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DECOMPOSITION DYNAMICS IN RESTORED AND NATURALLY RECOVERING ATLANTIC WHITE CEDAR (*CHAMAECYPARIS THYOIDES*) WETLANDS

by

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ABSTRACT

DECOMPOSITION DYNAMICS IN RESTORED AND NATURALLY RECOVERING ATLANTIC WHITE CEDAR (*CHAMAECYPARIS THYOIDES*) WETLANDS

Edward R. Crawford
Old Dominion University, 2002
Director: Frank P. Day

Restoration efforts and ecologically based management practices for Atlantic white cedar wetlands have recently focused on soil organic matter sequestration and aggradation as critical ecosystem functions in the maintenance of this imperiled community type. This work addresses how developmental stage, litter quality and environmental conditions influenced aboveground leaf litter and belowground root decay in naturally regenerating and restored Atlantic white cedar wetlands. Using standard litterbags for leaf litter and a modified litterbag technique for roots, decay dynamics of naturally regenerating and restored Atlantic white cedar stands were measured to compare ecosystem development trends with restoration conditions. Effects on rates of mass loss, nitrogen, phosphorus and carbon dynamics during decomposition of a common root and leaf litter type (*Chamaecyparis thyoides*) and native leaves and roots are discussed.

Native root decay was significantly faster at all depth intervals within the restoration setting compared to the stands along a chronosequence. In contrast, *Chamaecyparis* root decay was similar along the chronosequence and restoration setting. Native leaf litter decay was faster than *Chamaecyparis* leaf litter decay but no differences occurred among litter decay rates along the chronosequence and restoration setting.

Within all sites, native leaf litter and *Chamaecyparis thyoides* litter immobilized nitrogen over the course of the study, while phosphorus was released. Nitrogen in leaf litter was immobilized over two times initial amounts. Site hydrology and initial phosphorus content were strongly correlated with leaf litter decay rates.

Native roots and standard roots immobilized nitrogen and released phosphorus throughout the study. Roots accumulated nitrogen but increases were less pronounced relative to leaf litter. Root decay was highly correlated with initial phosphorus and lignin concentration and L:N ratio. Decay of *Chamaecyparis* roots were similar across all sites despite significant differences in site hydroperiod. Root decay was not correlated with site hydrology. With regards to native root material, these results suggest that within restored sites the current status of belowground carbon storage functions appear to be deficient in comparison to the naturally regenerating sites. Continued long-term study of these and similar restoration sites are needed to provide greater insight into appropriate recovery models for various wetland functions of Atlantic white cedar.

This dissertation is dedicated to my family.

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CHAPTER I

INTRODUCTION

OVERVIEW OF THE RESEARCH PROBLEM

This research represents a portion of a larger collaborative systems-level study on Atlantic white cedar wetland restoration between researchers from Christopher Newport University and Old Dominion University, Virginia, USA. An integrated suite of environmental parameters were measured in Atlantic white cedar wetlands to better understand important ecosystem processes in this imperiled community type. Hydrologic regimes, soil nutrient flux, pollution fate and effects, atmospheric gas exchange, plant and animal diversity and production, and decomposition were studied within naturally recovering and restored Atlantic white cedar stands to help identify potential ecological metrics suitable to evaluating the success of current restoration and management attempts.

The primary objective of the project was to evaluate carbon cycling dynamics in Atlantic white cedar wetlands because of its importance in ecosystem structure, function, and self-maintenance of this community type. Soil organic matter sequestration and subsequent peat accumulation are a critical component of carbon cycling in Atlantic white cedar wetlands. This work is a result of efforts to quantify decay dynamics in naturally regenerating and restored Atlantic white cedar wetlands as part of the larger effort to develop whole system models of carbon cycling for this community type.

The journal model used for this dissertation is Wetlands.

ATLANTIC WHITE CEDAR ECOLOGY AND RESTORATION

Atlantic white cedar [*Chamaecyparis thyoides* (L.) B.S.P.] Cupressaceae, is an arborescent, obligate, hydrophyte (Tiner 1996). The distribution of *C. thyoides* is restricted to freshwater wetlands in a narrow band along the eastern coastal United States ranging from mid-Maine to Mississippi (Laderman 1989). These tall, slender branched monoecious conifers typically form monotypic stands that primarily occur on organic soils (histosols); however, stands also occur over a sand or sand/gravel base in Florida and Mississippi (Laderman 1989). Species composition and canopy structure within stands are dependent on soil characteristics (Korstian and Brush 1931), fire regime and fire characteristics (Little 1950), hydroperiod (Laderman 1989) and region (Ward and Clewell 1987). At the time of European settlement, there was an estimated 200,000 hectares of *C. thyoides* wetlands throughout its range (Kuser and Zimmermann 1995). North Carolina alone may have contained over half of the original Atlantic white cedar swamp acreage (Kuser and Zimmerman 1995).

Historically, the largest known stand in the entire known range of Atlantic white cedar, estimated at 26,000 – 45,000 ha, was found in the Great Dismal Swamp (Frost 1987, Moore and Allen 1998). The current study was conducted in the mid-Atlantic region where cedar stands often occur in dense, monotypic, even-aged stands with scattered hardwood tree species such as red maple (*Acer rubrum* L.), black gum (*Nyssa sylvatica var. biflora* Marsh.) and a well developed layer of ericaceous shrubs and various lianas. The regeneration and development of this unique community type is dependent on the interplay of several environmental drivers including the catastrophic disturbance of fire, fire intensity, and the ground water elevation at the time of fire

(Laderman 1989). Catastrophic fire at a period of high water table is optimal for the natural regeneration of an even-aged cedar stand (Little 1950). The rapid and extremely dense seedling recruitment that results from these conditions reduces colonization rates of faster growing hardwood species, thus aiding Atlantic white cedar regeneration (Korstian and Brush 1931).

Ehrenfeld (1995) has identified the development of deep peat substrate as a key component of the structure and function of Atlantic white cedar wetlands. Peat deposits strongly affect the hydrology of Atlantic white cedar wetlands by increasing the water holding capacity of the soil (Levy and Walker 1979), and are required for seedling recruitment (Beull and Cain 1943). The wetter hydrologic conditions can lead to anaerobic conditions and reduced soil pH, which can lead to decreasing decay rates (Day 1982, Tupacz and Day 1990) ultimately affecting nutrient availability and production. As a result, hydrologic regimes and carbon cycling are tightly coupled mechanisms that either directly or indirectly affect other ecosystem functions.

As a result of extended hydroperiods, high litter production rates coupled with slow decomposition rates, Atlantic white cedar is typically found on deep organic soils (Day 1987). The dystrophic soil conditions found within Atlantic white cedar wetlands reduces turnover of organic matter, nutrient availability and production rates. According to Laderman (1998), Atlantic white cedar is a poor competitor able to survive in nutrient poor, saturated soils that inhibit the encroachment of faster growing hardwood species. Once these other species become established, they can outcompete Atlantic white cedar, ultimately replacing it.

Thus, the process of paludification, a gradual rise in the water table as peat accumulation impedes drainage, is of paramount importance for the self-regulation and maintenance of Atlantic white cedar wetlands.

The role of wetlands in maintaining the carbon cycle and atmospheric stability has only recently been appreciated since increased air pollution has begun to affect global balances (Odum 1989). The edaphic conditions found within Atlantic white cedar wetlands result in sequestration and aggradation of soil organic matter leading to the production of histosols. This peat accumulation in Atlantic white cedar wetlands has important regional and global implications. On a regional scale, not only are these wetlands important sinks for carbon, the accumulating peat decreases nutrient loading to coastal rivers and estuaries, thus improving downstream surface-water quality (Hinesly and Wicker 1999). On a global scale, histosol development within Atlantic white cedar wetlands represent an important carbon sink. While histosols cover approximately 1% of the world's land area, they hold 20% of the global soil carbon (Brady and Weil 1996).

Following European settlement, dramatic decline of the species and ecosystem has been attributed to commercially valuable attributes of the wood, along with concomitant hydrologic modifications, harvest without replanting, fire suppression, and extensive development of coastal areas (Frost 1987). These anthropogenic alterations of Atlantic white cedar wetlands have reduced this forested wetland type by as much as 95% throughout its former range (Frost 1987). In Virginia and the Carolinas, remnant Atlantic white cedar swamps are mostly second-growth, isolated and fragmented (Levy 1987).

Extensive Atlantic white cedar forests that occurred at the periphery of the Great Dismal Swamp prior to lumbering in 1899 (Musselman et al. 1977) have declined to relatively minor importance at present. By comparison, the importance of red maple and other euryhydric species in the forest canopy has been increasing, ultimately replacing Atlantic white cedar (Levy and Walker 1979, Day 1985).

Recently, the interest in restoring Atlantic white cedar wetlands along the Atlantic coast of the United States is on the rise (Kuser and Zimmerman 1995, Atkinson et al. 1996). Pocosins and associated wetlands (including Atlantic white cedar swamps) are among the least studied ecosystems in the United States (Richardson 1991). However, the United States Department of Interior Fish and Wildlife Service, the Department of Defense and various conservation groups have recently launched initiatives for the purpose of better understanding how to manage, maintain, and restore Atlantic white cedar ecosystems.

The majority of Atlantic white cedar restoration efforts have centered around the harvesting and regeneration of *C. thyoides* as a commercial crop (Korstian and Brush 1931). These early restoration efforts utilized a myopic approach to Atlantic white cedar regeneration ignoring the ecological functions and processes of these systems. The ecosystem is the functional ecological unit, and ecological restoration means more than simply replacing the dominant plant cover or habitat structure (Pratt 1994). Restoration ecology takes a holistic, systems level approach to restoration of ecosystem structure and function ultimately resulting in self-maintaining ecosystems (Jordan et al. 1987).

A more ecologically based restoration effort of Atlantic white cedar swamps requires this holistic approach. According to Jordan et al. (1987), elucidation of how ecosystem level processes recover through time following allogenic and autogenic perturbations is a primary concern in restoration ecology. Experimental evidence of the effects of various disturbances on Atlantic white cedar wetland function (Ehrenfeld and

Schneider 1991, Day and Megonigal 1993, Zhu and Ehrenfeld 2000) can provide valuable insight for management and restoration strategies. Cairns and Heckman (1996) proposed that the modeling of natural recovery patterns may facilitate the development of assessment tools for restoration and management decisions in mitigation programs.

Currently, there are only a few studies of long-term temporal and spatial recovery patterns for belowground systems, especially in forested communities (Berish 1982, Gleeson and Tilman 1990). In terms of belowground biomass and production following disturbance, Fahey and Hughes (1994) and Jones et al. (1996) have reported rapid recovery of biomass and production. Bridgham et al. (1991) determined that belowground cellulose decay rates in North Carolina peatlands were up to 10 times faster on disturbed sites compared to natural sites. Peat accumulation is relevant to global atmospheric carbon balance, and may be critical to long-term self-maintenance of Atlantic white cedar wetlands. Further investigation of long-term decomposition dynamics in relation to ecosystem recovery will aid in an understanding of the controls and processes important in creating self-sustaining ecosystems. According to Cairns and Heckman (1996), elucidation of the primary factors that control ecosystem health and self maintenance coupled with the inter-relations of these factors provides the foundation of restoration strategies.

This collaborative effort between researchers from Christopher Newport University and Old Dominion University has initiated an extensive examination of carbon budgets for Atlantic white cedar wetlands in the mid-Atlantic region to integrate multiple factors important to Atlantic white cedar ecosystems into a central model of ecosystem health. The underlying assumption of this approach is that soil carbon accumulation rates will help to assess the ecological condition of Atlantic white cedar communities in addition to providing a quantifiable metric for restoration success.

It is widely recognized that belowground processes play an important role in ecosystem dynamics (McClaugherty et al. 1982, Nadelhoffer et al. 1985, Mckane et al. 1990, Perry 1994, Brady and Weil 1996). Accurate assessments of whole-system carbon budgets require that belowground components of the community be estimated, especially in forested ecosystems. However, according to Vogt et al. (1986), our knowledge concerning the ecological processes in the belowground environment lags far behind the advances made in understanding aboveground dynamics. This is especially true of decay dynamics within wetland ecosystems. A general lack of belowground decomposition research within wetlands historically can be attributed to the technical difficulties encountered in the study of belowground systems and the time consuming nature of belowground measurements (Symbula and Day 1988, Tupacz and Day 1990, Conn and Day 1977). The present study will examine leaf litter and root litter decomposition dynamics within several naturally regenerating and restored Atlantic white cedar wetlands.

STUDY OBJECTIVES

The primary objectives of this research were to 1) quantify and compare aboveground and belowground organic matter decay rates along a chronosequence (intermediate, and mature age classes) of naturally recovering Atlantic white cedar wetlands; 2) compare above and belowground decay rates of the chronosequence to those of young Atlantic white cedar restoration plantings; and 3) determine if the influences of environment and substrate quality on leaf and root litter decay rates operate in similar ways within naturally regenerating sites and restored sites.

The questions addressed are: Do aboveground decomposition dynamics behave in ways similar to belowground decay dynamics in naturally occurring and restored Atlantic white cedar wetlands? Do influences of environment and substrate quality operate in similar ways in naturally occurring and restored Atlantic white cedar wetlands? Answers to these questions were approached by determining mass loss over time of decomposing root and leaf litter and by studying environmental and substrate quality controls on carbon, nitrogen, phosphorus and lignin dynamics of root and litter decay. Additionally, this research was conducted along a chronsequence of nutrient limited Atlantic white cedar wetlands that provided the opportunity to evaluate environmental influences and the unique physical, chemical and biological influences associated with site age on the decay dynamics of both leaf litter and roots.

The central hypothesis of this research was that litter and root decomposition differs between age classes of naturally regenerating Atlantic white cedar wetlands and that litter and root decomposition is faster in restored systems relative to all age classes of naturally recovering Atlantic white cedar wetlands. In addition, the null hypothesis that restored and naturally recovering sites do not differ in soil pH and hydroperiod was tested in an attempt to identify potential environmental factors associated with observed decomposition dynamics.

The following chapters present the research findings in detail. Chapter II compares above and belowground trends in decay dynamics along a chronosequence (intermediate and mature-aged sites) of naturally regenerating Atlantic white cedar wetlands to those of the restoration settings. Chapter III evaluates weight loss and nutrient changes in decomposing leaf litter in regenerating and restored sites. How these dynamics differ in response to differences associated within each site was quantified. Chapter IV 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 within restoration efforts were evaluated. Chapter V summarizes the research results. Results of above and belowground decomposition dynamics within an Atlantic white cedar restoration planting at Pocosin Lakes National Wildlife Refuge, Washington County, North Carolina is presented in the appendix.

The results from this research constitute a major component of a whole-system analysis of carbon dynamics in restored and naturally recovering Atlantic white cedar wetlands. Specifically, this research will provide a clearer understanding of the importance of above and belowground decomposition rates in the establishment of critical ecosystem functions and processes in restored or created forested wetlands.

STUDY SITES

Atlantic white cedar wetlands in Virginia and North Carolina are primarily located on the Pamlico Terrace east of the Suffolk Scarp. The sites selected for study are located in the mid-Atlantic coastal plain in the vicinity of southeastern Virginia and northeastern North Carolina (Figure 1.) In an effort to minimize site effects in the comparative aspects of this project, we selected was made to select only those Atlantic

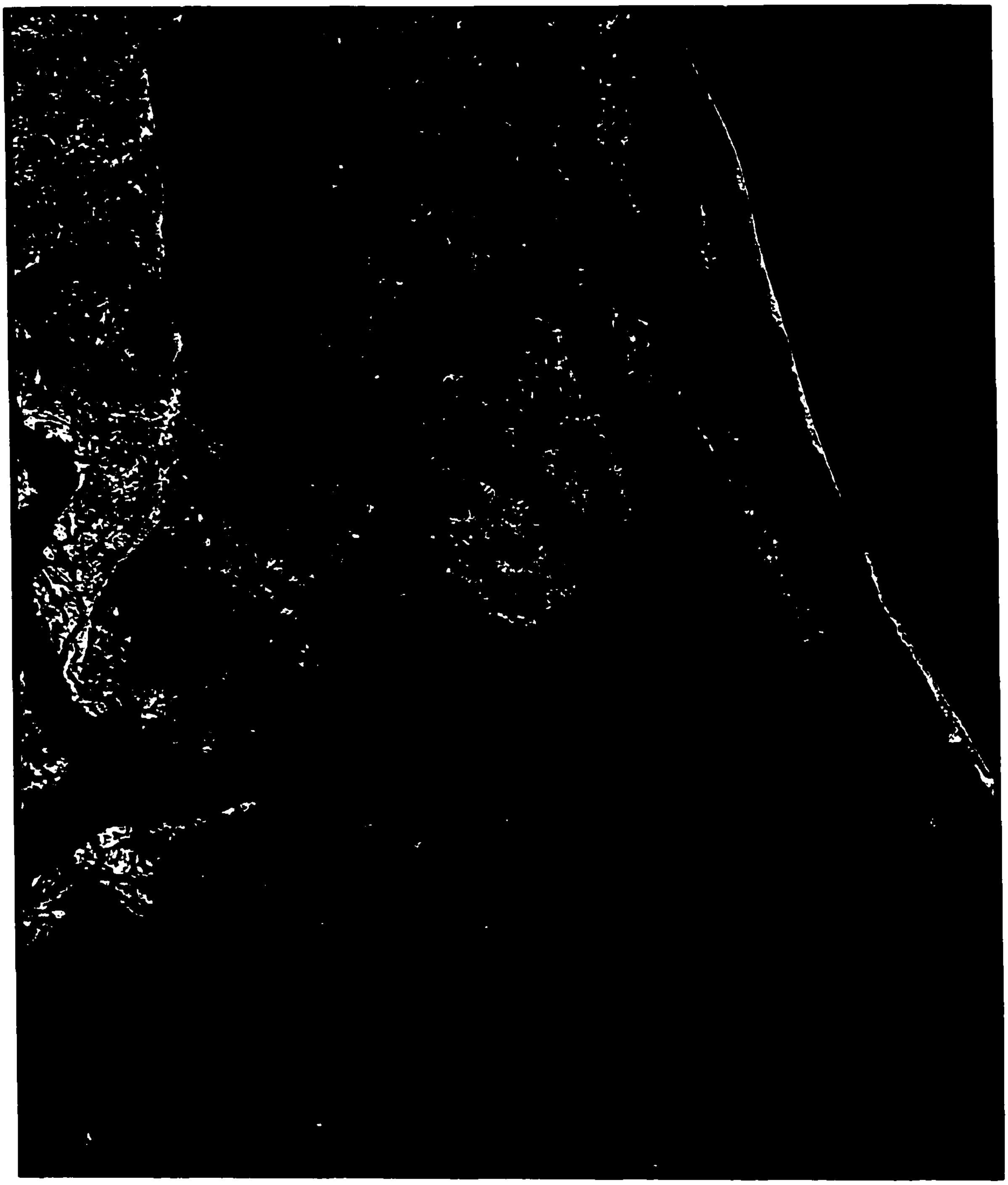

Figure 1. Satellite imagery of the study region. Study sites were located in the Great Dismal Swamp National Wildlife Refuge, Virginia/North Carolina, the Alligator River and Pocosin Lakes National Wildlife Refuges, North Carolina, and the White Cedar LLC Mitigation Bank located on the eastern boundary of the Great Dismal Swamp National Wildlife Refuge, Virginia.

white cedar stands that exhibited the structural characteristics of less disturbed historic conditions (Korstian and Brush 1931, Levy 1987). Given the declining numbers of remaining Atlantic white cedar forests in the mid-Atlantic region, site selection was generally limited to the Great Dismal Swamp National Wildlife Refuge and Alligator River National Wildlife Refuge. Atlantic white cedar wetlands found within these refuges are the nearest to undisturbed conditions for this region.

Selection of local restoration sites for study were limited to a few small-scale replanting projects, a <1 year old restoration pilot study within Pocosin Lakes National Wildlife Refuge, North Carolina, and an Atlantic white cedar mitigation bank located along the eastern boundary of the Great Dismal Swamp National Wildlife Refuge, known as the White Cedar LLC Mitigation Bank. These sites are on agricultural fields that are prior converted wetlands of the Great Dismal Swamp. Since the mitigation bank was already established and likely reflects typical conditions under which Atlantic white cedar restoration is expected to take place, it was selected for extensive examination in this study.

The Great Dismal Swamp (GDSNWR) is a seasonally flooded, non-riverine forested wetland located in the coastal plain of southeastern Virginia and northeastern North Carolina. Approximately 40% of the GDSNWR is located in Virginia and 60% in North Carolina. The Dismal Swamp is one of the few large forested wetlands remaining in the eastern United States (Levy and Walker 1979, Lichtler and Walker 1979).

Alligator River (ARNWR) and Pocosin Lakes (PLNWR) National Wildlife Refuges are both located within the Albermarle-Pamlico Peninsula in North Carolina. The ARNWR was created in 1984 when Prudential Life Insurance Company donated approximately 61,000 hectares of pocosin, marsh, and forested wetlands to the U.S. Fish and Wildlife Service (Richardson 1991). Much of these natural areas have endured extensive ditching, nutrient loading, and fire-suppression over the centuries (Richardson 1991). In 1991, PLNWR was established. Prior to public ownership, most of the area was cleared, ditched and drained for commercial farming and in anticipation of being mined for peat. The histosols formed on the Albermarle-Pamlico Peninsula (the old East Dismal Swamp) have developed over the last 9,000 years since the Wisconsin period of glaciation (Hinesly and Wicker 1999). Dolman and Buol (1967), as cited in Hinesly and Wicker (1999), purport that peat formation in these areas started about the same time as it did in the Dismal Swamp in Virginia, 8,900 ± 160 years before present.

Atlantic white cedar wetlands found within the GDSJNWR and ARNWR are the nearest to undisturbed conditions found within this region. As a reference for various ecological parameters of Atlantic white cedar wetlands, a chronosequence of age classes of naturally regenerating Atlantic white cedar wetlands was established for this study. Within the GDSNWR, three sites representing an age class gradient of wetlands recovering from canopy removal were selected: young (1 year since tree harvest), intermediate (26 years since harvest), and mature (68 years since harvest). The three wetlands were selected because 1) they were in close proximity to each other and therefore shared similar environmental conditions, 2) they shared the same watershed as the restored sites, and 3) their species components and stand structure were typical for the region (Levy and Walker 1979). The three sites were located within 2 km of each other along Corapeake Ditch Road at the North Carolina/Virginia state border. The mature and intermediate stands were located south of Corapeake Ditch Road in Camden Co., North

Carolina approximately 6 km west of the refuge boundary.

The mature stand (36° 32' 38" N, 76° 29' 21" W) was characterized by a nearly monotypic and even-aged canopy of Atlantic white cedar with scattered *Acer rubrum* L., *Nyssa sylvatica* Marsh., *Persea borbonia* Spreng., and *Pinus taeda* L. The understory was dominated by *Toxicodendron radicans* L., *Lyonia lucida* C. Koch, *Vaccinium corymbosum* L., *Smilax laurifolia* L., and *Clethra alnifolia* L. As with most areas within the Great Dismal Swamp, the hydroperiod has been altered by ditching, road construction, and various water management practices that have resulted in lower ground water elevations and alteration of natural seasonal fluctuations (Whitehead 1972). The soils within this site are Pungo soils, classified as Dysic-Thermic Typic Medisaprists (U.S. Department of Agriculture 1995), with pH values near 3.3.

The intermediate-aged stand (36° 32' 23" N, 76° 28' 43" W) was also characterized by a monotypic and even-aged canopy of Atlantic white cedar, with the major difference being the greater density of trees. Several authors have described stand development in Atlantic white cedar wetlands as beginning with very dense seedling establishment followed by density-dependent stand thinning as the canopy closes (Korstian and Brush 1931, Buell and Cain 1943, DeBerry 2000). The understory and ground cover strata of the intermediate site were similar to the mature wetland in species composition, although vegetative cover was greatly reduced. The soils within this site are classified as Pungo soils, Dysic-Thermic Typic Medisaprists (U.S. Department of Agriculture 1995), with pH values near 3.4.

The young site (36° 33' 09" N, 76° 28' 43" W) was located approximately 2 km northeast of the mature site in Suffolk City, Virginia. This site was harvested of nearly all Atlantic white cedar in the spring of 1997 using low impact harvesting methods to reduce ground compaction and understory disturbance. The remaining slash was left on site. At the time of initial sampling on site, the wetland was approximately 1 year since harvesting and vegetation consisted of remnant understory species (especially *Toxicodendron radicans* L., *Vaccinium corymbosum* L., and *Clethra alnifolia* L.) and emerging seedlings of Atlantic white cedar and *Acer rubrum* L. Soils at this site were classified as Pungo Muck soils, which are deep histosols (>2m deep), classified as Dysic-Thermic Typic Medisaprists (U.S. Department of Agriculture 1981), with pH values near 3.4.

The restoration sites (Edge Farm Restoration) (36^o 36' 35" N, 76^o 25' 17" W) are located on a 1 km^2 former agricultural area located on the eastern edge of the Great Dismal Swamp National Wildlife Refuge in southeastern Virginia. This site was under rotational crop cultivation for several decades prior and had been fallow for > 5 years before conversion to an Atlantic white cedar mitigation bank (known as the White Cedar LLC Mitigation Bank). Restoration efforts for this site included minor regrading to remove agricultural field crowns and furrows, plugging of existing drainage ditches, planting Atlantic white cedar saplings, and localized herbicide treatments to control encroaching hardwood species.

Atlantic white cedar saplings were planted on 3-m (±) centers in two phases, with plantings in 1992 and 1994. Supplemental plantings occurred in 1996 to offset localized mortality of planted material. The vegetation, which was in transition from a fallow agricultural field to an emergent freshwater wetland, contained components of old field vegetation, emergent freshwater marsh vegetation, and a developing canopy of planted

Atlantic white cedar. Dominant species included *Andropogon virginicus* L., *Eupatorium capillafolium* (Lam.) Small., *Panicum dichotomoflorum* Michx., *Juncus effusus* L., *Euthamia tenuifolia* (Pursh) Nutt., and *Chamaecyparis thyoides* (L.) B.S.P. Soils within the restoration sites are currently classified as Made Land but prior to cultivation were classified as Typic Umbraqualts, very poorly drained loam soils with high fractions of organic matter (U.S. Department of Agriculture 1953). Decades of intensive cultivation have resulted in the loss of much of the organic fraction typical of the surficial soils in the adjacent forested wetlands.

Two naturally regenerating Atlantic white cedar wetlands were selected for intensive study in ARNWR, Dare County, North Carolina. These two sites (intermediate and mature) are located approximately 90-km southeast of the intermediate and mature sites within the GDSNWR. The mature site was located approximately 0.5 km to the northwest terminus of North Sandy Ridge Road, located in the central section of the refuge. This site was harvested approximately 62 year ago and has since regenerated with a dense, monotypic canopy of Atlantic white cedar. Scattered throughout the canopy were individuals of *Acer rubrum* L., *Gordonia lasianthus* L. Ellis., and *Pinus taeda* L.

Vegetation in the understory was similar to that of the Great Dismal Swamp mature site, with *Lyonia lucida* C. Koch, *Clethra alnifolia* L., *Smilax rotundifolia* L., and *Toxicodendron radicans* L. The soils at the site are Pungo Muck with Belhaven inclusions and are classified as a Terric Medisaprist (U.S. Department of Agriculture 1992), with average pH values around 3.4.

The intermediate site was located approximately one kilometer south of the mature site, adjacent to North Sandy Ridge Road. This site was logged around 25 years ago and has since regenerated with a dense monotypic stand of Atlantic white cedar with scattered individuals of the aforementioned species throughout. The shrub layer was less prominent, but contained the same species found within the mature stand. The soils at this site are Pungo Muck with Belhaven inclusions and are classified as a Terric Medissaprist (U.S. Department of Agriculture 1992), with soil pH values near 3.3.

METHODS

Aboveground and belowground decay rates were determined and compared among two restored sites within the Great Dismal Swamp periphery (Edge Farm sites 1 and 2) and with sites that formed a chronosequence of naturally recovering stands within the GDSNWR and ARNWR. Results from the restoration site within PLNWR will be presented in the appendix. However, the following methodologies used were the same for all sites.

Within each site, two 10 x 15 m plots (each one consisting of 48 evenly dispersed stations) were identified for intensive above and belowground process and microenvironmental measurements. Within each of the sampling plots, nylon mesh litter bags containing roots were inserted into the soil profile during November 1998. The litter bags were constructed to integrate decay processes over a vertical soil profile (Tupacz and Day 1990, Conn and Day 1997). The litterbag technique using known amounts of selected vegetation has been successfully used in forests (Berg et al. 1984), tundra (Heal and French 1974), grasslands (Clark 1970), and wetlands (Day 1982, Tupacz and Day 1990, Thormann and Bayley 1997). Mesh bags permit organic matter quickly to become part of the natural litter layers as well as provide reasonable estimates of decay rates (Chamie and Richardson 1978). Using nylon mesh with 1mm openings permits maximum movement of all but the largest decomposer organisms and minimizes possible vegetation loss from bags due to fragmentation (Chamie and Richardson 1978). Although there has been much criticism directed at the use of litterbags (Witkamp and Olson 1963), they do provide a reproducible approximation of decomposition rates that integrate the effects of daily or weekly environmental variation (Gallagher 1978).

Belowground plant materials (roots and rhizomes, where applicable) were collected via pit excavations during the summer of 1998 from within each of the sites, were representative of the dominant communities at each site. A heterogeneous assortment of litter more closely approximates the decay dynamics of the entire community (Day 1982, Dwyer and Merriam 1983). Root material collected from each site represented the dominant species at each site. Upon harvesting, the root material was washed free of peat and air dried. 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).

Roots of approximately 9,000 *Chamaecyparis thyoides* seedlings were used as standard substrates across all sites to elucidate environmental/site effects. Within each site, comparison of *Chamaecyparis thyoides* seedling root decay with native "community" level root decay demonstrated litter quality influences under similar environmental conditions. Roots native to each site were buried to evaluate community decay dynamics and the influence of litter quality.

Known weights of air-dried roots were placed in 1 mm nylon mesh litter bags. The bags were constructed of 1 mm pore size nylon mesh and were 40 cm long, divided into four 10 cm sections that were inserted lengthwise into a vertical slit in the soil. Approximately 3 g of root material was placed in each of 4 10-cm sections in each litter bag. Most roots were 2-5 mm in diameter (all < 10 mm) and about 10-20% by volume were less than 2 mm in diameter. Subsamples were oven dried for 48 hr at 75° C to constant mass for air dry:oven dry mass ratios.

In the field, 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. Within each plot, litterbags were randomly assigned to a station. Six bags per site (3 from each plot) were collected at each sampling interval from randomly selected stations (within each plot) throughout the course of the study. Samples were installed in the field in November 1998 and sampling continued on a regular basis through August 2000. Over the course of the first year, sampling intervals were approximately one month intervals (when logistically possible); during the second year, samples were collected on a quarterly basis. Root decay rates and nutrient dynamics were compared among all sites.

Upon retrieval, the root bags were rinsed with tap water to remove adhering peat, and roots growing into bags were plucked out using forceps. The decomposing substrate was oven dried and weighed to determine mass loss. In order to determine ash free dry weight conversion ratios for the samples, individual samples were ground in a Wiley mill (40 mesh) and ashed in a muffle furnace at 550° C for 5 hours (Allen et al. 1986).

Decay rates and nutrient dynamics of leaf litter were also quantitatively compared among the sites. Recently senesced leaf litter was collected from tarps setup within each site during the fall of 1998. Approximately 3 g of air-dried leaves were placed in 20 x 20 cm nylon mesh (1 mm hole size) bags. Subsamples of leaves were oven dried at 75° C for 48 hours to constant mass for air dry:oven dry mass ratios. A second group of litterbags that contained *Chamaecyparis thyoides* leaf litter served as site controls. The *C. thyoides* leaf litter was collected during the fall of 1998 from an individual tree that fell during the late summer within the mature stand at the GDSNWR. Samples were deployed in January 1999 and collection coincided with root sample collection. Six litterbags of each type (native/standard) were removed from each site following the same protocol described earlier for the root litterbags.

Statistical Analyses

The data were evaluated using both linear and exponential decay models to test for the best fit. Relative decomposition rates (k [yr^{-1}]) for native/standard leaf litter and roots were derived from a fixed-intercept negative exponential decay model (Weider and Lang 1982) according to the following formula:

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

Where X = the proportion of initial mass remaining, k is the decay constant and t is time. Significant differences ($p = 0.05$) among all decay coefficients (k) at each depth for native and standard root decay and for litter decay across all sites were detected by the Tukey-Kramer method (Sokal and Rohlf 1981). Within each site, significant differences in decay coefficients between *Chamaecyparis* roots and native roots and *Chamaecyparis* leaf litter and native leaf litter were detected by t-tests (Zar 1998). Using the derived k values, time required to reach 1 percent mass remaining was extrapolated.

For all one-way and two-way ANOVA'S, assumptions of normality and homogeneity of variance were evaluated and transformations (arcsine, log, square root) were performed, if needed. Differences between means were detected using Tukey's Honestly Significant Difference ($p = 0.05$) test. ANOVA tests were conducted using the GLM procedure in SAS (SAS Institute 1985).

On the 1st, 3rd, and 6th sampling periods and on the 9th (370 days) and the 13th (670 days) for roots and 12th (610 days) for leaf litter, 3 bags of root material and leaf litter were randomly chosen for chemical analysis. Individual root samples were bulked by depth, and along with leaf samples were ground in a Wiley mill (40 mesh). Nutrient analysis was done on material left at the termination of the study to determine rates of nitrogen, phosphorus, carbon, and lignin loss from all tissues. Total carbon and nitrogen were analyzed using a CNS elemental analyzer (Elemental Vario Max CNS Analyzer). Phosphorus was determined by dry ashing of sample, followed by digestion in hydrochloric acid then digestate is analyzed by inductively coupled plasma emission spectroscopy (AOAC 1996). For each site and treatment combination (native/standard), ground replicates from subsamples were bulked and analyzed for lignin-like constituents. This approach sacrificed statistical testing but significantly reduced the time and cost required for analysis. Carbon quality was analyzed by an acid detergent fiber fractionation method (Ceramic Fiber Filter Method, AOAC 1998), resulting in an acid-insoluble residue. This fraction also contains non-lignin acid-insoluble substances, but is collectively referred to as lignin due to similarities in decomposability (Berg and McClaugherty 1989).

Researchers from Christopher Newport University and Old Dominion University measured the following variables on varying sampling schedules: stand structural characteristics, floristic surveys, aboveground production, belowground production (fine roots), hydrology, air and soil temperature, volumetric water content, soil nutrient content, and soil water content. With the exception of some edaphic parameters, these data are not presented in this dissertation, but are integral to the development of whole-system assessments of carbon cycling and other processes important to the overall objectives of the project.

Microsite environments are important in regulating decomposition rates (Day 1995). Over the course of this study, hydroperiod and soil pH were measured within the plots at each site. Monitoring microenvironmental variation over depth allowed for tight coupling between biological processes and the corresponding microenvironmental influences. Soil pH was measured from soils collected adjacent to regions where litterbags were removed during each sampling period. Four depths in the soil profile were sampled (0-10 cm, 10-20 cm, 20-30 cm and 30-40 cm). At each site, samples were collected, placed on ice in a cooler and brought back to the laboratory for analysis. Soil pH was measured using a portable pH meter (Orion, 290A) and combination glass and reference electrode immersed in a 50:50 soil:deionized water slurry.

Depth of rusting on steel rods was used as a means of determining depth to water table and the reducing zone within each of the sites (Bridgham et al. 1991, Thormann and Bayley 1997). Six uncoated mild steel welding rods, 81-cm long, were cleaned with steel wool and inserted in the soil within 1 plot at each site to a depth of 71 cm. After a one month incubation period (steel rod collection coincided with sample bag collection), the six rods were removed from the soil and six new rods (scored with steel wool) were inserted back into the soil. Upon collection, the steel rods were brought back to the laboratory and the depth of oxidation (rusting depth) was recorded. After measurements where made, the steel rods where inoculated (scored with steel wool) before being installed back in the field.

CHAPTER II

DECAY DYNAMICS IN REGENERATING SERAL STAGES AND RESTORATION SETTINGS: A CHRONOSEQUENCE APPROACH

INTRODUCTION

Historically, the net trend around the world has been toward the destruction of wetlands. However, significant efforts are now being focused on restoration and creation of these habitats (Mitsch and Gosselink 2000). The primary goal of wetland restoration and creation is to establish self-sustaining ecosystems that are similar in structure and function to the natural systems that they are designed to emulate, or one that will become like the natural system through succession of the flora and fauna (Broome 1990, Zedler 1992). While most wetland restoration studies characterize the temporal dynamics of vegetation composition (Broome et al. 1986, Broome 1990), few studies document the maturation of ecosystem processes, such as primary productivity and nutrient accumulation (Richardson 1994, Craft et al. 1999). In a recent review of the literature, Atkinson and Cairns (2001) could not find any estimates of plant decomposition rates in created wetlands. This finding is disconcerting as soil organic matter sequestration and subsequent carbon accumulation are critical functions in natural wetlands. It is crucial that these processes develop in restored and created wetlands if they are expected to reach functional equivalency with their natural counterparts.

Wetland restoration and creation are frequently used to replace ecological functions and values lost when natural wetlands are degraded or destroyed (Craft et al.

1999). According to Havens et al. (1997), in the United States, the use of constructed wetlands to replace natural wetlands is becoming pandemic, and the literature suggests (Zedler 1996, 1999, 2000, Mitsch and Wilson 1996, Mitsch and Gosselink 2000, Ness 2001) that these replacement wetlands are not reaching functional parity with their natural counterparts. With the exception of a 25-year study of soils in coastal North Carolina marshes (Craft et al. 1999), the long-term development of restored wetland ecosystems is poorly recorded (Zedler 2000).

Pocosins and associated wetlands (including Atlantic white cedar wetlands) are among the least studied ecosystems in the U.S. (Richardson 1991). These wetlands are highly recognized as peat storing wetlands (Mitsch and Gosselink 2000). With our limited knowledge of the ecosystem structure and function of these types of wetlands, is it possible to create or restore the soil organic matter sequestration functions that are critical to the development and self-maintenance of these wetlands? Brinson and Rheinhardt (1996) suggested that these peat-based wetlands cannot be created without either removing peat from existing wetlands or waiting the decades to millennia for sufficient peat to accumulate. According to Whittecar and Daniels (1999), forested pocosins are more likely to be developed only by restoring saturated conditions to former pocosins or by regrading transitional areas that fringe existing pocosins. Cole et al. (2001) found no evidence of increasing levels of soil organic matter within created wetlands that varied in time since development. Ecosystem-level research and ecosystem model development may provide guidance on when restored and created wetlands can reasonably be expected to comply with criteria that measure their success (Mitsch and Wilson 1996).

above and belowground organic matter decay along a chronosequence (intermediate and mature age classes) of naturally recovering Atlantic white cedar wetlands and 2) compare these trends to those of Atlantic white cedar restoration settings.

METHODS

Study Design

The current study was conducted along a chronosequence of naturally regenerating Atlantic white cedar wetlands within the GDS and AR National Wildlife Refuges and within restored Atlantic white cedar sites along the eastern periphery of the GDSNWR. The study sites along the chronosequence and within restoration efforts were selected based on similarities of site age, vegetative composition, topography and soils. This approach was taken to obtain replicate sites that were as similar as possible. Although it is rarely possible to select identical sites for replication of field experiments, the use of sites meeting a series of criteria of similarity allows for the results of the study to be generalized (Hurlbert 1984, Ehrenfeld and Schneider 1991). Whole-ecosystem experiments are often difficult to replicate. However, ecosystem experiments on this scale are important because they include major processes not often found in smaller-scale experiments (Mitsch et al. 1998). Decay measurements quantified along the chronosequence and restoration treatment are based on 2 replicates per treatment.

RESULTS

Leaf Litter Decay

Patterns of mass loss of aboveground leaf litter were similar along the chronosequence and within the restored sites (Figure 2). Native leaf litter decay rates (*k*) ranged from 0.60 to 0.65 yr^{-1} with no significant differences occurring along the chronosequence or within the restoration setting (Table 1). In general, it took approximately 7 years for leaf litter to reach 1 % mass remaining within all treatments. *Chamaecyparis* leaf litter exhibited less mass loss relative to native litters and decay rates (*k*) ranged from 0.33 to 0.43 yr^{-1} (Table 1). No significant differences occurred in *Chamaecyparis* leaf litter decay rates among sites. Under similar environmental conditions (within sites) *t*-tests between native leaf litter and *Chamaecyparis* leaf litter revealed significant differences in decay rates ($p = 0.05$) (Table 1). Decay of native leaf litter was faster than *Chamaecyparis* leaf litter.

Native Root Decay

In contrast to aboveground decomposition trends, percent mass loss was substantially greater for native roots in the restoration setting compared to native roots along the chronosequence (Figure 3). There was a pronounced vertical decay gradient of decreased mass loss with increasing depth in the restoration setting. Patterns of mass loss of native roots were similar along the chronosequence. Decay rates of native roots were similar along the chronosequence, but differed significantly from native root decay in the restored sites (Table 2). Along the chronosequence, native root decay ranged from 0.32 to 0.37 yr^{-1} with no significant differences in decay rates across the vertical soil profile.

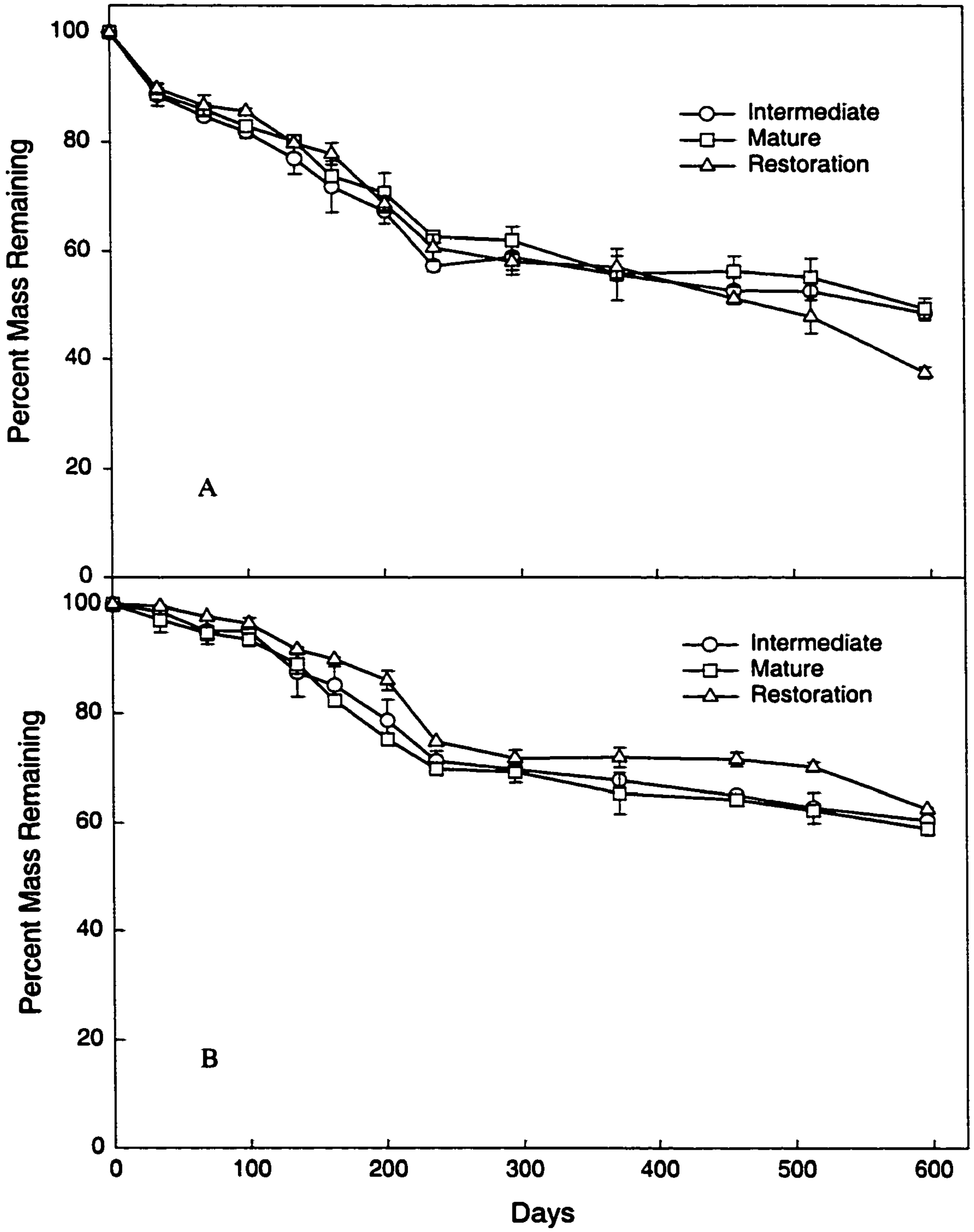

Figure 2. Percent mass remaining of native leaf litter (A), and *Chamaecyparis thyoides* leaf litter (B), along chronosequence and restoration treatment. Values represent means with one standard error.

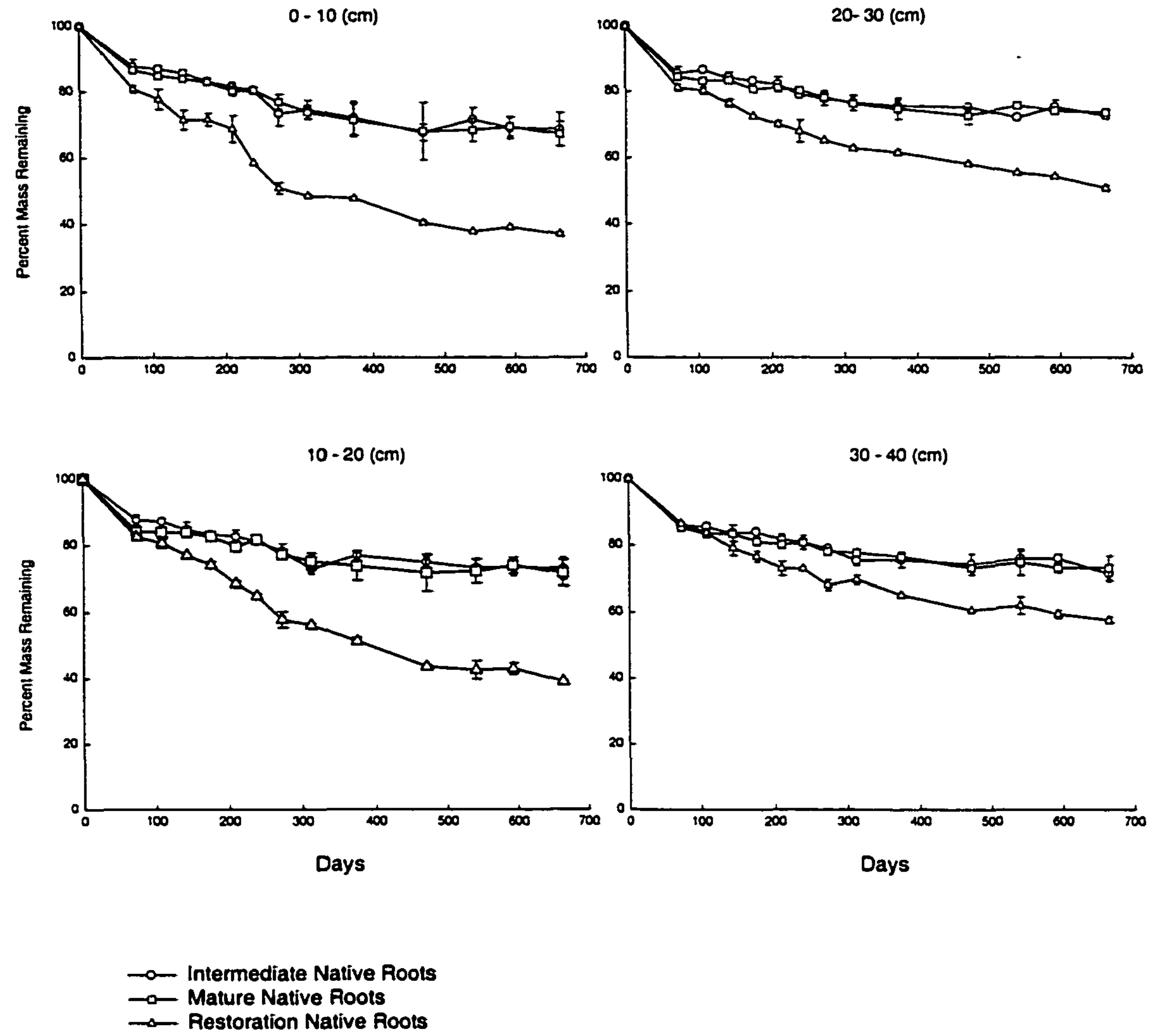

Figure 3. Percent mass remaining of native roots along chronosequence and in restoration setting. Values represent means with one standard error.

there a significant difference in decay rates and this occurred between the restored and mature treatments. Trends of decreasing decay with increasing depth in the vertical soil profile were variable along the chronosequence, but were apparent within the restoration treatment (Table 3). Under the same environmental conditions (within sites) *t*-tests revealed that significant differences ($p = 0.05$) occurred between decay rates of native roots and decay rates of *Chamaecyparis* roots within the restoration treatment

Table 2. Decay rate constants [$-k(\mathrm{yr}^{-1})$], coefficient of determination (r^2), time to reach 1% mass remaining ($t_{0.01}$), and percent mass remaining after 665 days of decay (% M) for native roots. All regressions are significant at $p = 0.0001$. Different uppercase letters indicate significant differences ($p = 0.05$) between sites. Different lowercase letters indicate significant differences ($p = 0.05$) between depths.

Site	Depth Class	k	SE	r^2	$t_{0.01}$ (yr)	Final % Mass
Mature	0-10 cm	0.37^{Aa}	0.02	0.96	12.52	67.15
	10-20 cm	0.36^{Aa}	0.03	0.94	13.04	71.68
	20-30 cm	0.35^{Aa}	0.03	0.93	13.12	73.54
	30-40 cm	0.34^{Aa}	0.03	0.93	13.59	73.14
Intermediate						
	0-10 cm	0.36^{Aa}	0.02	0.96	12.88	68.45
	10-20 cm	0.32^{Aa}	0.02	0.94	14.41	72.79
	20-30 cm	0.34^{Aa}	0.03	0.94	13.56	72.70
	30-40 cm	0.33^{Aa}	0.03	0.94	14.07	72.41
Restoration						
	0-10 cm	0.83^{Ba}	0.03	0.98	5.55	37.01
	10-20 cm	0.71^{Bb}	0.01	0.98	6.53	38.98
	20-30 cm	0.59^{Bc}	0.03	0.96	7.79	50.78
	30-40 cm	0.50^{Bc}	0.02	0.97	9.21	57.61

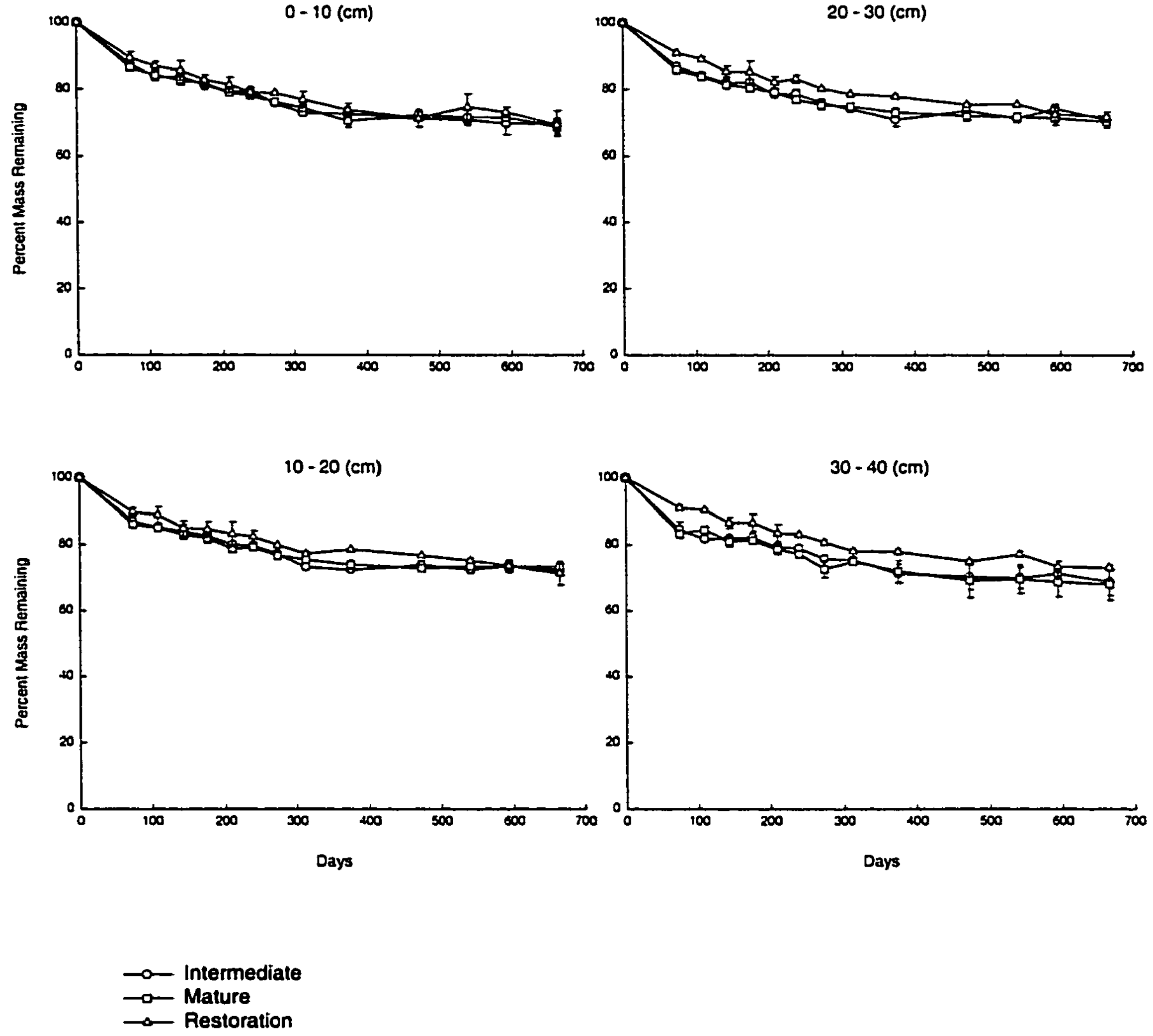

Figure 4. Percent mass remaining of *Chamaecyparis thyoides* roots along the chronosequence and restoration setting. Values represent means with one standard error.

(Tables 2 and 3). This difference was maintained across all depths of the vertical soil profile. No significant differences occurred between native root decay and *Chamaecyparis* root decay along the chronosequence.

In the upper soil profile (0 – 20 cm) of the restoration setting, less than 40 % mass remained for native roots following almost two years of incubation in the field. In the lower soil profile (20 –40 cm), approximately 53 % of native root mass remained over the

Table 3. Decay rate constants [$-k$ (yr^{-1})], coefficient of determination (r^2), time to reach 1% mass remaining ($t_{0.01}$), and percent mass remaining after 665 days of decay (% M) for *Chamaecyparis thyoides* roots. All regressions are significant at $p = 0.0001$. Different uppercase letters indicate significant differences ($p = 0.05$) between sites. Different lowercase letters indicate significant differences ($p = 0.05$) between depths.

Location	Depth Class	k	SE	r^2	$t_{0.01}$ (yr)	Final % Mass
Mature	0-10 cm	0.39^{ABa}	0.02	0.96	11.80	68.99
	10-20 cm	0.36^{ABa}	0.03	0.95	12.79	73.31
	20-30 cm	0.38^{ABa}	0.02	0.95	12.11	70.31
	30-40 cm	0.40^{Aa}	0.02	0.95	11.51	68.09
Intermediate						
	0-10 cm	0.37^{ABa}	0.02	0.96	12.44	69.79
	10-20 cm	0.36^{ABa}	0.02	0.97	12.79	72.23
	20-30 cm	0.38^{ABa}	0.02	0.96	12.11	70.89
	30-40 cm	0.39^{ABa}	0.03	0.95	11.80	68.72
Restoration						
	0-10 cm	0.35^{ABa}	0.02	0.96	13.15	69.40
	10-20 cm	0.31^{ABa}	0.02	0.95	14.85	71.35
	20-30 cm	0.30^{ABa}	0.02	0.96	15.35	71.73
	30-40 cm	0.29^{Ba}	0.02	0.97	15.87	72.05

course of the same time period. Mass loss of *Chamaecyparis* root material was similar within the restoration setting relative to the chronosequence; however, marked differences in mass loss occurred between the native root material and *Chamaecyparis* roots within this treatment. In the restoration setting, *Chamaecyparis* roots had about 70% mass remaining across all depths of the vertical soil profile after almost two years of incubation in the field. The native roots collected from the restored treatment were representative of the extant dominant vegetative community on both sites. The vegetation within these sites was dominated by various graminoid and forb species. The dominant woody species within the restoration sites was planted *Chamaecyparis thyoides*. The native root material for the restoration sites included 0.3 grams of *Chamaecyparis* roots within each pocket of each 40 cm long vertically oriented litterbags. This fraction of woody root material was included in each litterbag to simulate community level vegetation decay dynamics within this treatment. Unlike native root material in the restoration setting, patterns of mass loss for *Chamaecyparis* roots were not as pronounced with increasing depth in the vertical soil profile.

DISCUSSION

Aboveground Decay Trends

A primary concern with wetland creation and restoration projects is whether these wetlands successfully replace functional attributes that are lost when natural wetlands are destroyed or degraded. Rates of decomposition influence soil fertility, nutrient cycling and organic matter accumulation in wetlands and are a forcing factor controlling ecosystem structure and function. In spite of the fundamental role of decomposition in the structure and function of restored or created wetlands, few studies have measured this process, and there is a paucity of information to indicate and predict functional development over time. This is also the case within seral stages of natural wetlands undergoing succession. In the present study, leaf litter decay rates did not differ between seral stages of Atlantic white cedar ecosystem development. Other studies have demonstrated slower decay rates within early developmental stages. Atkinson and Cairns (2001) determined that decomposition of emergent vegetation in created depressional wetlands was faster in 20-yr-old sites than in 2-yr-old sites. However, they stated that wetland functional equivalence in regard to decomposition had not been achieved, and that decomposition functions of these wetlands were still developing after 20 years. Bakker et al. (1997) examined organic matter accumulation rates along a sere from open water to carr forest in the Netherlands and determined that an intermediate seral stage had the highest organic matter accumulation rates compared to earlier or later developmental stages.

Interestingly, aboveground decay in the restored treatment was also similar to that occurring along the chronosequence. This result was unexpected as the litter from the restored treatment was dominated by emergent graminoids and forbs. Benner et al. (1985) found that the lignocelluloses from herbaceous plants were mineralized several times faster relative to woody species under similar environmental conditions. Whigham et al. (1989) determined that litter that contained only leaves of herbaceous vegetation, lost weight faster than litter that contained both leaves and stem material. Perhaps the inclusion of stems and other aboveground parts led to a decrease in mass loss within the restoration setting. The lack of a canopy within the restoration treatment may have influenced the microclimate at the soil surface. Based on qualitative observations between the restoration treatment relative to chronosequence treatments, photosynthetic photon flux density was greater and exhibited a longer diel periodicity, fetch was greater within this setting leading to greater sustained wind movement, and relative humidity was reduced while temperatures were more variable. The interplay of these environmental variables, although not directly measured, could have potentially produced inimical conditions for microbial decay, resulting in decreased decay rates associated with the restoration treatment.

Decay rates of leaf litter along the chronosequence were higher compared to other studies in Atlantic white cedar wetlands. In a mature Atlantic white cedar stand in the GDSNWR, Day (1982) determined a decay rate of 0.34 yr^{-1} for mixed litter and 0.34 yr^{-1} for cedar litter, while Yates and Day (1983) calculated a decay rate of 0.48 yr^{-1} for mixed litter using an exponential decay model. Differences between previously determined decay rates and the decay rates determined in this study may be the result of the interplay of numerous environmental factors within sites at the time of the studies, differences in species composition of native litter in litter bags, as well as the use of fixed versus non-fixed intercept models. According to Wieder and Lang (1982), fixed intercept models estimate higher (*k*) values relative to unfixed intercept models.

Differences in decay rates between this study and previous studies in Atlantic white cedar wetlands may also be due to natural climatological variability during the time of the studies. Working within a bottomland hardwood forested wetland in Louisiana, Rybczyk et al. (2002) found that annual leaf litter decay rates varied from 0.49 to 1.71 yr^{-}

^{1} over the course of a four year study. Starting date of experiment and initial condition of litter collected were some reasons cited as potential sources of annual variation of decay rates for their study. However, the annual rates of aboveground decomposition measured during this study fell within the range of other forested wetlands (Brinson 1990, Conner and Day 1991, Mitsch and Gosselink 2000, Rybczyk et al. 2002). Native and *Chamaecyparis* leaf litters exhibited a period of rapid mass loss after about 200 days of incubation followed by a period of slow decay. This period coincided with flooding events caused by major hurricanes that struck the study area during late summer/early fall of 1999. Day (1982, 1983) determined that surface waters can accelerate mass loss via leaching, and after surface flooding recedes, decay slows and becomes more linear.

Belowground Decay Trends

In the GDSNWR, Megonigal and Day (1988) estimated that roots contribute 65% of the annual increment of soil organic matter in an Atlantic white cedar stand. Bridgham et al. (1991) found the highest rates of belowground cellulose decay in an agricultural site, with high nutrients and less acidic conditions and relatively low soil moisture. In the current study, native root decay was significantly faster within the restoration treatment relative to the chronosequence. The restoration setting in this study was an abandoned agricultural site with less acidic soil conditions compared to the chronosequence.

The finding of significantly higher rates of decomposition across the vertical soil profile within the restored treatment is of paramount importance. This suggests that native root contributions to soil organic matter pools are significantly less compared to the chronosequence of regenerating Atlantic white cedar stands. Broome et al. (1986)

determined that belowground biomass in a restored saltmarsh was similar to a reference marsh after four growing seasons. Craft and Broome (2000) suggested that macro-organic matter (the living and dead mat of roots and rhizomes) pools can achieve similarity with natural marshes in 15 to 30 yr. Evidence of soil organic matter sequestration in restored/created wetlands is limited despite studies indicating recovery of above and belowground production.

Broome et al. (2000) determined that low soil organic matter contents of restored marsh soils were associated with low nutrient concentrations and slowed the rate of functional development of the restored marshes. According to Craft et al. (1999), while it seems likely that with sufficient time, correctly designed constructed salt marshes will become similar to natural marshes, it is not clear how much time is required for these ecosystems to achieve levels of community structure and ecosystem function equivalent to natural counterparts. Craft (2001) determined that soil-nutrient concentrations, ratios, pools and accumulation in a 42-year-old restored marsh provided the same level of biogeochemical and water quality improvement functions as a natural reference marsh. However, these estimates of reaching functional equivalence in biogeochemical properties are for structurally simple salt marshes. The biogeochemistry of forested wetlands is considered by Lockaby and Walbridge (1998) to be the most difficult and complex to study with any type of forested ecosystem. The mechanism by which organic matter is incorporated into soils is generally attributed to saturated conditions that serve to retard decomposition (Collins and Kuehl 2001). Despite above and belowground biomass exceeding that of reference freshwater marshes in Pennsylvania, Cole et al. (2001) found no relationship of biomass to soil organic matter in created marshes. Also working within created freshwater marshes, Cambell et al. (2002), determined that reference wetlands had significantly higher organic matter than created wetlands and after more than 10 years of development, the created wetlands appear not to be accumulating meaningful amounts of soil organic matter.

It does appear that created and restored wetlands can become structurally equivalent (with respect to plant biomass) with their natural counterparts, but functionally different relative to the presence of soil organic matter and associated functions. Significantly faster native root decay occurred across all depth intervals in the restored treatment. Native root decay was almost 120% faster compared to that of the chronosequence in the 0 –20 cm depth interval, with the fastest decay rate occurring in the upper 0 – 10 cm interval. In a concomitant study, Rodgers (2001) determined that the fraction of fine roots in the upper 10 cm of soil accounted for 69% of the roots found over a 60 cm depth profile in the restored treatment. Additionally, based on calculations of mass-based root length production, Rodgers (2001) determined that belowground carbon inputs from fine roots were significantly less in restored sites and root turnover rates were significantly higher relative to the naturally regenerating sites. The finding of significantly faster belowground decay rates within the restoration treatment is important, because significantly higher rates of decomposition across the vertical soil profile within this treatment suggests that root contributions to soil organic matter pools are significantly less compared to the sites along the chronosequence.

Production and decomposition are counterbalancing processes that control ecosystem structure, function and development. In naturally occurring Atlantic white cedar wetlands high litter production rates coupled with low decomposition rates typically result in the production of deep organic soils (Day 1987). Higher planting densities of Atlantic white cedar and associated shrub species in the restoration sites may be required in order to achieve similar contributions of litter and roots to accumulating soil organic matter (DeBerry 2000). The results of the current study utilizing *Chamaecyparis thyoides* leaf litter and roots as standard substrates support this suggestion. There were no significant differences in above or belowground decay coefficients among the restoration treatment or chronosequence sites. Decay rates in the 20 – 40 cm depth interval were actually slower in the restoration treatment compared to the chronosequence.

Findings of this research suggest that while decomposition of native material is significantly faster within the restored treatment relative to the chronosequence, future increases in aboveground and belowground production of Atlantic white cedar coupled with the low decay rates of cedar litter could result in increased contributions to soil organic matter pools.

CHAPTER III

WEIGHT LOSS AND NUTRIENT CHANGES IN DECOMPOSING LEAF LITTER WITHIN REGENERATING AND RESTORED ATLANTIC WHITE CEDAR (*CHAMAECYPARIS THYOIDES*) WETLANDS

INTRODUCTION

Primary production of forested wetlands is closely tied to hydrology, with productivity typically highest in moderately wet conditions relative to either drier or wetter conditions. The effects of hydrology on decomposition pathways in forested wetlands are less clear than the effects on primary productivity (Mitsch and Gosselink 2000). Mechanisms controlling decomposition are extremely complex in seasonally flooded systems where terrestrial and aquatic influences alternate during a given year and year to year (Day 1987). Since wetlands combine attributes of both terrestrial and aquatic ecosystems but are neither, they have unique properties that are not adequately covered by present ecological paradigms and by fields such as freshwater and terrestrial ecology (Mitsch and Gosselink 2000).

Working in a riparian tupelo swamp in North Carolina, Brinson (1977) found leaf litter decay to be greatest in the wettest sites. Conner and Day (1991) found leaf litter decay rates were slowest in an impounded forested wetland site in Louisiana relative to decay rates in an impoundment where hydroperiod was experimentally manipulated. Day (1982) determined that decay rates of red maple were similar within four forested wetland sites with differing hydroperiods. The decomposition of organic matter and resultant release of nutrients involves as least two processes. Abiotic leaching is usually attributed to an initial loss of soluble materials. Respiration, denitrification and incorporation into decomposer organisms also results in nutrient release. Antithetically, accumulation of materials by components of the microfaunal detritus community and by abiotic factors (throughfall, aeolian deposition etc.) can cause increased nutrient content in decomposing litter. The end result of abiotic and biotic interactions during decomposition is that some materials are released (and potentially used in plant growth), while others are immobilized or stored temporarily or permanently (Whigham et. al. 1989). Rates of organic decomposition are most rapid in the presence of oxygen and slower for electron acceptors such as nitrates and sulfates (Mitsch and Gosselink 2000). Megonigal and Day (1988) estimated that leaf litter contributed 6-28% of the annual increment to soil organic matter within forested wetlands of the GDSNWR. Therefore, leaf litter represents a significant contribution to soil organic matter pools within forested wetland ecosystems. Aboveground decay processes within Atlantic white cedar wetlands are poorly understood (Day 1982, Yates and Day 1983, Ehrenfeld 1995)

The objectives of this study were to evaluate environmental and substrate quality factors influencing leaf litter decomposition within recovering stands of Atlantic white cedar and compare those measurements with decay dynamics of restored Atlantic white cedar wetlands. Regulatory factors influencing aboveground decomposition and nutrient cycling were tested by the following hypotheses: (1) leaf litter will decay more slowly in recovering stands relative to the restored sites, (2) leaf litter with high initial nitrogen content will have faster decay than leaf litter with low nitrogen content.

METHODS

Environmental influences (hydroperiod, pH) on decay were tested directly by deploying a standard substrate (*Chamaecyparis thyoides* leaf litter) at all sites. The native litter decay study incorporated both environmental and litter quality factors. In order to separate the influence of both factors, native litter decay and standard litter (*Chamaecyparis*) decay were compared within each site and interpreted in relation to differences in litter quality.

Statistical Analyses

Initial nitrogen and carbon concentrations of native and *Chamaecyparis* leaf litter were analyzed using one-way ANOVA's. Two way ANOVA (site x time) tested for differences in percent nitrogen and carbon remaining in the litter. Annual means of soil pH and depth to water table were analyzed by one-way ANOVA's. The relationships among annual environmental factors (hydroperiod, soil pH), initial chemical composition of the litter and annual decay rates (*k*) within all sites were examined by correlation analysis.

RESULTS

Decomposition Rates

Despite marked differences in edaphic characteristics between the recovering and restored Atlantic white cedar wetlands (Table 4), patterns of native leaf litter mass loss were similar across refuges and within all sites (Figure 5). Annual decay rate constants

Table 4. Average soil pH, bulk density, volumetric water content, organic matter content and groundwater levels within restored and naturally regenerating Atlantic white cedar wetlands. Alligator River National Wildlife Refuge = (ARNWR), Great Dismal Swamp National Wildlife Refuge = (GDSNWR) and Edge Farm Restoration = (EFR). Groundwater level determined by oxidation depth on steel rods. An (A*) indicates data from Thompson (2001).

	ARNWR		GDSNWR			EFR	
	Mature	Intermediate	Mature	Intermediate	Young	Site 1	Site2
Soil pH	3.4	3.2	3.3	3.4	3.4	4.5	4.4
Bulk Density* (g/cm3)	0.084	0.097	0.117	0.163	0.153	0.567	0.705
Volumetric Water* Content (%)	32.6	37.8	33.2	24.2	29.0	35	31
Organic Matter* Content (%)	97.6	97.3	93.2	92.2	92.9	38.6	23.3
Groundwater Level (cm) relative to soil surface	-8.8	-7.5	-34.7	-32.6	-14.7	-11.2	-11.3

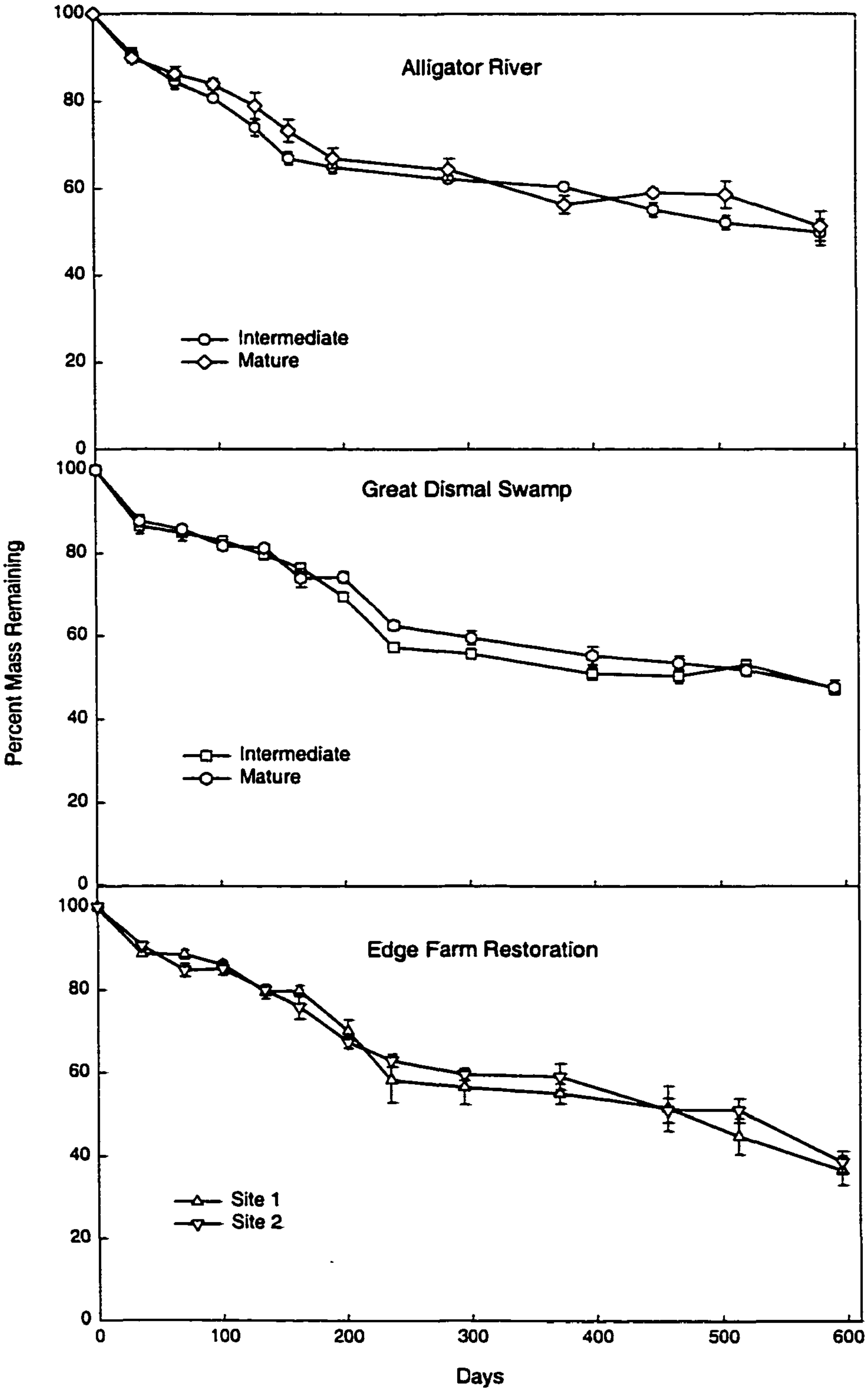

Figure 5. Percent mass remaining of native leaf litter within all sites. Values represent means with one standard error.

Table 5. Decay rate [-k (yr^{-1})], coefficient of determination (r^2) and fraction remainin for native litter decay among Atlantic white cedar restored and regenerating sites. All regressions are significant at p = 0.0001. One standard error in parentheses. Different upper case letters indicate significant differences (p = 0.05) between sites.

Site	*k* (yr^{-1})	r^2	Fraction Remaining
Alligator River N.W.R.			
Mature	0.60 (0.03)^{A}	0.97	0.563
Intermediate	0.62 (0.05)^{A}	0.93	0.604
Dismal Swamp N.W.R.			
Mature	0.60 (0.02)^{A}	0.98	0.552
Intermediate	0.68 (0.03)^{A}	0.98	0.508
Edge Farm Restoration			
Site 1	0.65 (0.03)^{A}	0.97	0.549
Site 2	0.61 (0.02)^{A}	0.98	0.590

Table 6. Decay rate [-k (yr^{-1})], coefficient of determination (r^2) and fraction remainin for *Chamaecyparis thyoides* litter decay among Atlantic white cedar restored and regenerating sties. All regressions are significant at p = 0.0001. One standard error in parentheses. Different upper case letters indicate significant differences (p = 0.05) between sites.

Site	*k* (yr^{-1})	r^2	Fraction Remaining
Alligator River N.W.R.			
Mature	0.40 (0.02)^{AB}	0.97	0.691
Intermediate	0.41 (0.02)^{AB}	0.96	0.685
Dismal Swamp N.W.R.			
Mature	0.45 (0.02)^{A}	0.96	0.615
Intermediate	0.38 (0.03)^{AB}	0.94	0.669
Young	0.32 (0.01)^{B}	0.96	0.730
Edge Farm Restoration			
Site 1	0.35 (0.02)^{AB}	0.94	0.701
Site 2	0.31 (0.02)^{B}	0.93	0.737

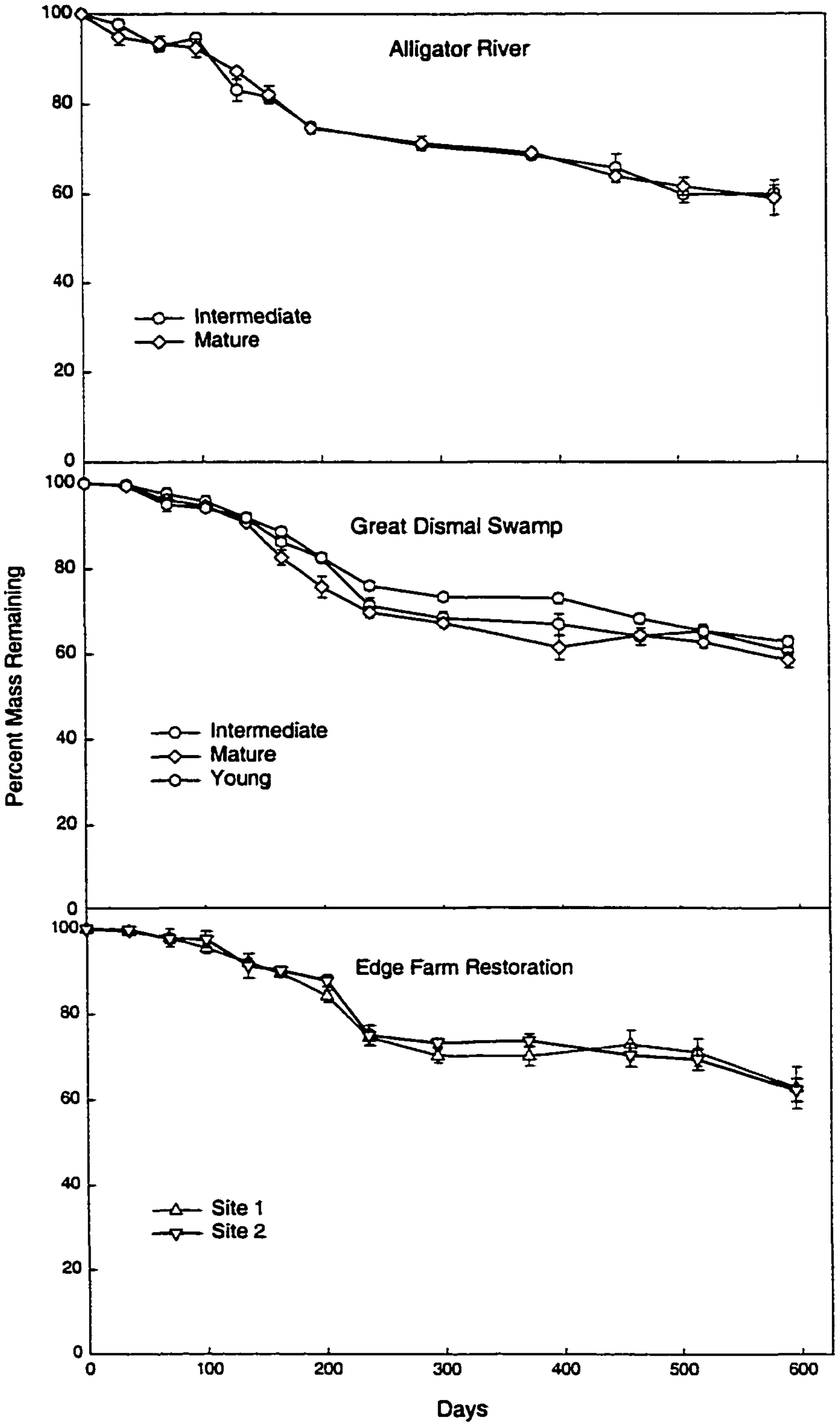

Figure 6. Percent mass remaining in *Chamaecyparis thyoides* leaf litter within all sites. Values represent means with one standard error.

Table 7. Initial native leaf litter quality indices (0) and after 1.6 years of decay (1.6) for nitrogen concentration (%N), phosphorus concentration (%P), carbon concentration (%C), and carbon:nitrogen ratio (C:N). One standard error in parentheses. Different lowercase superscripts between rows indicate significant differences (p = 0.05). N=3 for all % P where n=1.

	%N		%P		%C		C:N	
	0	1.6	0	1.6	0	1.6	0	1.6
Alligator River								
Mature	1.03 (0.06)^{a}	1.56 (0.09)^{a}	0.12	0.08	50.36 (0.02)^{a}	50.59 (0.11)^{a}	49	32
Intermediate	1.03 (0.06)^{a}	1.39 (0.09)^{a}	0.12	0.09	50.36 (0.02)^{a}	51.23 (0.14)^{a}	49	37
Dismal Swamp								
Mature	0.79 (0.13)^{a}	2.01 (0.07)^{b}	0.14	0.11	48.26 (1.61)^{ab}	49.06 (0.08)^{a}	64	24
Intermediate	0.79 (0.13)^{a}	2.29 (0.03)^{b}	0.14	0.12	48.26 (1.61)^{ab}	49.26 (0.04)^{a}	64	22
Edge Farm								
Site 1	0.72 (0.07)^{a}	1.48 (0.05)^{a}	0.25	0.17	45.62 (0.28)^{b}	43.39 (0.11)^{b}	64	29
Site 2	0.72 (0.07)^{a}	1.38 (0.08)^{a}	0.25	0.14	45.62 (0.28)^{b}	45.19 (0.18)^{b}	64	33

Table 8. Initial *Chamaecyparis thyoides* leaf litter quality indices (0) and after 1.6 years of decay (1.6) for, nitrogen concentration (%N), phosphorus concentration (%P), carbon concentration (%C), and carbon:nitrogen ratio (C:N). One standard error in parentheses. Different lowercase superscripts indicate significant (p = 0.05) differences. N=3 for all indices except % P where n=1.

	%N		%P		%C		C:N	
	0	1.6	0	1.6	0	1.6	0	1.6
Alligator River								
Mature	1.37 (0.11)	1.77 (0.01)^{a}	0.17	0.13	51.56 (0.32)	51.18 (0.06)^{a}	38	31
Intermediate	1.37 (0.11)	1.69 (0.01)^{b}	0.17	0.14	51.56 (0.32)	51.95 (0.03)^{b}	38	29
Dismal Swamp								
Mature	1.37 (0.11)	1.91 (0.01)^{c}	0.17	0.13	51.56 (0.32)	51.07 (0.06)^{a}	38	27
Intermediate	1.37 (0.11)	1.89 (0.01)^{c}	0.17	0.12	51.56 (0.32)	51.25 (0.02)^{a}	38	27
Edge Farm								
Site 1	1.37 (0.11)	1.92 (0.01)^{c}	0.17	0.13	51.56 (0.32)	47.91 (0.08)^{c}	38	25
Site 2	1.37 (0.11)	1.81 (0.01)^{a}	0.17	0.11	51.56 (0.32)	49.69 (0.03)^{d}	38	26

to all other sites (Tables 7 and 8). After 1.6 years of incubation, *Chamaecyparis* leaf litter accumulated nitrogen within all sites (Table 8). Nitrogen accumulation in *Chamaecyparis* leaf litter within the restored sites was similar to naturally regenerating sites within both refuges. Phosphorus was released within all sites and after 1.6 years of incubation. Initial carbon content was similar in *Chamaecyparis* litter and native litter within the naturally regenerating sites. After 1.6 years of incubation, carbon content of *Chamaecyparis* leaf litter was significantly lower in the restored sites relative to the naturally regenerating sites (Table 8).

Trends in Nitrogen and Phosphorus Dynamics

Significant site (F = 141.03, $p < 0.0001$), time (F = 88.46, $p < 0.001$) and site x time (F = 5.87, $p < 0.001$) effects resulted in different patterns of nitrogen behavior in native leaf litter within the naturally regenerating sites compared to the restored sites (Figure 7). Sites within the GDSNWR immobilized nitrogen amounts to over twice the initial amounts. After 1.6 years, greater than 100% of original nitrogen remained within all study sites with significantly higher amounts of nitrogen remaining within the stands in the GDSNWR (Figure 7 B).

Native leaf litter decay showed dynamic phosphorus behavior over time and between all the sites (Figure 8). Due to a finite amount of leaf litter available, phosphorus content could not be tested statistically (n = 1). While differences in remaining phosphorus were not statistically tested, the phosphorus data presented here may suggest trends operating within these sites. Net phosphorus immobilization (> 100%) occurred within the intermediate-aged site within the GDSNWR and the mature

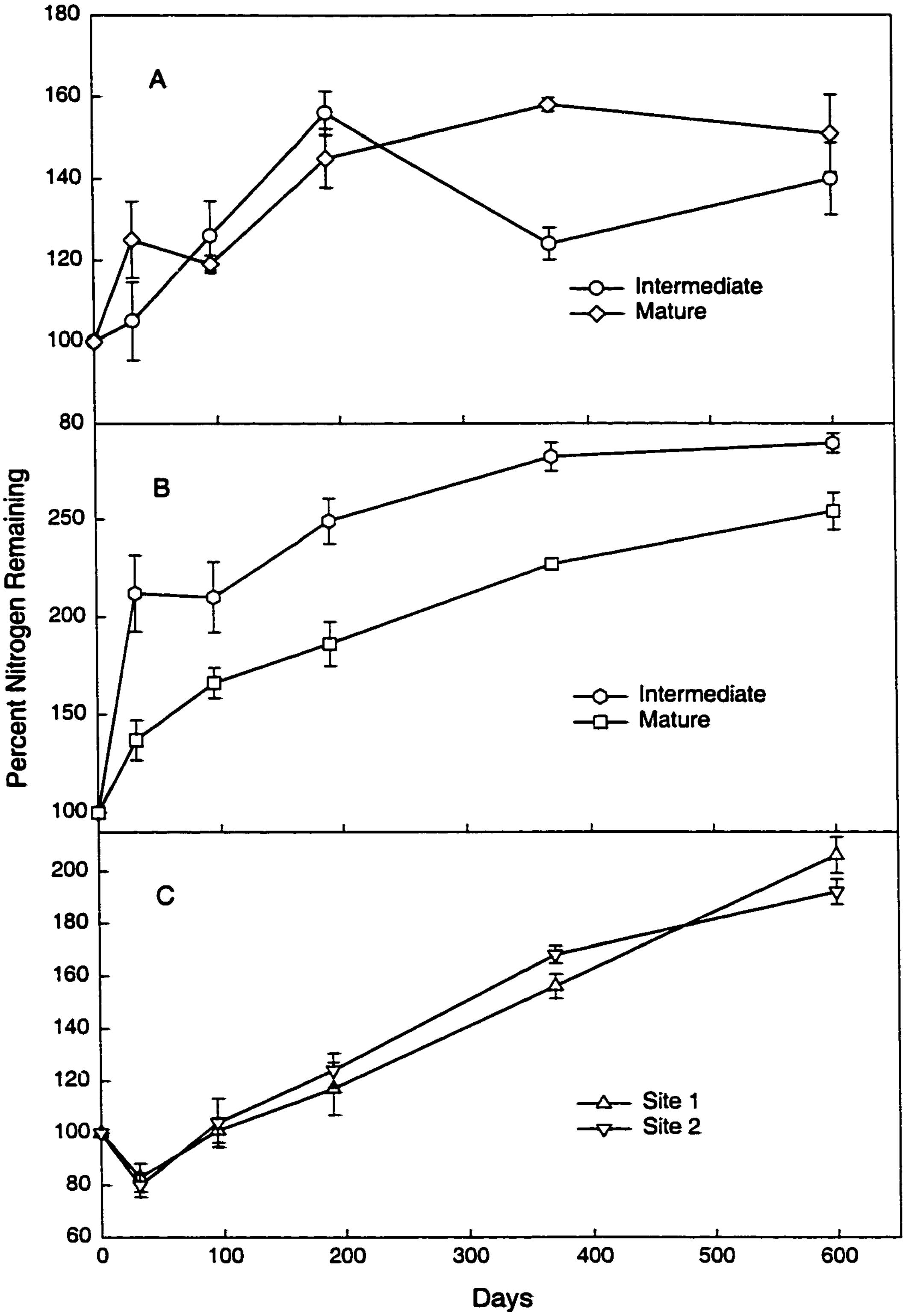

Figure 7. Percent nitrogen remaining in native leaf litter in (A), Alligator River N.W.R., (B), Great Dismal Swamp N.W.R., and (C) Edge Farm Restoration. Values represent means with one standard error.

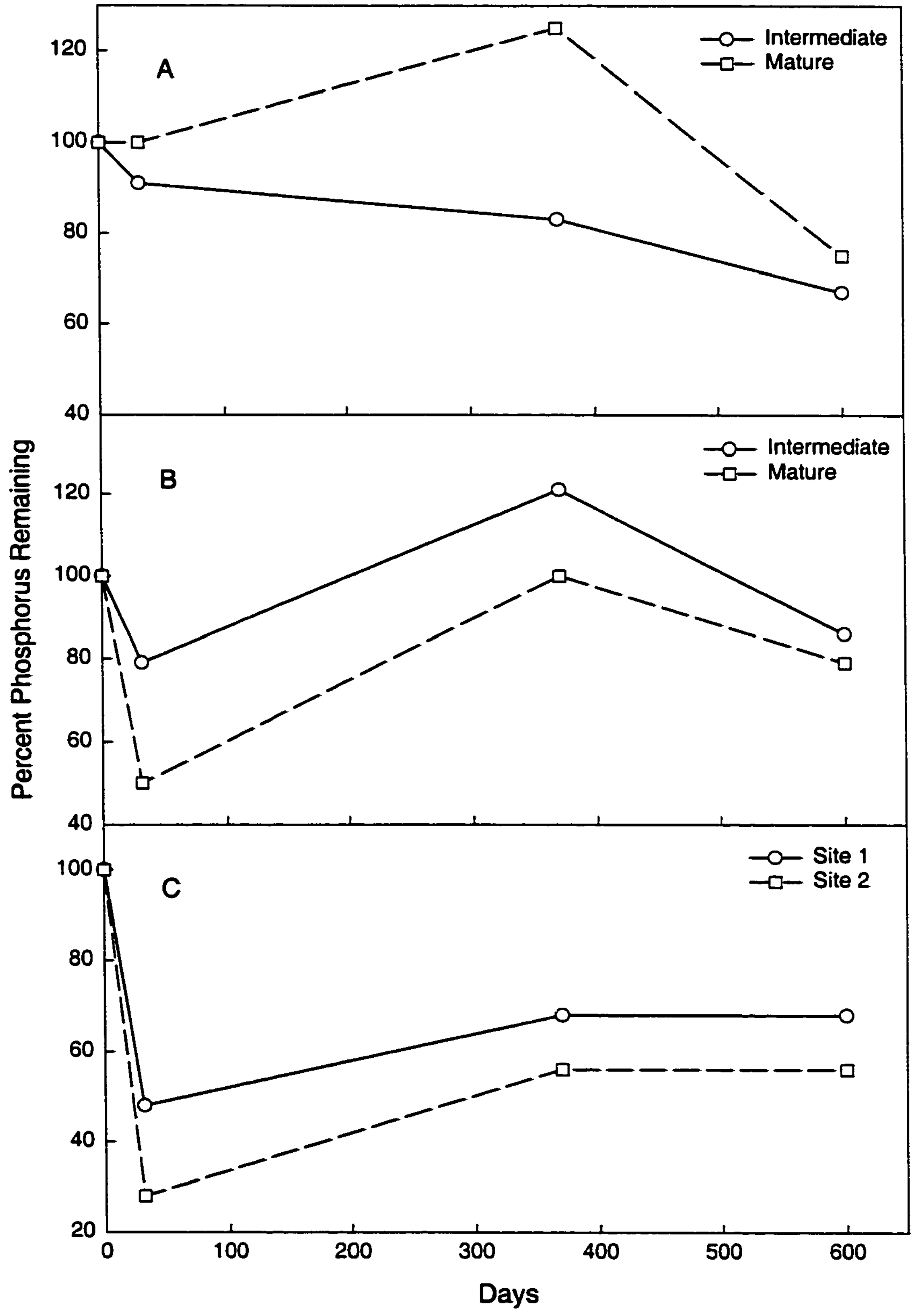

Figure 8. Percent phosphorus remaining in native leaf litter in (A) Alligator River N.W.R., (B) Great Dismal Swamp N.W.R., and (C) Edge Farm restoration.

stand in ARNWR, at the end of the first year of the study, although these trends were short-lived (Figure 8 A and B).

Significant site (F = 9.22, *p* = < 0.0001), time (F = 139.59, p = < 0.0001), and site x time (F = 4.49, *p* = < 0.0001) effects resulted in different patterns of nitrogen behavior in *Chamaecyparis thyoides* leaf litter over time and between sites (Figure 9). All sites experienced nitrogen accumulation over the course of the study and all sites immobilized nitrogen. After 1.6 years, all sites had exhibited net nitrogen immobilization with significantly higher amounts occurring within the sites in the GDSNWR and Site 1 of the restored sites, relative to the remaining sites.

Phosphorus behavior in *Chamaecyparis thyoides* leaf litter decay varied over time and between all the sites (Figure 10). Only Site 1 of the restoration sites exhibited net phosphorus immobilization (122%), but this period was short lived.

Lignin Dynamics

Initial lignin content of native leaf litter could not be statistically tested (n = 1). Qualitative comparisons of initial lignin content within the naturally regenerating and restored Atlantic white cedar wetlands showed similar amounts which ranged from a low of 29.66 % within litter from the GDSNWR to a high of 34.32 % within the restored sites (Table 9). The native litter from the restored sites had a slightly higher lignin content compared to those of the naturally regenerating sites. This may have been attributable to the woody nature (i.e. higher recalcitrant fraction) of standing dead graminoid stems and other aboveground components (relative to leaves) of the old field vegetation present within both sites. After a year of incubation, lignin content exhibited considerable

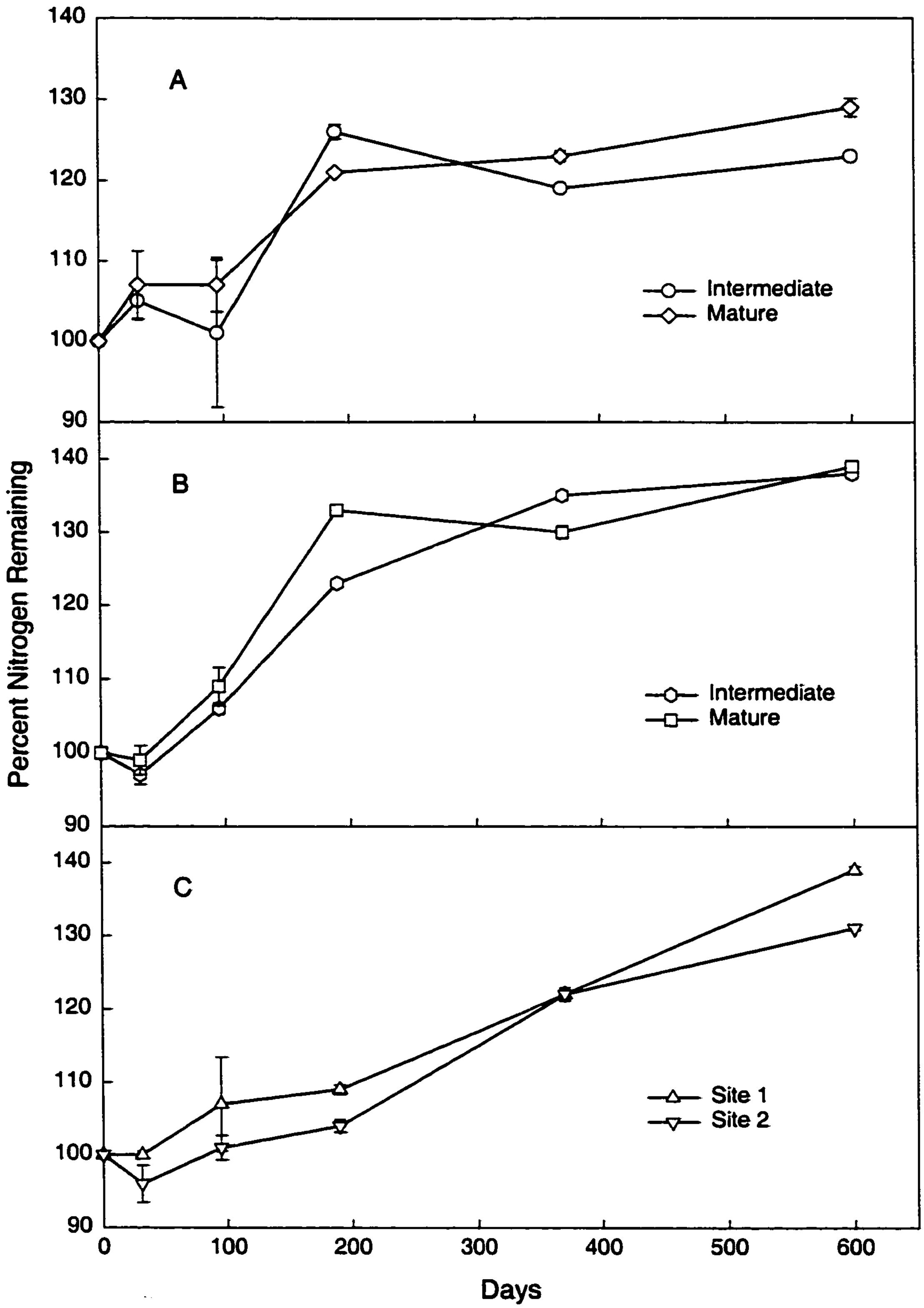

Figure 9. Percent nitrogen remaining in *Chamaecyparis* leaf litter within (A) Alligator River N.W.R., (B) Great Dismal Swamp N.W.R. and (C) Edge Farm restoration. Values represent means with one standard error.

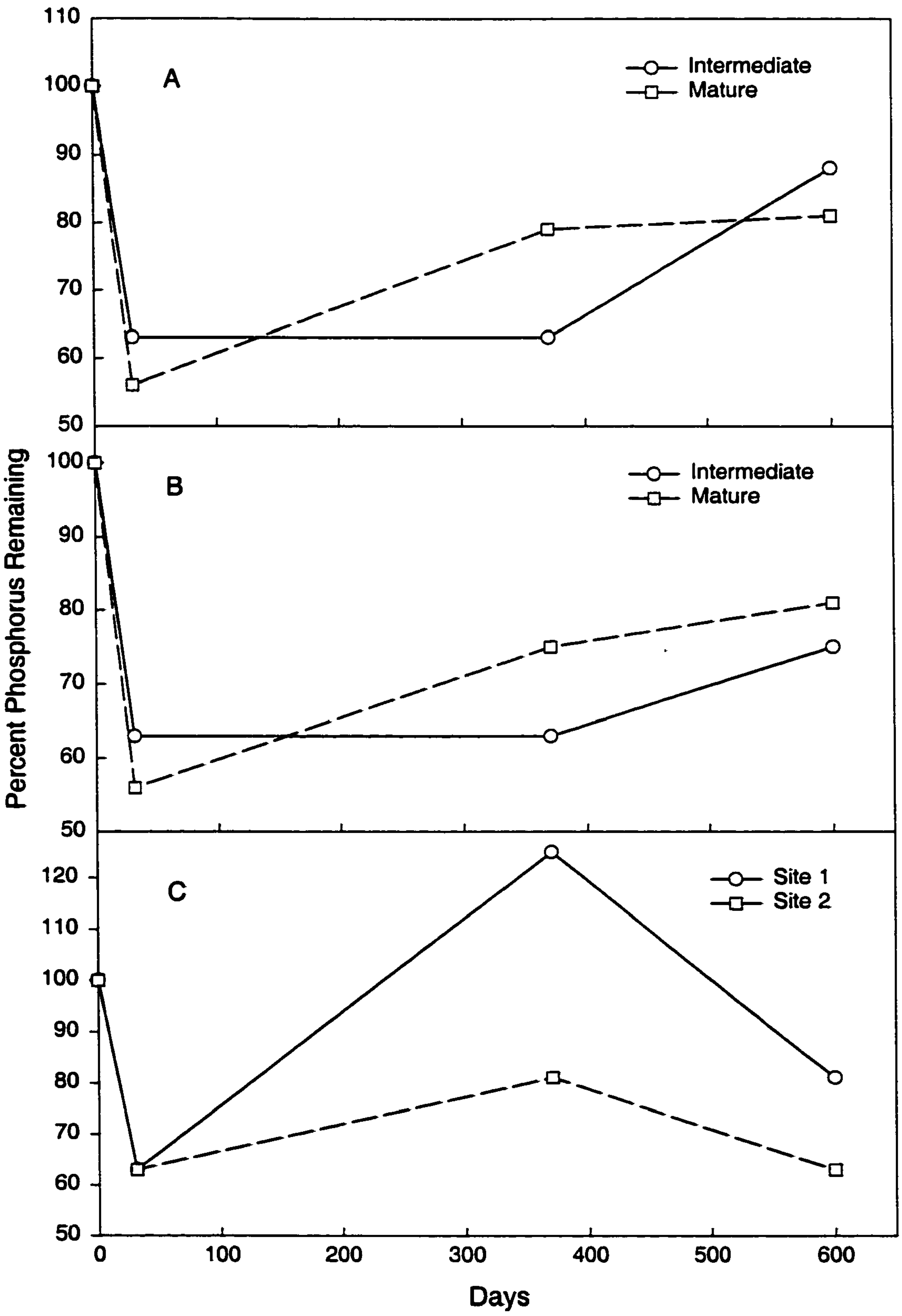

Figure 10. Percent phophorus remaining in *Chamaecyparis* leaf litter in (A) Alligator River N.W.R., (B) Great Dismal Swamp N.W.R. and (C) Edge Farm restoration.

Table 9. Changes in lignin derived indices for initial native litter (0) and after 1.0 years of decay (1.0) for lignin concentration (% L), lignin:nitrogen ratio (L:N), lignin:phophorus ratio (L:P), and nitrogen:phosphorus ratio (N:P). N=1 for all lignin indices.

	%L		L:N		L:P		N:P	
	0	1.0	0	1.0	0	1.0	0	1.0
Alligator River								
Mature	33.06	33.74	32	21	276	225	9	11
Intermediate	33.06	37.24	32	29	276	372	9	13
Dismal Swamp								
Mature	29.66	30.75	38	17	212	220	6	13
Intermediate	29.66	27.02	38	12	212	193	6	13
Edge Farm								
Site 1	34.32	30.66	48	27	137	180	3	7
Site 2	34.32	33.48	48	27	137	239	3	7

variation in remaining litters (Table 9).

Lignin to nitrogen ratios varied markedly between the naturally regenerating and restored sites. After a year, L:N ratios declined. The restored sites exhibited the lowest L:P ratio (137), while sites within the ARNWR had the highest L:P ratio (276). Nitrogen to phosphorus ratios exhibited the same trend.

Initial lignin content of *Chamaecyparis thyoides* litter was markedly higher compared to the native litters from within all sites (Table 10). Lignin content of *Chamaecyparis* litter increased within all sites after one year of incubation in the field. Initial L:N ratio for *Chamaecyparis* litter fell within the range of L:N ratios for the native litters (Tables 9 and 10). Initial L:P ratio for *Chamaecyparis* litter also fell within the range of L:P ratios for all native litters and tended to increase. Initial N:P ratio for *Chamaecyparis* litter fell within the range of N:P ratios for all native litters and after a year of incubation, N:P ratio generally increased (Table 10).

Environmental and Litter Quality Influences on Decay

Relationships between annual decay of *Chamaecyparis* litter and environmental influences resulted in correlations with hydrology ($r = -0.757$, $p = 0.048$), and weaker non-significant correlations with soil pH ($r = 0.506$, $p = 0.241$). With the inclusion of all independent variables, multiple regression explained 63 % of the variation of decomposition of *Chamaecyparis thyoides* litter ($F = 3.34$, $r^2 = 0.625$, $p = 0.140$). While these two variables were not significant, as the first variable selected, hydrology accounted for most of the explained variance ($F = 6.71$, $r^2 = 0.573$, $p = 0.048$).

A series of correlational analyses were performed to establish the potential

Table 10. Changes in lignin derived indices for initial *Chamaecyparis thyoides* litter (0) and after 1.0 years of decay (1.0) for lignin concentration (% L), lignin:nitrogen ratio (L:N), lignin:phophorus ratio (L:P), and nitrogen:phosphorus ratio (N:P). N = 1 for all lignin indices.

	%L		L:N		L:P		N:P	
	0	1.0	0	1.0	0	1.0	0	1.0
Alligator River								
Mature	45.47	50.21	33	30	268	456	8	15
Intermediate	45.47	52.47	33	32	268	524	8	16
Dismal Swamp								
Mature	45.47	49.46	33	28	268	412	8	15
Intermediate	45.47	54.03	33	29	268	540	8	19
Edge Farm								
Site 1	45.47	52.68	33	31	268	263	8	13
Site 2	45.47	52.57	33	31	268	404	8	8

influences litter quality characteristics had on decay dynamics. The variables included nitrogen, phosphorus and lignin content and the various ratios (C:N, L:N, N:P) listed in Tables 7 and 9 respectively. No significant correlations resulted. Initial C:N ratio yielded the highest (r) value ($r = 0.427$, $p = 0.397$), followed by nitrogen content ($r = -0.410$, $p = 0.418$), and phosphorus ($r = 0.239$, $p = 0.647$). With the remaining variables, (r) values tended to decrease (<0.35) while p values tended to increase. Thus suggesting that over the period of decay measured in this part of the study (one year), influences of initial litter quality may not be as important as within site environmental drivers (hydrology) on the decay process. Soil pH was positively correlated with native litter phosphorus ($r = 0.985$, $p = 0.003$).

Long-Term Decay Trends

The exponential decay constants reported in this study are on an annual basis to facilitate comparisons with the majority of values reported for other systems. However, we also wanted to evaluate leaf litter decay within these systems over longer temporal scales. This was done in an effort to determine if trends, apparent over the course of the first year of study, continued throughout the duration (1.6 years) of the study. In terms of mass loss of native leaf litter, the naturally regenerating sites had a greater fraction remaining relative to the restored sites (Table 11). The restored sites exhibited the fastest decay over the course of the study. The reverse was true of *Chamaecyparis* litter decay (Table 12). *Chamaecyparis* decay rates (k) within the young (recent clearcut) and restored sites were significantly lower than the decay rates within the remaining sites.

Table 11. Decay rate [-k (1.6yr^{-1})], coefficient of determination (r^2) and fraction remaining for native litter decay among Atlantic white cedar restored and naturally regenerating sites. All regressions are significant at p = 0.0001. One standard error in parentheses. Different upper case letters indicate significant differences (p = 0.05) between sites.

Site	*k* (1.6yr^{-1})	r^2	Fraction Remaining
Alligator River N.W.R.			
Mature	0.46 (0.03)^{A}	0.95	0.513
Intermediate	0.50 (0.03)^{AB}	0.94	0.498
Dismal Swamp N.W.R.			
Mature	0.51 (0.02)^{AB}	0.97	0.475
Intermediate	0.54 (0.03)^{AB}	0.95	0.472
Edge Farm Restoration			
Site 1	0.60 (0.02)^{B}	0.98	0.369
Site 2	0.56 (0.02)^{AB}	0.98	0.385

Table 12. Decay rate [-k (1.6yr^{-1})], coefficient of determination (r^2) and fraction remaining for *Chamaecyparis thyoides* litter decay among Atlantic white cedar restored and naturally regenerating sites. All regressions are significant at p = 0.0001 One standard error in parentheses. Different upper case letters indicate significant differences (p = *0.05)* between sites.

Site	*k* (1.6yr^{-1})	r^2	Fraction Remaining
Alligator River N.W.R.			
Mature	0.36 (0.01)^{A}	0.98	0.591
Intermediate	0.36 (0.01)^{A}	0.97	0.600
Dismal Swamp N.W.R.			
Mature	0.37 (0.02)^{A}	0.96	0.582
Intermediate	0.33 (0.01)^{AB}	0.96	0.606
Young	0.30 (0.01)^{B}	0.98	0.629
Edge Farm Restoration			
Site 1	0.29 (0.01)^{B}	0.95	0.627
Site 2	0.29 (0.01)^{B}	0.96	0.621

Relationships between *Chamaecyparis* litter decay and environmental parameters

were not tested over the remainder of the study. However, additional correlational analyses were performed to evaluate the potential influences litter quality characteristics exerted on decay dynamics. As before, variables included nitrogen, phosphorus and lignin content and the various ratios (N:C, L:N, L:P) listed in Tables 7 and 9. Native leaf litter decay rates were significantly correlated with nitrogen content ($r = -0.851$, $p = 0.03$) and phosphorus content ($r = 0.864$, $p = 0.026$). Carbon to nitrogen ratio ($r = 0.761$, $p = 0.078$) and lignin content ($r = 0.288$, $p = 0.579$) were not significantly correlated with decay. However, L:N ratio was highly correlated with decay ($r = 0.907$, $p = 0.012$). Litter quality influences on decay dynamics that were not apparent on a short term (1 year) basis, emerged as decay continued over longer temporal scales (> 1 year), thus underscoring the importance of long-term studies on decay dynamics within these and other ecosystems.

DISCUSSION

Decomposition Rates

Despite differences in depth to ambient water tables within the sites, there were no apparent discernable trends of native leaf litter decay within any of the sites over the first year of this study. While *Chamaecyparis* litter decay was strongly correlated with hydrology, too little moisture can limit decay as easily as too much moisture (Bunnell et al. 1977, Heal et al. 1987). Flooded conditions can result in enhanced leaching (Chamie and Richardson 1978), while anaerobic conditions can limit microbial processes. Alternating periods of aerobic and anaerobic conditions can enhance decomposition in natural wetlands (Brinson et al. 1981) and created wetlands (Atkinson and Cairns 2001).

similar to P levels from Maryland stands (Whigham and Richardson 1988). Foliar contents of nitrogen (1.50) and phosphorus (0.20) are the minimum concentrations needed for adequate growth (Epstien 1972). This suggests that the Atlantic white cedar present within these study sites may be nutrient deficient. Nitrogen accumulation patterns in this study were similar to those observed by Day (1982) in the GDSNWR and by Conner and Day (1991) in Louisiana forested wetlands. Immobilization such as this is likely to occur when a nutrient is limiting or when initial nutrient concentrations are low (Maclean and Wein 1978).

Initial C:N ratios ranged from 49 – 64 for native litters within this study. Working within coastal plain swamps of South Carolina, Shure et al. (1986) found that litter decomposition was slower and N immobilization was greater for leaf litter with high initial C:N ratios. Carbon to nitrogen ratios above 30 are representative of the passive fraction in soil organic matter and limit microbial decomposition (Brady and Weil 1996). Microbial immobilization throughout this study reduced the C:N ratio in all sites. Nitrogen is often the most limiting nutrient in flooded soils, whether the flooded soils are in natural wetlands or agricultural wetlands such as rice patties. Nitrogen fixation by blue-green algae is also important in northern bogs and rice cultures, which are often too acidic to support large bacterial populations (Mitsch and Gosselink 2000). Phosphorus is fixed as aluminum and iron phosphates in acid soils and is most bioavailable at slightly acidic to neutral pH (Mitsch and Gosselink 2000).

The patterns of nitrogen and phosphorus change indicate the potential role that decomposing litter might play in the retention of these materials within these wetland sites. An initial decline in P concentrations could be attributed to leaching or microbial metabolism of labile materials. Over the course of the first year of the study, phosphorus concentrations increased following initial losses and nitrogen accumulated throughout the duration of the study. Thus the litter may act as a short term sink for phosphorus (1 yr), and a long-term sink for nitrogen. Whigham et al. (1989) found that the litter layer in freshwater tidal wetlands acted as a short-term sink for both nitrogen and phosphorus. Whereas Chamie and Richardson (1978) and Bayley et al. (1985) found litter of emergent dominated wetlands to act as long-term sinks for nitrogen and phosphorus. Working in a marsh complex in Manitoba, Canada, van der Valk et al. (1991) found that marsh litter with initial lower nitrogen and phosphorus concentrations accumulated more nitrogen and phosphorus than litter with higher initial concentrations.

Lignin levels generally increased over the course of this study and L:N ratios were highly correlated with litter decay at the terminus of the study. Melillo et al. (1982) found that the mass of hardwood litter in the Hubbard Brook Experimental Forest after 1 year was more highly correlated with initial lignin to nitrogen ratios of leaf material than with lignin or nitrogen content alone. Benner et al. (1985) also found the lignin to nitrogen ratio to be a good predictor of biodegradability in litters from the Okefenokee Swamp and a coastal Georgia saltmarsh. During the decomposition process recalcitrant substances are produced which are analyzed as lignin and which often cause an apparent absolute increase in the amount of lignin (Berg and Theander 1984). These recalcitrant ligninlike substances can be derived from aromatic compounds produced during microbial metabolism or from the recondensation of lignin degradation products (Berg et al. 1984). Nitrogen was immobilized throughout the course of this study (ca. 20 months) in all litters and within all sites. Microbial biomass incorporated into the litter matrix or synthesis of nitrogenous compounds in the decomposing litter could have contributed to this nitrogen accretion. The temporal scale of this study may not have been sufficient to document nitrogen mineralization. Following decomposition of red pine needles, Melillo et al. (1989) determined that nitrogen accumulated and reached a maximum (N_{max}) at 22 months of decay. After that phase, a phase of net nitrogen mineralization continued for the next 55 months.

Lignin is probably not degraded in the absences of an available carbohydrate energy source (Berg et al. 1984). In partially decomposed litter, the degradation rate of lignin determines the decay rate of the litter that is turning into soil organic matter (Berg 2000). During this stage, high nitrogen concentrations will have a rate-retarding effect on lignin degradation and thus on the litter (Berg 2000). Benner et al. (1985) evaluated the effect of pH on lignin and lignocellulose degradation in a Georgia saltmarsh and in the Okefenokee Swamp. They determined that rates of the lignin component of lignocellulose were minimally affected within the range of pH 4-8, while mineralization of the polysaccharide component of lignocellulose increased 3 fold with increasing pH. Differences in biodegradability of lignocelluloses were observed with those coming from herbaceous plants being mineralized several times faster than those from woody species.

Benner et al. (1985) determined that organic acids present in Okefenokee Swamp water inhibit microbial degradation of lignocellulose primarily by lowering the ambient pH of the water rather than by other mechanisms such as the binding of extracellular degradative enzymes. Their results indicate that pH selectively influences the mechanism of biodegradation of the polysaccharide component of lignocellulose without substantially affecting the mechanism of lignin degradation and thus functions to partially uncouple lignin and polysaccharide degradation. However, the low pH associated with the naturally regenerating sites in the current study could directly inhibit degradation of polysaccharides that would indirectly decrease the degradability of lignin.

Annual aboveground decomposition rates in the restored sites were comparable to those found within the naturally regenerating sites. However, these findings may be misleading, while decay rates where similar over the course of a year, patterns of increased decay started to emerge over longer temporal scales. As the litter within these sites were beginning to be incorporated into the 02 litter layer (i.e. covered over by new litter etc.), changes in microclimate may have become more conducive to microbial decay. Further long-term studies are required to elucidate aboveground contributions to soil organic matter within these developing ecosystems.

CHAPTER IV

THE INFLUENCE OF LITTER QUALITY AND ENVIRONMENT ON ROOT DECOMPOSITION DYNAMICS IN NATURAL AND RESTORATION SETTINGS

INTRODUCTION

Decomposition of organic matter is a fundamental property within all ecosystems. By influencing soil fertility and nutrient cycling, decomposition is a forcing factor controlling ecosystem structure and function. The size of plant organic matter pools and decomposer activity affect the availability and mobility of mineral nutrients that in turn provide feedbacks on production and decay (Kuenzler et al. 1980). According to Swift et al. (1979), the decomposition of organic matter is regulated by three groups of variables: the decomposer organisms (invertebrates and microorganisms), the chemical composition of the resource (resource quality), and the physical rate determinants (primarily moisture and temperature). The physiological capacities of the bacteria and fungi are the ultimate factors determining the mineralization rates of organic carbon, with temperature and moisture operating at the cellular level as proximate controls (Anderson 1991).

More distal factors come into play and act as rate determinants as the scale increases from the cellular to the ecosystem level, with the macro-climate ultimately setting constraints within which the organism and resource quality factors operate (Anderson 1991). At a global scale, Aerts (1997) suggested that actual evapotranspiration is the best predictor of decay, whereas within a particular climatic region litter chemistry parameters were the best predictors of decay values. Microsite environments are also important in regulating decomposition rates (Day 1995). Decay dynamics on a local level are influenced by site specific factors such as micro-climate, soil texture, microtopography, soil moisture, oxygen availability, pH, and the types of decomposer communities present (Smith 1982, Cornejo et al. 1994).

Substrate quality also regulates rates of decay (Day 1982, Aerts 1997). Root material that is high in recalcitrant carbon fractions such as lignin and low in nitrogen and/or phosphorus, makes a poor substrate for decomposers. Decomposition is generally slower in conifer than temperate deciduous forests (Perry 1994). Tupacz and Day (1990) found slower rates of root decay within an Atlantic white cedar wetland relative to other forested wetland types within the Great Dismal Swamp. Decomposition rates of low-quality tree litters may be predicted from the initial concentration of lignin (Berendse et al. 1987) or the lignin/N (L/N) ratio (Aber and Melillo 1980, Melillo et at. 1982).

Many authors suggest that hydrology is the most significant force in forested wetlands controlling production and turnover of organic matter (Conner et al. 1981, Brinson et al. 1984, Day and Megonigal 1993). Carbon cycling is central to nutrient dynamics and accretion rates in wetlands. Wetlands contain a greater amount of detrital soil carbon per unit surface area than any other ecosystem (Schlesinger 1977). The accumulation of partially decomposed organic matter under anaerobic conditions is central to their development, hydrology, and nutrient status (Moore and Bellemy 1974). This is especially critical in Atlantic white cedar wetlands (Ehrenfeld 1995). Wetland hydrology regulates organic matter decay through abiotic factors (dystrophic conditions) and operates on horizontal scales and vertical scales (Brinson et al. 1981). Aboveground decay may be increased due to moisture availability and oxygen flux while belowground decay may be inhibited due to prolonged periods of soil anoxia.

Waterlogged soils, especially organic soils, develop a thin oxidized layer that is a few millimeters thick. Generally, the surface layer undergoes aerobic respiration, while the remaining areas undergo anaerobic respiration and fermentation (Chamie and Richardson 1978). Anaerobic decomposition is much slower and is done by obligate anaerobic and some facultative anaerobic bacteria. Working in a Michigan peatland, Chamie and Richardson (1978) determined that buried aerial parts consistently decayed at a slower rate than similar tissue exposed at the surface. Prolonged flooding or soil saturation induces anoxic conditions and slows rates of decay (Hackney and de la Cruz 1980, Brinson et al. 1981). Slower rates of decomposition with increasing depth in the soil profile are well documented and generally attributed to anaerobic conditions (Chamie and Richardson 1978, Hackney and de la Cruz 1980, Tupacz and Day 1990). Hydrologic regimes and carbon cycling are tightly coupled mechanisms that either directly or indirectly affect other ecosystem functions. Further investigation of long-term root decomposition dynamics in relation to ecosystem recovery will aid in our understanding of the controls and processes important in creating self-sustaining ecosystems.

The objectives of the current study were to evaluate environmental and substrate quality factors influencing root decomposition within recovering Atlantic white cedar wetlands and to compare those measurements with decay dynamics within restored Atlantic white cedar wetlands.

Regulatory factors influencing belowground decomposition and nutrient cycling were tested by the following hypotheses: (1) roots will decay more slowly in recovering stands relative to restored sites (2) regardless of site type, root litter with high initial litter quality will have faster decay than root litter with low initial quality.

METHODS

Study Design

Within each site, deployment of a standard root substrate (*Chamaecyparis thyoides*) allowed for evaluation of environmental influences (hydroperiod, pH) on decay. The native root decay study incorporated both environmental and litter quality factors. In order to separate the influence of both factors, native root decay and standard root (*Chamaecyparis*) decay were compared within each site and interpreted in relation to differences in litter quality. All decay and environmental measurements were conducted to a depth of 40 cm to incorporate the vertical dimension present in a soil profile.

Statistical Analyses

Initial nitrogen and carbon concentrations of native and *Chamaecyparis* roots were analyzed using one-way ANOVA's. Two way ANOVA (site x time) tested for differences in percent nitrogen, phosphorus and carbon remaining in the litter. Annual means of soil pH (depth combined) and within site (by depth) and depth to water table were analyzed by one-way ANOVA's. The relationships among annual environmental factors (hydroperiod, soil pH), initial chemical composition of the roots and annual decay rates (k) within all sites were examined by correlation analysis. A stepwise multiple regression tested for environmental influences on standard substrate decay across all sites.

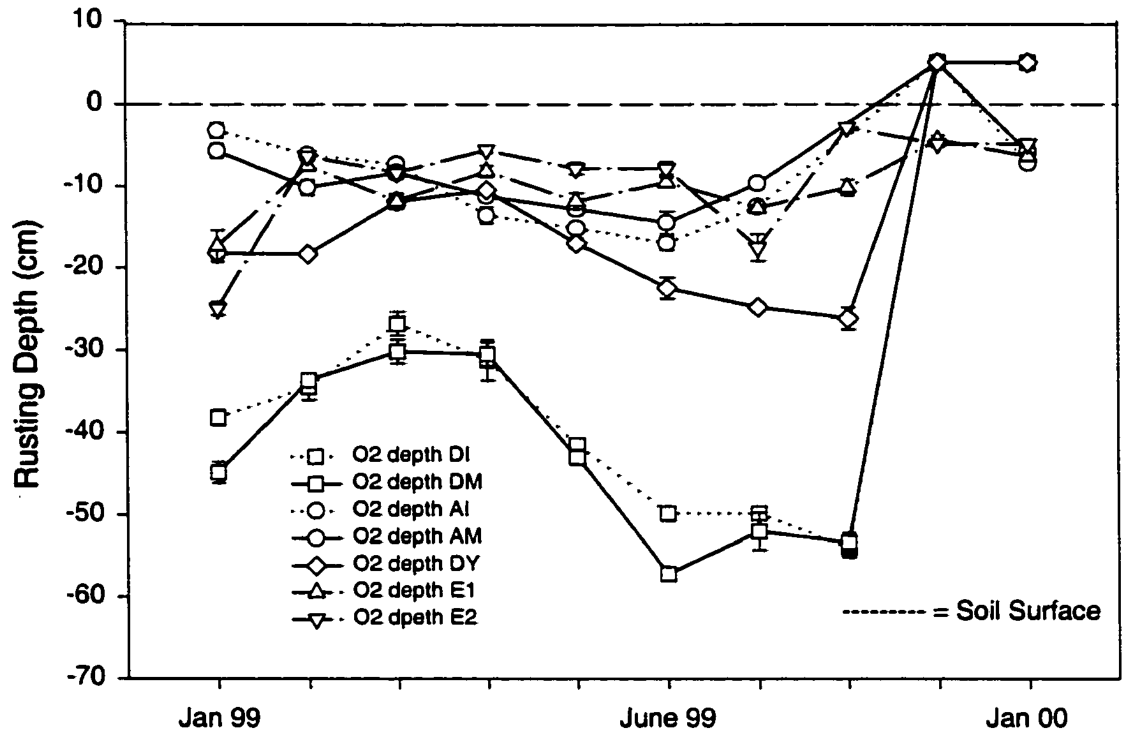

Figure 11. Hydroperiod as indicated by rusting depth on steel rods. Dismal Swamp mature (DM), Dismal Swamp intermediate (DI), Dismal Swamp young (DY), Alligator River mature (AM), Alligator River intermediate (AI), restoration site 1 (E1), restoration site 2 (E2). Values represent means with one standard error.

aged sites within the GDSNWR and all other sites. Site x time interactions (F = 116.49, p <0.001) resulted in differing water tables within sites from January 1999 through August 1999. After August 1999, water levels within all sites were near or at the surface (or ponded) throughout the remainder of the first year of the study.

Significantly greater (F = 271.05, p < 0.001) mean annual soil pH (depth combined) occurred in both restored sites relative to the naturally regenerating Atlantic white cedar sites (Table 13). Few consistent trends in soil pH levels were evident throughout the study except that soil pH within the restored sites was, on average, an order of magnitude higher compared to all other sites. This trend was maintained with

Table 13. Annual means for soil pH, bulk density, volumetric water content, organic matter content and groundwater levels within restored and naturally regenerating Atlantic white cedar wetlands. Alligator River National Wildlife Refuge = (ARNWR), Great Dismal Swamp National Wildlife Refuge = (GDSNWR) and Edge Farm Restoration = (EFR). Groundwater level determined by oxidation depth on steel rods. Different uppercase superscripts indicate significant differences (p = 0.05) between sites (average of depth). Different lowercase superscripts indicate significant differences (p = 0.05) between depths. One standard error in parentheses. An (*) indicates data from Thompson (2001).

	ARNWR		GDSNWR			EFR	
	Mature	Intermediate	Mature	Intermediate	Young	Site 1	Site 2
Soil pH	3.4 (0.01)^{A}	3.3 (0.02)^{A}	3.3 (0.01)^{A}	3.4 (0.01)^{A}	3.4 (0.02)^{A}	4.3 (0.05)^{B}	4.3 (0.05)^{B}
0-10 cm	3.4 (0.03)^{a}	3.2 (0.05)^{a}	3.3 (0.02)^{a}	3.4 (0.04)^{a}	3.4 (0.03)^{a}	4.5 (0.09)^{a}	4.4 (0.13)^{a}
10-20 cm	3.4 (0.01)^{a}	3.3 (0.04)^{a}	3.3 (0.02)^{a}	3.4 (0.02)^{a}	3.4 (0.02)^{a}	4.4 (0.07)^{a}	4.3 (0.09)^{a}
20-30 cm	3.4 (0.02)^{a}	3.3 (0.04)^{a}	3.3 (0.02)^{a}	3.4 (0.01)^{a}	3.3 (0.03)^{a}	4.3 (0.06)^{ab}	4.3 (0.07)^{a}
30-40 cm	3.4 (0.03)^{a}	3.3 (0.02)^{a}	3.3 (0.03)^{a}	3.4 (0.03)^{a}	3.4 (0.02)^{a}	4.1 (0.04)^{b}	4.4 (0.13)^{a}
Bulk Density* (g/cm^{3})	0.084	0.097	0.117	0.163	0.153	0.567	0.705
Volumetric Water* Content (%)	32.6	37.8	33.2	24.2	29.0	35	31
Organic Matter* Content (%)	97.6	97.3	93.2	92.2	92.9	38.6	23.3
Groundwater Level (cm) relative to soil surface	-8.1 (0.9)	-8.5 (0.8)	-33.5 (2.2)	-31.6 (2.6)	-13.9 (1.4)	-9.9 (0.6)	-9.1 (0.9)

depth within the restored sites relative to all the other sites. Other edaphic characteristics varied among the sites (Table 13).

Decomposition Rates

Vertical decay profiles within the stands in ARNWR exhibited similarities in mass loss over time for both native root material and *Chamaecyparis* roots (Figure 12). The trend of decreasing mass loss with increasing depth in the soil profile was not evident within ARNWR (Figure 12).

In contrast, there was a decrease in mass loss with an increase in depth of the soil profile within all sites in the GDSNWR (Figure 13). Mass loss of native roots and *Chamaecyparis* roots were similar across the entire soil profile in both the intermediate and mature stands. Only decay of *Chamaecyparis* roots were evaluated within the young (clear-cut) site. This was done primarily due to the fact that roots within sites would have been in various stages of senescence, which would have made collection and separation of live versus recently senesced material extremely difficult. Evaluating decay dynamics using *Chamaecyparis* roots within the young site allowed for the examination of differences in mass loss under varying hydroperiods within the GDSNWR. Mass loss of native roots and *Chamaecyparis* roots were strikingly different within the restored sites (Figure 14). Mass loss of native roots was substantially faster relative to root standards. Native root decay rates were similar within the naturally regenerating sites of both refuges regardless of site hydrology, but were statistically different from native root decay within the restored sites (Table 14). In general, native root decay within GDSNWR sites tended to decrease with increasing depth in the soil profile. This was not

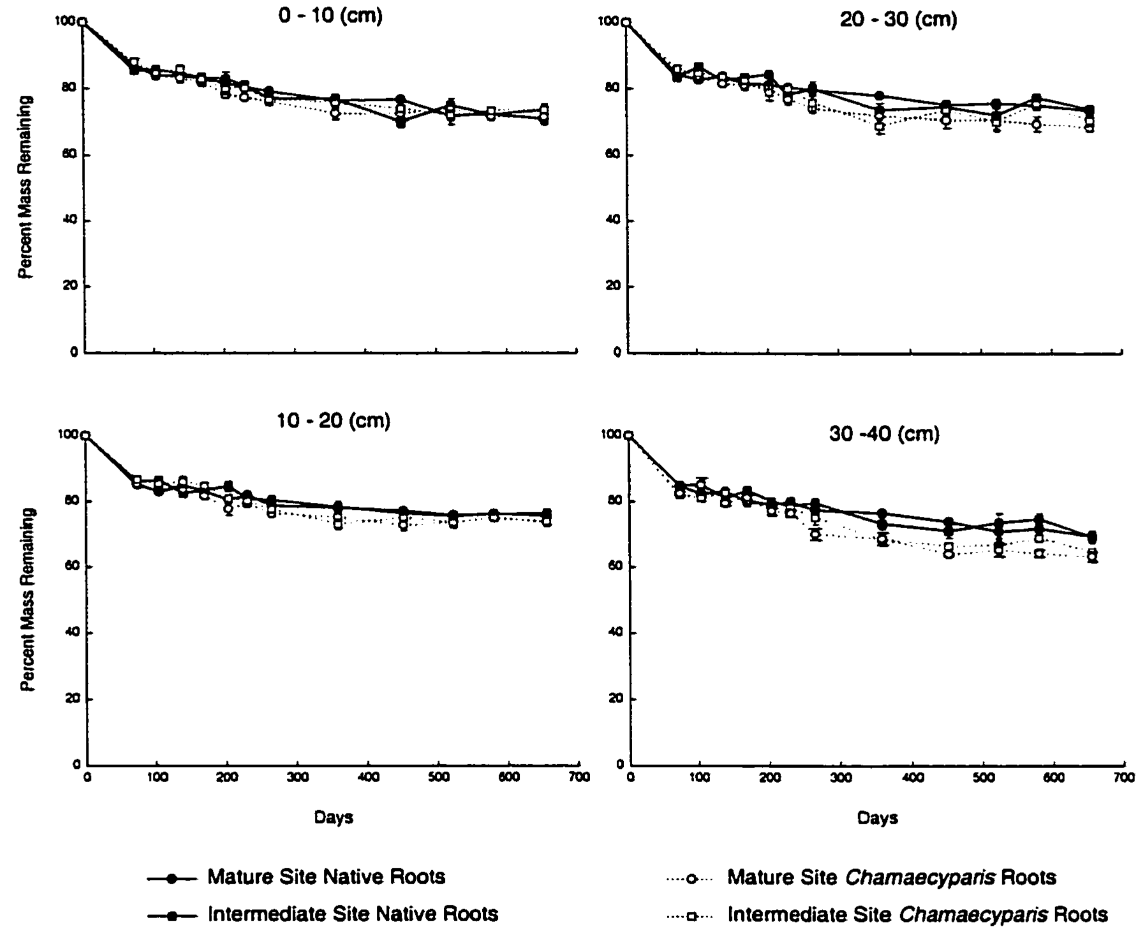

Figure 12. Percent mass remaing for native roots and *Chamaecyparis thyoides* roots within Alligator River National Wildlife Refuge. Values represent means with one standard error.

the case within the sites in the ARNWR where patterns of decay over the soil profile were variable. There were no significant differences in decay coefficients within all of the naturally regenerating sites regardless of individual site differences. Patterns of *Chamaecyparis* root decay over the soil profile were variable and exhibited similar trends relative to native root decay within each site (Table 15).

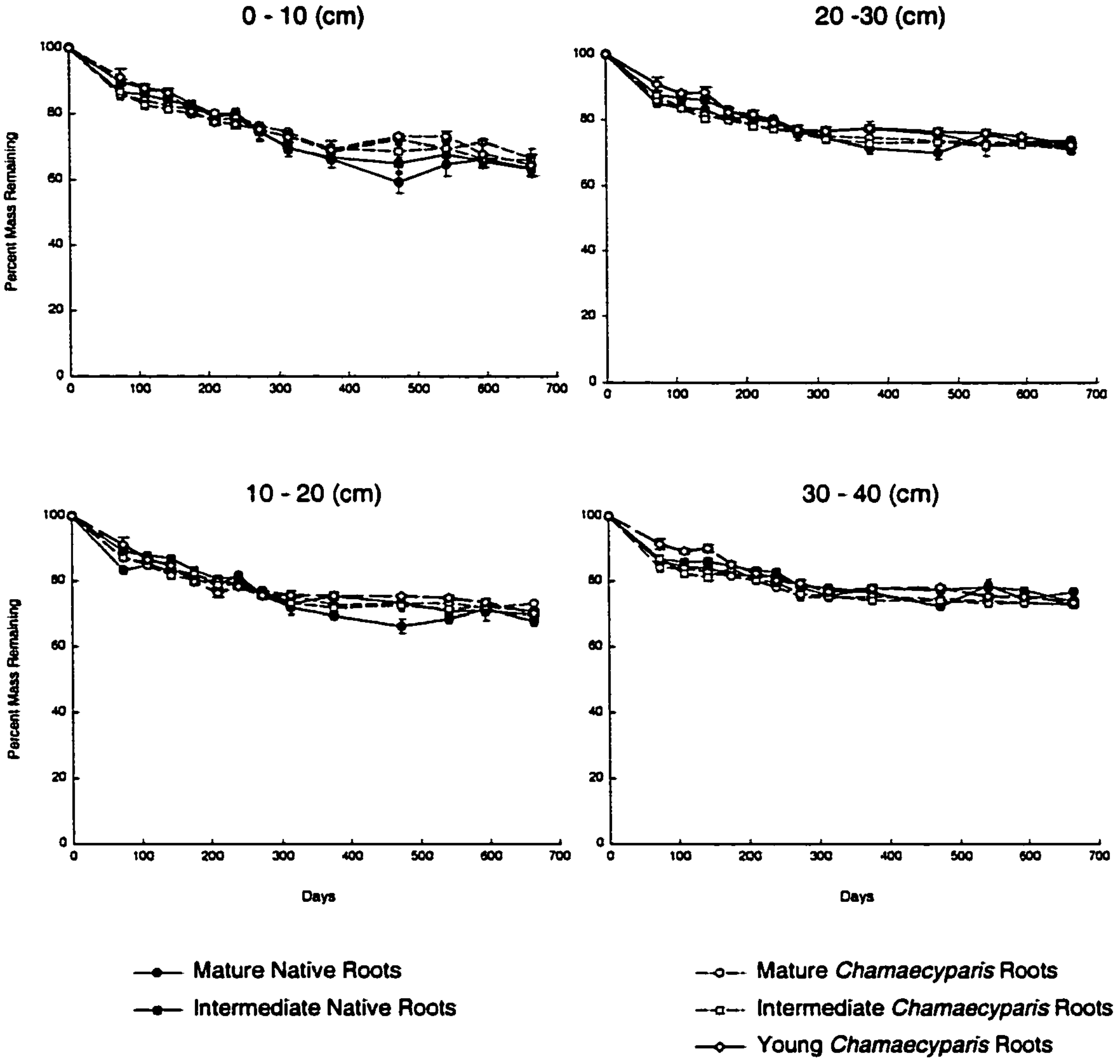

Figure 13. Percent mass remaining for native and *Chamaecyparis thyoides* roots within the Great Dismal Swamp National Wildlife Refuge. Values represent means with one standard error.

Influence of litter quality on decay

One-way ANOVAS between native roots and *Chamaecyparis* roots revealed significant differences for initial nitrogen content (F = 152.97, $p < 0.0001$), initial carbon content (F = 36.89, $p < 0.0001$), and initial C:N ratios (F = 178.51, $p < 0.0001$) (Tables 16 and 17).

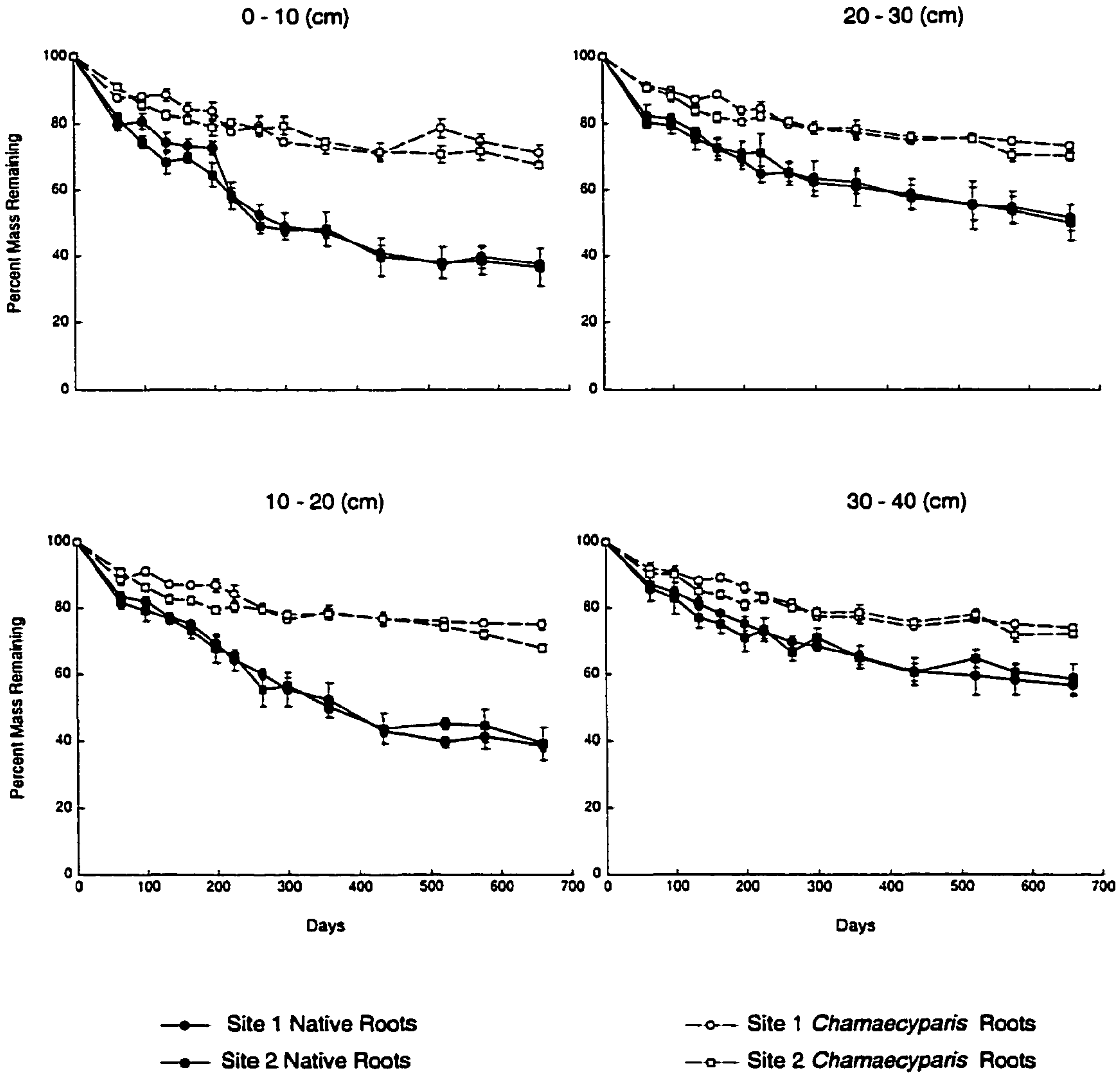

Figure 14. Percent mass loss remianing for native roots and *Chamaecyparis thyoides* roots within the Atlantic white cedar restoration sites. Values represent means with one standard error.

Initial phosphorus content was over twice as high within the restored sites' root litter relative to the naturally regenerating sites, but significant differences could not be statistically tested (n = 1) (Table 16). Initial C:N ratios were significantly higher

Table 14. Decay rate [-k(yr^{-1})] and coefficient of determination (r^2) for native root decay at each depth interval. All regressions are significant at $p = 0.0001$. One standard error in parentheses. Different uppercase letters between rows indicate significant differences ($p = 0.05$) between sites. Different lowercase letters between columns indicate significant differences ($p = 0.05$) between depths.

Site	Depth belowground (cm)							
	0-10		10-20		20-30		30-40	
	k(yr^{-1})	r^2	k(yr^{-1})	r^2	k(yr^{-1})	r^2	k(yr^{-1})	r^2
Alligator River								
Mature	0.34 (0.02)^{Aa}	0.94	0.33 (0.03)^{Aa}	0.91	0.34 (0.03)^{Aa}	0.90	0.36 (0.03)^{Aa}	0.92
Intermediate	0.33 (0.02)^{Aa}	0.94	0.31 (0.03)^{Aa}	0.92	0.35 (0.03)^{Aa}	0.94	0.36 (0.03)^{Aa}	0.94
Great Dismal Swamp								
Mature	0.40 (0.01)^{Aa}	0.98	0.38 (0.02)^{Aab}	0.96	0.36 (0.02)^{Aab}	0.96	0.32 (0.02)^{Ab}	0.94
Intermediate	0.39 (0.01)^{Aa}	0.99	0.33 (0.01)^{Ab}	0.97	0.33 (0.02)^{Aab}	0.95	0.30 (0.02)^{Ab}	0.95
Edge Farm Restoration								
Site 1	0.80 (0.03)^{Ba}	0.98	0.69 (0.01)^{Bb}	0.99	0.60 (0.03)^{Bb}	0.97	0.49 (0.01)^{Bc}	0.98
Site 2	0.86 (0.03)^{Ba}	0.98	0.72 (0.01)^{Bb}	0.99	0.58 (0.03)^{Bc}	0.96	0.51 (0.03)^{Bc}	0.96

Table 15. Decay rate [-*k*(yr^{-1})] and coefficient of determination (r^2) for *Chamaecyparis thyoides* root decay at each depth interval. All regressions are significant at *p* = 0.0001. One standard error in parentheses. Different uppercase letters between rows indicate significant differences (*p* = 0.05) between sites. Different lowercase letters between columns indicate significant differences (*p* = 0.05) between depths.

Site	Depth belowground (cm)							
	0-10		10-20		20-30		30-40	
	k(yr^{-1})	r^2	*k*(yr^{-1})	r^2	*k*(yr^{-1})	r^2	*k*(yr^{-1})	r^2
Alligator River								
Mature	0.39 (0.02)^{Aa}	0.96	0.37 (0.03)^{Aa}	0.94	0.40 (0.02)^{Aa}	0.96	0.45 (0.03)^{Aa}	0.96
Intermediate	0.35 (0.02)^{Aa}	0.96	0.35 (0.02)^{Aa}	0.97	0.39 (0.02)^{Aa}	0.97	0.42 (0.03)^{Aa}	0.95
Great Dismal Swamp								
Mature	0.38 (0.02)^{Aa}	0.97	0.35 (0.02)^{Aa}	0.97	0.36 (0.02)^{ABa}	0.95	0.35 (0.02)^{ABa}	0.94
Intermediate	0.39 (0.02)^{Aa}	0.97	0.37 (0.02)^{Aa}	0.97	0.37 (0.02)^{ABa}	0.96	0.35 (0.02)^{ABa}	0.95
Young	0.38 (0.01)^{Aa}	0.99	0.35 (0.02)^{Aab}	0.96	0.31 (0.01)^{AB}	0.97	0.29 (0.01)^{Bb}	0.98
Edge Farm Restoration								
Site 1	0.35 (0.01)^{Aa}	0.97	0.29 (0.01)^{Aab}	0.96	0.29 (0.01)^{Bab}	0.98	0.28 (0.01)^{Bb}	0.98
Site 2	0.34 (0.03)^{Aa}	0.95	0.33 (0.02)^{Aa}	0.94	0.31 (0.02)^{ABa}	0.94	0.30 (0.02)^{Ba}	0.96

Table 16. Initial native root litter quality indices (0) and after 1.8 years of decay (1.8) for nitrogen concentration (%N), phosphorus concentration (%P), carbon concentration (%C), and carbon:nitrogen ratio (C:N). One standard error in parentheses. Differences between lowercase superscripts indicate sgnificant (p =0.05) differences. N=3 for all indices except initial % P where n=1.

	%N		%P		%C		C:N	
	0	1.8	0	1.8	0	1.8	0	1.8
Alligator River								
Mature	0.52 (0.01)^{a}	0.56 (0.01)^{a}	0.11	0.04 (0.01)^{a}	49.59 (0.42)^{a}	51.37 (0.08)^{a}	96	90
Intermediate	0.52 (0.01)^{a}	0.63 (0.02)^{a}	0.13	0.04 (0.001)^{a}	49.59 (0.42)^{a}	50.23 (0.62)^{a}	96	81
Dismal Swamp								
Mature	0.84 (0.01)^{b}	1.05 (0.09)^{b}	0.09	0.04 (0.001)^{a}	47.51 (0.21)^{b}	50.85 (0.29)^{a}	57	49
Intermediate	0.84 (0.01)^{b}	0.96 (0.03)^{b}	0.12	0.05 (0.001)^{a}	47.51 (0.21)^{b}	49.84 (0.06)^{a}	57	50
Edge Farm								
Site 1	0.78 (0.03)^{b}	1.13 (0.04)^{b}	0.26	0.13 (0.01)^{b}	45.41 (0.22)^{c}	46.11 (0.30)^{b}	58	41
Site 2	0.78 (0.03)^{b}	1.27 (0.08)^{c}	0.26	0.15 (0.01)^{b}	45.41 (0.22)^{c}	45.41 (0.55)^{b}	58	36

Table 17. Initial *Chamaecyparis thyoides* root litter quality indices (0) and after 1.8 years of decay (1.8) for nitrogen concentration (%N), phosphorus concentration (%P), carbon concentration (%C), and carbon:nitrogen ratio (C:N). One standard error in parentheses. Different lowercase superscripts between rows indicate significant (p = 0.05) differences. N=3 for all indices except initial % P where n=1.

	%N		%P		%C		C:N	
	0	1.8	0	1.8	0	1.8	0	1.8
Alligator River								
Mature	0.38 (0.01)	0.52 (0.06)^{a}	0.13	0.05 (0.001)^{a}	45.83 (0.33)	49.51 (0.19)^{a}	121	98
Intermediate	0.38 (0.01)	0.52 (0.05)^{a}	0.13	0.04 (0.003)^{a}	45.83 (0.33)	49.63 (0.06)^{a}	121	98
Dismal Swamp								
Mature	0.38 (0.01)	0.54 (0.01)^{ab}	0.13	0.04 (0.003)^{a}	45.83 (0.33)	49.45 (0.09)^{a}	121	92
Intermediate	0.38 (0.01)	0.60 (0.02)^{ab}	0.13	0.05 (0.001)^{a}	45.83 (0.33)	49.41 (0.15)^{a}	121	82
Edge Farm								
Site 1	0.38 (0.01)	0.60 (0.01)^{ab}	0.13	0.11 (0.001)^{b}	45.83 (0.33)	47.26 (0.34)^{b}	121	80
Site 2	0.38 (0.01)	0.75 (0.05)^{b}	0.13	0.12 (0.01)^{b}	45.83 (0.33)	45.62 (0.10)^{b}	121	62

in the ARNWR relative to sites in the GDSNWR and the restored sites.

Chamaecyparis root litter had the lowest initial nitrogen content and accumulated nitrogen within all sites (Table 17). Initial phosphorus content of *Chamaecyparis* roots was similar to that of the native roots harvested from the naturally regenerating sites, and twice as low as the initial phosphorus content of native roots from the restored sites (Tables 16 and 17). Initial carbon content was similar between native roots of the restored sites and *Chamaecyparis* roots, but was significantly lower relative to the naturally regenerating sites.

Significant site (F = 126.41, p <0.0001) and time (F = 17.52, p <0.0001), but not site x time (F = 1.04, p = 0.4314), effects resulted in different patterns of nitrogen behavior in native root litter within the sites in ARNWR compared to all other sites (Figure 15). Net phosphorus immobilization potentials were nonexistent with no increases above 100 percent phosphorus remaining (Figure 16). Significant site (F = 137.14, p <0.0001), time (F = 56.95, p <0.0001), and site x time (F = 2.11, p = 0.0494) effects resulted in different patterns of phosphorus behavior in native roots within the naturally regenerating sites and restored sites.

Significant site (F = 6.77, p <0.0001), time (F = 26.20, p <0.0001), and site x time (F = 2.16, p = 0.0114) effects resulted in different patterns of nitrogen behavior in *Chamaecyparis* roots over time and between sites (Figure 17). Significant site (F = 29.86, p <0.0001), time (F = 9.10, p = 0.0006), and site x time (F = 8.94, p <0.0001) effects resulted in different patterns of phosphorus behavior in *Chamaecyparis* roots over time and between sites (Figure 18).

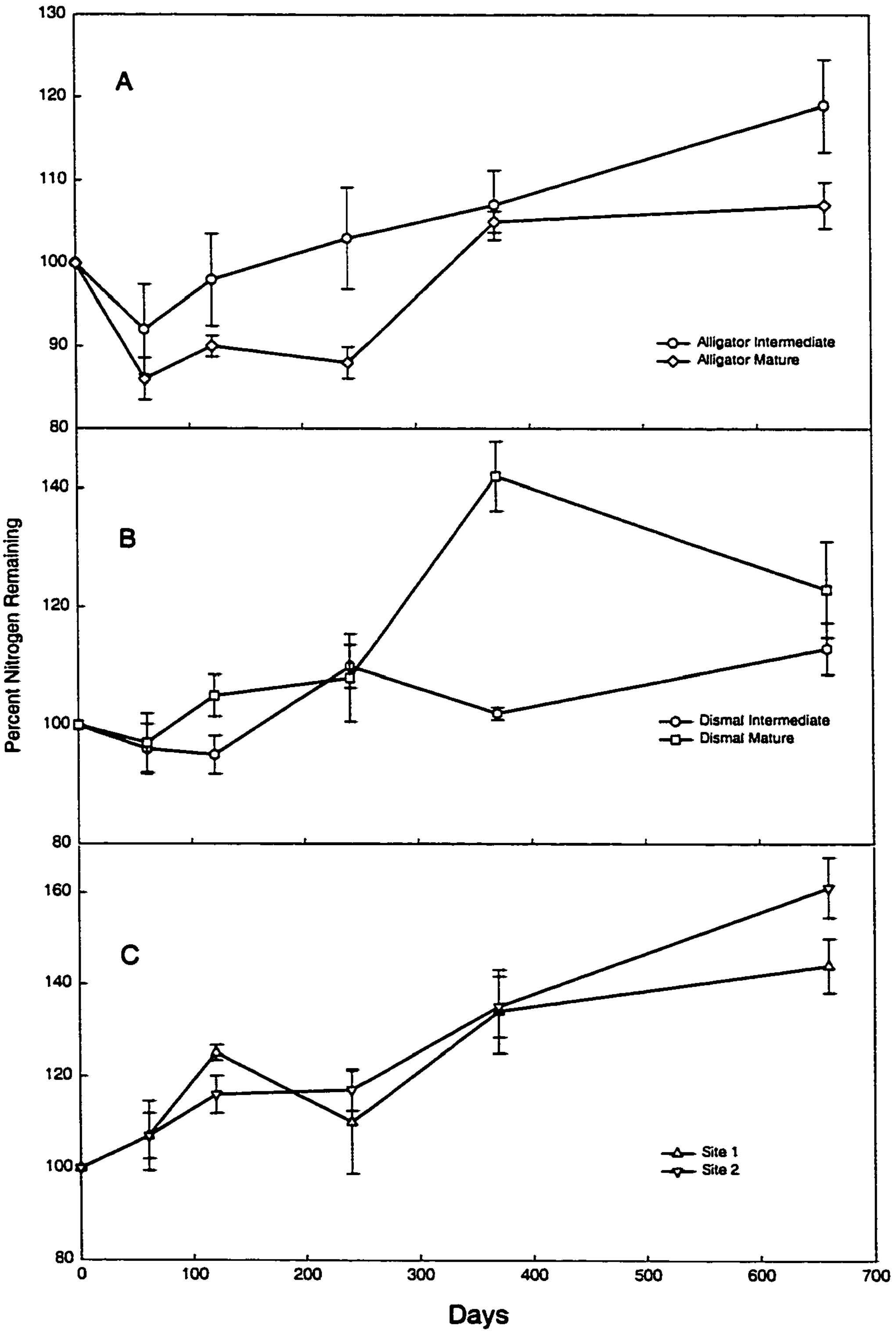

Figure 15. Percent nitrogen remaining from native roots in (A) Alligator River N.W.R., (B) Great Dismal Swamp N.W.R., and (C) Edge Farm restoration. Values represent means with one standard error.

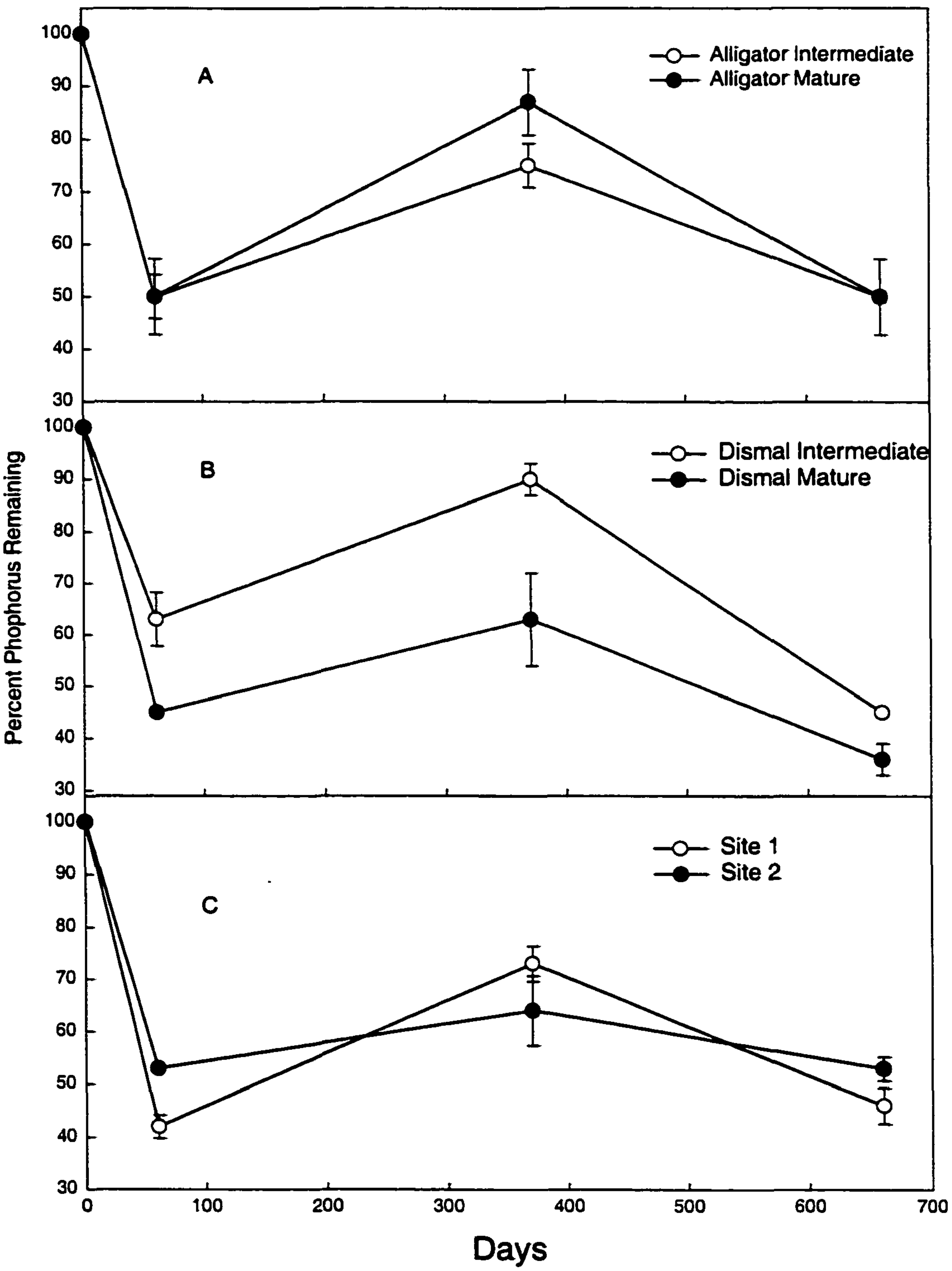

Figure 16. Percent phosphorus reamining in native roots from (A) Alligator River N.W.R., (B) Great Dismal Swamp N.W.R., and (C) Edge Farm Resotration. Values represent means with one standard error.

Initial lignin content of native root material could not be statistically tested (n = 1). Qualitative comparisons of initial lignin content within the naturally regenerating sites ranged from 52.39 % to 56.38 % (Table 18). In contrast, initial lignin content of native root materials from the restored sites was around 37.03 %. These dramatic differences can be attributed to the increased recalcitrant tissues common in woody roots compared to herbaceous root material. Following a year of incubation, lignin content increased in all roots. Significant differences in initial nitrogen content (Table 16) resulted in substantial differences in L:N ratios between the refuges and the restored sites (Table 18). The L:P ratio of native roots within the restored sites were substantially lower relative to all of the naturally recovering sites. Nitrogen to phosphorus ratios exhibited similar trends.

Initial lignin content and L:nutrient ratios of *Chamaecyparis* roots were variable compared to native root material within the naturally regenerating sites and the native roots from the restored sites (Tables 18 and 19).

Environmental influences on decay

Relationships between annual decay of *Chamaecyparis* roots and environmental influences resulted in strong correlations with soil pH ($r = -0.607$, $p = 0.0006$) and weaker non-significant correlations with hydrology ($r = 0.205$, $p = 0.294$). However, with the inclusion of all independent variables, multiple regression only explained 37% of the variation in decomposition of *Chamaecyparis thyoides* roots ($F = 7.41$, $r^2 = 0.37$, $p = 0.003$). As the first variable selected, soil pH accounted for most of the explained

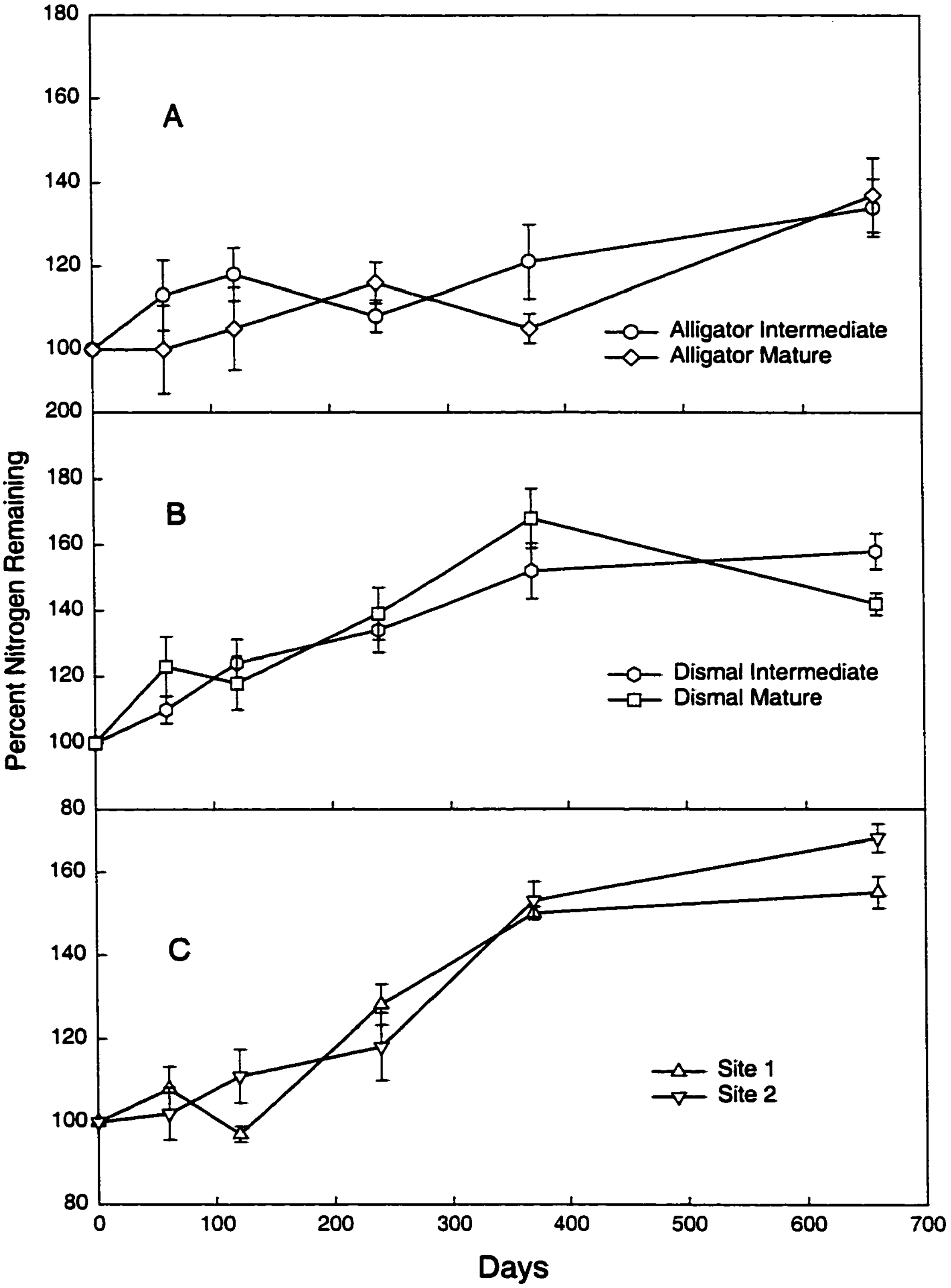

Figure 17. Percent nitrogen remaining in *Chamaecyparis* roots in (A) Alligator River N.W.R., (B) Great Dismal Swamp N.W.R., and (C) Edge Farm Restoration. Values represent means with one stadard error.

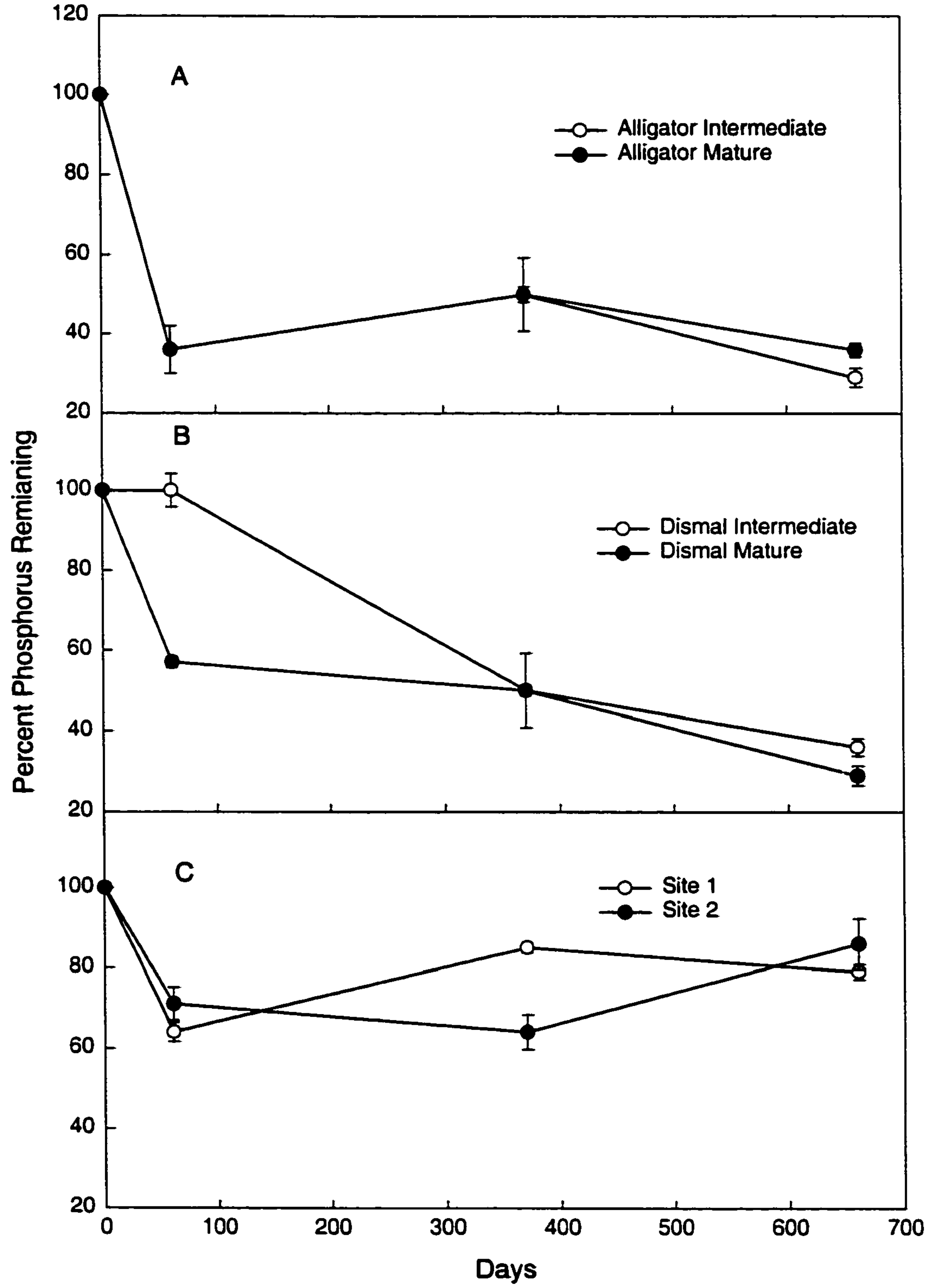

Figure 18. Percent phosphorus remaining in *Chamaecyparis* roots in (A) Alligator River N.W.R., (B) Great Dismal Swamp N.W.R., and (C) Edge Farm restoration. Values represent means with one standard error.

Table 18. Changes in lignin derived indices for initial native root litter (0) and after 1.0 years of decay (1.0) for lignin concentration (% L), lignin:nitrogen ratio (L:N), lignin:phophorus ratio (L:P), and nitrogen:phosphorus ratio (N:P). N=1 for all lignin indices.

	%L		L:N		L:P		N:P	
	0	1.0	0	1.0	0	1.0	0	1.0
Alligator River								
Mature	56.38	67.66	108	123	512	967	5	8
Intermediate	53.04	67.31	102	122	408	1121	4	9
Dismal Swamp								
Mature	55.78	65.80	66	55	619	940	9	17
Intermediate	52.39	69.69	62	80	437	697	7	9
Edge Farm								
Site 1	37.03	39.89	47	38	142	209	3	6
Site 2	37.03	41.86	47	39	142	233	3	6

Table 19. Changes in lignin derived indices for initial *Chamaecyparis thyoides* root litter (0) and after 1.0 years of decay (1.0) for lignin concentration (% L), lignin:nitrogen ratio (L:N), lignin:phophorus ratio (L:P), and nitrogen:phosphorus ratio N:P. N = 1 for all lignin indices.

	%L		L:N		L:P		N:P	
	0	1.0	0	1.0	0	1.0	0	1.0
Alligator River								
Mature	42.67	50.84	112	127	328	726	3	6
Intermediate	42.67	53.30	112	113	328	904	3	7
Dismal Swamp								
Mature	42.67	49.20	112	76	328	702	3	9
Intermediate	42.67	50.11	112	86	328	716	3	8
Edge Farm								
Site 1	42.67	54.52	112	96	328	454	3	6
Site 2	42.67	53.67	112	93	328	447	3	5

variance ($F = 15.23$, $r^2 = 0.369$, $p = 0.0006$). Addition of hydrologic variables did not result in improvements. The level of resolution allowed by the multiple regression technique could not identify specific depth related effects. Despite significant differences in groundwater levels across the sites, *Chamaecyparis thyoides* decay (Table 13) was generally similar across all sites. A direct gradient analysis examining annual decay rates (depth combined) of *Chamaecyparis* roots along a gradient of ambient water tables found no relationship ($F = 0.07$, $r^2 = 0.014$, $p = 0.795$) between the two variables.

Litter Quality Influences on Decay

A series of correlation 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 (C:N, L:N, N:P) listed in Tables 17 and 18. Initial nitrogen content was weakly correlated with decay ($r = 0.327$, $p = 0.117$). Conversely, all other variables were strongly correlated with decay. Phosphorus content was positively correlated with decay ($r = 0.866$, $p < 0.0001$). Carbon to nitrogen ratio was negatively correlated with decay ($r = -0.451$, $p = 0.0269$), as was lignin ($r = -0.870$, $p < 0.0001$), L:N ratio ($r = -0.659$, $p = 0.0005$) and N:P ratio ($r = -0.588$, $p = 0.0025$). Among all sites, high lignin content coupled with low phosphorus and L:N ratios corresponded with low decay. Soil pH was positively correlated with native root phosphorus levels ($r = 0.983$, $p = 0.0004$).

Differences in litter quality between woody and herbaceous roots produced different patterns of mass, nitrogen, and phosphorus loss when decomposing in the same site. *Chamaecyparis* roots (lower nitrogen, lower phosphorus, and higher lignin content) buried in the restored sites next to native roots showed slower decay and greater phosphorus and nitrogen retention.

Long-term Decay Trends

The exponential decay constants reported in this study are on an annual basis because they are comparable with the majority of values reported for other systems. However, we also wanted to evaluate root decay within these systems over longer temporal scales (Tables 20 and 21). This was done in an effort to determine if trends, apparent over the course of the first year of study, continued throughout the duration (1.8 years) of the study. While decay rates decreased in all sites, the trends in native root decay did not change within the recovering and restored sites (Table 14). The restored sites exhibited the fastest decay over the course of the study. Decay rates of *Chamaecyparis* roots were similar to the one year decay rates, although all rates were lower (Table 21).

Table 20. Decay rate [$-k(1.8yr^{-1})$] and coefficient of determination (r^2) for native root decay at each depth interval. All regressions are significant at $p = 0.0001$. One standard error in parentheses. Different uppercase letters between rows indicate significant differences ($p = 0.05$) between sites. Different lowercase letters between columns indicate significant differences ($p = 0.05$) between depths.

Site	Depth belowground (cm)							
	0-10		10-20		20-30		30-40	
	$k(yr^{-1})$	r^2	$k(yr^{-1})$	r^2	$k(yr^{-1})$	r^2	$k(yr^{-1})$	r^2
Alligator River								
Mature	$0.23\ (0.01)^{Aa}$	0.92	$0.21\ (0.02)^{Aa}$	0.86	$0.22\ (0.02)^{Aa}$	0.87	$0.25\ (0.02)^{Aa}$	0.91
Intermediate	$0.23\ (0.02)^{Aa}$	0.91	$0.20\ (0.02)^{Aa}$	0.88	$0.22\ (0.02)^{Aa}$	0.88	$0.24\ (0.02)^{Aa}$	0.90
Great Dismal Swamp								
Mature	$0.31\ (0.02)^{Aa}$	0.94	$0.27\ (0.02)^{Aab}$	0.92	$0.24\ (0.02)^{Aab}$	0.87	$0.21\ (0.02)^{Ab}$	0.87
Intermediate	$0.30\ (0.01)^{Aa}$	0.95	$0.25\ (0.01)^{Ab}$	0.94	$0.23\ (0.01)^{Aab}$	0.92	$0.20\ (0.01)^{Ab}$	0.89
Edge Farm Restoration								
Site 1	$0.66\ (0.03)^{Ba}$	0.96	$0.61\ (0.02)^{Ba}$	0.98	$0.45\ (0.03)^{Bb}$	0.94	$0.38\ (0.02)^{Bb}$	0.96
Site 2	$0.69\ (0.03)^{Ba}$	0.96	$0.59\ (0.01)^{Ba}$	0.97	$0.45\ (0.02)^{Bb}$	0.95	$0.37\ (0.02)^{Bb}$	0.92

Table 21. Decay rate [-*k*(1.8yr^{-1})] and coefficient of determination (r^2) for *Chamaecyparis thyoides* root decay at each depth interval. All regressions are significant at $p = 0.0001$. One standard error in parentheses. Different uppercase letters between rows indicate significant differences ($p = 0.05$) between sites. Different lowercase letters between columns indicate significant differences ($p = 0.05$) between depths.

Site	Depth belowground (cm)							
	0-10		10-20		20-30		30-40	
	k(yr^{-1})	r^2	*k*(yr^{-1})	r^2	*k*(yr^{-1})	r^2	*k*(yr^{-1})	r^2
Alligator River								
Mature	0.25 (0.02)^{Aa}	0.89	0.23 (0.02)^{Aa}	0.87	0.27 (0.02)^{Aa}	0.91	0.32 (0.02)^{Aa}	0.93
Intermediate	0.23 (0.02)^{Aa}	0.91	0.22 (0.02)^{Aa}	0.89	0.25 (0.02)^{Aa}	0.89	0.29 (0.02)^{Aa}	0.92
Great Dismal Swamp								
Mature	0.26 (0.02)^{Aa}	0.92	0.24 (0.02)^{Aa}	0.90	0.24 (0.02)^{Aa}	0.88	0.23 (0.02)^{ABa}	0.88
Intermediate	0.28 (0.02)^{Aa}	0.93	0.25 (0.02)^{Aa}	0.91	0.25 (0.02)^{Aa}	0.89	0.23 (0.02)^{ABa}	0.89
Young	0.27 (0.01)^{Aa}	0.93	0.24 (0.02)^{Aa}	0.90	0.22 (0.01)^{Aa}	0.91	0.21 (0.01)^{Ba}	0.93
Edge Farm Restoration								
Site 1	0.24 (0.02)^{Aa}	0.90	0.21 (0.01)^{Aa}	0.92	0.21 (0.01)^{Aa}	0.94	0.21 (0.01)^{Ba}	0.94
Site 2	0.26 (0.01)^{Aa}	0.93	0.24 (0.01)^{Aa}	0.92	0.23 (0.01)^{Aa}	0.93	0.22 (0.01)^{Ba}	0.92

DISCUSSION

Environmental Influences on Root Decay

Patterns of root decay over the soil profile were variable within each site. Within the GDSNWR sites and the restored sites, decreases in root decay were expected in response to increased depth and degree of saturation. Studies examining belowground decay, while incorporating a depth component in saturated soils, have demonstrated this diminishing effect (Hackney and de la Cruz 1980, Tupacz and Day 1990). Other studies have found no depth effect or relationship with soil redox potential (Hackney 1987, Blum 1993).

Decay of native and *Chamaecyparis* roots in ARNWR varied with depth, but not in a predictable manner. The highest rates of decay were found within the lowest depth interval in the soil profile, which was saturated over the course of this study. Continuously flooded and stagnant systems tend to be low in nutrients and oxygen deficient. Low oxygen levels inhibit decomposition and retard nutrient uptake due to poor aeration in the rooting zone (Schlesinger 1978). Ransom and Smeck (1986) determined that reduced soil conditions reflected the availability of inorganic electron donors and acceptors (including but not limited to O_2) and organic matter as opposed to the degree of soil saturation. According to Melillo et al. (1989), the presence of easily degradable carbohydrates can enhance the rate of degradation of complex carbohydrates such as lignin.

Enhanced decay within these sites under saturated soil conditions may be indicative of greater microbial activity responding to greater cometabolite availability and might explain why decay of native and *Chamaecyparis* roots within ARNWR sites does not decrease directly with increasing depth in the soil profile. Methanogenisis was found to occur at both sites within ARNWR and did not occur within the GDSNWR. Lower amounts of methane flux were recorded at the restored sites. In the Atlantic white cedar sites examined in this study, it took between six to eight months before methanogen activity was detected on decomposing substrates. Increased leaching could also have occurred within the sites at ARNWR as they exhibited the highest water tables over the course of the study.

Hydrologic differences among sites did not influence *Chamaecyparis* root decay even though the frequency and duration of saturation within the rooting zone differed, creating greater periods of oxic soil conditions within the intermediate and mature-aged stands in the GDSNWR. In a study experimentally mimicking hydroperiods typical of seasonally saturated soils, Neckles and Neill (1994) found no differences in belowground decay. However, native and *Chamaecyparis* root decay decreased with increasing depth in the soil profile across all other sites, similar to other woody root decay in wetland systems (Day et al. 1989, Tupacz and Day 1990).

According to Taylor et al. (1991), woody litter is actually more sensitive to microenvironmental differences than herbaceous litter. Excess moisture inhibits fungal activity important for lignin degradation (Fahey et al. 1988) and fragmentation of bark (Harmon and Hua 1991). Tissue fragmentation, either through fungal activity, live root activity or faunal activity, can stimulate decay in woody roots (Day et al. 1989, Harmon and Hua 1991). Increased fungal activity under drier, less anoxic conditions should have contributed to greater decay within sites in the GDSNWR, but did not. Day et al. (1989)

found similar rates of decay in bald cypress roots under contrasting hydroperiods. This evidence, coupled with the lack of correlation between *Chamaecyparis* root decay and hydrology, suggests that litter quality exerts a strong controlling factor regulating decay within the naturally regenerating Atlantic white cedar wetlands.

Patterns of soil pH with increasing depth in the vertical soil profile did not behave in a predictable manner. In all recovering sites, soil pH remained constant as the degree of saturation increased. In the restored sites, soil pH tended to decrease with increasing soil saturation. A consequence of flooding previously drained soils is that carbonic acid can form as a result of CO_2 build up and lead to a decrease in pH. The opposite can occur in peat soils where pH increases as a result of the reduction of ferric iron hydroxides (Mitsch and Gosselink 2000). The spatial soil pH dynamics within the recovering sites were virtually identical. Despite seasonal differences in ambient water tables, the extremely acidic conditions were maintained within these sites. Peat soils often remain acidic during submergence through the slow oxidation of sulfur compounds near the surface, producing sulfuric acid, and the production of humic acids and selective cation exchange by sphagnum mosses (Mitsch and Gosselink 2000). Other studies working in Atlantic white cedar wetlands have found an increasing pH with decreasing water table levels (Day 1982, Tupacz and Day 1990).

Soil pH levels along the recovering sites were 10 times more acidic compared to the restoration sites. The range of pH values measured in the recovering sites (3.1 to 3.4) were generally lower than most estimates including 3.55 to 4.01 in New Jersey (Zhu and Ehrenfeld 1999), 4.95 and 4.26 in Rhode Island (Golet and Lowry 1987), 5.34 in Maryland (Whigham and Richardson 1988), 4.8 to 5.0 in Mississippi (Eleuterius and Jones 1972), and 6.6 to 7.5 in Florida (Collins et al. 1964). They were similar to soil pH levels (3.4) that Bandle and Day (1985) found within an Atlantic white cedar stand in the GDSNWR. Working in Rhode Island, Golet and Lowery (1987) determined that *C. thyoides* maximum growth rates were highest at sites with a pH above 4.0. This would suggest that *Chamaecyparis* growth in the recovering sites may be inhibited by low soil pH relative to the restored sites.

Root Decay and Nutrient Dynamics

Plant nutrient status and carbon allocation patterns have a profound influence on the chemical composition and physical structure of litter types (Swift et al. 1979). The types of carbon available in the litter substrate, such as cellulose and lignin, which vary in quantity and degradability, also regulate decay rates (Day 1982, Berendse et al. 1987).

Decomposing root material (native/standard) within all sites immobilized nitrogen over the course of the study. Nitrogen dynamics within decaying litter exhibit a phase of leaching, followed by a period of nutrient accumulation, and terminate with a phase of net release (mineralization) (Melillo et al. 1989). These dynamics can be tentatively extended to phosphorus. Accumulation of nitrogen greater than twice 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 ratio drops 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).

nitrogen limited decay and may serve as an important mechanism for conserving nitrogen in these nutrient limited systems.

Nutrient concentrations and availability in wetlands are influenced by soil and groundwater acidity. Nitrogen and phosphorus availability is greatly affected by the acidic conditions found in peat soils common in Atlantic white cedar wetlands. Lucas and Davis (1961) evaluated the relationship between nutrient availability and pH in organic soils and determined that organic soils with a pH above 5.0 usually contain over 2% total nitrogen, but when the pH drops below 4.0 the total nitrogen content is typically less than one percent. The total nitrogen in the soil and the effect of pH on decomposers influence nitrogen release and availability. Highly acidic soils typically have poor microbial activity, low soil nitrogen, and an unfavorable carbon to nitrogen ratio that may limit plant growth (Lucas and Davis 1961). The initial nitrogen content of litter is generally considered a good predictor of decay rates, especially in similar habitats (Stump and Binkley 1989). Results of the current study seem to contradict these findings. Native roots and *Chamaecyparis* root decay under the same environmental conditions contradict the idea that initial nitrogen content can predict decay rates. Within each naturally regenerating Atlantic white cedar stand, *Chamaecyparis* roots that had a lower initial nitrogen content decayed at similar rates relative to native roots.

Phosphorus concentrations in soil water of natural peatlands are low (Paavilainen and Paivanen 1995). A very acidic peat soil often contains as little as 0.01 % phosphorus. Strongly acidic soil conditions tend to limit phosphorus availability for plant uptake (Day 1982). When the pH drops below 5.5, phosphorus availability is reduced due to increased solubility of iron and aluminum (Lucas and Davis 1961). In native roots phosphorus exhibited an initial leaching phase, with subsequent peaks of accumulation, followed by a decrease in remaining phosphorus. In standard roots, phosphorus was rapidly mineralized and susceptible to leaching. It has been suggested that belowground phosphorus cycles may lack an immobilization interval resulting from a predominance of unavailable forms of phosphorus in soils (Seastedt 1988).

Litter with high initial lignin content and lignin to nitrogen ratio are often associated with low decay (Berg et al. 1984, Melillo et al. 1982). These generalities are supported by my results. Native roots within the naturally regenerating stands and *Chamaecyparis* roots had high initial levels of lignin and L:N ratios relative to the native roots from the restored sites. Additionally, phosphorus was twice as high in native roots (and highly correlated with decay) in the restored sites compared to the naturally regenerating sites and *Chamaecyparis* roots. Seastedt (1988) determined that N:P ratios above 10 can impose phosphorus limitations on decomposers. Nitrogen to phosphorus ratios were lowest (3) for the native roots in the restored sites, relative to the native roots from the naturally regenerating sites.

Significant differences in native root decay coefficients occurred between restoration sites and the naturally regenerating Atlantic white cedar sites. This was expected as herbaceous roots tend to have lower lignin content and higher labile fractions relative to woody tissues. Native root decomposition rates in this study were highly correlated with lignin concentration and L:N ratios, which are assumed to be higher in the roots within the naturally regenerating sites due to greater densities of woody species (Benner et al. 1985).

The results of the current study suggest that decay of Atlantic white cedar roots appears to be strongly regulated by litter quality factors. Studies that neglect the potentially confounding effects of litter quality and site environmental drivers may result in erroneous interpretation of data. The influence of litter quality on decay is complex and may not rest solely on one pivotal factor such as initial lignin content and could be further complicated by integrative site effects. Studies that evaluate decay of native material among a variety of sites without adequate controls may be missing a more complex picture.

CHAPTER V

CONCLUSIONS

Recent interest in the management and restoration of Atlantic white cedar wetlands has resulted in numerous studies examining various aspects of ecosystem structure and function (Shear and Summerville 1999). Few studies have examined aboveground decay dynamics within these forested wetlands (Day 1982, Yates and Day 1983, Ehrenfeld 1995). Additionally, due to the limitations of studying belowground decay dynamics in natural settings, very few data regarding root decay processes are available for Atlantic white cedar ecosystems (Tupacz and Day 1990). Understanding above and belowground decay processes in developing Atlantic white cedar wetlands allows for more complete assessments of soil organic matter accrual and carbon storage functions in this community type. It is estimated leaf and root litter contribute over 80% of the annual increment of soil organic matter in Atlantic white cedar wetlands (Megonigal and Day 1988). Decomposition of this litter material plays a significant role in soil organic matter aggradation, an ecosystem process considered to be crucial for the long-term self-maintenance of this wetland type.

This study examined the regulatory control that litter quality and environmental influences impose on above and belowground decay dynamics and was unique in that a chronosequence of age classes was incorporated into the design. Considerable insight into Atlantic white cedar development, at the ecosystem level, can be revealed through chronosequence studies. Examination of above and belowground decay processes revealed similar rates of leaf litter decay and root decay within differing age classes along the chronosequence. In all naturally regenerating stands, leaf litter decomposed at faster rates than did roots. This result was expected as differences in litter quality between leaf litter and roots and differences in microclimates often result in increased decay at the soil surface relative to belowground. Vertical gradients found within a soil profile, such as environment, litter quality, root production and root mortality, all contribute to an added dimension of complexity that is absent in aboveground decay studies. In contrast, root decay within the 0 –20 cm depth interval exhibited faster decay rates than native leaf litter within the restored sites. This was unexpected because native leaf litter within the restored sites had comparable nitrogen and phosphorus levels and slightly lower levels of lignin compared to native roots. The differences in decay rates may be partly explained by environmental differences found within the leaf litter layer and root/soil matrix.

Root material was live at collection while leaf litter was senescent. The leaf material may have previously lost a greater proportion of water soluble organics and cellulose that are rapidly metabolized or leached during early decay. Decomposition processes in the restoration sites'soils have greater access to soil resources, such as moisture and nutrients, than on the soil surface. Standard leaf litter within the restored sites and young (recent clear-cut) exhibited the slowest decay rates relative to the forested regenerating sites. The microclimate at the soil surface within the restoration sites and young site was dramatically different compared to the closed canopied naturally regenerating sites. Working in a coastal dune environment, Conn (1994) found lower rates of leaf litter decay compared to root decay within the same dune complex. Decay patterns of native material within the restored sites increased significantly over longer temporal scales relative to the naturally regenerating sites, while *Chamaecyparis* leaf litter decomposed slower within these sites compared to the other sites. These emerging patterns suggest that litter fall from Atlantic white cedar within these sites has the potential to contribute greater amounts to soil organic matter pools while extant vegetation will be rapidly mineralized with increased time in the litter layer. The need for further examination of long-term aboveground decomposition patterns within these developing systems is warranted.

Nutrient dynamics were similar within all sites and between above and belowground materials. Nitrogen accumulated in all litters while phosphorus was released. In nutrient poor ecosystems, mechanisms exist to prevent nutrient losses, such as slower decay rates and greater immobilization of nutrients (Barbour et al. 1999). 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). Additionally, at least in early to mid stage development, nutrient outflows should decrease and production rates should increase (Vitousek and Reiners 1975). This was not the case in the current study. Across all age classes and in restoration settings, nitrogen was immobilized and continued to accumulate, while phosphorus was rapidly leached, accumulated over the first year, then was mineralized over the course of the study. Paradigms of ecosystem development based on upland systems may not apply to wetlands where hydrology is a primary driver of vegetation dynamics (Mitsch and Gosselink 2000).

Aboveground litters accumulated nitrogen to nearly twice their original levels, while root nitrogen accumulations were more modest. Aboveground litters potentially have more exogenous sources of nitrogen available via throughfall, cyanobacteria, diazotrophs and fugal hyphae. Nitrogen immobilization in aboveground litter is influenced by hyphal bridges that translocate nitrogen from the soil to the litter (Harmon and Hua 1991).

Rodgers (2001) found substantial differences in belowground allocation patterns between the naturally regenerating sites and restoration sites suggesting that root contributions to soil organic matter pools are substantially less in restoration settings. This finding coupled with the results of my study would imply that not only is root production less within restored sites, but these roots are decomposing at significantly faster rates compared to the naturally regenerating sites. In these restored sites, a simple shift from a herbaceous dominated community to one dominated by woody species may not be enough to substantially increase belowground contributions of roots to accumulating soil organic matter pools. Colonization and subsequent domination by species other than Atlantic white cedar within these sites could have deleterious consequences for carbon sequestration and accrual which are critical to ecosystem function and self-maintenance of this wetland type.

To date, the planted Atlantic white cedar in the restored sites have been decimated by herbivory, only 25% of the original planted stock remain, and the site is being colonized by *Acer rubrum*, *Nyssa spp.*, and *Taxodium distichum* (Steve Martin, U.S.A.C.O.E., Norfolk Disrtict, personal communication). Tupacz and Day (1990) determined that roots of Atlantic white cedar decomposed more slowly than those of *Taxodium distichum*, *Acer rubrum*, and *Nyssa sylvatica* var. *biflora*. Thus it would appear that these sites are currently not following a trajectory of ecosystem recovery in terms of successional development and above and belowground decay processes.

Management Implications

Laderman (1989) stated that planting Atlantic white cedar has proven to be so difficult that natural regeneration is preferred in areas where opportunities exist. However, restoration of this wetland type through planting new sites will be critical to reversing the trends of range wide habitat destruction. Reversing the trend of Atlantic white cedar habitat loss will require forging partnerships between governmental and non-governmental organizations as well as private and public entities. The results of this study suggest that decay rates of Atlantic white cedar leaf litter and root material in the restored sites are equal to and in some cases lower than the decay rates determined for the naturally regenerating stands.

Based on the results of this study, it also appears that decay dynamics of Atlantic white cedar are strongly regulated by litter quality factors rather than environmental conditions within sites. This would suggest that these restoration sites could achieve similar contributions of leaf litter and root litter to accumulating soil organic matter pools, if Atlantic white cedar are planted at densities that more closely emulate seedling densities found in natural settings. Continued long-term study of these and similar restoration sites are needed to provide greater insight into appropriate recovery models for various wetland functions of Atlantic white cedar.

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APPENDIX

DECAY DYNAMICS IN A RESTORATION SETTING AT POCOSIN LAKES NATIONAL WILDLIFE REFUGE

INTRODUCTION

Atlantic white cedar has been the most valuable timber species on the Albemarle-Pamlico peninsula since the mid-1970s. Elaborate networks of roads, canals and ditches were constructed to provide direct access to the pure, dense stands (Laderman 1989). Alligator River and Pocosin Lakes National Wildlife Refuges were established in this region over the past two decades in part to conserve and manage the areas unique wetlands, including Atlantic white cedar forests (Bryant 1999). They currently contain over 10,000 acres of Atlantic white cedar clearcuts and scattered disjunct remnants of Atlantic white cedar stands (Eagle 1999). The absence of post-harvest forest management coupled with poor logging practices and hydrologic modifications have resulted in poor Atlantic white cedar regeneration in many areas (Eagle 1999).

The primary objectives of these refuges are the preservation and restoration of unique habitats, and restoration of Atlantic white cedar habitat is a priority in Refuge management practices (Bryant 1999). While there are many recent studies examining various aspects of Atlantic white cedar restoration (see Shear and Summerville 1999), there are no studies documenting decay processes occurring in Atlantic white cedar restoration settings. Soil organic matter accumulation and sequestration are regarded as critical components to ecosystem function and self-maintenance of these wetlands.

The objectives of this study were to quantify aboveground and belowground decomposition rates within a restoration setting.

METHODS

The current study was conducted within a restoration effort of a former Atlantic white cedar wetland. The stand was located off of F2 road and was approximately 3 km south of Lake Phelps within Pocosin Lakes National Wildlife Refuge. The stand was planted with Atlantic white cedar seedlings during the fall of 1998. The site had burned two years prior to planting, and was colonized by bracken fern (*Pteridium aquilinum* (L.) Kuhn.), an unidentified *Solidago spp.* and barnyard grass (*Echinochloa crusgalli* (L.)). Atlantic white cedar seedlings were the dominant woody species on site. The site is on acidic organic soils which are ombrotrophic, and classified as Typic Haplosaprists (National Soil Survey Center (2000). Within site comparison of *Chamaecyparis thyoides* leaf and root decay with native leaf and root decay demonstrated litter quality influences under similar environmental conditions. Depth of ambient water table was determined by depth of rusting on steel rods, and soil pH was evaluated over a 0 – 40 cm soil profile.

RESULTS

Native leaf litter exhibited greater initial mass loss relative to *Chamaecyparis* litter mass loss and maintained this trend throughout the year (Figure 19). Native decay rates were over twice as fast compared to *Chamaecyparis* litter, with time to reach 1 percent mass remaining also doubled for standard litter (Table 22). T-tests between native leaf litter and *Chamaecyparis* leaf litter revealed significant differences ($p = 0.05$)

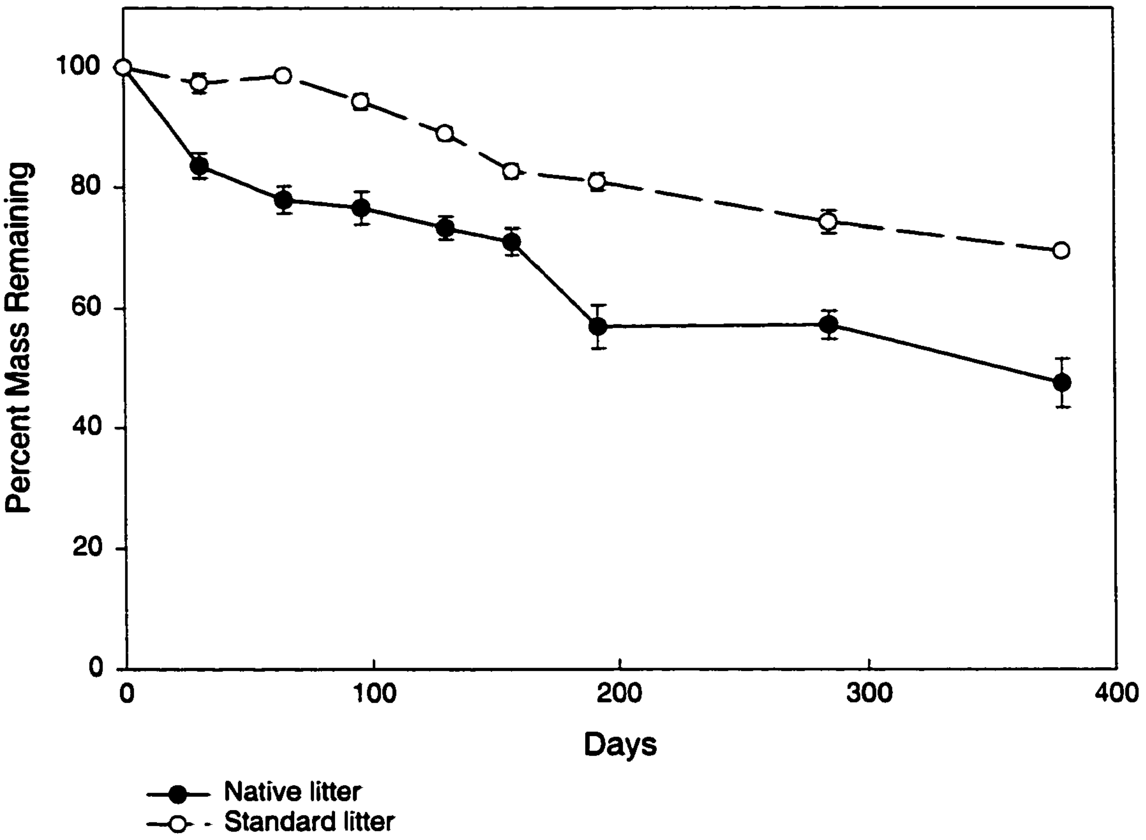

Figure 19. Percent mass remaining for native and *Chamaecyparis thyoides* leaf litter at Pocosin Lakes National Wildlife Refuge. Values represent means with one standard error.

between decay rates (Table 22).

Native roots exhibited greater mass loss over time relative to *Chamaecyparis* roots (Figure 20). There was a trend of decreasing mass loss with increasing depth of the vertical soil profile for both native and standard roots (Figure 20). Native root decay rates were more than doubled in the 0 - 10 cm depth interval and nearly doubled in the 10 –20 cm depth interval relative to standard roots (Figure 20). Across all depth intervals, *t*-tests revealed significant differences ($p = 0.05$) between native root decay and

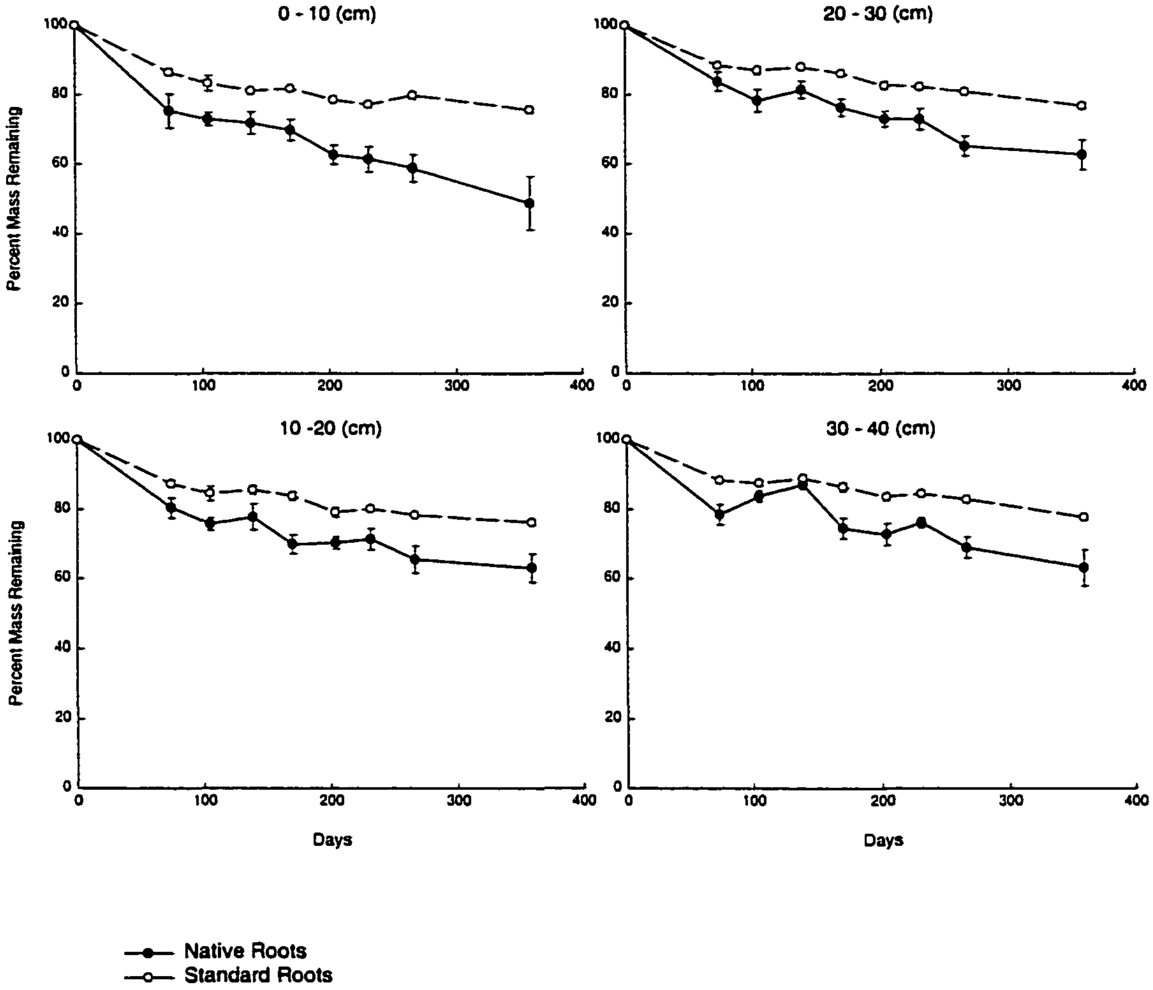

Figure 20. Percent mass remaining of native and *Chamaecyparis thyoides* root litter at Pocosin Lakes National Wildlife Refuge. Values represent means with one standard error.

Chamaecyparis root decay (Table 22).

Soil pH averaged around 3.5, and there was little temporal or spatial variation throughout the study (Figure 21). Depth of water table as indicated by oxidation depth on steel rods varied seasonally throughout the study (Figure 22).

Table 22. Decay rate constants [-*k*(yr^{-1})], coefficient of determiniation (r^2), time to reach 1% mass remaining ($t_{0.01}$), and percent mass remaining after 370 days of decay (%M). All regressions are significant at $p = 0.0001$.

Litter Type	Depth Class	*k*	SE	r^2	$t_{0.01}$ (yr)	Final % Mass
Leaf						
Native		0.79	0.05	0.96	5.82	47.50
Standard		0.36	0.07	0.98	12.79	69.54
Root						
Native						
	0-10 (cm)	0.78	0.03	0.98	5.82	48.76
	10-20 (cm)	0.57	0.04	0.95	8.07	62.97
	20-30 (cm)	0.54	0.02	0.97	8.52	62.59
	30-40 (cm)	0.50	0.03	0.95	9.21	63.06
Standard						
	0-10 (cm)	0.36	0.03	0.93	12.79	75.64
	10-20 (cm)	0.34	0.02	0.95	13.54	76.14
	20-30 (cm)	0.30	0.01	0.96	15.35	76.60
	30-40 (cm)	0.28	0.02	0.96	16.44	77.63

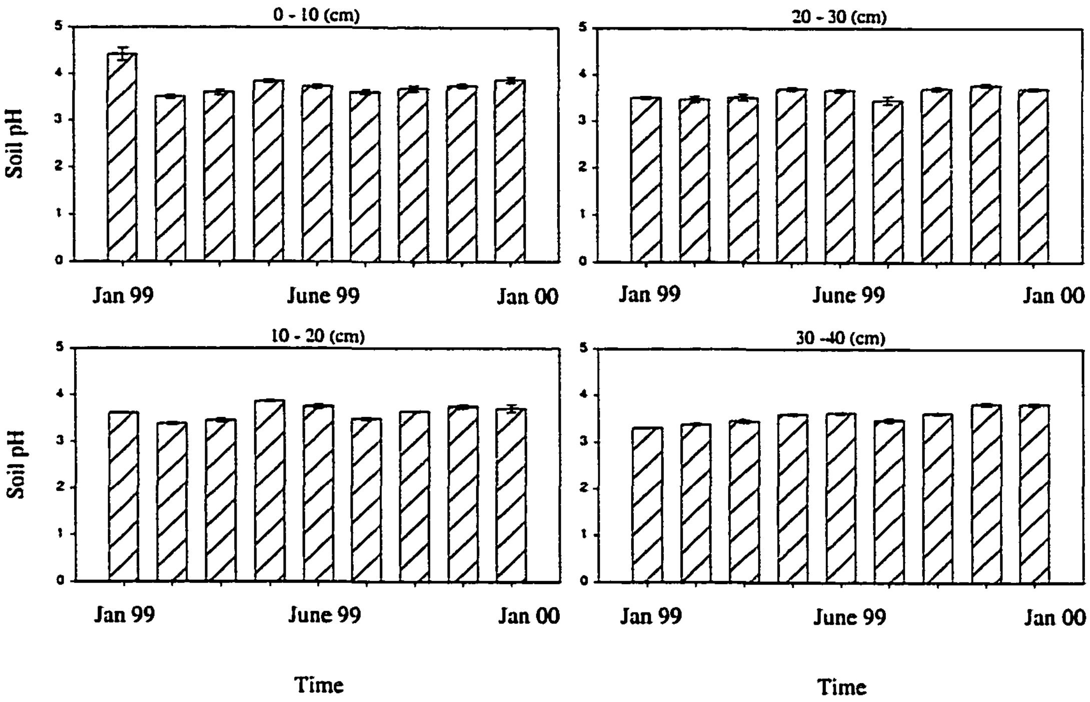

Figure 21. Vertical gradient in soil pH within Pocosin Lakes National Wildlife Refuge. Values represent means with one standard error.

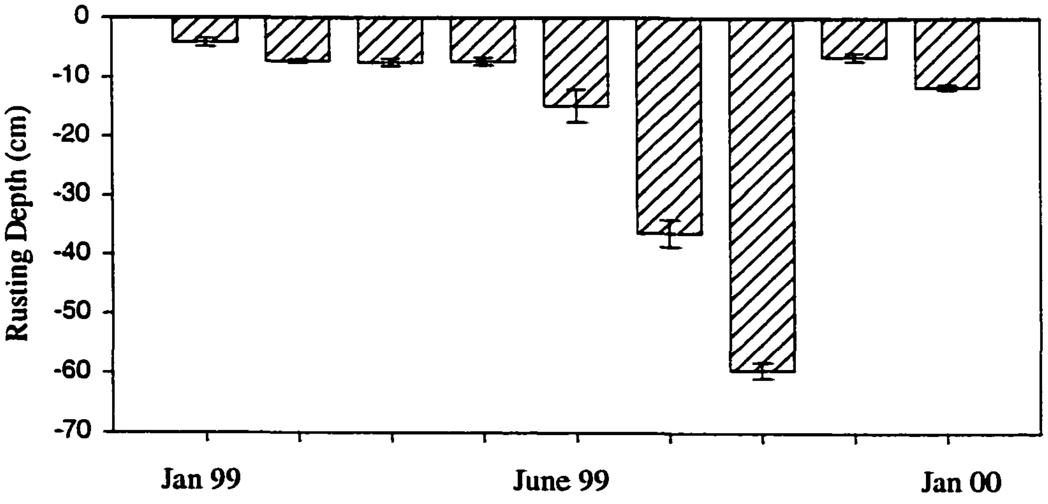

Figure 22. Depth to water table at Pocosin Lakes National Wildlife Refuge as determined by rusting depth on steel rods. Values represent means with one standard error.

DISCUSSION

Successful regeneration of Atlantic white cedar within its historic range has been hindered due to shade intolerance (Smith 2002), improper hydrologic conditions (Hinesley and Wicker 1999) and herbivory by deer, mice, and rabbits (Guidry 1999). These problems were experienced at the Pocosin Lakes restoration site over the course of this research. Summer drought coupled with intense herbivory decimated the plantings such that there were few to no seedlings remaining at the site by the summer of 1999 (personal observation). Additionally, the site was being rapidly colonized by southern wax myrtle (*Myrica cerifera* L.). This actinorhizal and mycorrhorizal species can rapidly colonize nutrient poor coastal habitats eventually forming dense monotypic stands. Despite the loss of Atlantic white cedar at this site, annual decay rates were measured and compared to other restoration attempts and naturally regenerating sites in this region.

Native leaf litter decay rates at PLNWR were faster than native litter decay rates in other restored and regenerating sites in the study region. Although not tested, these differences may be attributed to differences in litter quality as the dominant species in this restored site were *P. aquilinum*, an unidentified *Solidago spp.*, and *E. crusgalli.* The decay rate of *Chamaecyparis* litter (0.36 yr^{-1}) was well within the range of values reported for other regional restored and regenerating sites (this dissertation) and close to those reported for Atlantic white cedar by Day (1982) and Yates and Day (1983).

The average soil pH was also within the range of those reported for other restored/regenerating stands in the region (this dissertation), and also within the range found for other regional Atlantic white cedar stands (Tupacz and Day 1990, Whigham and Richardson 1988). Based on hydrology data inferred from rusting depth on steel rods, with the exception of summer drought during 1999, antecedent and post drought water tables were comparable with other East Coast Atlantic white cedar wetlands (Golet and Lowry 1987).

The trend of decreasing root decay with increasing depth in the soil profile was similar between native and *Chamaecyparis* roots. However, native root decay was significantly faster than *Chamaecyparis* within each depth interval. These trends were also exhibited in other Atlantic white cedar restoration sites in the study region (this dissertation). Native root decay rates at PLNWR were similar to those of other regional restoration sites. Decay rates of *Chamaecyparis* roots were similar to those found in all the study sites within this region (this dissertation). The highest native root decay rate occurred in the 0 – 10 cm depth interval and is likely a result of aerobic conditions found at that interval.

Litter quality appears to be the overriding factor influencing differences in decay rates between the dominant extant vegetation and *Chamaecyparis* litters. Thus it appears that the current input into the soil organic matter pool from extant above and belowground materials is deficient within this site compared to other naturally regenerating Atlantic white cedar stands in the region. According to Laderman (1989), while it may be necessary at times, planting Atlantic white cedar has proven to be so difficult that natural regeneration is preferred in areas where opportunity exists. The problems experienced during this restoration attempt are symptomatic of the difficulties encountered when trying to restore Atlantic white cedar within its historic range.

VITA

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Edward Ratcliffe Crawford received his Bachelor of Science in Marine Biology from the University of North Carolina-Wilmington in May 1989. Edward completed his Master of Science degree in Biology at Virginia Commonwealth University in 1995. He was awarded the Phi Sigma award for academic excellence during the spring of 1995. Edward began doctoral research at Old Dominion University, where he conducted the research presented in this work. He was inducted into the Phi Kappa Phi National Honor Society for superior academic achievement during the spring of 1999. He currently has three refereed publications in print, two in press and numerous published abstracts for oral and poster presentations at annual meetings of the Association of Southeastern Biologists, Ecological Society of America and Society of Wetland Scientists. Edward currently lives in Richmond, Virginia