	.81	33.06(6.26)^{a}	.29 (.02)	.76	65.89(3.36)^{a}
30-40	.59 (.03)	.80	43.64(7.41)^{a}	.23 (.01)	.84	69.91(1.57)^{a}

improvements. Hydrology was strongly and significantly intercorrelated with soil Eh ($r = -0.950$, $p < .0001$), salinity ($r = -0.878$, $p < .0001$) and soil temperature ($r = -0.825$, $p < .0001$), illustrating the influence hydrology exerted on other environmental parameters that potentially influenced decay. The level of resolution allowed by the multiple regression technique could not identify specific depth related effects. However, within swale sites, *Spartina patens* decay (Table 6) was often faster at depths exhibiting lower soil redox potential (Table 2).

Spartina patens root decay showed highly dynamic nitrogen behavior over time and between sites (site x time: $F = 2.15$, $p < .0001$, Figure 7 b). All sites experienced an initial release of nitrogen. More frequent periods of soil saturation and flooding in the 24 year swale may have promoted greater leaching losses apparent during early phase nitrogen dynamics. At no time did net nitrogen immobilization occur. After 1.7 years, between 47.20 and 73.24 % original nitrogen remained among all sites with no significant differences.

Environmental conditions strongly influenced phosphorus dynamics. Site main effects ($F = 33.82$, $p < .0001$) indicated no significant differences between swale sites and significantly greater percent phosphorus remaining in dunes when compared to swales of like age. Interaction effects ($F = 2.62$, $p < .0001$, Figure 7 c) operated primarily during early decay. Phosphorus was rapidly released in swale sites (greater leaching response), but by the end of the first year, percent phosphorus remaining between all sites converged. Site effects among dunes showed significantly greater amounts of phosphorus remaining in the 120 year dune, but these effects were not sustained through time. After 1.7 years, percent phosphorus in all dunes and swales ranged between 25.56 % and 49.05 % with no significant differences. Appendix 2 provides complete data on percent mass, nitrogen and phosphorus remaining during *Spartina patens* root decay.

Native root decay across the chronosequence

Analysis of variance on percent mass remaining of native roots found all main effects, first order interactions and the second order interaction significant. A separate discussion of swales and dunes will simplify the interpretation of these tests. Site main effects (F = 276.60, $p < .0001$) indicated a decay gradient across the dune chronosequence. Multiple comparison tests indicated significantly slower decay (more percent mass remaining) in the 6 year dune and faster decay (less percent mass remaining) in the 120 year dune. Across the dune chronosequence, decay rates ranged from .45 to .86 and required 10.23 to 5.35 years to reach 1 percent mass remaining (Table 7). A divergence in percent mass remaining occurred within the first 0.5 years of decay (site x time: F = 9.04, $p < .0001$, Figure 8 a). Near the end of the study, differences between the three older dunes began to disappear while decay still remained slowest in the youngest

(6 year) site. Across the swale chronosequence, multiple comparison tests indicated differences among all swale sites at the site main effect level. The 36 and 120 year swales showed the most percent mass remaining while the least occurred for the younger swales. Decay rates (Table 7) indicated 36 year swale roots exhibited the slowest decay, requiring 23.03 years to reach 1 percent mass remaining, and 6 year swale roots exhibited the fastest decay ($k = 0.41$, $t_{.01} =$ 11.23 years). Decay responses in swales diverged soon after initiation of the study (Figure 9 a). Differences between sites were generally maintained,

Table 7. Decay rates [-k (yr^{-1})], coefficient of determination (r^2) and time (yr) to reach 1 % mass remaining ($t_{.01}$) for native roots incubated across dune and swale chronosequences. One standard error in parentheses. All regressions are significant at p=.0001.

	k	r^2	n	$t_{.01}$ (yr)
Dune Age				
6 year	.45 (.02)	.86	120	10.23
24 year	.70 (.01)	.87	556	6.58
36 year	.65 (.01)	.85	564	7.08
120 year	.86 (.02)	.83	556	5.35
Swale Age				
6 year	.41 (.02)	.90	120	11.23
24 year	.28 (.01)	.75	280	16.45
36 year	.20 (.01)	.77	280	23.03
120 year	.25 (.01)	.81	280	18.42

Figure 8. Native root decay dynamics across dune chronosequence: a) percent mass remaining, b) percent nitrogen remaining, c) percent phosphorus remaining.

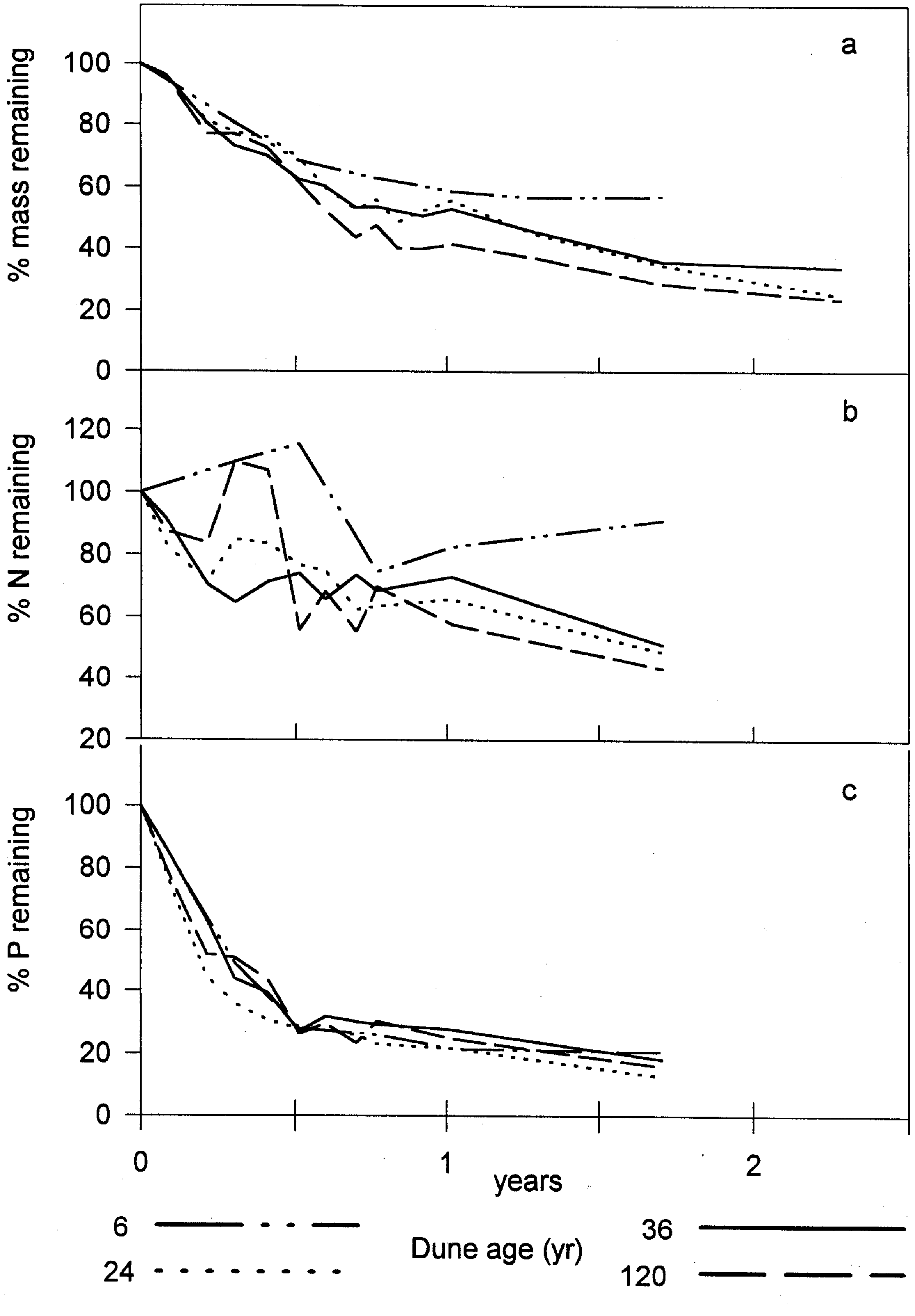
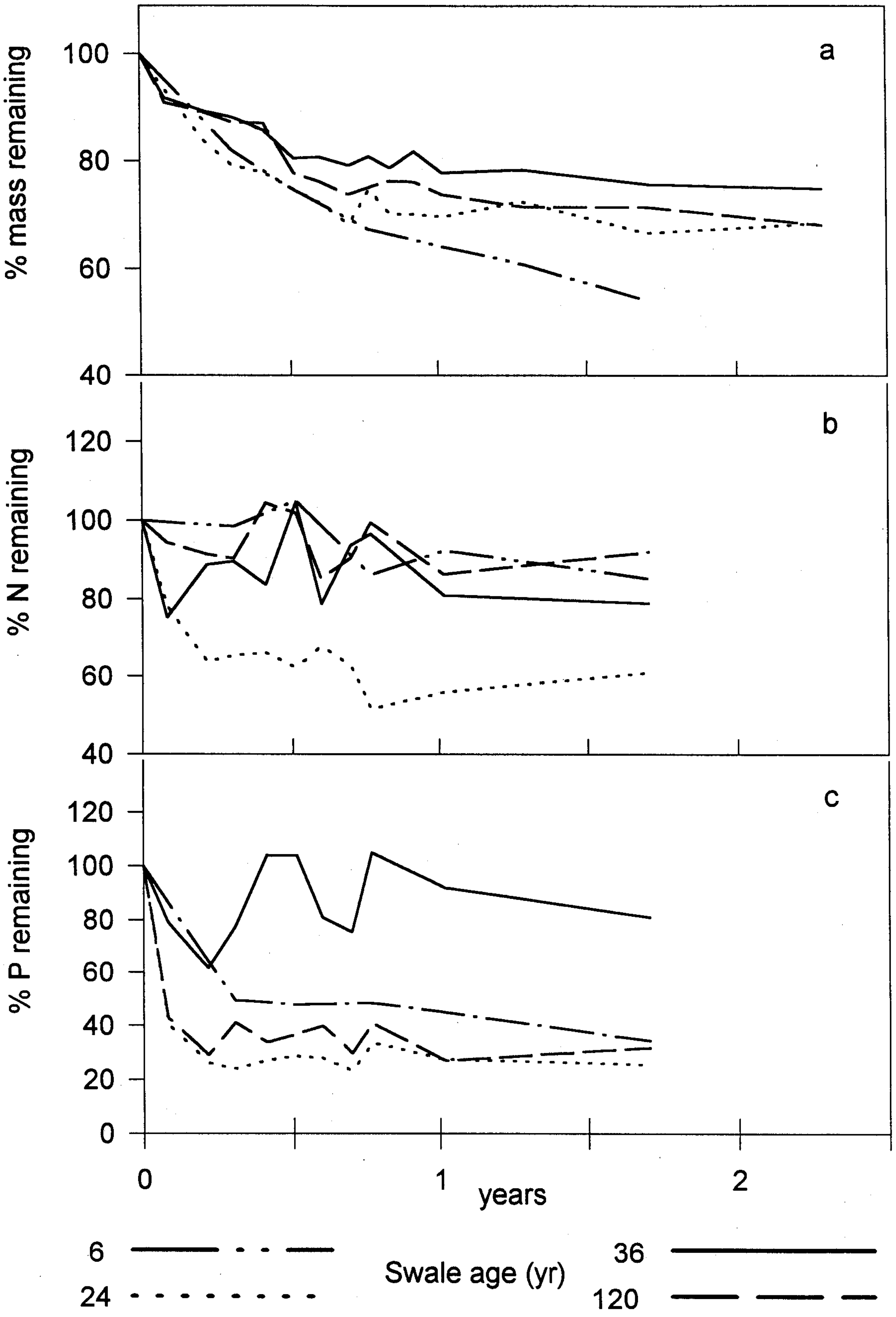

a
% mass remaining
0
20
40
60
80
100
b
% N remaining
20
40
60
80
100
120
c
% P remaining
0
20
40
60
80
100
0
1
2
years
6
24
Dune age (yr)
36
120

Figure 9. Native root decay dynamics across swale chronosequence: a) percent mass remaining, b) percent nitrogen remaining, c) percent phosphorus remaining.


% mass remaining
100
80
60
40
a
% N remaining
120
100
80
60
40
b
% P remaining
120
100
80
60
40
20
0
c
0
1
2
years
6
24
Swale age (yr)
36
120

although after one year, percent mass remaining between the 24 and 120 year swale became more similar. Between the three older adjacent dune and swale sites, dune root decay was always greater than swale root decay. Similar decay rates occurred between 6 year dune and swale roots.

Significant site x depth (F = 30.46, $p < .0001$) and site x depth x time interactions (F = 1.26, $p < .0090$) resulted in complex patterns of decay rates over depth. In the 6 year dune, decay increased with increased depth (Table 8). Older dune roots generally showed greater decay in the middle (10-30 cm) of the soil profile. Differences in percent mass remaining over depth were significant only for the 6 and 36 year dunes. The gradient in decay across the dune chronosequence, for the most part, continued to be expressed across depth intervals, although differences were not significant. Within swales, significantly slower decomposition occurred at 30-40 cm deep (Table 8). Faster decay occurred at the 0-10 cm depth, except for the 24 year swale where faster decay took place at the 10-20 cm depth. Among swales, significantly slower decay rates and more percent mass remaining occurred at the 36 year swale at all depths below 10 cm. Higher decay rates and significantly less percent mass remaining occurred in dunes than in adjacent swales, except between the 6 year dune and swale. At 0-10 cm, faster decay occurred in 6 year swale roots.

Significant site (F = 19.40, $p < .0001$), time (F = 8.19, $p < .0001$) and site x time (F = 1.99, $p < .0001$) effects resulted in very different patterns of nitrogen behavior across the chronosequence. Net nitrogen immobilization potentials were low to nonexistent for both dunes and swales as indicated by only small or no increases above 100 percent

Table 8. Decay rates [-k (yr^{-1})], coefficient of determination (r^2) and percent mass remaining after 2.25 years of decay (% M) for native root decay at each depth interval. All decay models are significant at p=.0001. One standard error in parentheses. Different lowercase superscripts indicate significant differences (p=.05) between depths.

	Dunes			Swales		
	k	r^2	% M	k	r^2	% M
Site age						
6 year			n=30	n=30		
0-10	.34 (.03)	.83	67.27 (3.25)^{a}	.51 (.03)	.91	47.47 (6.58)^{a}
10-20	.44 (.04)	.82	60.17 (3.43)^{ab}	.43 (.02)	.95	51.64 (2.96)^{a}
20-30	.47 (.02)	.93	51.27 (3.24)^{b}	.37 (.02)	.89	59.38 (3.64)^{a}
30-40	.55 (.03)	.91	48.68 (3.46)^{b}	.34 (.02)	.94	58.20 (7.88)^{a}
24 year			n=139	n=70		
0-10	.70 (.03)	.84	24.92 (3.03)^{a}	.29 (.02)	.75	68.26 (4.56)^{ab}
10-20	.81 (.03)	.87	19.66 (1.86)^{a}	.33 (.02)	.78	62.62 (3.03)^{b}
20-30	.69 (.02)	.90	26.93 (2.39)^{a}	.30 (.02)	.77	65.02 (3.14)^{ab}
30-40	.62 (.02)	.90	27.80 (1.45)^{a}	.21 (.01)	.74	77.65 (1.43)^{a}
36 year			n=141	n=70		
0-10	.46 (.01)	.87	43.93 (3.64)^{a}	.29 (.01)	.91	60.62 (2.58)^{b}
10-20	.74 (.02)	.90	26.24 (3.61)^{b}	.22 (.01)	.82	73.29 (2.11)^{ab}
20-30	.72 (.02)	.87	31.34 (4.09)^{ab}	.16 (.01)	.76	80.43 (1.93)^{a}
30-40	.68 (.02)	.88	33.47 (3.56)^{ab}	.13 (.01)	.74	84.70 (1.35)^{a}
120 year			n=139	n=70		
0-10	.68 (.02)	.85	28.07 (2.05)^{a}	.34 (.01)	.91	57.06 (2.66)^{b}
10-20	.97 (.04)	.83	22.01 (4.51)^{a}	.24 (.01)	.82	67.74 (4.34)^{ab}
20-30	.89 (.03)	.84	23.64 (6.03)^{a}	.20 (.01)	.78	75.87 (1.84)^{a}
30-40	.90 (.03)	.86	20.68 (3.73)^{a}	.22 (.01)	.78	71.42 (2.79)^{a}

nitrogen remaining (Figures 8 b and 9 b). Among dunes, initial leaching of nitrogen followed by accumulation took place in all sites except the 6 year dune. During the brief accumulation phase, net nitrogen immobilization occurred in both the 6 and 120 year sites. Although nitrogen dynamics in dunes showed unique patterns, differences among the three older dunes were short-term. Site effects were significant only between the 6 year dune and the older dunes. These differences continued throughout the study and were significant at the endpoint. Percent nitrogen remaining in the 6 year old dune root litter (91.12%) was significantly greater than all other dune sites (24 year = 48.76 %, 36 = 51.26 %, 120 year = 43.33 %). Periods of brief nitrogen immobilization (> 100%) occurred in all swales, except for the 24 year swale (Figure 9 b). Site main effects showed significantly less percent nitrogen remaining in the 24 year swale than other swales. At the endpoint of the study, no significant differences occurred, even though percent nitrogen remaining continued to be lower in the 24 year swale (61.01%) relative to other swales (6 year = 85.29 %, 36 year = 78.93 %, 120 year = 92.00 %). Generally, swales retained more original nitrogen than did adjacent dunes. Significant site effects occurred between the 36 year and 120 year dunes and swales, but after 1.7 years, significant differences in percent nitrogen remaining were limited to the 120 year dune and swale.

Dune sites exhibited similar phosphorus dynamics over time (Figure 8 c). Significant site effects ($F = 122.11$, $p < .0001$) indicated less percent phosphorus remained in the 24 year dune relative to the 36 year dune, although these differences were slight and short-term. After 1.7 years, no differences were found among dune sites (12.61 % to 20.52 %). Significant site x time interactions ($F = 4.69$, $p < .0001$) resulted in markedly different phosphorus dynamics for the 36 year swale compared to other swales and dunes (Figures 8 c and 9 c). A phase of accumulation occurred after initial leaching only in the 36 year swale. Although slight in magnitude and duration, accumulation was accompanied by a brief period of net phosphorus immobilization. Site main effects indicated significantly greater amounts of phosphorus remained in 36 year swale roots and suggested a similar response in 6 year roots compared to 24 and 120 year swale roots. After 1.7 years, percent phosphorus remaining in the 36 year swale

(81.01 %) continued to be significantly greater than other swales (25.56 % to 34.18 %) and the adjacent 36 year dune.

Root ingrowth

Multiple correlation analysis between root ingrowth mass and density and decay rates indicated significant relationships between decay and root density (r = 0.44, p = .0002) and between root mass and root density (r = 0.82, p < .0001) and a positive, but non-significant relationship between decay and root mass (r = 0.16, p = 0.1793). Within each site, faster decay rates generally coincided with greater root ingrowth density (Tables 8 and 9). Analysis of variance on root density and root mass resulted in similar conclusions. Only root ingrowth density data are discussed due to the significant relationship with decay. Site x depth interactions (F = 6.21, p < .0001) indicated, among dunes, greater root ingrowth density occurred at the 120 year dune for most depth intervals (Table 9). Within dune sites, significant differences over depth occurred only at the 120 year dune. Among swales, root ingrowth density was generally significantly greater at the 36 year swale. Within swale sites, significantly greater root ingrowth density occurred at shallow soil depths. Between adjacent dunes and swales,

Table 9. Average root ingrowth density from native root litterbags. One standard error in parentheses. Different uppercase superscripts indicate significant differences (p=.05) between sites. Different lowercase superscripts between rows within a site indicate significant differences (p=.05) between depth intervals.

	Site Age			
	6 year	24 year	36 year	120 year
Dunes	n=30	n=139	n=141	n=139
0-10 cm	3.53(1.17)^{aB}	11.81(1.89)^{aA}	2.27(0.33)^{aB}	6.96(1.05)^{bAB}
10-20 cm	4.13(0.92)^{aB}	10.79(1.25)^{aAB}	4.28(0.49)^{aB}	16.62(2.01)^{aA}
20-30 cm	3.97(0.88)^{aB}	6.80(0.73)^{aB}	3.16(0.43)^{aB}	15.27(1.72)^{aA}
30-40 cm	2.63(0.68)^{aB}	6.32(0.69)^{aAB}	3.53(0.66)^{aB}	11.84(1.54)^{aA}
Swales	n=30	n=70	n=70	n=70
0-10 cm	20.93(2.69)^{aA}	7.51(1.04)^{aB}	15.04(1.81)^{aAB}	9.74(1.52)^{aB}
10-20 cm	9.90(1.51)^{bAB}	5.56(0.66)^{aB}	16.91(2.23)^{aA}	4.77(0.90)^{abB}
20-30 cm	7.90(1.52)^{bAB}	4.60(0.70)^{aAB}	9.36(1.50)^{abA}	1.90(0.46)^{abB}
30-40 cm	4.73(1.04)^{bA}	3.67(0.60)^{aA}	3.56(0.82)^{bA}	0.57(0.27)^{bA}

mean root density was similar with the exception of greater root density in the 36 year swale (0-20 cm) and 120 year dune (10-40 cm).

Influence of litter quality on decay

Differences in initial litter quality among native dune and swale roots likely influenced rates of decay and nitrogen and phosphorus dynamics. Among dunes, initial nitrogen content of native roots increased with site age, paralleling the increase in exogenous nitrogen availability. Initial nitrogen content was significantly greater in 120 year roots than in 6 or 24 year roots (Table 10) while initial phosphorus content was similar (0.12 % to 0.15 %). Initial lignin content could not be statistically tested (n = 1), but demonstrated a concentration gradient across dunes. Native 6 year roots had 10.0 % lignin while 120 year roots had 20.0 % lignin. Across the swale chronosequence, significant increases in native root nitrogen content occurred, except between the 36 and 120 year swale (Table 10). Roots from the 120 year swale had significantly greater initial phosphorus concentration (0.13 %) than 36 year swale roots (0.05 %). Similar phosphorus content was found between the 6 and 24 year swales (0.07 % to 0.10 %). Qualitative comparison of initial lignin content showed very similar amounts among 6, 24 and 120 year swale roots (16.7 % to 17.2 %) and higher amounts in 36 year swale roots (27.0 %). Considerable intraspecific variation in lignification can occur (Hodson et al. 1984, Wardrop 1971). Roots under anaerobic conditions can accumulate indoleacetic acid (de Wit 1978) which has been linked to greater lignification in woody tissues (Wardrop 1971). More frequent or intense periods of anoxia in 36 year swale soils may have induced greater root lignification through this process.

Table 10. Initial litter quality indices (0) and after 1.7 years of decay (1.7) for nitrogen concentration (% N), phosphorus concentration (% P) and nitrogen:phosphorus ratio (N:P). One standard error in parentheses. Changes in lignin derived indices after 1 year of decay (1.0) for lignin concentration (L), lignin:nitrogen ratio (L:N) and lignin:phosphorus ratios (L:P). n=1 for all indices except % N and % P where n=3 for *Spartina patens* roots, swales and 6 year dune and n = 6 for 24, 36 and 120 year dunes.

	% N		% P		N:P		L		L:N		L:P	
	0	1.7	0	1.7	0	1.7	0	1.0	0	1.0	0	1.0
Spartina patens roots												
24 year dune	0.91 (0.03)	1.15 (0.03)	0.10 (0.01)	0.09 (0.01)	9	13	17.1	18.9	19	18	171	236
36 year dune	0.91 (0.03)	1.35 (0.11)	0.10 (0.01)	0.08 (0.01)	9	17	17.1	22.6	19	17	171	226
120 year dune	0.91 (0.03)	1.33 (0.05)	0.10 (0.01)	0.10 (0.01)	9	13	17.1	14.3	19	12	171	159
24 year swale	0.91 (0.03)	0.82 (0.04)	0.10 (0.01)	0.04 (0.001)	9	21	17.1	25.0	19	35	171	625
36 year swale	0.91 (0.03)	1.01 (0.04)	0.10 (0.01)	0.04 (0.001)	9	25	17.1	21.2	19	25	171	530
120 year swale	0.91 (0.03)	0.93 (0.01)	0.10 (0.01)	0.05 (0.003)	9	19	17.1	16.7	19	18	171	333
Native roots												
6 year dune	0.47 (0.03)	0.72 (0.02)	0.13 (0.001)	0.05 (0.01)	4	14	10.0	15.8	22	23	77	316
24 year dune	0.59 (0.01)	0.83 (0.05)	0.15 (0.02)	0.06 (0.004)	4	14	9.5	14.3	17	20	67	286
36 year dune	0.70 (0.02)	1.01 (0.06)	0.12 (0.001)	0.06 (0.002)	6	17	13.0	15.0	19	15	109	214
120 year dune	0.81 (0.10)	1.13 (0.23)	0.13 (0.01)	0.07 (0.01)	7	16	20.0	20.0	25	19	167	286
6 year swale	0.49 (0.02)	0.76 (0.03)	0.07 (0.001)	0.04 (0.003)	7	19	17.2	12.8	35	18	246	256

Table 10 continued.

	% N		% P		N:P		L		L:N		L:P	
	0	1.7	0	1.7	0	1.7	0	1.0	0	1.0	0	1.0
24 year swale	0.91 (0.03)	0.82 (0.04)	0.10 (0.01)	0.04 (0.001)	9	21	17.1	25.0	19	35	171	625
36 year swale	1.46 (0.03)	1.50 (0.03)	0.05 (0.001)	0.05 (0.002)	29	30	27.0	30.2	19	21	541	604
120 year swale	1.33 (0.04)	1.74 (0.26)	0.13 (0.001)	0.06 (0.01)	10	29	16.7	34.2	13	22	128	684

A series of correlational analyses were performed to establish the potential influences litter quality characteristics exerted on decay dynamics. The variables included nitrogen, phosphorus and lignin content and the various ratios (N:P, L:N, L:P) listed in Table 10. Available soil nitrogen was also included. Separate analyses of dunes and swales eliminated potentially confounding environmental effects, primarily hydroperiod. Low sample size reduced analytical power and produced mostly nonsignificant correlations, but certain trends may be important. Among dune sites, nitrogen content (r = 0.906, p = .0938), available soil nitrogen (r = 0.872, p = .1282) and lignin content (r = 0.770, p = .2295) showed the strongest relationships with decay rates. Among swale sites, high nitrogen content (r = -0.964, p = .0359), high soil nitrogen (r = -0.908, p = .0917) and high nitrogen:phosphorus ratios (r = -0.721, p = .2793) corresponded with low decay. A positive relationship existed between L:N ratios and decay rates (r = 0.871, p = .1288). A similar analysis was run to establish relationships with nitrogen dynamics. N_{max} generally represents maximum nitrogen immobilization potential (Melillo and Aber 1984). In the present study, N_{max} represented the maximum peak of nitrogen accumulated after initial leaching. No significant relationships between N_{max} and any other variable occurred. L:N ratios (r = 0.782, p = .2181) exhibited the strongest relationship with N_{max} among dune sites while soil nitrogen (r = 0.563, p = .4371) provided the strongest relationship among swales. Similar phosphorus dynamics between all sites (except 36 year swale) negated the need for correlation analysis. Unique litter quality differences for 36 year swale roots may have been responsible for high phosphorus retention coupled with immobilization. Thirtysix year swale roots contained the highest initial lignin content, lowest initial phosphorus content and exhibited an exceedingly high N:P ratio (29 vs. 4 to 10) and L:P ratio (541 vs. 67 to 246).

Differences in litter quality between herbaceous and woody roots produced different patterns of mass, nitrogen and phosphorus loss when decomposing in the same site. Roots from the 36 year swale (higher lignin and nitrogen content, lower phosphorus content) buried in the

24 year swale, next to *Spartina patens* roots, showed slower decay ($k = 0.12$ " .01 s.e., $r^2 = 0.73$) and net phosphorus immobilization ($P_{max} = 106.44$ %). No nitrogen immobilization during 36 year woody root decay occurred in the 24 year swale but root type effects ($F = 92.43$, $p < .0001$) indicated significantly greater percent nitrogen retention (Appendix X). These differences mirrored those occurring between herbaceous and woody roots in the 36 year swale (same root type pair) but not in the 120 year swale. Litter quality similarities (phosphorus and lignin content) between *Spartina patens* roots and 120 year *Myrica cerifera* roots produced similar decay rates (Table 5 and 7) and phosphorus dynamics (Figures 7 c and 9 c) but different nitrogen dynamics (Figures 7 b and 9 b).

Changes in litter quality during decay

Spartina patens decay, in dunes and swales, modeled how environmental factors transform chemically similar substrates into chemically different substrates. These effects can cascade through the decay continuum, influencing the eventual formation of stable organic matter. After 1.7 years of decay, environmental factors specific to swales decreased litter quality. *Spartina patens* roots in swales exhibited greater decreases in phosphorus content (0.04 % to 0.05 %) and smaller changes in nitrogen content (0.82 % to 1.01 %) relative to dunes (P = 0.08 % to 0.10 %, N = 1.15 % to 1.35 %). Greater increases in N:P ratios occurred in swales, inducing greater phosphorus limited decay (Table 10). In the most anoxic site (24 year swale), lignin content increased to 25.0 % while other sites showed smaller changes. Dunes showed lower percent lignin remaining than swales (Table 11). Within topographic classes, older sites had less percent lignin remaining than younger sites. Lignin and nutrient dynamics in swales yielded higher L:N and L:P ratios after 1 year of decay.

Native root decay modeled how different initial litter quality and environmental influences during decay affected eventual litter quality. In all sites, nitrogen content generally increased after 1.7 years of decay while phosphorus content generally decreased (Table 10). Initial differences in nitrogen content continued to be maintained. Phosphorus content among all native roots became more similar. N:P ratios increased in all sites and showed greater similarity between swales. Across dunes, lignin concentration became more similar and greater decay across the chronosequence resulted in more decay of lignaceous compounds (Table 11). Across swales, lignin content increased and became more similar in the three older swales but decreased in the 6 year site, which also demonstrated higher rates of lignin degradation. The 24 and 120 year swales experienced absolute gains in percent lignin remaining after 1 year. Excluding the 24 year swale, L:N ratios among all sites became more similar. L:P ratios increased more in swales than dunes.

Roots exposed to identical environments (native vs. *Spartina patens* transplants) generally continued exhibiting litter quality differences. Some convergence in litter quality

Table 11. Percent lignin remaining in *Spartina patens* roots and native roots after 1 year of decay (n=1).

	Spartina patens roots	Native roots
Dune Age		
6 year		92.51
24 year	63.71	83.17
36 year	67.84	60.70
120 year	34.27	41.37
Swale Age		
6 year		47.64
24 year	114.86	101.93
36 year	86.90	86.90
120 year	74.92	151.20

parameters did occur. Across dunes, N:P ratios became more similar between native and *Spartina patens* roots. Other convergences were isolated cases and not representative of any consistent trends.

DISCUSSION

Influences on belowground rates of mass loss

Hydrologic influences produced marked differences in decay of *Spartina patens* roots between dunes and swales and likely influenced native root decay similarly between dunes and swales. However, hydroperiod differences among swales did not influence *Spartina patens* decay even though frequency and duration of surface flooding differed, creating greater periods of oxic soil conditions in older swales. Neckles and Neill (1994) experimentally mimicked hydroperiods typical of seasonally saturated soils and found no differences in belowground decay. An annual drawdown of water can alleviate low oxygen tension and minimize differences in anoxia that would otherwise inhibit decay (Day and Megonigal 1993, Brinson et al. 1981) and may explain why *Spartina patens* decay did not respond to hydroperiod variation among swales. Similar inhibitions on *Spartina patens* decay through hydroperiod influences were found across a broader spatial scale on Hog Island (Appendix 3).

Woody root decay across swales responded to hydroperiod variability. Woody litter is more sensitive to microenvironmental differences than non-woody litter (Taylor et al. 1991). Excess moisture inhibits fungal activity important for lignin degradation (Fahey et al. 1988, McClaugherty et al. 1985) and fragmentation of bark (Harmon and Hua 1991). Increased fungal activity under drier, less anoxic conditions may have contributed to the increase in 36 year *Myrica cerifera* decay between the 24 year swale (k = .12) and 36 year swale (k = .20).

Decreases in swale root decay were expected in response to increased depth and degree of saturation. Studies incorporating a depth component to belowground decay in saturated environments demonstrated this effect (Hackney and de la Cruz 1980, Tupacz and

Day 1988) while others found no depth effect or relationship with soil redox potential (Blum 1993, Hackney 1987). Decay of *Spartina patens* roots varied with depth, but not predictably. Higher rates of decay were associated with lower soil redox potentials. Couto et al. (1985) and Ransom and Smeck (1986) found reduced soil conditions reflected the availability of inorganic electron donors and acceptors (including but not limited to O_2) and organic matter, rather than the degree of saturation. The presence of easily degradable carbohydrates can enhance the rate of complex carbohydrate (ie. lignin) degradation (Kirk et al. 1976, Melillo et al. 1989). Enhanced decay at lower soil redox potentials might be indicative of greater microbial activity responding to greater cometabolite availability and could explain why decay of *Spartina patens* roots does not decrease directly with increases in depth.

In contrast, decay of woody roots in all swale sites demonstrated decreased decay with increased depth, similar to other studies of woody root decay in wetland systems (Tupacz and Day 1988, Day et al. 1989). If cometabolites affected the vertical pattern of *Spartina patens* root decay, woody root decay may have been unresponsive to these influences due to structurally more complex root tissue. Tissue fragmentation, either through fungal activity, live root activity or faunal activity, stimulates decay in woody roots (Day et al. 1989, Harmon and Hua 1991). In the present study, decay rates for woody roots, and dune grass roots as well, were correlated with root ingrowth density.

Differences in litter quality were important during decay, and may have been influenced by site characteristics. Among dune sites, high initial root nitrogen, high initial root lignin and high soil nitrogen availability were correlated with high native root decay . High soil nitrogen generally increases litter nitrogen (Cuevas and Medina 1988, Vitousek et al. 1994) and is considered an important feedback loop for regulating decay rates (Aber and Melillo 1982, Shaver and Melillo 1984). Similar soil nitrogen and root nitrogen gradients occurred across Hog Island on a broader spatial scale (Appendix 3). The insensitivity of *Spartina patens* root decay to nitrogen availability across dunes demonstrated the superiority of litter nitrogen over exogenous nitrogen as an important control on decay. Typically, higher lignin content suppresses decay (Meentenmeyer 1978, Berg et al. 1984, Fogel and Cromack 1977), but native dune roots with the highest lignin content decomposed fastest. Nutrient content is important during early decay, but lignin assumes a greater role during later decay (Berg and Stååf 1980, Berg and Ågren 1984). Taylor et al. (1989) reported C:N ratios and nitrogen concentrations predicted decay rates better for litter below 20.5 % lignin, but above this breakpoint, lignin content and L:N ratios were better predictors. After 2.25 years of decay, similar levels of percent mass remaining between 24 and 120 year native roots may have reflected the increasing importance of lignin content.

Low root nitrogen, low available soil nitrogen, low nitrogen:phosphorus ratios and high lignin:nitrogen ratios correlated with high native root decay among swales sites. High root nitrogen content and soil nitrogen availability associated with the nitrogen fixing activity of *Myrica cerifera* linked woody tissues with high nitrogen content and low L:N ratios (13-19) in contrast to 6 year roots (L:N=35). N:P ratios above 10 impose phosphorus limitations to decomposers (Seastedt 1988) and may have played a role in the slow decay of 36 year roots (N:P=29, k=.20) and the faster decay of 6 year roots (N:P=7, k=.41).

Influences on nutrient and carbon dynamics during belowground decomposition

Environmental gradients influenced rates of lignin degradation. Roots incubated in swales experienced less lignin degradation than in dunes. Additionally, more initial lignin remained in *Spartina patens* roots and 36 year swale woody roots decomposing in the highly anoxic 24 year swale in contrast to older swales. Under anoxic conditions, selective degradation of non-lignified compounds and subsequent humification of secondary metabolites can be enhanced (Howarth and Hobbie 1982), resulting in a net increase of lignin-like residue. Under identical site conditions, litter quality attributes affected lignin dynamics. Woody 120 year swale roots showed 151 % lignin remaining after 1 year in contrast to 75 % in *Spartina patens* roots even though decay rates and initial lignin content were similar. Higher nitrogen content in woody roots possibly contributed to greater formation of decay resistant nitrogenous compounds registering as lignin (Vitousek et al. 1982, Aber and Melillo 1982). More phenols, terpenes and tannins, which are common in bark, would provide surplus precursory compounds for more refractory residues (Fogel and Cromack 1977, Horner et al. 1988). Among dunes, percent lignin remaining in native roots decreased in response to greater decay.

All litters exhibited an initial leaching phase of nitrogen with subsequent peaks of accumulation, followed by a stabilization or decrease in percent nitrogen remaining. When net nitrogen immobilization (> 100 %) occurred, the magnitude of increase was slight and brief. Among dunes, high L:N ratios were related to net nitrogen immobilization. Nitrogen immobilization during 6 year native root decay (low lignin, low nitrogen, L:N=22) was expected due to greater nitrogen limited decomposition (Van Vuuren et al. 1993, Berendse et al. 1987). This would also explain the nitrogen immobilization observed during 6 year native swale root decay (L:N=35). By this reasoning, less immobilization should have occurred during decay of older, more nitrogen enriched, native dune roots. High initial nitrogen and lignin found in 120 year dune roots (L:N=25) likely enhanced lignin-nitrogen complexing and produced immobilization (Camiré et al. 1991, Wilson et al. 1986). These effects were short-term. Once lignin degradation began, nitrogen release occurred and differences between the three older dunes disappeared. Lignin-nitrogen interactions also influenced nitrogen immobilization in woody swale roots. Surplus exogenous nitrogen likely enhanced immobilization. Woody 36 year roots decomposing under lower nitrogen availability in the 24 year swale showed no immobilization, although greater leaching rates could be important under more flooded site conditions. Additionally, *Spartina patens* roots in the 24 year swale experienced greater leaching losses.

Phosphorus was rapidly mineralized and susceptible to leaching. Seastedt (1988) suggested belowground phosphorus cycles may lack an immobilization interval due to predominance of phosphorus in soil in unavailable forms. Vitousek and Sanford (1986) implied phosphorus cycles can be decoupled from carbon cycles since ester-linkages binding orthophosphate to carbon can be easily cleaved by extracellular phosphatases. Vesicular arbuscular mycorhizze (VAM) are considered important to this process and critical for plant phosphorus nutrition, especially in sand dune environments (Koske and Polson 1984). High initial N:P and L:P ratios in 36 year swale roots may have induced microbial immobilization or promoted immobilization through lignin-phosphorus interactions (Berg and McClaugherty. 1989, Borie and Zunino 1983). Additionally, much of the initial phosphorus may have been lignin encased as is often true for nitrogen (Berendse et al. 1987).

In the present study, herbaceous roots unexpectedly exhibited very low to no net nitrogen immobilization while phosphorus was rapidly mineralized. Although woody roots retained and accumulated nitrogen and phosphorus to greater degrees, the increases were not as great as expected. Black alder roots (similar in lignin and nitrogen content to 36 year *Myrica cerifera* roots) immobilized nitrogen to 170 % of original amounts after 462 days and were still increasing (Camiré et al.1991). However, the saturated to flooded soil conditions of this study may have decreased potential immobilization through inhibition of decay and increased leaching effects (Day et al. 1989). All herbaceous roots, by virtue of their lignin and nitrogen chemistry, should have immobilized nitrogen as predicted by Aber and Melillo (1982). However, low to no nitrogen immobilization potential of roots have been documented elsewhere. Seastedt et al (1992) reported very low nitrogen immobilization potential for tall grass prairie roots concurrent with rapid phosphorus mineralization. Small fine roots of deciduous temperate forests rapidly mineralized nitrogen and were not important for belowground nitrogen and phosphorus immobilization (Fahey et al. 1988). Buried leaves accumulated less nitrogen than surficial leaves during decomposition (McLachlan and van der Merwe 1991). In this system, belowground decomposition favors early release of nitrogen and phosphorus. Competition among roots and soil fauna, grazer activity, or the influence of fungal hyphae linkages may transfer nutrients away from the decaying litter, removing possible sources of nitrogen and phosphorus for immobilization (Harmon and Hua 1991, Schomberg et al. 1994, Seastedt et al. 1992). In other dune chronosequences, VAM density increases with age (Koske and Polson 1984). Competitive interactions for nitrogen may have been less intense in the 6 year dune, enhancing nitrogen immobilization and retention. Separate from decomposition processes, greater nutrient accumulation aboveground can be enhanced through autotrophic bacteria or blue-green algae colonization; an influence not likely to occur belowground (Odum and Heywood 1978, Chamie and Richardson 1978).

Melillo et al (1989) likened early stages of decay, or Phase I decay, to a "decay filter" that results in marked changes in mass loss, carbon and nutrients to produce chemically similar organic matter from initially different precursors. Overall, chemically different root material decomposing under similar environments, and very dissimilar environments, continued to exhibit different litter quality attributes. Environmental controls were particularly influential and produced dramatic shifts in litter quality from identical precursor material The end of Phase I decay is generally marked by an 80 % mass loss (Aber et al. 1990). This study was not designed for long-term evaluation of decomposition dynamics and different decay rates across the island confound appropriate points of comparison. Therefore, it was not surprising that litter quality continued to differ.

On Hog island, these patterns of decay dynamics have important implications for ecosystem nutrient cycling. The nutrient pool in swale soils is higher than dunes and may be receiving groundwater export of leachates from decomposing litter in dunes. In many of the dune sites, decay after 2.2 years yields as little as 20 % mass remaining, indicating rapid rates of organic matter turnover in relation to swales which are likely to accumulated carbon. Additionally, a short-term study on rates of aboveground decay on Hog Island suggest burial, at least in dune soils, enhances the rate of decay (Appendix 4). Gradients across the chronosequence indicated increased soil fertility through increased soil organic matter and available nitrogen in older sites. An increase in nitrogen retention occurs across swales, mediated by the introduction of *Myrica cerifera*. Across dunes, short-term nitrogen immobilization may decrease the potential for leaching in the 120 year dune, but slower decay, greater duration of nitrogen immobilization and less nitrogen mineralization conserves nitrogen in the 6 year site.

Belowground decay dynamics on Hog Island are under many of the same controls that regulate aboveground decay. Attributes, such as landscape position and nutrient status influence decomposition processes directly, and indirectly, through species-level controls in a predictable manner. Soil nutrient status influenced plant nutrient status. Species characteristics (ie. *Myrica cerifera*), in turn, influenced soil nutrient characteristics. Lignin content of root tissue and hydrologic influences modified decay rates and nutrient dynamics in swales while nitrogen content was operative in dune root decay. Biological immobilization of nitrogen occurred in response to nitrogen limited decay. Lignin-nitrogen and, perhaps, lignin-phosphorus interactions, produced physicochemical immobilization of nutrients. However, compared to aboveground decay, nutrient immobilization/mineralization dynamics were different. This may be mediated through complex soil interactions that do not necessarily occur aboveground. How these belowground processes differ from system to system, differ in response to different quality litters (herbaceous vs. woody roots) or in response to abiotic controls are fruitful questions which can lead to better understanding of soil fertility issues and global biogeochemical cycles.

CHAPTER III

THE INFLUENCE OF NITROGEN AVAILABILITY ON ROOT DECOMPOSITION DYNAMICS

INTRODUCTION

Exogenous nitrogen supplies have significant effects on decomposition rates and nutrient dynamics. However, influences exerted by nitrogen availability generally operate by controlling litter quality characteristics which then influence decay and nitrogen dynamics (Shaver and Melillo 1984, Vitousek 1982, Nadelhoffer et al. 1985). Greater turnover, both in fine root material (Aber et al. 1985, Nadelhoffer et al. 1985, Cuevas and Medina 1988) and aboveground litter types (Pastor et al. 1987, Vitousek 1982) occurs in more nutrient rich sites. Intuitively, one would expect that higher nitrogen availability would compensate for nitrogen limitations imposed by litter quality on decomposer activity and serve to increase decomposition. Additionally, since exogenous sources are required for nitrogen immobilization, fertilization should increase nitrogen immobilization, especially in low nitrogen plant material or ecosystems. Tests of the effects of variable exogenous nitrogen availability have produced conflicting results. McClaugherty et al (1985) found that enhanced decay and nitrogen immobilization of litter in response to a nitrogen mineralization gradient only occurred in low quality (low nitrogen, high lignin) material. High nitrogen and low lignin material showed no decay or nitrogen dynamic responses to this gradient although other site effects may have confounded the results. Vitousek et al. (1994) observed an increase in decay of a common substrate placed along a nitrogen availability gradient, but, interactions with abiotic site factors, such as temperature and moisture, were indicated.

Direct testing through fertilization experiments can remove site and litter quality effects. Hunt et al (1988) found aboveground decay and nitrogen immobilization increased for a variety of litter types in forested, meadowland and prairie ecosystems as a result of fertilization. Jordan et al. (1989) and Triska and Sedell (1976) found no aboveground decay or nitrogen immobilization responses as a result of nitrogen enrichment.

Nitrogen immobilization in aboveground litter is influenced by hyphal bridges that translocate nitrogen from the soil to the litter (Harmon and Hua 1991, Fahey 1983). Fungi respond well to increases in nitrogen availability and can increase nitrogen content three fold (Kaushik and Hynes 1971) which may partially explain greater nitrogen immobilization in response to fertilization. Fungi are considered better competitors aboveground for nitrogen uptake, but may be outcompeted belowground by roots and microbial prokaryotes (McGill et al. 1981, Holland and Coleman 1987). The influence nitrogen fertilization may have belowground is uncertain.

This fertilization experiment was designed not only to test how belowground decay dynamics respond to increased nitrogen availability, but also how this response is mediated by differences in nitrogen status of both root material and soils. Across Hog Island dunes, soil nitrogen availability, root nitrogen content and root decay increases with site age (Chapter II). Nitrogen amendment would hypothetically increase decay on all sites due to the inherent nutrient poor status of barrier islands. Additionally, responses of both decay and nitrogen immobilization would be greater in younger sites that are presumably more nitrogen limited.

By artificially increasing exogenous soil nitrogen, the study posed the following questions. Is decomposition of dune roots limited by soil nitrogen? Do these responses differ in accordance with ambient soil nitrogen resources? Is nitrogen immobilization limited by available soil nitrogen?

METHODS

In order to determine if root decomposition and nitrogen immobilization were nitrogen limited, a nitrogen fertilization experiment was conducted on the three older dunes (24, 36 and 120 year sites). Within each site, two designated areas were treated identically to control areas with regards to size, vegetation composition and number of native litter bags buried. Throughout the study period (2.25 years), these areas were fertilized four times on an annual basis, using a broadcast application technique, resulting in a delivery rate of 60 g N m^{-2} yr^{-1}. The fertilizer contained 41.8 % nitrogen (urea) and consisted of 30 % quick release pellets and 70 % slow release pellets in order to ensure elevated levels until the next fertilizing event. Percent mass remaining, nitrogen remaining and phosphorus remaining in response to fertilization were evaluated on a site basis using the same ANOVA procedure described in Chapter Two. Similar methods, as previously described, were also used to evaluate fertilization effects on soil redox potential, soil pH and soil temperature on a site basis.

RESULTS

Soil responses to fertilization

Fertilization produced a significant decrease in mean annual (depth combined) soil redox potential at the 36 and 120 year dunes but not the 24 year dune site (Table 12). In both control and fertilized plots, soil redox potential remained well within levels representative of oxidized soils (> 300 mV, Gambrell and Patrick 1978). In all sites, soil redox potential showed a slight, but generally nonsignificant, decrease in depth regardless of treatment (data not presented). Fertilization produced a significant decrease in mean annual soil pH (depth combined) only on the 120 year dune. Within each site x treatment combination, mean annual soil pH was not significantly different between depth intervals (data not presented). Mean annual soil temperature was similar between fertilized and control plots and ranged from 22 to 24E C.

All forms of nitrogen in soil and soil water showed a significant (p=.05) increase as a result of fertilization (Table 12). Increases were greater in the older dune site than in the younger sites. For example, mean annual soil ammonium between control dunes was not significantly different and ranged from 2.11 to 2.46 % dry weight. Fertilization increased ammonium levels to 36.67 % dry weight in the 120 year dune in contrast to 18.98 % dry weight in the 24 year dune. Greater nitrogen limitation in the 24 year dune site likely induced proportionally greater nitrogen uptake in response to fertilization, thus decreasing available soil nitrogen relative to older sites. In control areas, soil nitrite-nitrate increased across the chronosequence implying more extreme nitrogen limitation in younger dunes. Additionally, nitrogen mineralization rates showed a greater increase in response to

Table 12. Response of soil Eh (n = 304), soil pH(n = 288-304), soil (n = 106) and soil water nutrients (n = 43-46) and nitrogen mineralization rates to fertilization. One standard error in parentheses. Different lowercase superscripts indicate significant differences ($p < .05$) between treatments within a site.

	24 year dune		36 year dune		120 year dune	
	control	fertilized	control	fertilized	control	fertilized
Soil Eh (mV)	488 (5)^a	461 (5)^a	529 (5)^a	474 (5)^b	541 (5)^a	468(5)^b
Soil pH	6.2 (0.1)^a	5.8(0.1)^a	5.9(0.1)^a	5.9 (0.1)^a	5.7(0.1)^a	5.1(0.1)^b
Soil nutrients (%dry weight)						
NH_4	2.11 (0.17)^a	18.98(1.93)^b	2.54(0.22)^a	23.86 (2.10)^b	2.46(0.25)^a	36.67(3.81)^b
NO_2-NO_3	0.17 (0.01)^a	1.39(0.15)^b	0.28(0.01)^a	1.69 (0.15)^b	0.44(0.03)^a	2.19(0.22)^b
Soil water nutrients (mg/l)						
NH_4	0.10 (0.02)^a	2.91(1.13)^b	0.08(0.02)^a	19.86 (6.84)^b	0.11(0.03)^a	19.88(4.26)^b
NO_2-NO_3	0.14 (0.03)^a	8.08(2.39)^b	0.29(0.06)^a	29.28 (5.93)^b	0.26(0.08)^a	38.33(7.43)^b
TKN	1.01 (0.34)^a	7.25(4.73)^b	0.79(0.13)^a	25.96 (11.96)^b	0.81(0.12)^a	31.86(8.27)^b
T	0.07 (0.01)^a	0.13(0.04)^b	0.07(0.01)^a	0.16 (0.04)^b	0.09(0.02)^a	0.10(0.03)^b
Nitrogen mineralization rate (g m^{-2} yr^{-1})	0.20	1.45	0.02	0.87	0.19	0.23

fertilization in the 24 and 36 year old sites. Although no differences in soil water orthophosphate levels (ranged from 0.02 to 0.03 mg/l) occurred in response to fertilization, total phosphorus showed a significant increase due to fertilization in the 24 and 36 year dune sites (Table 12). Greater biological uptake of phosphorus under release from nitrogen limitations could produce more organically bound phosphorus in soil water.

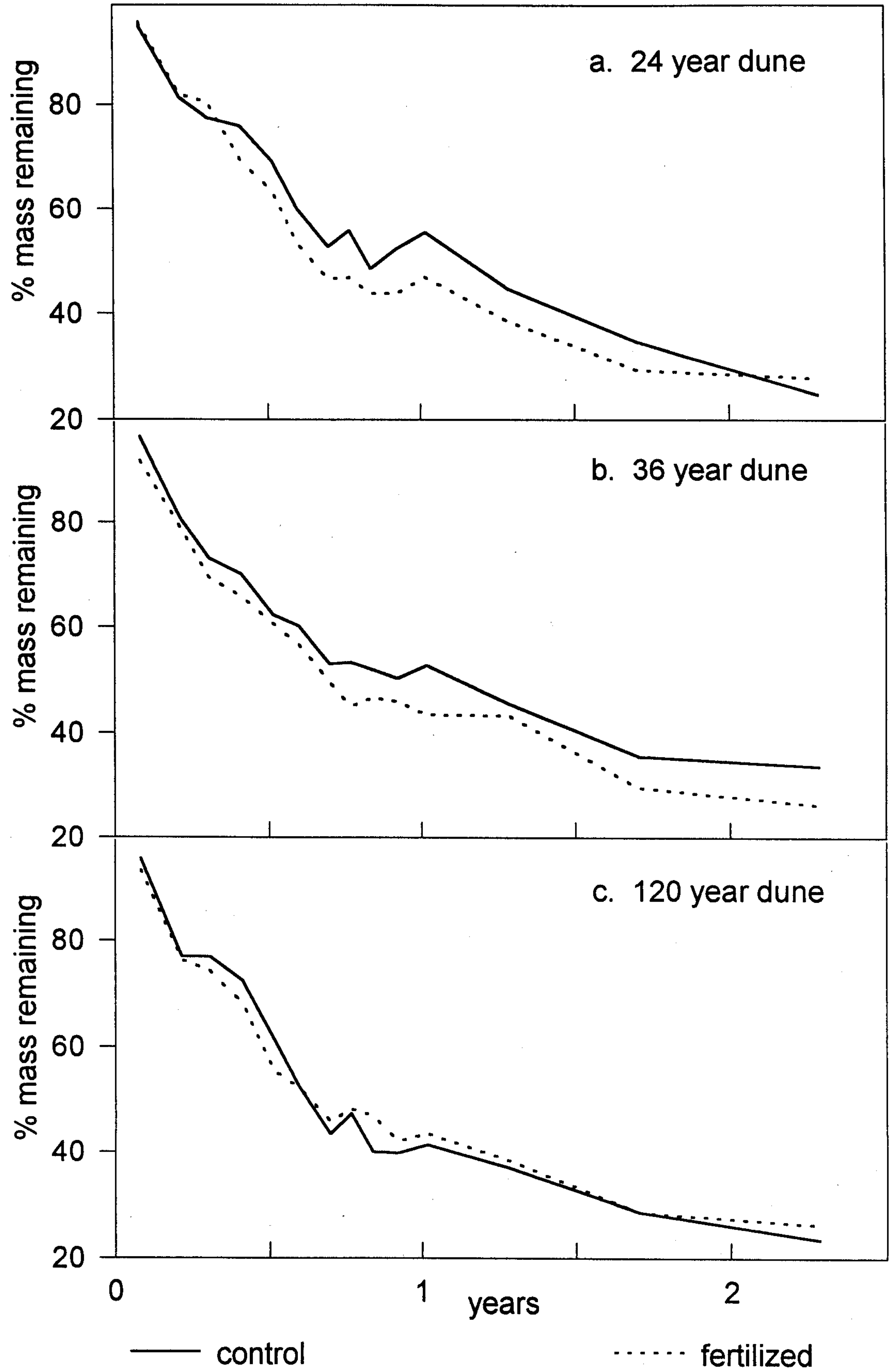
Response of decay dynamics to fertilization

Analysis of variance on percent mass remaining showed significant treatment effects for both the 24 year (F = 30.81, p < .0001) and 36 year (F = 34.73, p < .0001) dune sites while fertilization produced no significant decay response on the 120 year dune site (F = 0.06, p < .8001). Faster decay occurred in the fertilized areas of the 24 and 36 year sites, but the decrease in time required to reach 1 % of initial mass remaining was only 1 year for the 36 year site and 0.5 years for the 24 year site (Table 13). In contrast, decay rates indicated fertilization may have had a negative effect on the 120 year dune. Decay rates decreased from 0.86 to 0.79 with an increase of 0.5 years needed to reach 1 % mass remaining in fertilized areas (Table 13). Figures 10 a-c demonstrate the influence of fertilization on decay over time on each of the three dune sites. Significant treatment x time effects occurred only for the 24 year dune site (F = 2.16, p < .0119). Initially fertilization stimulated decomposition on the 24 year dune, but the effects were not sustained. On the 36 year dune site, fertilization increased decay throughout the study period while a slightly negative response (not significant) to fertilization took place at the 120 year dune site. Chapter II demonstrated that decay of native roots increased across the chronosequence and is likely a response to increased tissue nitrogen content. With

Table 13. Decay rates [-k (yr^{-1})], coefficient of determination (r^2) and time (yr) to reach 1 % mass remaining ($t_{.01}$) across dune chronosequence in response to fertilization. One standard error in parentheses. All regressions are significant at p=.0001.

	Control			Fertilized		
	k	r^2	$t_{.01}$ (yr)	k	r^2	$t_{.01}$ (yr)
Dune Age						
24 year	.70 (.01)	.87	6.58	.76 (.01)	.88	6.06
36 year	.65 (.01)	.85	7.08	.76 (.01)	.88	6.06
120 year	.86 (.02)	.83	5.35	.79 (.01)	.87	5.83

Figure 10. Effect of fertilization on percent mass remaining in a) 24 year dune, b) 36 year dune, c) 120 year dune.



a. 24 year dune
b. 36 year dune
c. 120 year dune
% mass remaining
80
60
40
20
0
1
2
years
control
fertilized

the addition of nitrogen, decay rates became more similar (Table 13). Fertilization partially offset low tissue nitrogen content but other factors limiting decay also operated. Part of this response was due to a slight, but non-significant, inhibition on the 120 year site.

In control plots, the disappearance of initial amounts of lignin parallelled decay rates. The 120 year dune, which had faster unfertilized decay rates, also demonstrated greater lignin decay relative to initial amounts after 1 year (Table 14). Under high nitrogen availability, a slight negative response in lignin degradation occurred on the 24 and 36 year site in contrast to a greater response on the 120 year dune (Control = 41.37 %, Fertilized = 54.45 %). The inhibition of lignin degradation may have been more pronounced at this site due to initially greater amounts of lignin in tissues on the 120 year dune (20.0 %) than the younger sites (9.5 - 13.0 %). This could have contributed to the slight inhibition of decay noted on the 120 year dune.

On the 24 and 120 year dunes, all depth x treatment and depth x treatment x time interactions were nonsignificant. On all sites, significant depth effects indicated slower decay at the 0-10 cm depth although significant differences after 2.25 years of decay were not apparent (Table 15). Significant depth x treatment effects ($F = 5.85$, $p < .0006$) on the 36 year dune related to faster unfertilized decay at the 10-20 cm depth and faster fertilized decay at the 20-30 cm depth. Decay rates for specific depths increased in response to fertilization on the 24 and 36 year dunes, but significant differences in percent mass remaining after 2.25 years did not exist.

Within all sites, fertilization produced a significant increase in percent nitrogen

Table 14. Percent lignin remaining in response to fertilization (n=1).

	Control	Fertilized
Dune Age		
24 year	83.17	86.99
36 year	60.70	61.40
120 year	41.37	54.45

Table 15. Effects of fertilization on decay rates [-k (yr^{-1})], coefficient of determination (r^2) and percent mass remaining after 2.25 years of decay (% M) for depth intervals across the dune chronosequence. All regressions are significant at p=.0001. One standard error in parentheses. Different lowercase superscripts indicate significant differences (p=.05) between depths.

	Control			Fertilized		
	k	r^2	% M	k	r^2	% M
Dune age			n = 139	n = 140		
24 year						
0-10	.70 (.03)	.84	24.94 (3.03)^{a}	.72 (.02)	.90	26.27 (1.56)^{a}
10-20	.81 (.03)	.87	19.66 (1.86)^{a}	.86 (.03)	.89	25.50 (1.87)^{a}
20-30	.69 (.02)	.90	26.93 (2.39)^{a}	.76 (.02)	.89	28.46 (2.16)^{a}
30-40	.62 (.02)	.90	27.80 (1.45)^{a}	.70 (.02)	.88	31.21 (2.18)^{a}
36 year			n = 140	n = 139		
0-10	.46 (.01)	.87	43.93 (3.64)^{a}	.63 (.02)	.91	28.43 (2.70)^{a}
10-20	.74 (.02)	.90	26.24 (3.61)^{b}	.78 (.02)	.89	26.33 (2.80)^{a}
20-30	.72 (.02)	.87	31.34 (4.09)^{ab}	.84 (.02)	.90	22.13 (2.40)^{a}
30-40	.68 (.02)	.88	33.47 (3.56)^{ab}	.78 (.02)	.88	28.18 (2.48)^{a}
120 year			n = 139	n = 140		
0-10	.68 (.02)	.85	28.07 (2.05)^{a}	.64 (.02)	.90	31.77 (4.85)^{a}
10-20	.97 (.04)	.83	22.01 (4.51)^{a}	.83 (.03)	.87	25.45 (3.41)^{a}
20-30	.89 (.03)	.84	23.64 (6.03)^{a}	.85 (.03)	.89	23.92 (3.03)^{a}
30-40	.90 (.03)	.86	20.68 (3.73)^{a}	.84 (.03)	.88	23.70 (3.35)^{a}

remaining that was unconfounded by interactions with time (Figures 11 a-c). Treatment effects on the 24 year dune (F = 65.34, p = .0001) and 36 year dune (F = 24.28, p = .0001) were immediate, or nearly so. While control areas in these sites showed increases in percent nitrogen remaining after initial decreases, there were no periods of net nitrogen immobilization (>100 %). A period of net nitrogen immobilization in response to fertilization occurred on the 24 year dune. After 1.7 years, percent nitrogen remaining was significantly greater (p=.05) in fertilized areas than in control areas for both the 24 year dune (48.76 % v. 70.65 %) and the 36 year dune (51.26 % v. 68.71 %). Treatment effects for the 120 year dune (F=5.45, p=.0153) were not immediate nor lasting (Figure 11 c). Initially, nitrogen dynamics were similar. Decaying roots in both control and fertilized plots underwent a period of net nitrogen immobilization. After 0.5 years of decay, greater nitrogen retention continued in the fertilized roots, but, by 1.7 years of decay, percent nitrogen remaining in control and fertilized substrate was nearly identical (43.33 % v. 41.17 %). In Chapter II, nitrogen immobilization in 120 year dune native roots was attributed to higher initial lignin content and subsequent lignin-nitrogen interactions. Initially, exogenous nitrogen had no effect on nitrogen accumulation and immobilization, but did influence nitrogen dynamics later. After 1 year of decay, greater lignin concentration in fertilized roots may have enhanced lignin-nitrogen interactions (Table 16). Lignin content was only slightly greater in fertilized substrate from the 24 and 36 year dunes relative to control substrate. Coupled with higher nitrogen availability, these differences may also have contributed to greater nitrogen retention.

Fertilization had no effect on phosphorus dynamics (Figure 12 a-c). Analysis of

Figure 11. Effect of fertilization on percent nitrogen remaining in a) 24 year dune, b) 36 year dune, c) 120 year dune.

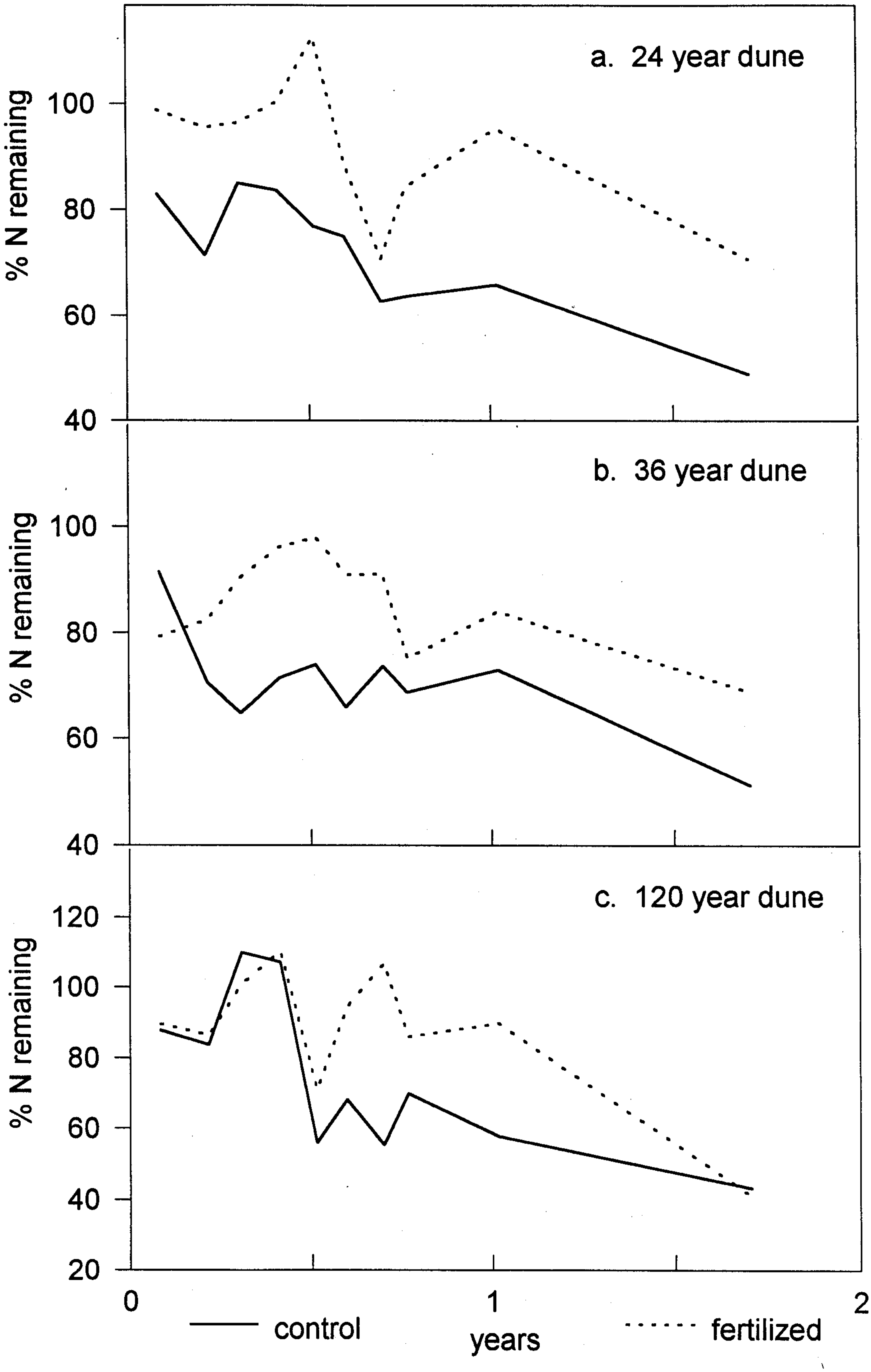

a. 24 year dune
b. 36 year dune
c. 120 year dune
% N remaining
% N remaining
% N remaining
100
80
60
40
100
80
60
40
120
100
80
60
40
20
0
1
2
years
control
fertilized

Table 16. Initial litter quality indices and after 1.7 years of decay for nitrogen concentration (% N), phosphorus concentration (% P) and nitrogen:phosphorus ratio (N:P). One standard error in parentheses. Changes in lignin derived indices after 1 year of decay for lignin concentration (L), lignin:nitrogen ratio (L:N) and lignin:phosphorus ratios (L:P). n=1 for all indices except % N and % P where n=6.

		24 year dune		36 year dune		120 year dune	
		control	fertilized	control	fertilized	control	fertilized
N	initial	0.59 " 0.01		0.70 " 0.02		0.81 " 0.10	
	1.7 yr	0.83 " 0.05	1.43 " 0.05	1.01 " 0.06	1.62 " 0.12	1.13 " 0.23	1.39 " 0.09
P	initial	0.15 " 0.02		0.12 " 0.001		0.13 " 0.01	
	1.7 yr	0.06 " 0.004	0.07 " 0.01	0.06 " 0.004	0.07 " 0.004	0.07 " 0.01	0.08 " 0.003
N:P	initial	4		6		7	
	1.7 yr	14	20	17	23	16	17
L	initial	9.5		13.0		20.0	
	1.0 yr	14.3	17.7	15.0	18.4	20.0	25.0
L:N	initial	17		19		25	
	1.0 yr	20	15	15	15	19	18
L:P	initial	67		109		167	
	1.0 yr	286	295	214	307	286	357

variance on percent phosphorus remaining revealed no significant treatment or treatment x time effects in any of the three sites. After 1.7 years of decay, percent phosphorus remaining in all site and treatment combinations ranged from 12.61 % to 18.33 %.

Fertilization produced changes in litter quality indices that were mediated through influences on nitrogen content, and to a smaller degree, lignin content (Table 16). Greater L:P ratios occurred in fertilized substrate than in control substrate after 1 year due to higher lignin concentrations. In the 36 and 120 year fertilized substrates, increases in lignin content balanced increases in nitrogen content, resulting in similar L:N ratios after 1 year. However, the L:N ratio for 24 year fertilized substrate was lower (15) compared to control substrate (20) suggesting a greater demand for nitrogen in relation to lignin at this site. After 1.7 years, nitrogen content in all roots increased relative to initial amounts and, within sites, roots incubated in fertilized areas had higher nitrogen concentrations than roots decomposing in control areas. In contrast, phosphorus content decreased in all roots relative to initial amounts. On the 24 and 36 year dunes, changes in the N:P ratios of roots buried in fertilized plots produced substrates with greater potential for phosphorus limited decay. After 1.7 years, the N:P ratio of control roots was lower than fertilized roots on the 24 and 36 year dunes while fertilization had little effect on N:P ratios of 120 year dune roots.

Response of root ingrowth to fertilization

Analysis of variance showed root ingrowth density (Table 17) increased in response to fertilization on the 24 year dune ($F = 77.17$, $p < .0001$) and 36 year dune ($F = 74.53$, $p < .0001$), but not the 120 year dune ($F = 0.72$, $p = .4069$). Treatment x depth interactions

Figure 12. Effect of fertilization on percent phosphorus remaining in native roots on a) 24 year dune, b) 36 year dune, c) 120 year dune.

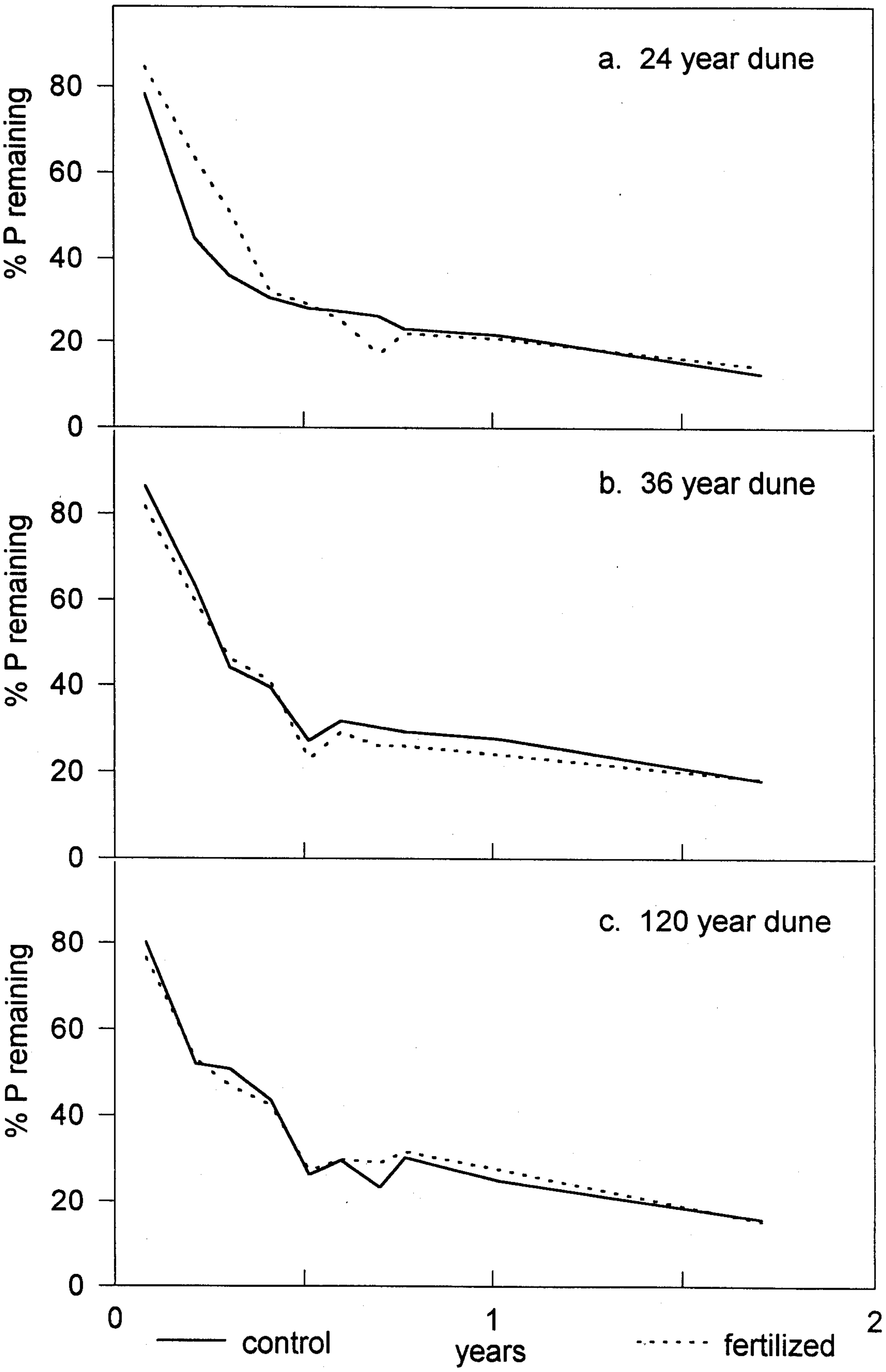

a. 24 year dune
b. 36 year dune
c. 120 year dune
% P remaining
0
20
40
60
80
0
1
2
years
control
fertilized

Table 17. Effects of fertilization on average root ingrowth density. One standard error in parentheses. Within sites, different uppercase superscripts indicate significant differences (p=.05) between treatment level. Different lowercase superscripts indicate significant differences (p=.05) between depths.

	24 year Dune		36 year Dune		120 year Dune	
	control	fertilized	control	fertilized	control	fertilized
Depth (cm)						
0-10	11.81 (1.89) ^{aA}	20.26 (1.57)^{abB}	2.27 (0.33)^{aA}	12.96 (2.28)^{bB}	6.96 (1.05)^{bA}	9.79 (1.39)^{bA}
10-20	10.79 (1.25)^{aA}	25.61 (1.82)^{aB}	4.28 (0.49)^{aA}	23.27 (2.54)^{aB}	16.62 (2.01)^{aA}	14.64 (1.71)^{abA}
20-30	6.80 (0.73)^{aA}	21.28 (1.46)^{abB}	3.16 (0.43)^{aA}	20.12 (2.03)^{abB}	15.27 (1.72)^{aA}	16.48 (2.04)^{aA}
30-40	6.32 (0.69)^{aA}	19.01 (1.50)^{bB}	3.53 (0.66)^{aA}	15.27 (1.51)^{bB}	11.84 (1.54)^{abA}	15.50 (1.94)^{abA}

were not significant on any site. Greater root ingrowth density occurred at 10-20 cm on the 24 and 36 year sites and 20-30 cm on the 120 year site. Treatment effects were maintained at particular depths within each site.

DISCUSSION

In a literature review on decomposition responses to fertilization, Fog (1988) found a wide range of responses indicating enhanced decay, inhibited decay and no effect at all. A large majority of these cases fell into neutral or negative categories and were attributed to a number of factors. Under conditions supporting nitrification, soil pH may drop in response to urea or ammonium fertilization as these forms of nitrogen are oxidized to nitric acid. Significant decreases in soil pH as a result of fertilization parallelled a neutral to negative response on the 120 year dune. High nitrogen levels can suppress lignolytic activity (Fenn et al. 1981, Scheu 1993) and can increase formation of toxic nitrogenous compounds, originating from lignin- or humic-nitrogen interactions, that may be inhibitory to decomposers (O'Connell 1994, Horner et al. 1988, Fog 1988). The initially greater and sustained lignin concentrations during decay found in the fertilized 120 year dune roots, coupled with decreased lignin degradation, may explain why a slight decrease in decay occurred. Another factor to consider may be trace metal contamination of the fertilizer. The fertilizer was not analyzed for contaminants, but, if present, could influence microbial activity.

In terrestrial systems (Hunt et al. 1988, Pastor et al. 1987) and, more often, in aquatic systems (Almazon and Boyd 1978, Jensen et al. 1978, Howarth and Fisher 1976, Kaushik and Hynes 1971), fertilization increased decomposition. Enhanced decay has been linked to a release of nitrogen limitation, especially for low nitrogen litter (Hunt et al. 1988, Almazon and Boyd). Similar conclusions, gathered in less direct ways, indicate nitrogen availability operates more strongly on low quality litter rather than high quality litter (McClaugherty et al. 1985, Taylor et al. 1991). Decomposition was limited by a combination of low nitrogen content in roots and soils of the 24 and 36 year dunes. Significant increases in root ingrowth density and mass also indicated other nitrogen limited responses in younger dunes.

Effects on nitrogen dynamics by fertilization also show a variety of responses. Jordan et al. (1989) and Triska and Sedell (1976) found that neither increased decay nor increased nitrogen immobilization occurred. Holland and Coleman (1987) and O'Connell (1994) showed an increase in nitrogen immobilization due to lignin-nitrogen interactions since decay responses were either neutral or negative. In studies confirming a positive link between decay and fertilization, immobilization of nitrogen also increased (Kaushik and Hynes 1971, Howarth and Fisher 1976, Hunt et al. 1988). Fertilization increased nitrogen retention in roots from the 24 and 36 year dunes. Since fertilization also stimulated decay, biological immobilization rather than physicochemical immobilization was implicated.

Nitrogen limited decomposition occurred on the younger (24 and 36 year) sites but not older (120 year) site. This statement must be tempered with the knowledge that fertilization may influence decay in indirect ways, such as the inhibition responses documented by Fog (1988). Although decay was stimulated on the 24 and 36 year site by nitrogen amendment, native unfertilized root decay on the 120 year site was still faster. Increased exogenous nitrogen did not fully alleviate limitations imposed by low litter nitrogen content. Additional factors, both internal and external to substrate quality, may also be important. Across the chronosequence, other lines of evidence, besides a small, but significant decay response, demonstrate greater nitrogen limitation on younger sites. Nitrogen mineralization rates showed greater increases on the 24 and 36 year sites with fertilization than on the 120 year site as did root ingrowth responses. Greater increases in soil nitrogen availability occurred on the 120 year dune with fertilization than younger dunes even though all sites received identical quantities of nitrogen. Although fertilization had no effect on soil water orthophosphate, soil water total phosphorus increased on the two younger sites. Increased organically bound phosphorus could be an indication of greater biological uptake of phosphorus due to release from nitrogen limitations. However, nitrogen immobilization potential associated with belowground decay was low, even with added nitrogen, and served to maintain leaky nutrient cycles typical of barrier island ecosystems.

CHAPTER IV

CONCLUSIONS

The dune soils of Hog Island, like many other barrier islands, are nitrogen poor in relation to other ecosystems and influence plant nutrient status. Alpine tundra ecosystems, considered to be nitrogen limited, exhibited soil ammonium in the range of 6 to 14 mg/kg and soil nitrite-nitrate from 1 to 7 mg/kg (Bowman et al. 1993). In contrast, a survey of nitrogen storage in forests floors showed ranges in soil ammonium from 10.7 to 97 mg/kg and in soil nitrite-nitrate from 0.2 to 11.9 mg/kg (Vitousek et al. 1982). Comparatively, the available soil nitrogen capital in Hog island dune soils is very low (NH_4: 0.17 - 0.44 mg/kg, NO_2-NO_3: 2.1 - 2.4 mg/kg).

Tall grass prairie roots, produced in a fire-induced nitrogen limited system, exhibited 0.49 % nitrogen and 0.05 % phosphorus (Seastedt 1988). Roots from *Calamagrostis canadensis* (Michx.) Nutt. (perennial, rhizomatous grass) grown under low nitrogen and phosphorus availability ranged from 0.56 to 0.70 % nitrogen and 0.06 to 0.07 % phosphorus (Shaver and Melillo 1984). Under high nitrogen and phosphorus availability, *Calamagrostis* roots ranged from 1.48 to 1.74 % nitrogen and 0.18 to 0.25 % phosphorus. Nitrogen content in leaves produced under low nitrogen availability by a nutrient conserving species was 1.22 % (Aerts and van der Peijl 1993). Nitrogen status of Hog Island dune roots (0.47 to 0.81 %) is comparable to roots from other nitrogen limited systems while phosphorus content reflects less phosphorus limitation (0.12 to 0.15 %) or more efficient allocation systems. Young soils typically exhibit greater phosphorus availability (Walker and Syers 1976). Hog Island swales supporting herbaceous vegetation showed similar soil nitrogen availability and root nitrogen and phosphorus content as dune soils and vegetation. The introduction of *Myrica cerifera* increased soil nitrogen availability (NH_4: 4.65 to 5.16 mg/kg, NO_2-NO_3: 0.78 to 1.25 mg/kg) and root nitrogen content (1.33 to 1.46 %) in older swales.

In nutrient poor ecosystems, mechanisms exist to prevent nutrient losses, such as slower decay rates and greater immobilization of nutrients (Vitousek and Sanford 1986, Barbour et al. 1987) . Developing ecosystems should show increasing nutrient capital through increases in biomass and soil organic matter components and greater amounts of total nutrients should be recycled rather than lost (Vitousek and Howarth 1991, Odum 1969). In addition, at least in early to mid stage development, nutrient outflows should decrease and production rates should increase (Vitousek and Reiners 1975). Concurrent with these patterns, young systems should be more nitrogen limited than older systems (Vitousek and Matson 1991, Stevens and Walker 1970). Under ideal circumstances, where major state factors (climate, parent material, relief and organisms) are held constant, soil chronosequences can be useful evaluative models (Jenny 1980). While barrier island chronosequences offer temporal gradients, considerable spatial heterogeneity confounds the effects of time by imposing physical gradients (wind, salt spray, relief and moisture) that, in turn, impact vegetational characteristics. However, taken holistically, these are the processes that make barrier islands unique. Considerable insight into barrier island development, at the ecosystem level, can be revealed through chronosequence studies.

Soil attributes and soil driven processes, such as root decay dynamics, across the Hog Island chronosequence exhibit certain trends expected in developing ecosystems and in response to nitrogen limitation. Pools of soil organic matter and inorganic soil nitrogen increase along dune and swale chronosequences. Fertilization responses indicated greater nitrogen limitations occur on younger dunes (24 and 36 year). Nitrogen content of root material, in response to soil nitrogen availability, influences decay rates predictably across the dune chronosequence. Slower root decomposition on younger, more nitrogen limited sites demonstrated the expected response to nitrogen limitation. However, nitrogen and phosphorus immobilization potential was either low or nonexistent on all dune sites. Higher decay rates, lower to no nutrient immobilization and higher soil nitrogen availability increased leaching potential in older dune sites (24 to 120 year) and could lead to increased nutrient losses rather than increased nutrient retention as hypothesized in accordance with Odum (1969). Rather, these process rates and system level attributes served to conserve nutrients in the more nitrogen limited 6 year dune. Greater production in older dunes could short-circuit potential nutrient losses. However, data on production from this study are limited to inferences based on root ingrowth measurements. Greater ingrowth mass and density occurred on the older dune. However, other studies on Hog Island that deal exclusively with seasonal variations in aboveground and belowground biomass and production indicated greater peak aboveground (Dilustro, pers. comm.) and belowground (Stevenson, pers. comm.) biomass allocation in younger sites and lower root production on the older site (Stevens, pers. comm.).

The introduction of a woody nitrogen fixing species, *Myrica cerifera*, along the chronosequence strongly influenced nutrient dynamics in both dunes and swales by increasing nitrogen capital and long-term nutrient storage and by introducing substantially different quality litter. Among swales, decay dynamics reflect both hydrologic controls and litter quality controls (woody vs. herbaceous). Although lignin content suppressed decay for 36 year woody roots compared to herbaceous roots, woodiness doesn't necessarily mean greater lignin content and slower decay. However, the biochemical and structural complexity of *Myrica cerifera* roots (ie. presence of bark) appeared to influence nitrogen retention and immobilization.

The introduction of *Myrica cerifera* affects dune nutrient dynamics. The likelihood of interactions between dunes and swales intensifies in the 36 and 120 year sites due to closer spatial proximity. Leaf litterfall inputs from adjacent stands of *Myrica cerifera* could have contributed nitrogen and organic matter to dune soils. The litter quality of senesced *Myrica cerifera* leaves likely undergoes different decay responses than dune roots. How this might have affected edaphic attributes is unknown. In a Hog Island minirhizotron study, Weber (pers. comm.) reported *Myrica cerifera* roots encroached dune soils in the 36 year site (other sites not measured). These interactions may provide another possible source of belowground organic matter and nitrogen and an additional nutrient uptake mechanism. These questions offer many avenues for further research.

Barrier islands are highly dynamic features of coastal environments. The processes governing island geomorphology and ecosystem structure and function are disturbance driven and serve to maintain barrier islands in early successional stages. Considerable heterogeneity in these stages is revealed by the diversity in island landscape features. The unforested dunes of Hog Island have low nutrient capital in soil and vegetation components. Belowground nutrient cycles are rapid and leaky and do not appear to slow or tighten in response to site age. As such, dunes are vulnerable to disturbance, especially if vegetation is impacted. The loose nutrient cycles of dunes are juxtaposed with swales that demonstrate slower turnover rates and greater storage of nutrients in soil and vegetation, particularly with the introduction of *Myrica cerifera*. In time, Hog Island dunes may support woody species, such as loblolly pine (*Pinus taeda*) and red cedar (*Juniperus virginiana*), that are found in more developed chronosequences of Southeastern Atlantic Coast barrier islands (Dueser et al. 1976) and add additional features of stability.

LITERATURE CITED

Aber, J.D and J.M. Melillo. 1982. Nitrogen immobilization in decaying hardwood leaf litter as a function of initial nitrogen and lignin content. Canadian Journal of Botany 60: 2263-2269.

Aber, J.D., J.M. Melillo and C. McClaugherty. 1990. Predicting long-term patterns of mass, N dynamics and SOM formation from initial fine litter chemistry in temperate forest ecosystems. Canadian Journal of Botany 68: 2201-2208.

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 (Berlin) 66: 317-321.

Aerts, R. and M.J. van der Peijl. 1993. A simple model to explain the dominance of low-productive perennials in nutrient-poor habitats. Oikos 66: 144-147.

Almazon, G. and C.E. Boyd. 1978. Effects of nitrogen levels on rates of oxygen consumption during decay of aquatic plants. Aquatic Botany 5: 119-126.

Anderson, J.M. 1981. Ecology for environmental sciences: biosphere, ecosystems and man. Edward Arnold, London.

Atkinson, D. 1973. Observations on the phosphorus nutrition of two sand dune communities at Ross Links. Journal of Ecology 61: 117-133.

Atlas, R.M. and R. Bartha. 1987. Microbial ecology: Fundamentals and applications, 2nd. ed. Benjamin/Cummings Publishing Co., Inc., California.

Barbour, M.G., J.H. Burk and W.D. Pitts. 1987. Terrestrial plant ecology, 2nd. ed. Benjamin/Cummings Publishing Co., Inc., California. pp 634.

Bargali, S.S., S.P. Singh and R.P. Singh. 1993. Patterns of weight loss and nutrient release from decomposing litter in an age series of eucalypt plantations. Soil Biology and Biochemistry 25: 1731-1738.

Berendse, F., B. Berg and E. Bosatta. 1987. The effect of lignin and nitrogen on the decomposition of litter in nutrient-poor ecosystems: a theoretical approach. Canadian Journal of Botany 65: 1116-1120.

Berg, B. and G.I. Ågren. 1984. Decomposition of needle litter and its organic chemical components: theory and field experiments. Long-term decomposition in a Scots pine forest. III. Canadian Journal of Botany 62: 2880-2888.

Berg, B., G. Ekbohm and C. McClaugherty. 1984. Lignin and holocellulose relations during long-term decomposition of some forest litters. Long-term decomposition in a Scots pine forest. IV. Canadian Journal of Botany 62: 2540-2550.

Berg, B. and C. McClaugherty. 1989. Nitrogen and phosphorus release from decomposing litter in relation to the disappearance of lignin. Canadian Journal of Botany 67: 1148-1156.

Berg, B. and H. Stååf. 1980. Decomposition rate and chemical changes in decomposing needle litter of Scots pine. II. Influences of chemical composition. Ecological Bulletin (Stockholm) 32: 373-390.

Berg, B. and O. Theander. 1984. The dynamics of some nitrogen fractions in decomposing Scots pine needles. Pedobiologia 27: 161-167.

Blum, L.K. 1993. *Spartina alterniflora* root dynamics in a Virginia marsh. Marine Ecology Progress Series 102: 169-178.

Borie, F. and H. Zunino. 1983. Organic matter-phosphorus associations as a sink in P-fixation processes in allophanic soils of Chile. Soil Biology and Biochemistry 15: 599-603.

Bowman, W.D., T.A. Theodose, J.D. Schardt and R.T. Conant. 1993. Constraints of nutrient availability on primary production in two alpine tundra communities. Ecology 74: 2085-2097.

Brady, N.C. 1990. The nature and properties of soils. Macmillan Publishing Co., New York.

Brinson, M.M., A.E. Lugo and S. Brown. 1981. Primary productivity, decomposition and consumer activity in freshwater wetlands. Annual Review of Ecology and Systematics 12: 123-161.

Camiré, C., B. Côté and S. Brulotte. 1991. Decomposition of roots of black alder and hybrid poplar in short-rotation plantings: nitrogen and lignin control. Plant and Soil 138: 123-132.

Chamie, J.P.M. and C.J. Richardson. 1978. Decomposition in northern wetlands, pp. 115-130. *In* R.E. Good, D.F. Whigham, and R.L. Simpson (eds). Freshwater wetlands: Ecological processes and management potential. Academic Press, New York.

Chapin, F.S. 1980. The mineral nutrition of wild plants. Annual Review of Ecology and Systematics 11: 233-260.

Cicchetti, D.V. 1972. Extension of multiple-range tests to interaction tables in the analysis of variance: a rapid approximate solution. Psychological Bulletin 77: 405-408.

Clayton, J.L. 1972. Salt spray and mineral cycling in two California coastal ecosystems. Ecology 53: 74-81.

Cleary, W.J. and P.E. Hosier. 1974. Geomorphology, washover history, and inlet zonation: Cape Lookout, North Carolina to Bird Island, North Carolina, pp. 237-272. *In* S.P. Leatherman (ed.), Barrier islands from the Gulf of St. Lawrence to the Gulf of Mexico. Academic Press, New York. .

Cornejo, F.H., A. Varela and S.J. Wright. 1994. Tropical forest litter decomposition under seasonal drought: nutrient release, fungi and bacteria. Oikos 70: 183-190.

Couto, W., C. Sanzonowicz and A. De O. Barcellos. 1985. Factors affecting oxidation-reduction processes in an oxisol with a seasonal water table. Soil Science Society of America Journal 49: 1245-1248.

Cuevas, E. and E. Medina. 1988. Nutrient dynamics within amazonian forests. II. Fine root growth, nutrient availability and leaf litter decomposition. Oecologia 76: 222-235.

Day, Jr., F.P. 1982. Litter decomposition rates in the seasonally flooded Great Dismal Swamp. Ecology 63: 670-678.

Day, Jr., F.P., J.P. Megonigal and L.C. Lee. 1989. Cypress root decomposition in experimental wetland mesocosms. Wetlands 9: 263-282.

de Wit, M.C.J. 1978. Morphology and function of roots and shoot growth of crop plants under oxygen deficiency. pp. 333-350. *In* D.D. Hook and R.M.M. Crawford (eds.). Plant life in anaerobic environments. Ann Arbor Science Publications, Inc., Ann Arbor, Michigan.

Donnelly, P.K., J.A. Entry, D.L. Crawford and K. Cromack, Jr. 1990. Cellulose and lignin degradation in forest soils: response to moisture, temperature and acidity. Microbial Ecology. 20: 289-295.

Dueser, R.D., M.A. Graham, G.J. Hennessy, C. McCaffrey, A.W. Niederoda, T.W. Rice and B. Williams. 1976. Ecosystem description: The Virginia Coast Reserve study. The Nature Conservancy. Arlington, Virginia.

Dwyer, L.M. and G. Merrian. 1983. Decomposition of natural litter mixtures in a deciduous forest. Canadian Journal of Botany 62: 2340-2344.

Ehrenfeld, J.G. 1990. Dynamics and processes of barrier island vegetation. Aquatic Sciences 2: 437-480.

Enríquez, S., C.M. Duarte and K. Sanci-Jensen. 1993. Patterns in decomposition rates among photosynthetic organisms: the importance of detritus C:N:P content. Oecologia (Berlin) 94: 457-471.

Ernst, W.H.O. 1983. Element nutrition of two contrasted dune annuals. Journal of Ecology 71: 197-209.

Etherington, J.R. 1967. Studies of nutrient cycling and productivity in oligotrophic systems. I. Soil potassium and wind-blown sea-spray in a South Wales dune grassland. Journal of Ecology 55: 743-752.

Fahey, T.J. 1983. Nutrient dynamics of aboveground detritus in lodgepole pine (*Pinus contorta* ssp. *latifolia*) ecosystems, southeastern Wyoming. Ecological Monographs 53: 51-72

Fahey, T.J., J.W. Hughes, P. Mou and M.A. Arthur. 1988. Root decomposition and nutrient flux following whole-tree harvest of Northern hardwood forest. Forest Science 34: 744-768.

Fauci, M.F. and R.P. Dick. 1994. Plant response to organic amendments and decreasing inorganic nitrogen rates in soils from a long-term experiment. Soil Science Society of American Journal 58: 134-138.

Faulkner, S.P., W.H. Patrick, Jr. and R.P. Gambrell. 1989. Field techniques for measuring wetland soil parameters. Soil Science Society of American Journal 53: 883-890.

Fenn, P., C. Chois and T.K. Kirk. 1981. Lignolytic activity of *Phanerochaete chrysoporium*: physiology and suppression by NH_4^+ and L-glutamate. Archives of Microbiology 130: 66-91.

Fog, K. 1988. The effect of added nitrogen on the rate of decomposition of organic matter. Biological Review 63: 433-462.

Fogel, R. and K. Cromack, Jr. 1977. Effect of habitat and substrate quality on douglas fir litter decomposition in western Oregon. Canadian Journal of Botany 55: 1632-1640.

Gallagher, J.L. 1978. Decomposition processes: summary and recommendations, pp. 145-151. *In* R.E. Good, D.F. Whigham, and R.L. Simpson (eds). Freshwater wetlands: Ecological processes and management potential. Academic Press, New York.

Gambrell, R.P. and W.H. Patrick, Jr. 1978. Chemical and microbiological properties of anaerobic soils and sediments. pp. 375-423. *In* D.D. Hook and R.M.M. Crawford (eds.). Plant life in anaerobic environments. Ann Arbor Science Publications, Inc., Ann Arbor, Michigan.

Godfrey, P.J., S.P. Leatherman and R. Zaremba. 1979. A geobotanical approach to classification of barrier beaches, pp. 99-126. *In* S.P. Leatherman (ed.), Barrier islands from the Gulf of St. Lawrence to the Gulf of Mexico. Academic Press, New York. .

Hackney, C.T. 1987. Factors affecting accumulation or loss of macroorganic matter in salt marsh sediments. Ecology 68: 1109-1113.

Hackney, C.T. and A.A. de la Cruz. 1980. In situ decomposition of roots and rhizomes of two tidal marsh plants. Ecology 61: 226-231.

Harmon, E.M. and C. Hua. 1991. Coarse woody debris dynamics in two old-growth ecosystems. BioScience 41: 604-610.

Hawk, V.B. and W.C. Sharp. 1967. Sand dune stabilization along the North Atlantic coast. Journal of Soil and Water Conservation 22: 143-146.

Hayden, B.P., R.D.Dueser, J.T. Callahan and H.H. Shugart. 1991. Long-term research at the Virginia Coast Reserve. BioScience 41: 310-318.

Hendrick, R.L. and K.S. Pregitzer. 1993. The dynamics of fine root length, biomass and nitrogen content in two northern hardwood ecosystems. Canadian Journal of Forest Research 23: 2507-2520.

Hodson, R.E., R.R. Christian and A.E. Maccubbin. 1984. Lignocellulose and lignin in saltmarsh grass *Spartina alterniflora*: initial concentrations and short-term, post-depositional changes in detrital matter. Marine Biology 81: 1-7.

Holland, E.A. and D.C. Coleman. 1987. Litter placement effects on microbial and OM dynamics in an agroecosystem. Ecology 68: 425-433.

Horner, J.D., J.R. Gosz and R.G. Cates. 1988. The role of carbon-based plant $2^{\#}$ metabolites in decomposition in terrestrial ecosystems. American Naturalist 132: 869-883.

Howard, P.J.A., and D.M. Howard. 1974. Microbial decomposition of tree and shrub leaf letter. I. Weight loss and chemical composition of decomposing litter. Oikos 25: 341-352.

Howarth, R.W. and S.G. Fisher. 1976. Carbon, nitrogen and phosphorus dynamics during leaf decay in nutrient-enriched stream microecosystems. Freshwater Biology 6: 221-228.

Howarth, R.W. and J.E. Hobbie. 1982. The regulation of decomposition and heterotrophic microbial activity is salt marsh soils: a review, pp. 183-207. *In* V.S. Kennedy (ed.), Estuarine Comparisons. Academic Press, New York.

Hunt, H.W., E.R. Ingham, D.C. Coleman, E.T. Elliot and C.P.D. Reid. 1988. Nitrogen limitation of production and decomposition in prairie, mountain meadow and pine forest. Ecology 69: 1009-1016.

James, W.P.T. and O. Theander. 1981. The analysis of dietary fiber in food. Marcel Dekker, Inc., New York, New York.

Jenny, H. 1980. Soil genesis with ecological perspectives. Springer-Verlag, New York.

Jensen, C.L., J.M.Melillo and J.D. Aber. 1978. The effect of nitrogen on the decomposition of *Spartina patens*. Biological Bulletin 155: 446.

Jordan, T.E., D.F. Whigham and D.L. Correll. 1989. The role of litter in nutrient cycling in a brackish tidal marsh. Ecology 70: 1906-1915.

Kachi, N. and T. Hirose. 1983. Limiting nutrients for plant growth in coastal sand dune soils. J. Ecology 71: 937-944.

Kaushik, N.K. and H.B.N. Hynes. 1971. The fate of dead leaves that fall into streams. Archív fur Hydrobiologie 68: 465-515.

Kirk, K.T., W.J. Connors and J.G. Zeikus. 1976. Requirement for a growth substrate during lignin decomposition by two wood-rotting fungi. Environmental Microbiology 32: 192-194.

Koske, R.E. and W.R. Polson. 1984. Are VA mycorrhizae required for sand dune stabilization? BioScience 34: 420-424.

Martin, W.E. 1959. The vegetation of Island Beach State Park, New Jersey. Ecological Monographs 29: 1-46.

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.

McClaugherty, C.A., J.D. Aber and J.M. Melillo. 1984. Decomposition dynamics of fine roots in forested ecosystems. Oikos 42: 378-386.

McClaugherty, C.A., J Pastor and J.D. Aber. 1985. Forest litter decomposition in relation to soil nitrogen dynamics and litter quality. Ecology 66: 266-275.

McGill, W.B., H.W. Hunt, R.G. Woodmansee and J.O. Reuss. 1981. Phoenix, a model of the dynamics of carbon and nitrogen in grassland soils. *In* F.E. Clark and T. Rosswall (eds). Ecological Bulletins-NFR 33: 49-115.

McKane, R.B., D.F. Grigal and M.R. Russelle. 1990. Spatiotemporal differences in ^{15}N uptake and the organization of an old-field plant community. Ecology 71: 1126-1132.

McLachlan, A. and D. van der Merwe. 1991. Litter decomposition in a coastal dune slack. Journal of Coastal Research 7: 107-112.

Meentenmeyer, V. 1978. Macroclimate and lignin control of litter decomposition rates. Ecology 59: 465-472.

Megonigal, J.P. and F.P. Day. 1988. Organic matter dynamics in four seasonally flooded forest communities of the Dismal Swamp. American Journal of Botany 75: 1334-1343.

Melillo, J.M. and J.D. Aber. 1984. Nutrient immobilization in decaying litter: an example of carbon-nutrient interactions. pp. 193-215. *In* J.H. Cooley and F.B. Golley (eds). Trends in ecological research for the 1980s. Plenum Press, New York.

Melillo, J.M., J.D. Aber, A.E. Linkins, A. Ricca, B. Fry and K.J. Nadelhoffer. 1989. Carbon and nitrogen dynamics along the decay continuum: plant litter to soil organic matter. Plant and Soil 115: 189-198.

Melillo, J.M., J.D. Aber and J.F. Muratore. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63: 621-626.

Mitsch, W.J. and K.C. Ewel. 1979. Comparative biomass and growth of cypress in Florida wetlands. The American Midland Naturalist 101: 417-426.

Montague, K.A. and F.P. Day, Jr. 1980. Belowground biomass of four plant communities of the Great Dismal Swamp, Virginia. The American Midland Naturalist 103: 83-87.

Nadelhoffer, K.J., J.D. Aber and J.M. Melillo. 1985. Fine roots, net primary production and soil nitrogen availability: a new hypothesis. Ecology 66: 1377-1390.

Neckles, H.A. and C. Neill. 1994. Hydrologic control of litter decomposition in seasonally flooded prairie marshes. Hydrobiologia 286: 155-165.

O'Connell, A.M. 1994. Decomposition and nutrient content of litter in a fertilized eucalypt forest. Biology and Fertility of Soils 17: 159-166.

Odum, E.P. 1969. The strategy of ecosystem development. Science 164: 262-270.

Odum, W.E. and M.A. Heywood. 1978. Decomposition of intertidal freshwater marsh plants. pp. 89-97. *In* R.E. Good, D.F. Whigham and R.L. Simpson (eds). Freshwater wetlands: Ecological processes and management potential. Academic Press, New York, New York.

Oertel, G.F. 1974. Barrier island development during the holocene recession, southeastern United States, pp. 273-290. *In* S.P. Leatherman (ed.), Barrier islands from the Gulf of St. Lawrence to the Gulf of Mexico. Academic Press, New York.

Oosting, H.J. 1945. Tolerance to salt spray of plants of coastal dunes. Ecology 26: 85-89.

Parker, L.W., P.F. Santos, P.F. Phillips, Jr. and W.G. Whitford. 1984. C and N dynamics during the decomposition of litter and roots of a Chihuahuan desert annual *Lepidium lasiocarpum*. Ecological Monographs 54: 339-360.

Parton, W.J., D.S. Schimel, C.V. Cole and D.S. Ojima. 1987. Analysis of factors controlling soil organic matter levels in the Great Plains grasslands. Soil Science Society of American Journal 51: 1173-1179.

Pastor, J., M.A. Stillwell and D. Tilman. 1987. Little bluestem litter dynamics in Minnesota old fields. Oecologia (Berlin) 72: 327-330.

Ransom, M.D. and N.E. Smeck. 1986. Water table characteristics and water chemistry of seasonally wet soils of Southwestern Ohio. Soil Science Society of America Journal 50: 1281-1289.

Rastetter, E., M.G. Ryan, G.R. Shaver, J.M. Melillo, K.J. Nadelhoffer, J.E. Hobbie and J.D. Aber. 1991. A general biogeochemical model describing the response of the C and N cycles in terrestrial ecosystems to changes in CO_2, climate, and N deposition. Tree Physiology 9: 101-126.

Scheu, S. 1993. Litter microflora-soil macrofauna interactions in lignin decomposition: a laboratory experiment with ^{14}C-labelled lignin. Soil Biology and Biochemistry 25: 1703-1711.

Schlesinger, W.H. 1985. Decomposition of chaparral shrub foilage. Ecology 66: 1353-1359.

Schomber, H.H., J.L. Steiner and P.W. Unger. 1994. Decomposition and nitrogen dynamics of crop residues: residue quality and water effects. Soil Science Society of America Journal 58: 372-381.

Seastedt, T.R. 1988. Mass, nitrogen and phosphorus dynamics in foilage and root detritus of tall grass prairie. Ecology 69: 59-65.

Seastedt, T.R., W.J. Parton and D.S. Ojima. 1992. Mass loss and nitrogen dynamics of decaying litter of grasslands: the apparent low nitrogen immobilization potential of root detritus. Canadian Journal of Botany 70: 384-391.

Shaver, G.R. and J.M. Melillo. 1984. Nutrient budgets of marsh plants: efficiency concepts and relation to availability. Ecology 65: 1491-1510.

Smith, O.L. 1982. Soil microbiology: a model of decomposition and nutrient cycling. CRC Press Inc., Boca Raton, Florida.

Stevens, P.R. and T.W. Walker. 1970. The chronosequence concept and soil formation. Quarterly Review of Biology 45: 333-350.

Swift, M.J., O.W. Heal and J.M. Anderson. 1979. Decomposition in terrestrial ecosystems. University of California Press, Berkeley, California.

Symbula, M and F.P. Day, Jr. 1988. Evaluation of two methods for estimating belowground production in a freshwater swamp forest. The American Midland Naturalist 120: 405-415.

Taylor, B.R., D. Parkinson and W.J.F. Parsons. 1989. Nitrogen and lignin content as predictors of litter decay rates: a microcosm test. Ecology 70: 97-104.

Taylor, B.R., C.E. Prescott, W.J.F. Parsons and D. Parkinson. 1991. Substrate control of litter decomposition in four Rocky Mountain coniferous forests. Canadian Journal of Botany 69: 2242-2250.

Tiffney, Jr., W.N., and D.E. Eveleigh. 1983. Nitrogen-fixing plants for coastal management. Coastal Zone '83: 102-111.

Triska, F.J. and J.R. Sedell. 1976. Decomposition of four species of leaf litter in response to nitrate manipulation. Ecology 57: 783-792.

Tupacz, E.G. and F.P. Day. 1989. Decomposition of roots in a seasonally flooded swamp ecosystem. Aquatic Botany 37: 199-214.

Tyndall, R.W. and G.F. Levy. 1978. Plant distribution and succession within interdunal depressions on a Virginia barrier dune system. Journal of the Elisha Mitchell Scientific Society 94: 1-15.

van der Valk, A.G. 1974. Mineral cycling in coastal foredune plant communities in Cape Hatteras National Seashore. Ecology 55: 1349-1358.

Van Vuuren, M.M.J., F. Berendse and W. De Visser. 1993. Species and site differences in the decomposition of litters and roots from wet heathlands. Canadian Journal of Botany 71: 167-173.

Vitousek, P. 1982. Nutrient cycling and nutrient use efficiency. American Naturalist 119: 553-572.

Vitousek, P.M., J.R. Gosz, C.C. Grier, J.M. Melillo and W.A. Reiners. 1982. A comparative analysis of potential nitrification and nitrate mobility in forest ecosystems. Ecological Monographs 52: 155-177.

Vitousek, P.M. and R.W. Howarth. 1991. Nitrogen limitation on land and in the sea: how can it occur? Biogeochemistry 13: 87-115.

Vitousek, P.M. and P.A. Matson. 1985. Disturbance, N availability and N losses in an intensively managed loblolly pine plantation. Ecology 66: 1360-1367.

Vitousek, P.M. and W.A. Reiners. 1975. Ecosystem succession and nutrient retention: a hypothesis. BioScience 25: 376-381.

Vitousek, P.M. and R.L. Sanford. 1986. Nutrient cycling in a moist tropical forest. Annual Review of Ecology and Systematics 17: 137-168.

Vitousek, P.M., D.R. Turner, W.J. Parton and R.L. Sanford. 1994. Litter decomposition on the Mauna Loa environmental matrix, Hawai'i: patterns, mechanisms and models. Ecology 75: 418-429.

Vogt, K.A., C.C. Grier and D.J.Vogt. 1986. Production, turnover and nutrient dynamics of above- and belowground detritus of world forests. Advances in Ecological Research 15: 303-378.

Walker, T.W. and J.K. Syers. 1976. The fate of phosphorus during pedogenesis. Geoderma 15: 1-19.

Wardrop, A.B. 1971. Occurrence and formation in plants. pp. 19-41. *In* K.V. Sarkanen and C.H. Ludwig (eds.). Lignins: Occurrence, formation, structure and function. Wiley-Interscience, New York.

Wells, B.W. 1942. Ecological problems of the southeastern United States Coastal Plain. Botanical Review 8: 533-561.

Wieder, R.K. and G.E. Lang. 1982. A critique of the analytical methods used in examining decomposition data obtained from litter bags. Ecology 63: 1636-1642.

Willis, A.J. 1963. Braunton Burrows: the effects on the vegetation of the addition of mineral nutrients to the dune soils. Journal of Ecology 51: 353-374.

Willis, A.J., B.F. Folkes, J.F. Hope-Simpson and E.W. Yemm. 1959. Braunton Burrows. Part I: the dune system and its vegetation. Journal of Ecology 47: 1-24.

Willis, A.J. and E.W. Yemm. 1961. Braunton Burrows: mineral nutrient status of the dune soils. Journal of Ecology 49: 377-390.

Wilson, A.T. 1959. Surface of the ocean as a source of air-borne nitrogenous material and other plant nutrients. Nature 184: 99-101.

Wilson, J.O., D. Valiela and T. Swain. 1986. Carbohydrate dynamics during decay of litter of *Spartina alterniflora*. Marine Biology 92: 277-284.

APPENDIX 1

LANDSCAPE VARIABILITY STUDY

INTRODUCTION

The belowground decomposition study conducted across the Hog Island chronosequence indicated gradients in nitrogen availability and rates of organic matter turnover existed. Environmental factors influenced decay between dunes and swales. Due to the need for vehicular access required by the research coupled with the intensive sampling regime, sites were located along a single transect. As such, generalizations of ecosystem wide trends are limited to inference. It is possible the patterns observed across the chronosequence resulted from random phenomena. In order to strengthen the degree of inference, an island wide survey of soil nitrogen and root nitrogen and phosphorus status was conducted. Additionally, the influence of environmental variability on belowground decomposition processes, at the island level, was determined using *Spartina patens* root material as a common substrate. These measurements provided rough estimates of landscape variability useful for gauging the applicability of the study's results to the ecosystem level.

METHODS

The northern two thirds of Hog Island possesses clearly identifiable dune ridges continuous with those used in the main study. Three transects crossing the island at the north end, mid-section and south end of this region were identified. All dunes and swales supported similar vegetation as sites of like age in the main study. At each of three randomly selected localities on every dune and swale (6, 24, 36 and 120 years old), one soil sample (10 cm deep, 7 cm wide) and one native root sample were collected. One litterbag, constructed identically to those used previously and containing *Spartina patens* roots (gathered from one locality), was inserted vertically in the soil. Sampling took place on July 2, 1992 and litterbags were retrieved on November 21, 1992 (141 day incubation). All root samples (native, pre- and post-incubated *Spartina patens*) were analyzed for total Kjeldahl nitrogen and total phosphorus. Soils were analyzed for ammonium and nitrite-nitrate. Percent mass remaining determinations provided approximations of decay. Chapter One described the methods used.

A nested one-way analysis of variance run on soil ammonium, nitrite-nitrate and root nitrogen and phosphorus content tested for site effects while accounting for variability between transects. Percent mass, nitrogen and phosphorus remaining in decomposed *Spartina patens* roots could not be tested similarly since some of the bags were not found. Hence, design became unbalanced and incompatible for nested analysis of variance. A split-plot anova tested for site and depth effects on percent mass remaining and a one-way anova tested for site effects on percent nitrogen and phosphorus remaining (depth bulked). A modified Tukey's Honestly Significant Difference method (Cicchetti 1972) tested for significant differences ($p = .05$) between means.

RESULTS

Significant site effects on soil ammonium ($F = 9.52$, $p < .0001$) and nitrite-nitrate ($F = 3.09$, $p = .0291$) were apparent. Significant differences among dune ages did not occur, although soil ammonium tended to increase with increased age (Table a). Significant differences in soil nitrogen availability did occur among swale ages where older swales had greater extractable soil ammonium and nitrite-nitrate than did younger swales. Older swales generally had greater soil nitrogen availability than dunes of like age although significant differences were confined to soil ammonium levels between the 120 year old pair. Site effects explained a portion of root nitrogen ($F = 9.92$, $p < .0001$) and root phosphorus ($F = 4.65$, $p = .0052$) variability. Higher nitrogen content occurred in native roots from the 120 year dunes relative to younger dunes but differences were not significant (Table a). Roots from 36 and 120 year swales had significantly higher nitrogen content than younger swale roots and dune roots of like age. Native root phosphorus content was similar among dune ages and generally higher than swale roots, especially between the older (36 and 120 year) dunes and swales (Table a). Herbaceous swale roots (6 and 24 year) had greater (not significant) phosphorus content than woody roots from older swales.

Site effects ($F = 10.61$, $p < .0001$), but not depth effects or site x depth interaction, influenced *Spartina patens* decay. Percent mass remaining was similar among different aged dunes and significantly less than swales of like age (except 36 year swale, Table b). Swales exhibited similar levels of percent mass remaining. Site effects on percent nitrogen ($F = 6.77$, $p < .0001$) and phosphorus ($F = 23.12$, $p < .0001$) remaining also occurred. Among swale ages, significantly less nitrogen remained in roots decomposing in 24 year swales (Table b). Otherwise, nitrogen dynamics were similar among all dune and swale ages. Swales always had significantly less phosphorus remaining in *Spartina patens* roots

Table a. Soil ammonium (NH_4), soil nitrite-nitrate (NO_2-NO_3), root nitrogen and root phosphorus content in *Spartina patens* roots decomposing across dune and swale chronosequence. n=9.

	Age			
	6 year	24 year	36 year	120 year
Soil NH_4 (mg/kg)				
Dunes	0.83(0.14) ^{aA}	2.27(0.31) ^{aA}	2.93(0.49) ^{aA}	2.63(0.22) ^{aA}
Swales	1.01(0.28) ^{aA}	2.50(0.27) ^{aAB}	7.25(0.90) ^{aBC}	10.13(2.14) ^{bC}
Soil NO_2-NO_3 (mg/kg)				
Dunes	0.54(0.11) ^{aA}	0.34(0.07) ^{aA}	0.39(0.06) ^{aA}	0.58(0.09) ^{aA}
Swales	0.19(0.05) ^{aAB}	0.03(0.01) ^{aB}	1.01(0.42) ^{aA}	0.87(0.24) ^{aAB}
Root nitrogen (%)				
Dunes	0.70(0.06) ^{aA}	0.62(0.03) ^{aA}	0.58(0.04) ^{aA}	0.82(0.04) ^{aA}
Swales	0.74(0.04) ^{aA}	0.84(0.06) ^{aAB}	1.35(0.12) ^{bC}	1.22(0.09) ^{aBC}
Root phosphorus (%)				
Dunes	0.17(0.03) ^{aA}	0.15(0.01) ^{aA}	0.16(0.01) ^{aA}	0.14(0.01) ^{aA}
Swales	0.14(0.01) ^{aA}	0.13(0.01) ^{aA}	0.06(0.01) ^{bA}	0.070.01 ^{aA}

Table b . Percent mass, nitrogen and phosphorus remaining in *Spartina patens* roots decomposing across dune and swale chronosequence. n=28-36 (% mass remaining), n=3-9 (% nitrogen and phosphorus remaining).

	Age			
	6 year	24 year	36 year	120 year
% mass remaining				
Dunes	74.08(1.84) ^{aA}	71.85(1.49) ^{aA}	74.43(1.02) ^{aA}	72.98(1.47) ^{aA}
Swales	80.64(0.94) ^{bA}	81.34(0.93) ^{bA}	79.82(0.88) ^{aA}	79.43(0.75) ^{bA}
% phosphorus remaining				
Dunes	76.15(4.98) ^{aA}	76.54(1.90) ^{aA}	78.92(2.45) ^{aA}	87.54(2.36) ^{aA}
Swales	84.99(3.11) ^{aA}	69.85(2.18) ^{aB}	89.14(2.18) ^{aA}	92.62(4.60) ^{aA}
% nitrogen remaining				
Dunes	76.71(7.06) ^{aA}	75.62(2.92) ^{aA}	68.09(3.85) ^{aA}	66.04(3.33) ^{aA}
Swales	51.44(11.21) ^{bA}	23.56(1.20) ^{bB}	40.83(4.18) ^{bAB}	38.11(3.92) ^{bAB}

than dunes of like age (Table b). Phosphorus was also lost more readily from roots decomposing in the 24 year swales than in other aged swales. At the point in time litterbags were retrieved from the field, evidence of nitrogen or phosphorus immobilization did not exist.

DISCUSSION

Similar patterns and levels of soil nitrogen availability and root nitrogen and phosphorus content across the island wide chronosequence existed in relation to those observed in the main study (Tables a and b). *Myrica cerifera* has a strong influence on soil and vegetation nitrogen status. Higher root nitrogen content in roots from 120 year dunes may feedback to higher decay rates.

Environmental influences also operated in a like manner across the island wide landscape as they did in the main study. Decay was inhibited in swales relative to dunes and was likely a result of greater soil saturation to the point of anoxia. Differences between topographic classes were minimal, underscoring the insensitivity of *Spartina patens* decay to differences in soil nutrient status or other environmental differences besides hydroperiod. Nutrient dynamics paralleled those previously observed. Stronger leaching effects in swales promoted greater phosphorus losses, and, to a certain extent (24 year swales), greater nitrogen losses. As in the main study, evidence for nutrient immobilization was absent, although the sampling protocols may have missed any brief periods that might have occurred.

Admittedly, the data collected from this abbreviated study did not demonstrate significant trends that were apparent in the main study. Several factors confound adequate comparison between studies. The main study had the benefit of rigorous sampling conducted throughout an entire year and thus, the statistical tests employed were more powerful. Seasonal influences on root nutrient content also confound direct comparisons with the main study. Root collection for the main study occurred in the winter; a time when nutrients have been translocated to perennial roots or rhizomes for the dormant season. In contrast, root collection for the landscape variability study took place in July; a time when available nutrients are allocated to all growing parts of the plant body.

Even under the burden of these limitations, the data presented offer an additional piece of evidence suggesting that the influences of nitrogen availability, litter quality and hydroperiod observed in the main study are not random phenomena. The inference that these controls operate similarly on belowground decay dynamics at the ecosystem level is strengthened.

APPENDIX 2

ABOVEGROUND DECAY STUDY

INTRODUCTION

In order to balance observations on belowground decomposition dynamics, this study addressed aboveground decomposition dynamics. The scope of the study provided limited data on decay rates and nutrient dynamics for early phase decomposition of aboveground shoots. The study was confined to the 24 and 120 year dune sites and sought to answer the following questions: 1) Are rates of aboveground decomposition of shoots similar to belowground decomposition of roots? 2) Does shoot litter quality respond to increases in nitrogen availability across the chronosequence and, if so, do these differences produce differences in decay or nutrient dynamics? 3) Are the nutrient dynamics of decomposing shoots similar to decomposing roots? and 4) Does nitrogen amendment influence the decomposition dynamics of shoots?

METHODS

During December 1993, recently senescent shoots (still standing with a touch of yellow) were collected from dune grasses (primarily *Ammophila breviligulata* and *Spartina patens*) on the 24 and 120 year dunes. Litter was air-dried and placed in nylon mesh bags. Oven-dried subsamples provided conversion factors for air-dried to oven-dried weight. On each dune site, 8 litterbags were randomly located in each of 8 permanent plots (25 m^2) developed for a separate vegetation study. Four of these plots were fertilized following the specifications outlined in Chapter III. Litterbags were placed on bare mineral soil on March 12, 1994. At monthly intervals, 2 randomly selected litterbags were removed from each plot for a total of 4 sampling events. Initial litter and decomposed litter after the first two sampling events were analyzed for nitrogen and phosphorus content (methods in Chapter I). Percent mass loss estimated decay. Two way analysis of variance evaluated the effects of site and time on decomposition dynamics of shoots placed in non-fertilized plots. Similar analyses for each dune site tested for fertilization and time effects on decomposition dynamics. Tukey's Honestly Significant Difference method determined significant differences ($p < .05$) between means.

RESULTS

Table a presents a summary of results. Similar rates of decay occurred between 24 and 120 year dune shoots in unfertilized plots ($F = 3.98$, $p = .0582$). Percent mass remaining significantly decreased with time ($F = 25.49$, $p < .0001$) over 4 months of decay and site x time interactions were not significant. Initially, no significant differences existed in nitrogen content (24 year dune = 0.63%, 120 year dune = 0.55%) or in phosphorus content (24 year dune = 0.16%, 120 year dune = 0.14%) of shoots. Although no immobilization of nitrogen or phosphorus occurred during the first 2 months of decay, decomposing shoots on the 120 year dune retained significantly ($F = 17.68$, $p = .0012$) more percent initial nitrogen than 24 year dune shoots while percent phosphorus remaining between the two sites was similar ($F = 2.79$, $p = .1272$). Only the 120 year dune demonstrated a significant increase in nitrogen accumulation after an initial loss.

Fertilization produced a significant increase in shoot decay for both the 24 year dune

Table a. Percent mass, nitrogen and phosphorus remaining in 24 and 120 year dune shoots decomposing in unfertilized and fertilized plots. Multiple comparison tests performed by days. Different uppercase letters between columns indicate significant differences due to fertilization. Different lowercase letters between rows indicate significant differences due to site. n=4.

Days	Site age	Unfertilized	Fertilized
		Percent mass remaining	
31	24 year	98.34(0.31)^{aA}	97.52(0.54)^{A}
	120 year	100.18(0.55)^{aA}	97.31(0.35)^{B}
61	24 year	98.92(0.61)^{aA}	96.84(0.50)^{B}
	120 year	98.94(0.75)^{aA}	96.02(0.45)^{B}
92	24 year	95.51(0.80)^{aA}	95.09(0.25)^{A}
	120 year	96.62(0.89)^{aA}	95.20(0.15)^{A}
122	24 year	94.72(0.56)^{aA}	93.30(0.52)^{A}
	120 year	94.42(0.59)^{aA}	92.57(0.70)^{A}
		Percent nitrogen remaining	
31	24 year	71.24(4.00)^{aA}	71.49(1.98)^{A}
	120 year	79.24(3.19)^{aA}	86.02(2.48)^{A}
61	24 year	70.43(4.88)^{aA}	77.67(3.50)^{A}
	120 year	94.64(2.94)^{bA}	91.02(5.43)^{A}
		Percent phosphorus remaining	
31	24 year	78.69(2.83)^{aA}	95.61(2.55)^{B}
	120 year	76.12(6.42)^{aA}	72.60(4.62)^{A}
61	24 year	81.61(2.70)^{aA}	82.46(2.83)^{A}
	120 year	69.87(4.44)^{aA}	77.19(4.49)^{A}

(F = 11.09, p = .0028) and the 120 year dune (F = 35.78, p < .0001). However, these effects were significant only for the first two months of decay. The only effect on nutrient dynamics as a result of fertilization occurred on the 24 year dune where more initial phosphorus was retained in shoots decomposing in fertilized plots (F = 10.58, p = .0069). These effects did not carry over to the second month of decay.

DISCUSSION

The most striking difference between belowground root decomposition and aboveground shoot decomposition occurred in the rates of decay. After 111 days of decomposition, 24 and 120 year dune roots exhibited approximately 77 % mass remaining in contrast to approximately 94 % mass remaining in dune shoots after 122 days. Direct comparison is tenuous since the studies occurred in different years. However, decay intervals for both studies spanned similar times of the year which reduced the potential for differential seasonal influences, particularly temperature. Other factors also cloud straightforward comparison. Root material was live at collection while shoot material was senescent. Shoots may have previously lost a greater proportion of water soluble organics and cellulose that are rapidly metabolized or leached during early decay. Differences in litter quality between roots and shoots may also have influenced decay. Although shoot nitrogen and phosphorus content was within ranges exhibited by dune roots, lignin content was unknown. The production of sclerophyllous tissues in maritime environments is a common adaptation (Ehrenfeld 1990) and may operate differently in shoots than in roots. Additionally, shoots confined in litterbags do not receive the mechanical breakdown or burial impacts of wind that may be important for decomposition of aboveground litter on coastal dunes (McLachlan and van der Merwe 1991)

The effects of site, litter quality and fertilization on the decomposition dynamics of roots generally became apparent after the first 0.5 years of decay. A longer time interval may be necessary to observe whether similar influences operate on aboveground decay of shoots. Unlike roots, shoot nitrogen content did not reflect differences in available soil nitrogen between dune sites. Although shoot nitrogen content was not significantly different between the 24 and 120 year dune, lower nitrogen content in 120 year dune shoots may be responsible for nitrogen accumulation observed during the second month of decay. Whether nitrogen immobilization would have followed is uncertain. In decaying roots, fertilization induced an immediate effect on nitrogen dynamics in 24 and 36 year roots that resulted in significantly greater nitrogen retention followed by accumulation. In contrast, shoot nitrogen dynamics were initially unresponsive to soil nitrogen enrichment. If fungal mycelia are necessary for translocation of nitrogen from soil reserves to aboveground litter during decay, a certain lag time is to be expected for colonization and growth.

This study does not conclusively demonstrate that the nutrient dynamics during decomposition of aboveground material are different than belowground dynamics on Hog Island. A coordinated, longer-term study would be necessary to fully evaluate similarities and differences. The evidence presented does suggest that belowground decay may be faster. Environmental influences and/or litter quality influences are likely important determinants. Decomposition processes in Hog Island dune soils have greater access to soil resources, such as moisture and nutrients, than on the soil surface. Burial of aboveground litter may speed decay.

VITA

Christine Elizabeth Conn was born in Denver Colorado on December 5, 1962. She received her first Bachelor of Science degree in Business Administration at Towson State University (1986). She continued her education at Towson State University, receiving the Bachelor of Science degree in Biological Sciences (1989). She completed the Master of Science degree in Biological Sciences at Old Dominion University (1991). During the academic 1993-94 year, she received a Special Doctoral Research Assistantship.

Her publications include one refereed publication: "Belowground biomass patterns on a coastal barrier island in Virginia" published in the Bulletin of the Torrey Botanical Club (1993) and eleven published abstracts for oral and poster presentations at annual meetings of the Association of Southeastern Biologists and the Ecological Society of America. At the Association of Southeastern Biologists 1994 conference, she received the Ecological Society of America Southeastern Chapter Eugene P. Odum Award for the Best Ecological Paper presented by a student entitled "Nitrogen dynamics of root decomposition in response to nitrogen availability gradients".

Christine Conn married Douglas Thomas on August 1, 1992 and currently lives in Virginia Beach, Virginia.