Fall 1980

Litter Production and Nutrient Content of Litter in the Seasonally Flooded Dismal Swamp

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LITTER PRODUCTION AND NUTRIENT CONTENT OF LITTER IN THE SEASONALLY FLOODED GREAT DISMAL SWAMP

by

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B.A. December 1977, Duke University

A Thesis Submitted to the Faculty of
Old Dominion University in Partial Fulfillment
of the Requirements for the Degree of

MASTER OF SCIENCE

BIOLOGY

OLD DOMINION UNIVERSITY
December, 1980

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ABSTRACT

LITTER PRODUCTION AND NUTRIENT CONTENT OF LITTER IN THE SEASONALLY FLOODED GREAT DISMAL SWAMP

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Old Dominion University, 1980
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Litter production was studied in four plant communities in the Great Dismal Swamp, Virginia, that differ primarily in species composition and flooding regime. Greatest leaf deposition occurred in the more flooded communities, maple-gum (*Acer-Nyssa*) with 536 g m^{-2} yr^{-1} and cypress (*Taxodium distichum* (L.) Richard) with 528 g m^{-2} yr^{-1}, followed by the cedar (*Chamaecyparis thyoides* (L.) BSP) and mixed hardwood (*Quercus-Acer-Nyssa-Liquidambar*) communities with 506 g m^{-2} yr^{-1}. and 455 g m^{-2} yr^{-1}, respectively. Litter nutrient concentrations were generally higher in the cypress and maple-gum stands, indicating greater nutrient availability and uptake than in the two less flooded and more acidic stands. Higher leaf fall rates and litter nutrient concentrations resulted in greater nutrient deposition in the cypress and maple-gum communities. Relative abundance of elements differed between the two more flooded and the two less flooded stands. Deposition of tree boles and large branches, nutrient concentrations and nutrient deposition in the macrolitter was also investigated in three of the communities.

ACKNOWLEDGEMENTS

This thesis is based upon work supported by the National Science Foundation under grant number DEB-7708609. I am very grateful to my academic advisor, Dr. Frank P. Day Jr., for his patience and guidance during my graduate career. I greatly appreciate the help of Dr. Gerald F. Levy and Dr. Kneeland Nesius, who provided valuable advice in the preparation of this thesis. Many thanks to Dr. James Matta, friend and statistical consultant. I extend my special gratitude to Joseph Atchue for his friendship and assistance. I am also indebted to Elizabeth Breidling for help in almost every facet of this project -- and, thank you Allen.

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INTRODUCTION

Swamps and marshes are extremely productive biological systems (Kuenzler *et al* 1980, Odum 1969) which play an important ecological role. Wetlands, due to their water-holding capacity, are important in lowering flood crests, in decreasing the destructiveness of severe floods and in minimizing erosion. The ability of wetlands to remove pollutants from waste waters and to aid in sediment removal is also of great ecological significance (Goodwin and Niering 1974, Kitchens *et al* 1980). It is evident that wetlands are of great importance to man, yet these habitats are being destroyed by various types of human activity. Goodwin and Niering (1974) report that of the original 51,400,000 ha of wetlands in the United States (inland and coastal) only 28,300,000 ha now remain. These systems must be better understood in order to properly maintain them.

Penfound (1952) in his classic review of southern swamps and marshes, defines swamps as woody communities occurring in areas where surface water is present for one or more months of the growing season. Swamplands are characterized by different flooding regimes, that is, time of inundation (hydroperiod) and water depth. These differences may be reflected in variability in ecosystem structure, nutrient recycling processes and productivity.

Recent studies have demonstrated differences in productivity between swamp environments experiencing stagnant conditions for most of the year, and systems that are only seasonally flooded. An example of the former is the Okefenokee Swamp in Georgia, characterized by slow moving surface waters, low productivity (Schlesinger 1978) and low nutrient availability (Schlesinger and Chabot 1977). High productivity estimates for swamplands receiving periodic inputs of water have been obtained in Louisiana (Conner and Day 1976) and North Carolina (Brinson *et al* 1980, Kuenzler 1980).

Litter fall represents a major pathway of energy flow through the transfer of plant debris to the forest floor, and is useful as an indicator of minimum levels of net primary production (NPP) (Bray and Gorham 1964, Ricklefs 1973, Woodwell and Marples 1968). The continued monitoring of this process provides information that is helpful in measuring changes to community structure and NPP, and recovery of the ecosystem following disturbance (Armentano and Woodwell 1976, Woodwell and Marples 1968). Litter fall also provides the major input of nutrients to the forest floor (Blow 1955, Garstka 1932, O'Neill *et al* 1973, Ovington 1965) and may help explain the distribution and productivity of forest species (Cotrufo 1977).

There is extensive literature on litter production in various types of forested systems. Two reviews of world-wide production were conducted by Bray and Gorham (1964) and Rodin and Bazilevich (1967). Litter fall in mixed hardwood forests of the U.S. has been studied by Cotrufo (1977, Cromack and Monk (1975), Dixon (1976), Gosz *et al* (1972), Lang (1974), Rochow (1974), Wells *et al* (1972) and Whittaker and Woodwell (1969). Literature on litter fall in swamp systems include studies in Florida (Carter *et al* 1973), Louisiana (Conner and Day 1976), Georgia (Schlesinger 1978), North Carolina (Brinson *et al* 1980, Kuenzler *et al* 1980) and Minnesota (Reiner 1972, Reiners and Reiners 1970).

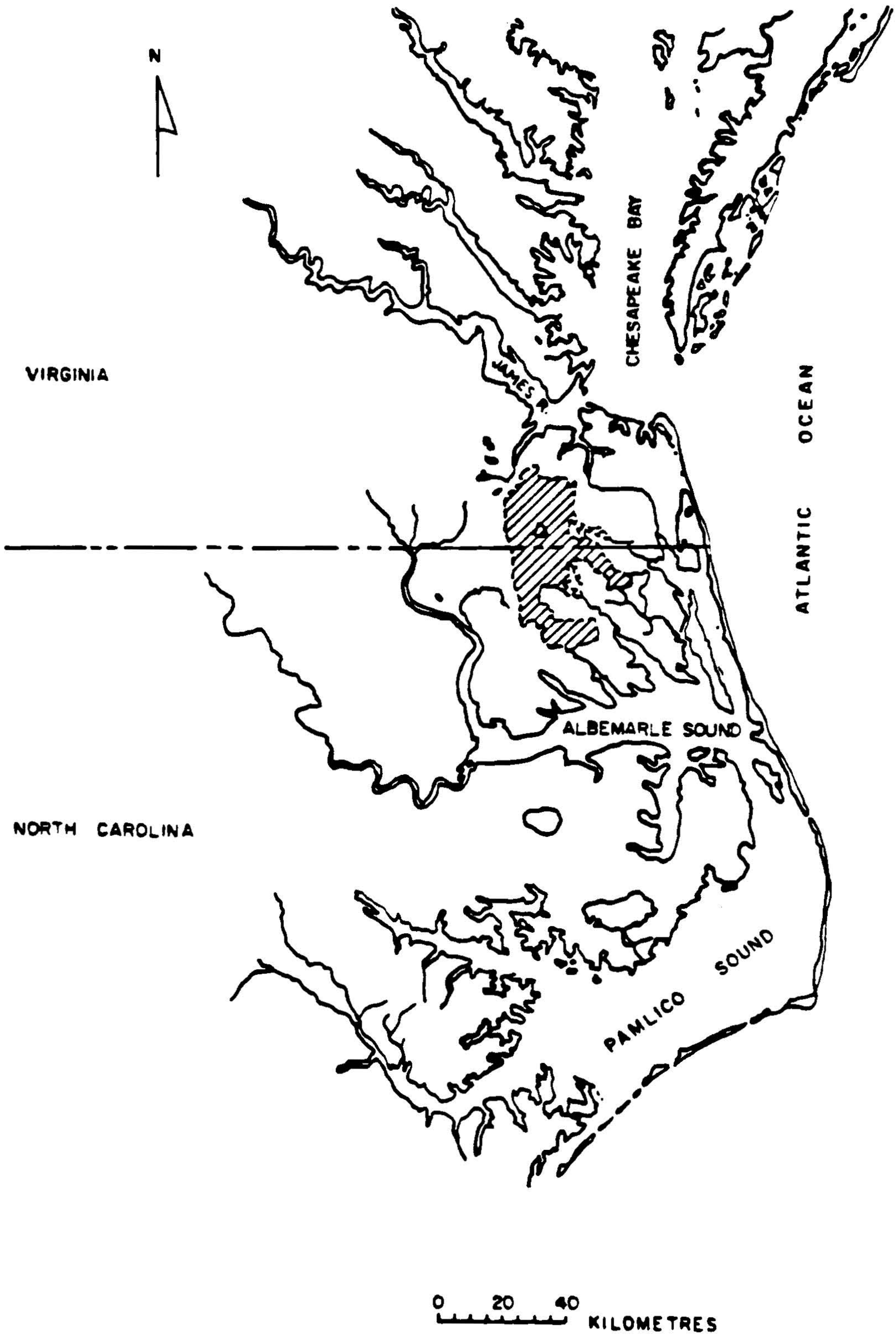
The present study was conducted in the seasonally flooded Great Dismal Swamp, which has been subjected to various human disturbances. The importance of such a study is that it might produce generalizations concerning effects of human disturbance on existing swamplands. Effective application of ecological principles in the management of the Dismal Swamp system requires a sufficient understanding of how this ecosystem functions. The study of litter production and nutrient content of the litter will contribute to better comprehension of this swamp. Quantification of mineral nutrient deposition provides information of practical and economic importance in the conservation (and reforestation) of existing swamplands.

Research was conducted in four plant communities that differ primarily in spcies composition and flooding regime. The major objective was to determine whether differences between the communities were reflected in litter production and litter nutrient concentrations. In order to do this, litter fall rates were measured and nutrient concentrations determined. Results obtained were used in calculating nutrient deposition via litter fall, thus providing preliminary information on the relative abundance of elements in the four stands. Data collected were used in statistical analyses to evaluate quantitative seasonal and site differences. Litter fall data were also used to make comparisons between the Great Dismal Swamp and other swamp and forest ecosystems.

DESCRIPTION OF STUDY AREA

The Great Dismal Swamp is a non-riverine swamp located on the Coastal Plain in southeastern Virginia and northeastern North Carolina (Figure 1). The Swamp is bordered on the west by the Suffolk Scarp (elevation approximately seven to eight m above mean sea level), a marine shore-line formed during the Pleistocene Epoch when sea level was approximately 14 m higher than at present (Lichtler and Walker 1979). Deep Creek swale bounds the Dismal Swamp on the eastern side. From this north-south swale, the land rises from the center westward to the Dismal Swamp and eastward to the Fentress rise (U.S. Department of the Interior, Fish and Wildlife Service 1974). The Fentress rise is a subtle north-south linear rise consisting of inter-glacial marine and barrier sediments. The Dismal Swamp extends northward to the headwaters of the Nansemond River and southward to the Churchland flat. The present area of the Swamp is estimated to be 85,000 ha, as compared to precolonial times when the Dismal Swamp encompassed an area of 202,000 ha (Bureau of Sports, Fisheries and Wildlife, GDSNWR 1974). In 1973, approximately 25,000 ha in Virginia became the Great Dismal Swamp National Wildlife Refuge. Lake Drummond,one of only two natural lakes in Virginia, is found near the center of the Swamp.

The principal factors controlling the hydrology are climate, topography and geology of the area. The surface of the Dismal Swamp slopes eastward approximately 0.2 m per km from an altitude of about seven m near the top of the Suffolk Scarp, to approximately five m at Deep Creek


N
VIRGINIA
NORTH CAROLINA
CHESAPEAKE BAY
JAMES R.
ATLANTIC OCEAN
ALBEMARLE SOUND
PAMLICO SOUND
0 20 40
KILOMETRES

swale (Lichtler and Walker 1979). Thus, streamflow enters the Swamp from the Suffolk scarp and leaves to the south, east and north (Carter 1979). The clay rich layers of the Yorktown Formation underlie the entire area and form and effective seal preventing the movement of water (Oaks and Whitehead 1979).

Surface inflow to the Dismal Swamp varies with season. Inflow may be up to three to four times greater in winter than summer, with approximately 90% occurring from November to April (Oaks and Whitehead 1979). The principal outflow is through the Dismal Swamp Canal to the Pasquotank and Elizabeth Rivers and to the Nansemond River watershed in the northern section (Freston 1973). The drainage ditches (e.g. Jericho and Portsmouth) also constitute water outlets, and many of them drain into Lake Drummond, which in turn drains to the Dismal Swamp Canal through the Feeder Ditch (U.S. Department of the Interior, Fish and Wildlife Service, 1974).

Most of the Dismal Swamp soils are highly organic soils, i.e. mucky peats (Henry 1970). The organic soils are classified as Typic Medisaprists and Terric Medisaprists. The first soil type, which includes all of the mucks and peats that are 130 cm or more thick, extends throughout most of the Swamp. The soils of the second type have organic materials underlain by mineral materials at depths of less than 130 cm, but more than 41 cm. These are found in the southern and eastern border areas of the Dismal Swamp. Mineral soils found in the Swamp have at least 20 cm of peat and muck but less than 41 cm, and are classified as Histic Humaquepts. This type is found in the southern portion of the Swamp and extends in a narrow band along the western and northern boundaries (U.S. Department of the Interior, Fish and Wildlife Service, 1974). Thickness of the Dismal Swamp peat is variable and reflects the wavy nature of the underlying surface. The maximum depth of the peat seems to be approximately 3.5 m (Whitehead 1972).

The Dismal Swamp lies at the northern end of the Warm Temperate climate zone, being characterized by long, humid summers and relatively mild winters. The climate is more temperate than that of more inland areas of the same latitude, due to the moderating influence of the warm waters of the Gulf Stream a few miles to the east (Freston 1973).

Precipitation data recorded at the Suffolk Lake Kilby station during the study period (1977 - 1978) showed that total precipitation was greater in 1978 than 1977 (124.43 cm and 114.09 cm, respectively). The wettest months were August in 1978 with 20.57 cm and May in 1977 with 15.30 cm. The driest months were September in 1978 with 2.43 cm and August in 1977 with 5.99 cm. Temperature data recorded at the same station showed temperatures fluctuated more in 1977, when temperatures ranged from -15°C in January to 37°C in July. In 1978, temperatures ranged from -11°C in January to 35°C in July (National Oceanographic and Atmospheric Administration, 1977 and 1978).

The forests of the Great Dismal Swamp have undergone dramatic changes. Cypress (*Taxodium distichum* (L.) Richard) and cedar (*Chamaecyparis thyoides* (L.) BSP), typical swamp species, were once extremely abundant and are now relatively uncommon. At present, the vegetation of the Swamp is estimated to consist of approximately 65% hardwoods, 20% pine species (*Pinus* spp.), 6% cedar, 2% cypress and the remaining 7% comprise unidentified species. The hardwoods consist of gum species (*Nyssa* spp.)(31%), red maple (*Acer rubrum* L.)(26%) and sweetgum (*Liquidambar styraciflua* L.), oak species (*Quercus* spp.) and tulip tree (*Liriodendron tulipifera* L.) combined (8%)

(Bureau of Sports, Fisheries and Wildlife, GDSNWR, 1974).

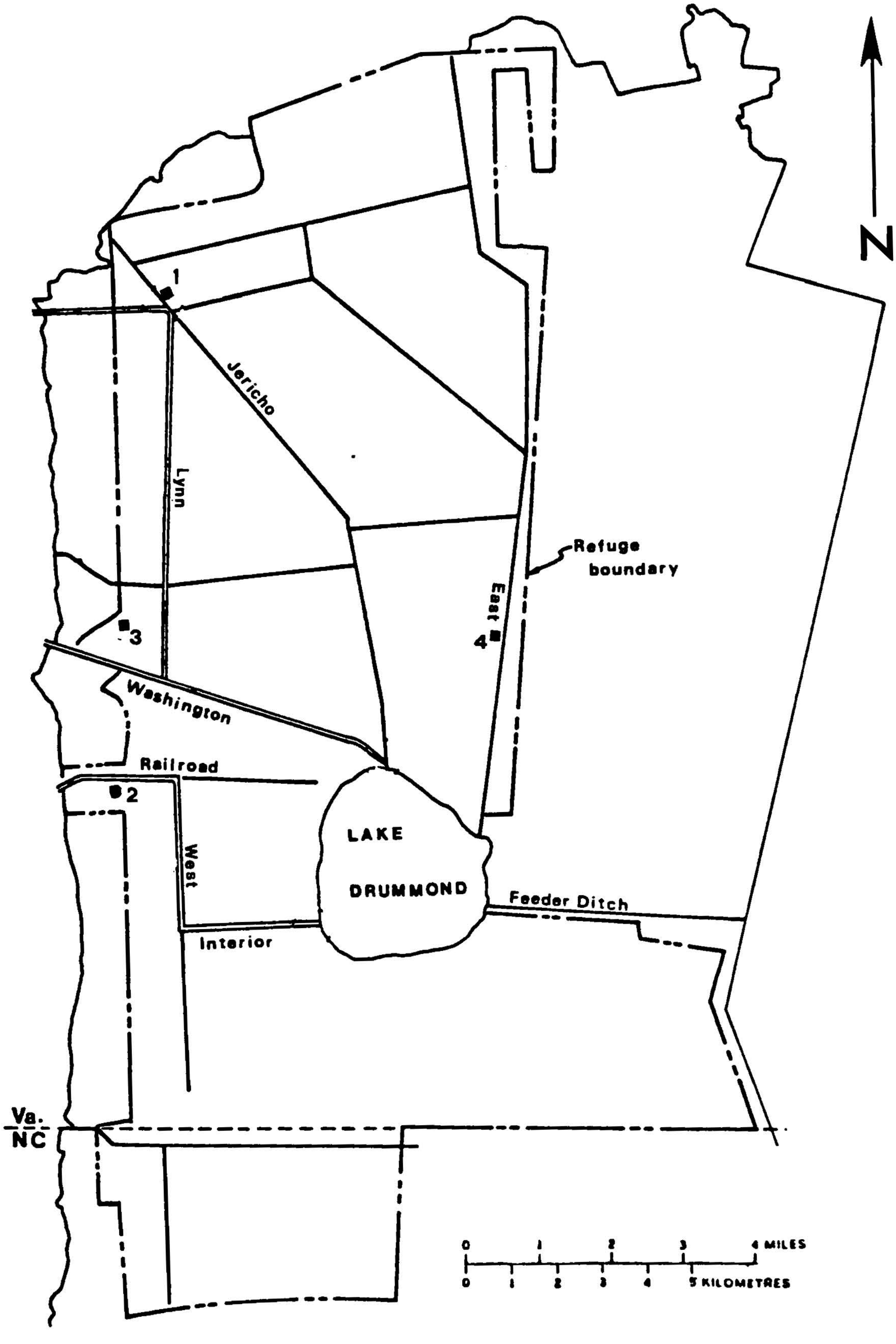
Forests presently found in the Swamp are characterized by differences in structure and species composition. Distribution of the vegetation is controlled by differences in moisture, soil and light conditions, i.e. length of hydroperiod, thickness of peat and successional stage (Carter 1979, Whitehead 1972). Previous research concerning the vegetation component of the Dismal Swamp include numerous lists of the flora (Meanley 1968, Musselman *et al* 1977, Waters *et al*1974) studies describing community types (Braun 1967, Dean 1969, Freston 1973, Kearney 1901, Meanley 1968), causes of tree distribution (Jantzen 1974), forest dynamics (Levy and Walker 1979), plant succession (Walker 1972) and herbaceous production in cut and uncut burned areas of a cedar stand (McKinley and Day 1979). Gammon (1978) identified and mapped specific vegetative communities using color infrared photographs.

The early history of the Great Dismal Swamp is fragmentary. The Swamp was so impenetrable that for over a century after the English first occupied Virginia there was little interest in the Dismal Swamp. William Byrd II desribed the Great Dismal Swamp as a "horrible desert" and "a blot on His Majesty's Kingdom" (Stewart 1979). Since the early 1700's the Dismal Swamp system has been subjected to various human disturbances that have resulted in severe alteration of the natural vegetation. Disturbances such as logging ,land-clearing and canal digging began in the late 1700's. Peat fires have also been frequent, especially in the eastern portion of the Swamp (Dean 1969). These perturbations have played a dominant role in determining the present composition of the Dismal Swamp's vegetation. Changes in moisture relations that are normally brought about after centuries of aggradation of organic and inorganic matter have been accelerated by ditch construction (Levy and Walker 1979). Logging practices have resulted in the complete elimination of the natural vegetation from extensive areas, and along with frequent fires have led to the replacement of original forest communities.

Four plant communities in the Great Dismal Swamp have been most extensively studied. They include mixed hardwood, maple-gum, bald-cypress and Atlantic white cedar communities. Research efforts have been directed towards a clearer understanding of ecological dynamics in these four communities. Data obtained to date include information on structural comparisons of the four stands (Dabel and Day 1977), phytomass budgets (Day and Dabel 1978), litter accumulation (Day 1979), root production (Montague and Day 1980), tree growth (Day,unpublished) and population age structures (Train and Day,unpublished). Current research involves process studies on decomposition and nutrient recycling.

A detailed description of the four plant communities follows. Figure 2 indicates the specific location of each community within the Great Dismal Swamp National Wildlife Refuge.

*Mixed hardwood community.*__ This stand developed in a mesic area, which is reflected in its species richness and well developed forest stratification. It is characterized by having the largest ground cover biomass and second largest shrub biomass, compared with the other three stands. The community experiences only minimal flooding. The most prominent species ranked in order of importance based on total community biomass are: laurel oak (*Quercus laurifolia* Michaux), white oak(*Q. alba* L.), sweet gum, black gum (*Nyssa sylvatica* var. *biflora* Walter) red maple, swamp chestnut oak(*Q. michauxii* Nuttal), beech (*Fagus grandifolia* Ehrhart) and tulip tree. An important subcanopy species is American



N
1
Jericho
Lynn
Refuge boundary
East
4
3
Washington
Railroad
2
West
LAKE
DRUMMOND
Feeder Ditch
Interior
Va.
NC
0 1 2 3 4 MILES
0 1 2 3 4 5 KILOMETRES

holly (*Ilex opaca* Aiton). This community has the lowest total biomass and tree stratum biomass, although not significantly lower than the maple-gum stand. The various species of oak contribute 57.7% to the total above-ground biomass, red maple contributes 9.5% and other species make up the remainder (Dabel and Day 1977). It appears that the plant species constituting this community have achieved a stable age distribution (Train and Day, unpublished).

*Maple-gum community.*__The area in which this community is located was logged approximately 30 years ago (P. Gammon, USGS, GDSNWR, personal communication),and the cypress that covered this area previously have not regenerated. This stand is extensively flooded, but not as frequently as the cypress community. Peaks in flooding were recorded during the months of January, March and June of 1978. The most prominent species ranked in order of importance on the basis of total biomass are: water gum(*Nyssa aquatica* L.), red maple, black gum, hop hornbeam (*Ostrya virginiana* (Miller) K. Koch), and laurel oak; with water gum contributing 46.7% to the total biomass, red maple 32.9%, black gum 16%, and the other species make up the remainder. This stand has the second lowest total biomass and tree stratum biomass (Dabel and Day 1977). It has a poorly developed herbaceous layer and a well developed shrub layer. The water gum population has an even distribution of age classes, while the red maple population is expanding (Train and Day, unpublished).

*Cypress community.*__ This stand is characterized by more extensive flooding than at the other three communities. It was continuously underwater from December 1977 to May 1978 and again in June 1978. Logging in this area has resulted in a relatively even aged stand of cypress, ranging from 70 to 95 years of age. The oldest stand of trees, of the four study areas, occurs in this community (Day and Train, unpublished). There is a conspicuous lack of younger aged cypress trees, probably due to reduced light and competition from hardwood seedlings. The shrub layer is lacking, but the herb layer is well developed. The most prominent plant species ranked in order of importance based on total biomass are: bald cypress, red maple, water gum, black gum, sweet gum, beech, swamp ash (*Fraxinus caroliniana* Miller) and laurel oak. Cypress contributes 50% to total biomass, while red maple contributes 18%. This stand had the highest total biomass and tree stratum biomass (Dabel and Day 1977). It appears that hardwoods are increasing in importance, as red maple is increasing in numbers while cypress is declining. The water gum population was found to be constant (Day and Train, unpublished).

*Cedar community.*__ The cedar community and the cypress community are representative of pre-disturbance (pre-logging) vegetation types formerly found in abundance in the Great Dismal Swamp. It is the only community of the four that is located on a peat deposit (Day and Dabel 1978). The cedar and mixed hardwood communities exhibit the most acidic conditions. This stand is flooded for about four months with peaks in standing water recorded in March and June of 1978. The cedar trees have attained maturity and are dying due to natural senesence. This has resulted in a relatively large accumulation of woody litter on the forest floor. There is no evidence of cedar regeneration, which is probably due to the combined effects of fire prevention management and competition from hardwood seedlings. The red maple and black gum populations are rapidly increasing and replacing the cedar as dominant tree species. This stand is characterized by a well developed shrub layer, probably due to increased light and space caused by openings in the tree canopy. This dense shrub layer does not permit the development of thick herbaceous growth. The most prominent species are: Atlantic white cedar, black gum, red maple, red bay (*Persea borbonea* (L.) Sprengel), sweet bay (*Magnolia virginiana* L.) and sweet pepperbush (*Clethra alnifolia* L.). Cedar contributes 46.8% to total biomass, black gum 30.9% and red maple 19.5%. This community had the second highest total and tree stratum biomass (Dabel and Day 1977).

METHODS

Litter fall measurements

Fieldwork was conducted from October 8, 1977 to December 19, 1978. Litter production was measured by collecting fallen litter in traps (baskets) placed in the four stands. Time elapsed between collection dates varied, ranging from seven days in autumn to two months the remainder of the year, depending on rate of litter fall. Fifteen litter collectors were randomly placed along two parallel transects at each community. Lloyd and Olson (1974) studied the precision and repeatability of such a sampling technique and reported that it gave reliable results. Newbould (1967) suggested conditions that a trap for falling litter should meet. The requirements concerned mainly the addition to or loss from the trap of material other than by litter fall and ensuring that the collector catches the litter that would normally be deposited on the area presented by the trap if it were absent. Litter collectors used in the present study were designed to meet these requirements.

Litter traps set out in the four stands consisted of 0.25 m^2 aluminum screen baskets set on 50 cm high wooden frames. The baskets had a depth of 20 cm. This depth ensured that fallen litter would not be blown out of the trap. Armentano and Woodwell (1976) using traps ten cm deep showed that losses from the traps due to wind amounted to less than five percent of the total collection. Height of the wooden frames was such that baskets were placed above maximum flooding levels. Although some animal activity was noticed (bear and deer), most of the damage incurred was to the wooden frames. From observation of the calculated annual standard errors (of the mean), it appeared that 15 traps at each stand were sufficient for concentrated sampling in these communities. However, this sampling system was designed primarily for leaves, and was not adequate for the collection of small woody litter or fruit and miscellaneous litter, which had distributions that were highly aggregated (standard errors were greater than 10% of the mean).

Litter fall was collected from the baskets, placed in paper bags, brought to the lab and separated by tissue type and species. If wet, the litter was allowed to air dry before proceeding with the separation. Plant tissues were placed in the categories of leaf, wood, flower, fruit and miscellaneous.

Leaf tissue was separated into the major species of each community and species that were common to the four stands. The remainder of the species at each community were placed in the category of Other. During litter fall collections made from July 28 to December 19, 1978, plant species considered minor contributors to total leaf fall at each community were also separated and identified. The woody tissue category consisted of small twigs less than four cm in diameter and pieces of bark. A miscellaneous classification was added when needed (e.g. insect frass, bud scales and lichens). After separation by tissue type and species, samples were placed into paper bags, oven dried at 70°C for 48 hours and weighed. They were then ground in a Wiley Mill using a size 40 mesh for nutrient analyses, conducted at a later date.

Deposition of macrolitter, i.e. large branches (greater than four cm in diameter) and tree boles was also investigated. Ten 10 m^2 ground plots were randomly located along two parallel transects at each of the four stands. Plots were located at the maple-gum and cypress communities on November 11, 1977, and at the mixed hardwood and cedar communities on December 4, 1977. Plots were initially cleared of all large woody litter. At the conclusion of the study period, macrolitter that fell into the plots was weighed in the field using a spring balance. Subsamples were taken, placed into paper bags, brought to the laboratory and weighed. They were dried in an oven at 70°C until a constant weight was achieved and used in the calculation of wet weight - dry weight conversion factors. Samples were ground in the same manner as the leaf material for chemical analyses. It was impossible to relocate the ground plots at the cedar stand, so information on the deposition of large woody litter in this stand is lacking. It is expected that this study will be repeated, since the data are needed to more completely characterize the Atlantic white cedar stand. Nomenclature follows Radford *et al* (1968).

Nutrient analyses

Analyses for concentrations of the macronutrients N, P, K, Ca and Mg were carried out on subsamples of the litter fall. The material used for nutrient analyses consisted of samples collected during peak deposition periods in the communities. Samples were lumped at each stand in order to obtain three samples from 15 litter collectors. Lumping was done by tissue type, and by species in the case of leaf tissue. Three subsamples were taken at each community for the macrolitter.

Ground samples were wet digested in a Technicon BD-40 Block Digestor, using the sulfuric acid (H_2SO_4)-hydrogen peroxide (H_2O_2) method. Approximately 0.26 g of each sample was weighed and added to a digestion tube along with several alundum boiling chips. Seven ml of digestion solution were added and mixed so as to thoroughly wet the plant material. The digestion solution was prepared by dissolving 97.0 g of selenous acid (H_2SeO_3) in 100 ml of deionized water, which was added to a 2.23 l bottle of concentrated H_2SO_4. After addition of the digestion solution three ml of 30% H_2O_2 were added. Samples were then placed into the block and digested for one hour and ten minutes. Standard reference material 1571 (orchard leaves) obtained from the National Bureau of Standards was used for verification of the digestion procedure. Orchard leaf samples were processes in the same manner as litter fall samples, beginning with the digestion.

After digestion, samples were cooled and diluted to volume (75 ml) with deionized water. Samples were then mixed by inversion and decanted into polyethylene bottles. The digestate was filtered if it appeared cloudy. The original digestate was then used in the various analyses for concentrations of N, P, K, Ca and Mg.

Nitrogen and P were analyzed using a Technicon AutoAnalyzer I. The procedure used for the N analysis is a modification of the Kjeldahl technique. Phosphorus was analyzed by the molybdate-blue method. Two separate dilutions with deionized water were made from the original digestate. Dilutions for the determination of N and P content were 1:100 and 1:5, respectively. Standards used for both N and P were 0.25 ppm, 0,50 ppm, 1,0 ppm, 2.0 ppm, 3.0 ppm and were made by diluting NH_4Cl and KH_2PO_4 with deionized water. The stock solutions were subsequently diluted to obtain the concentrations mentioned above.

Concentrations of K, Mg and Ca were determined using a Perkin-Elmer Model 603 Atomic Absorption Spectrophotometer. Two separate dilutions (1:50) were made: one for analysis of K and one for analysis of Mg and Ca. For K, the 1:50 dilution consisted of one ml sample, five ml 1.0%

lanthanum solution, five ml 1.5% sodium solution and 39 ml deionized water. For Mg and Ca, the 1:50 dilution consisted of one ml sample, five ml 10.0% lanthanum solution and 44 ml deionized water. The stock lanthanum and sodium solutions were made using lanthanum chloride ($LaCl_3$) and sodium chloride (NaCl). These solutions were added to overcome ionization interferences.

Standards were made using Certified Atomic Absorption Standard K, Mg and Ca Reference Solutions (1000 ppm). The K and Mg Standard Reference solutions were initially diluted to 100 ppm. Reference solutions were then used to make the stock solutions. These were diluted to obtain four working standards: 0.5, 1.0, 3.0 and 5.0 ppm Ca; 0.05, 0.10, 0.30 and 0.50 ppm Mg; and 0.20, 0.40, 1.20 and 2.0 ppm K. 50 ml of 10% $LaCl_3$ were added to the Mg and Ca standards, and 50 ml each of 1.0% $LaCl_3$ and 1.5% NaCl were added to the K standards.

Statistical analyses

Statistical analyses of the data were carried out using the Statistical Package for the Social Sciences run on the Old Dominion University Dec-10 system. Analyses included descriptive statistics, t-tests, Duncan multiple range test, multiway analysis of variance (ANOVA) and oneway ANOVA. All results were considered significant at the $p = 0.05$ level.

Duncan multiple range tests and t-tests were used as *a posteriori* tests. The Duncan test was used in order to contrast stands in amounts of litter production and nutrient concentrations of the litter, while t-tests were run to establish whether differences between stands in a amounts of large woody litter deposition and nutrient concentrations were significant. A multiway ANOVA was run to test for differences in amounts of litter fall due to the simultaneous effects of seasonality and stand differences. Since all factors were considered to be fixed, a fixed effect or linear hypothesis model (Model I) was used (Sokal and Rohlf 1969). The subprogram ANOVA produces a table for multiple classification analysis (MCA). The MCA table was used when there was no significant interaction between these two factors (Nie *et al* 1975). A oneway ANOVA (Model I) was used when testing only for differences between communities. A oneway was also conducted whenever the two way ANOVA showed a significant interaction between effects of site and date.

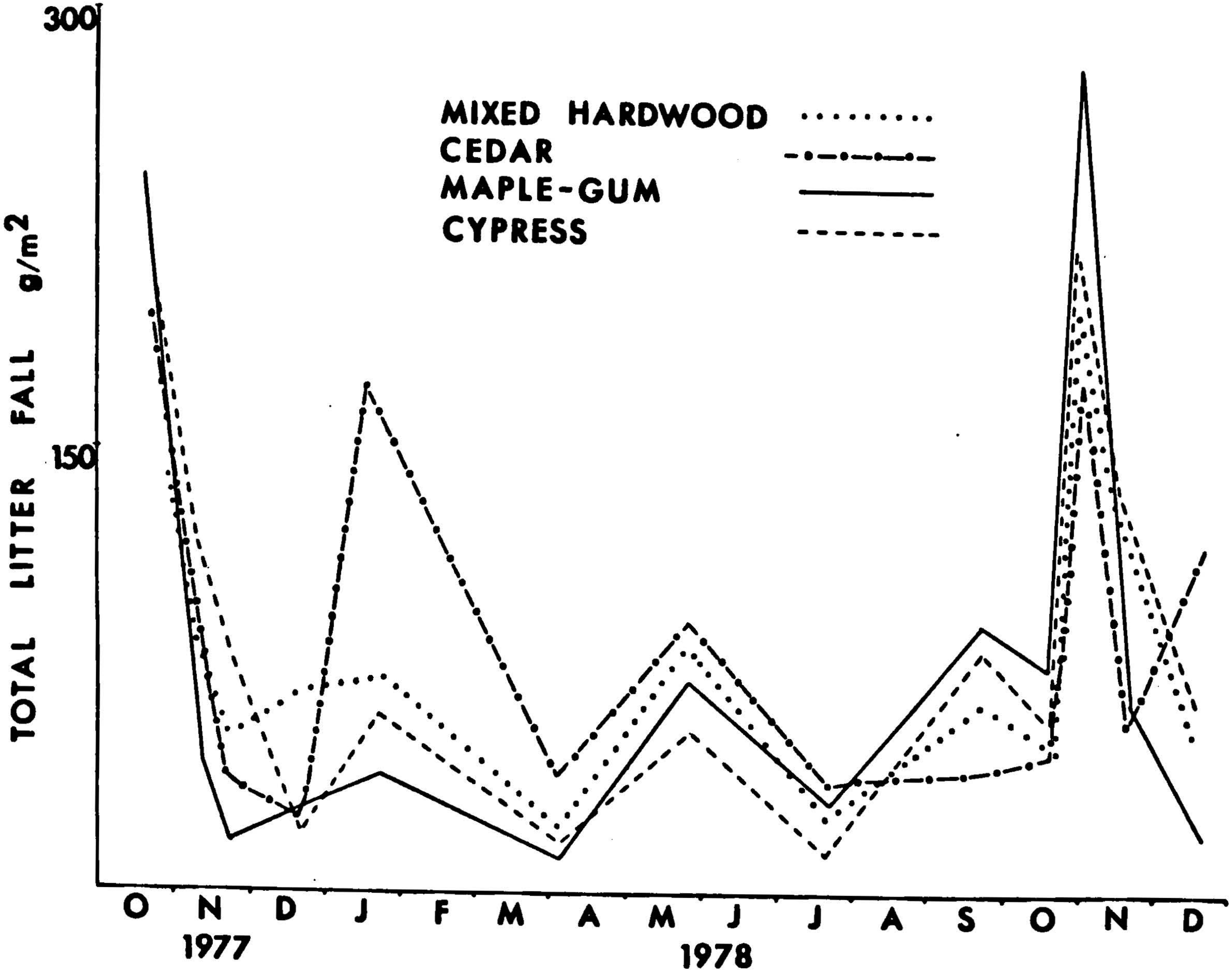
RESULTS

Litter production

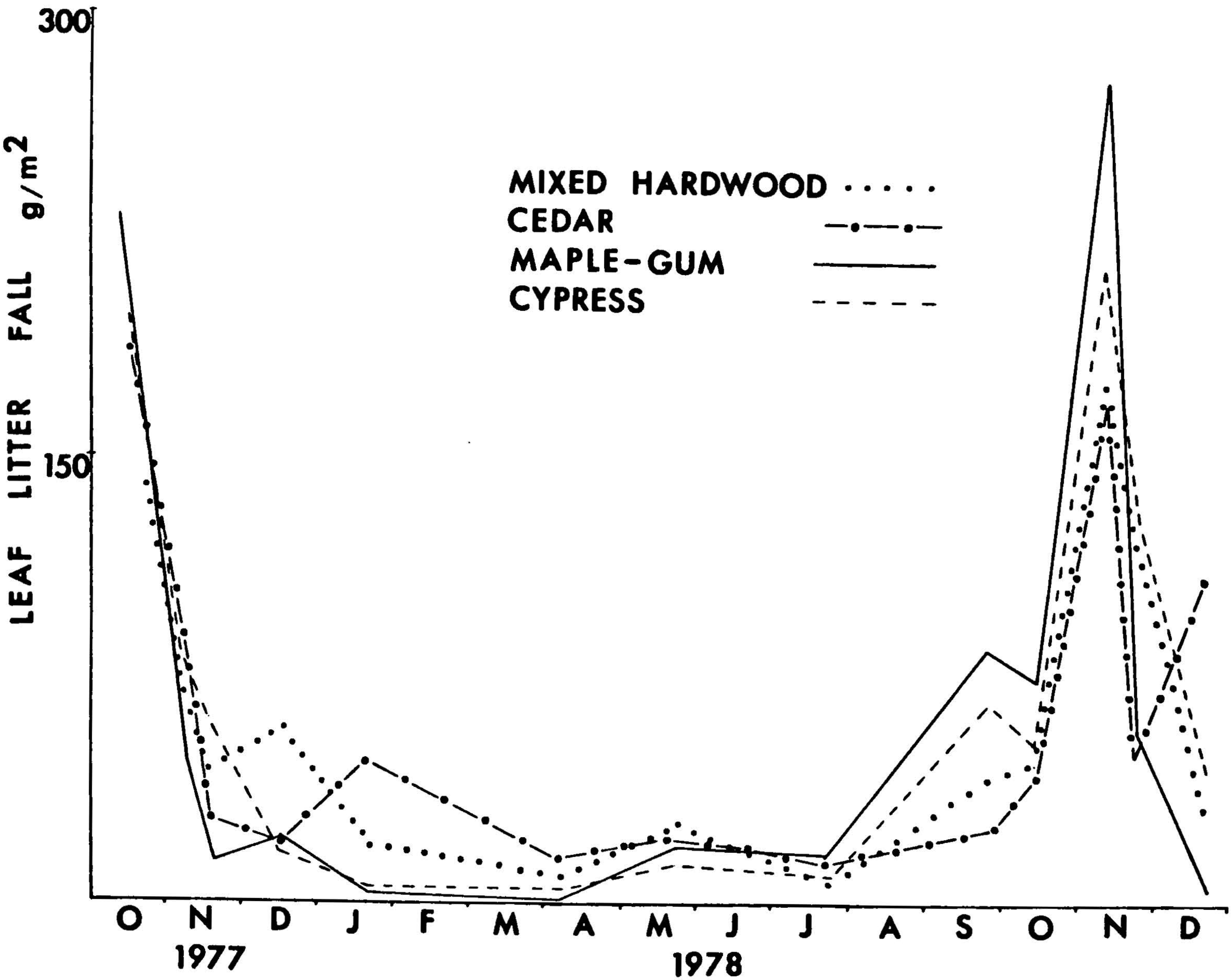
The plant communities exhibited four periods of peak litter deposition for the period October 1977 to December 1978 (Figure 3). Peaks occurring in October and November correspond to autumn leaf fall, while peaks in January and May were due to some leaf litter combined with a large amount of woody litter. The maple-gum and cypress communities exhibited greater autumn maximum deposition than the cedar and mixed hardwood communities. Peaks composed mostly of woody litter were consistently greater at the cedar stand. Total litter deposition in the three deciduous communities during autumn of 1978 was complete after the leaf fall maximum. However, litter deposition at the cedar community again increased directly after the autumn peak, due mainly to a large deposition of cedar needles.

Leaf.__ Maximum leaf deposition occurred between October 8 and October 31 in 1977 and between October 21 and November 5 in 1978 (Figure 4). Both the cedar and mixed hardwood communities exhibited smaller increases in leaf fall during early winter, reflecting the leaf fall patterns of dominant species at these communities. Smaller peaks were recorded in the four communities during early summer. Autumn leaf fall began in August during 1978 due to early leaf shedding by the gum species.

Leaf fall patterns for major species at each community are shown in Figures 5 through 8. The category of Other represents the remaining



TOTAL LITTER FALL g/m²
300
150
MIXED HARDWOOD
CEDAR
MAPLE-GUM
CYPRESS
O N D J F M A M J J A S O N D
1977
1978


LEAF LITTER FALL g/m2
300
150
MIXED HARDWOOD
CEDAR
MAPLE-GUM
CYPRESS
O N D J F M A M J J A S O N D
1977
1978

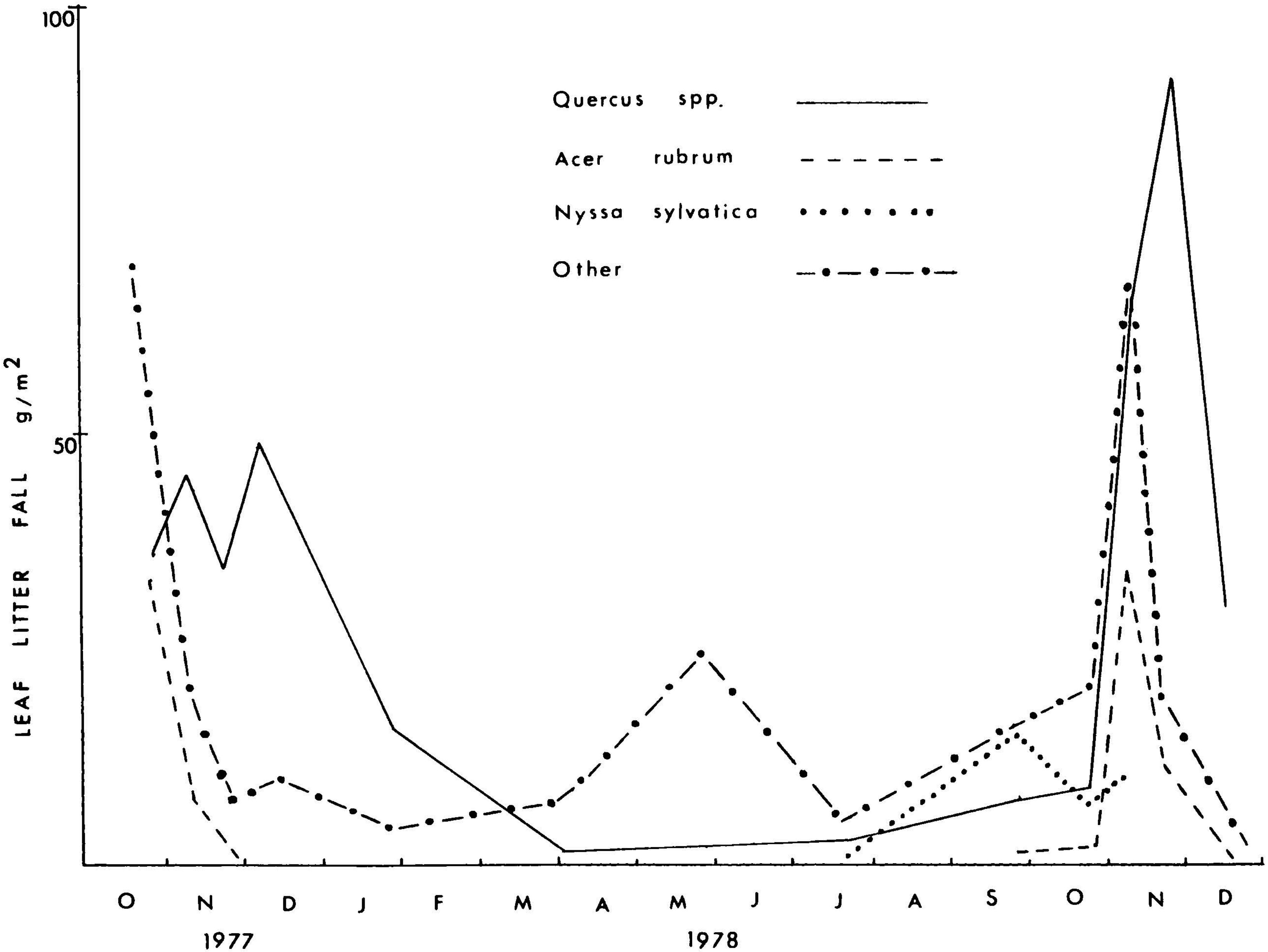
species found at each community, excluding dominant species, red maple and black gum. However, this category does include black gum for litter collections made in 1977. The figures show autumn leaf fall had just begun or was in progress when litter collectors were set out in 1977, therefore peak deposition for some species may have already occurred.

Oak leaf fall at the mixed hardwood stand peaked later than the other species in this community and continued into early spring (Figure 5). Several species of oak are marcarescent, dropping their leaves later than other species. Leaf shedding by red maple was relatively abrupt during both autumns. In contrast, black gum leaf deposition began earlier than other species and was complete by early November.

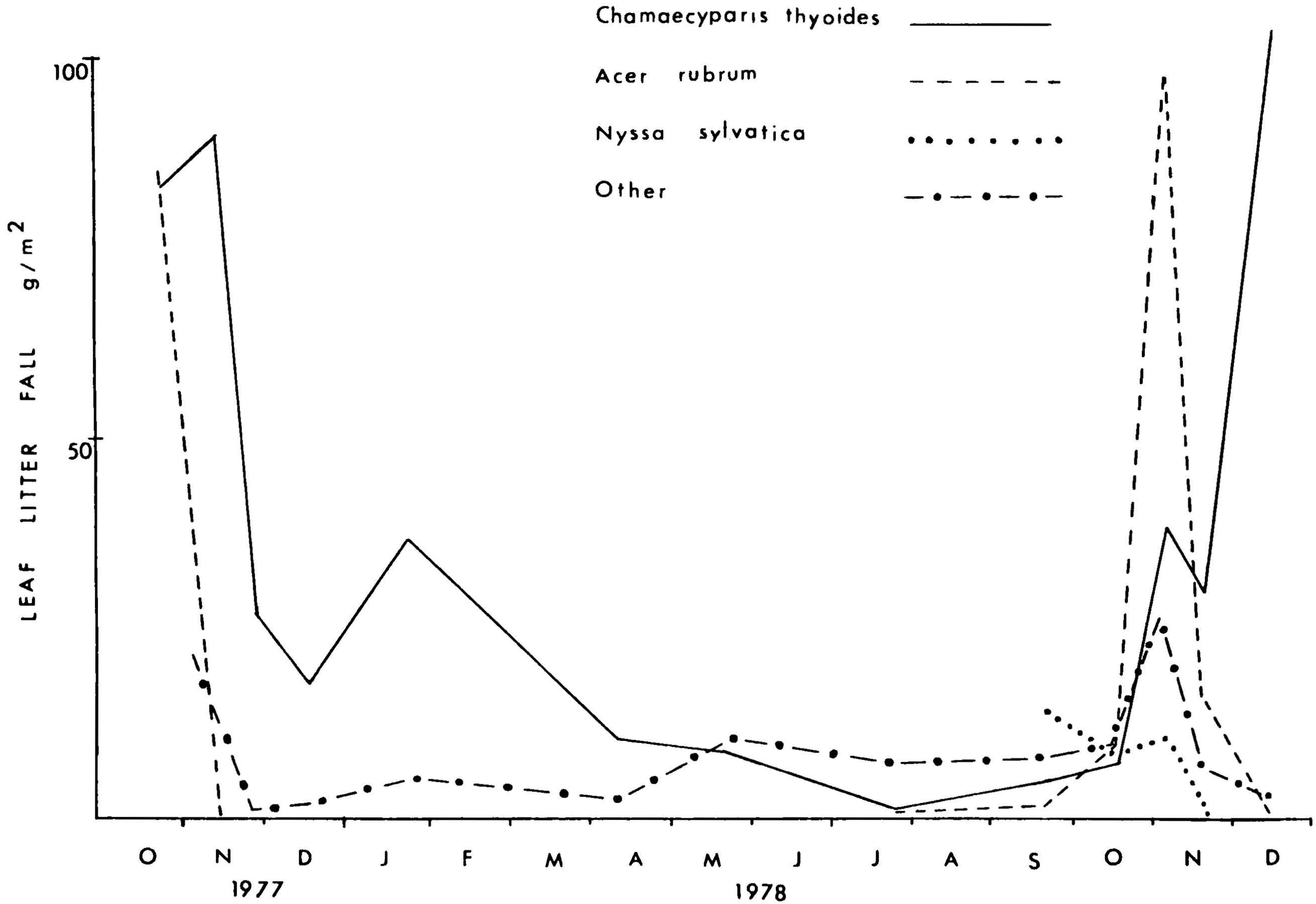
Peak cedar needle deposition occurred later than other species at the cedar community (Figure 6). This species also exhibited a smaller peak during later January, which could have been caused by snow storms. Leaf deposition by red maple and black gum was similar to patterns exhibited by these species at the mixed hardwood community.

Peak leaf fall for all species at the maple-gum community appeared to occur simultaneously in 1977 (Figure 7). However, during the autumn of 1978, water gum and black gum began to shed their leaves earlier than other species. Red maple exhibited a different leaf pattern compared with red maple at the mixed hardwood and cedar stands, in that, although shedding was still abrupt, a second, smaller peak was evident during later December.

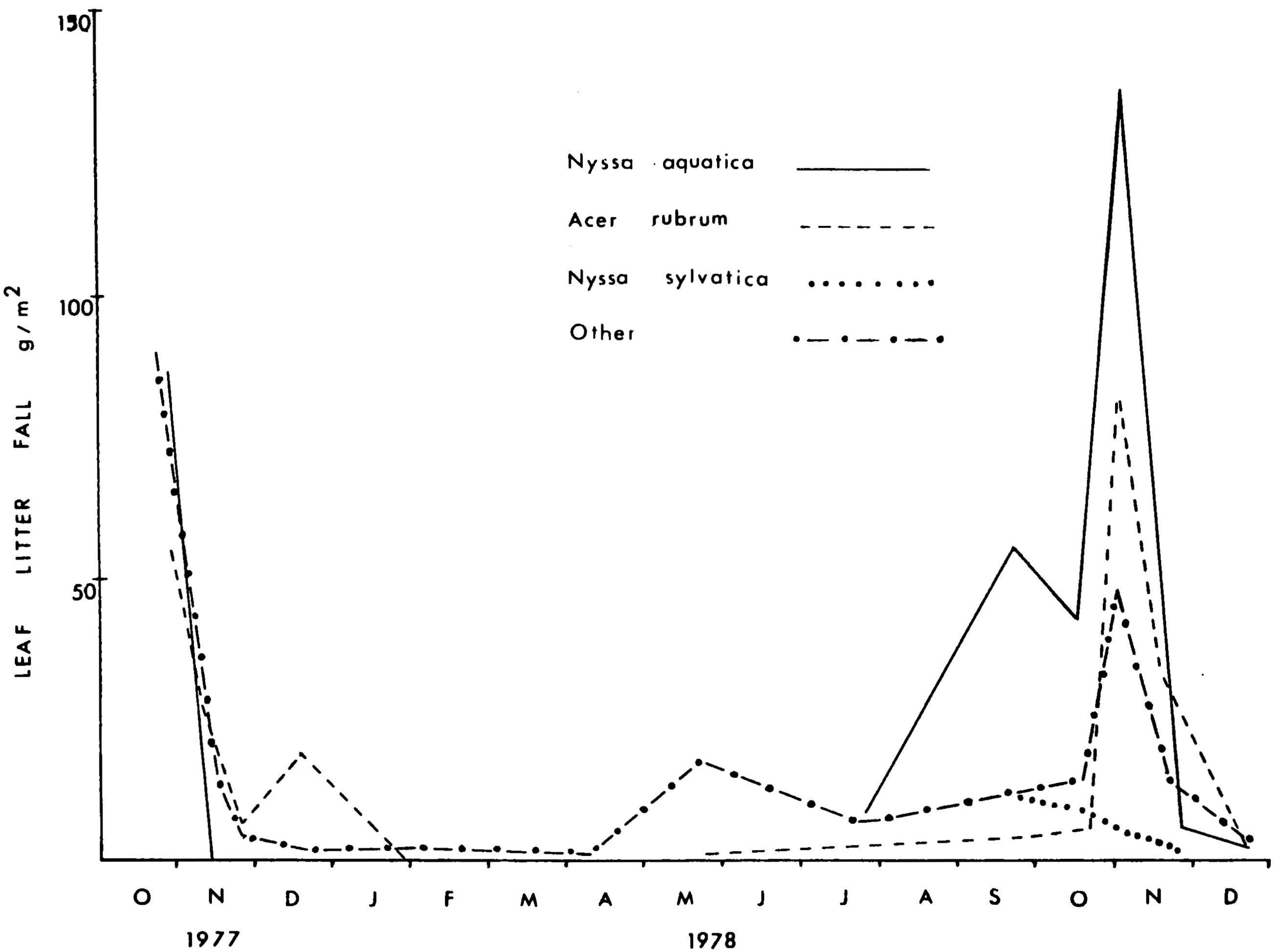
Cypress leaf fall peaked later than other plant species at the cypress stand, and exhibited two peaks during the autumn of 1977 (Figure 8). Water gum leaf fall again began early and was almost complete when litter collections were begun in 1977. Red maple leaf deposition was

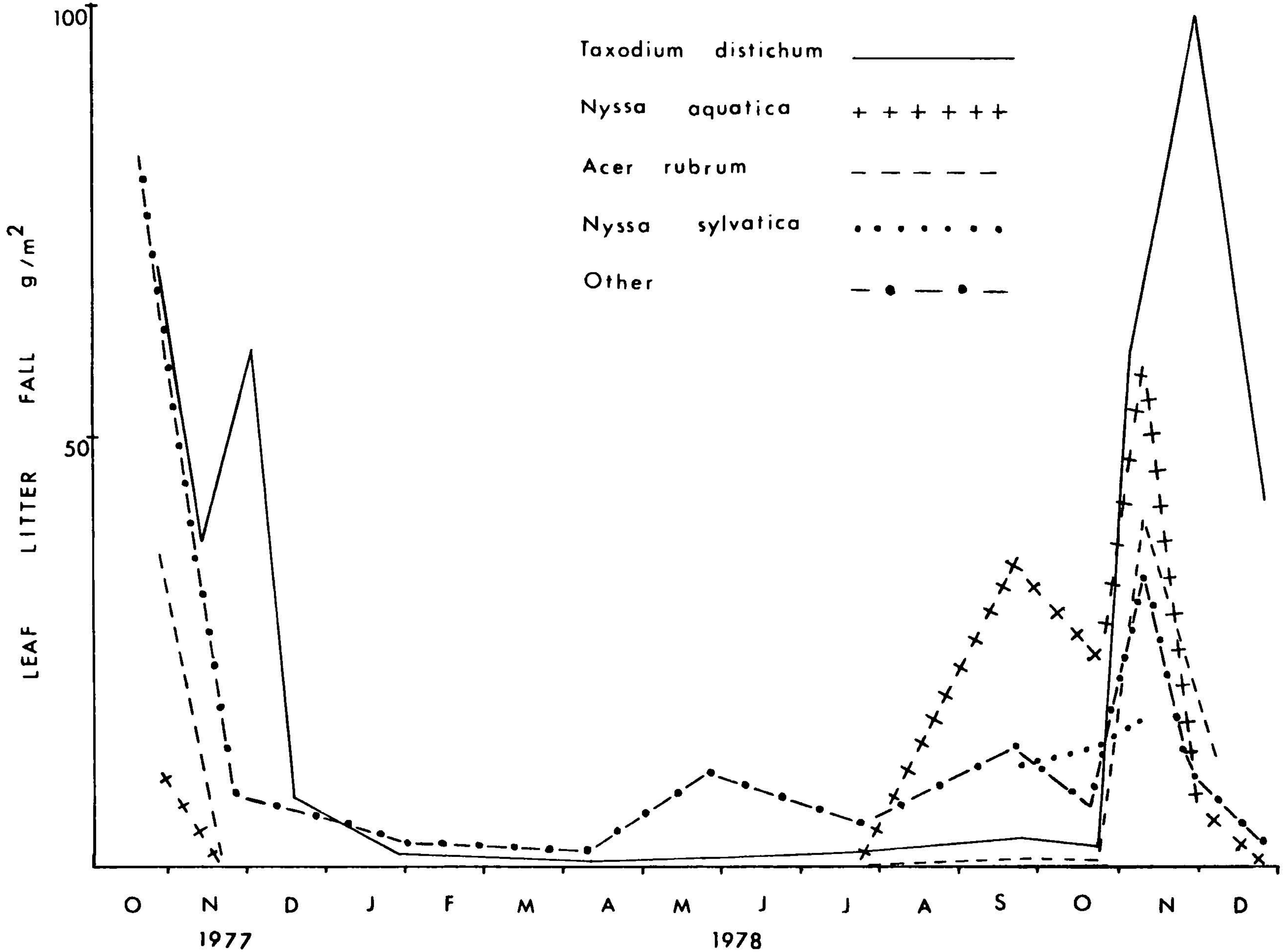


100
50
LEAF LITTER FALL g/m²
Quercus spp.
Acer rubrum
Nyssa sylvatica
Other
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
1977
1978



Chamaecyparis thyoides
Acer rubrum
Nyssa sylvatica
Other
LEAF LITTER FALL g/m2
100
50
O N D J F M A M J J A S O N D
1977
1978


150
100
50
LEAF LITTER FALL g/m2
Nyssa aquatica
Acer rubrum
Nyssa sylvatica
Other
O N D J F M A M J J A S O N D
1977
1978



Taxodium distichum
Nyssa aquatica
Acer rubrum
Nyssa sylvatica
Other
100
50
LEAF LITTER FALL g/m^2
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
1977
1978

complete within a short period of time, as in the mixed hardwood and cedar communities. Peak deposition for black gum differed from that at the other communities, since maximum leaf fall coincided with that of other species at this stand.

The category of Other at the four communities exhibited a small peak in early summer, due mostly to shedding of leaves by understory plant species that were either shaded out after closure of the tree canopy or damaged by insects. Most of the foliage collected during this time was green, indicating possible premature abscission of leaves. However, whether true abscission occurred could not be determined by this study.

*Wood.*__ Woody litter fall, consisting of bark and small branches (less than four cm in diamter) was continuous and variable throughout the study (Figure 9). Peaks occurred in late January, May and December of 1978. The cedar community consistently exhibited greatest deposition in January and May, while the cypress stand had highest deposition in December. The extremely high value recorded at the cedar stand in January was due to a single cedar branch with a large number of twigs which was totally contained in the litter collector.

*Annual litter production.*__Litter fall collected from December 11, 1977 to December 19, 1978 was used in calculating annual deposition rates (Table 1). Breakdown of total litter fall by plant tissue showed that the maple-gum stand had the greatest percentage of leaf tissue in litter fall, followed by the cypress, mixed hardwood and cedar communities. The sequence was reversed for percentages of woody litter. The combined percentages for the remaining tissues (flower, fruit and miscellaneous) were less than 15% of total litter fall at any of the

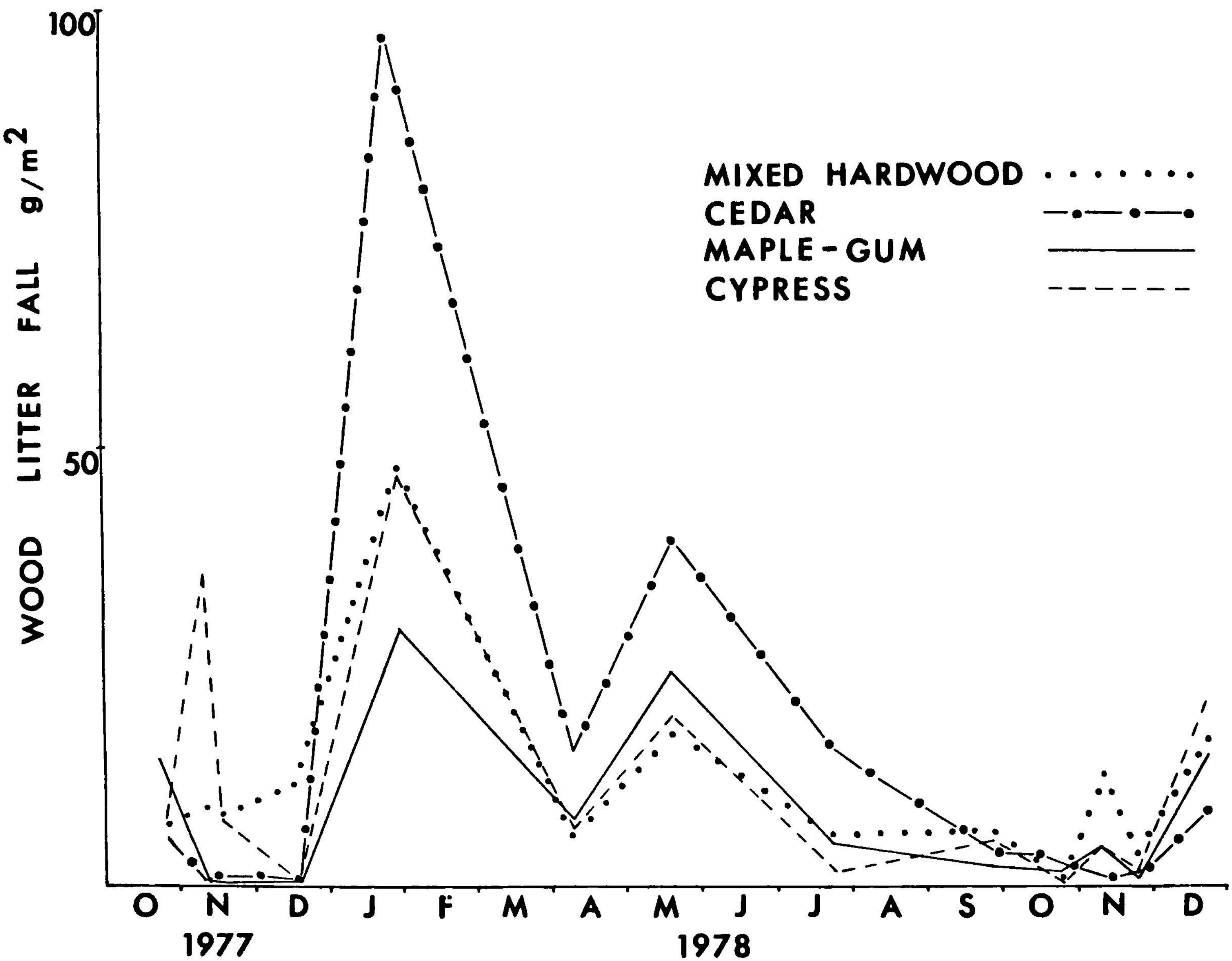

100
50
WOOD LITTER FALL g/m2
MIXED HARDWOOD
CEDAR
MAPLE-GUM
CYPRESS
O N D J F M A M J J A S O N D
1977
1978

Table 1. Mean annual total above-ground litter production for the period December 11, 1977 to December 19, 1978. Values are in g m^{-2} yr^{-1}.

	Maple-gum	%	Cypress	%
Leaf	536.40 (20.28)	81.5	528.32 (22.68)	78.0
Wood	87.52 (16.64)	13.3	109.76 (16.16)	16.2
Flower	6.04 (0.56)	0.9	14.48 (1.52)	2.1
Fruit	10.60 (2.52)	1.6	5.36 (0.88)	0.8
Miscellaneous	17.88 (2.00)	2.7	20.12 (2.52)	2.9
TOTAL	658.56 (29.00)	100.0	678.08 (35.36)	100.0
	Cedar	%	Mixed Hardwood	%
Leaf	506.56 (10.76)	66.9	455.56 (22.52)	69.9
Wood	188.60 (30.20)	24.9	108.32 (16.40)	16.6
Flower	10.20 (1.12)	1.3	14.40 (0.76)	2.2
Fruit	37.84 (3.60)	5.0	44.84 (7.68)	6.9
Miscellaneous	14.36 (1.88)	1.9	29.20 (4.04)	4.4
TOTAL	757.16 (35.16)	100.0	652.16 (29.48)	100.0

four communities, and ranged from 5.2% at the maple-gum stand to 13.5% at the mixed hardwood stand.

The cedar community exhibited the highest annual total litter fall (757.16 g m^{-2} yr^{-1}) followed by the cypress, maple-gum and mixed hardwood communities (652.16 g m^{-2} yr^{-1}). The latter community differed significantly from the other three stands. Annual leaf fall was highest in the maple-gum community (536.40 g m^{-2} yr^{-1}), followed by the cypress, cedar and mixed hardwood communities. The maple-gum stand differed significantly from the other three. Annual wood deposition was greatest at the cedar community, followed by the cypress, mixed hardwood and maple-gum communities. Statistical analysis indicated that the cedar and maple-gum stands were significantly different, while wood deposition at the other two communities was similar.

The mixed hardwood forest, characterized by lower total and leaf litter fall, generally exhibited greatest deposition of fruit, flower and miscellaneous litter. Annual deposition of inflorescence and cone litter was greatest at the cypress and mixed hardwood communities exhibiting almost identical values, while the maple-gum stand had the lowest estimate (6.00 g m^{-2} yr^{-1}). Results from statistical analysis indicated a significant difference between these two and the maple-gum communities. Annual fruit fall was greatest at the mixed hardwood and cedar communities. Variation in fruit litter deposition was significant between these two and the maple-gum and cypress communities. The category of miscellaneous included mainly insect frass (early summer) and to a lesser degree lichens and bud scales. Most of the miscellaneous litter was collected from May to October. Highest estimates were recorded at the mixed hardwood and cypress communities.

Differences between the communities were not statistically significant.

Results from multiway ANOVA's indicated a significant interaction between effects of site and date on litter deposition for all categories except miscellaneous. Analysis of the Multiple Classification Analysis (MCA) table showed 64% of the variation in miscellaneous litter fall was explained by the effect of date , while 65.40% was explained by the combined effects of site and date.

Leaf litter fall in each community was dominated by a single species or an association of species (Table 2). Red maple at the cedar and maple-gum communities exhibited similar percent contribution to total leaf fall, as did red maple in the cypress and mixed hardwood stands. Each of the communities was also characterized by several different species that were minor contributors to total leaf fall. These species were combined into the category of Other in order to clarify comparisons between stands.

*Seasonal leaf fall.*__The seasonal input of leaf litter is reported in table 3. Seasons are based on the phenology of the forest and correspond to periods of dormancy (mid-December to late January), growth (early April to late July) and leaf fall (late July to mid-November). Leaf deposition occurring after November 18 was not utilized in order to avoid overlap; therefore, the data do not coincide with annual leaf data reported in tables 1 and 2. Leaf fall was collected throughout the year, but seasonal trends were obvious. Smallest amounts of leaf deposition occurred during the dormancy period, with the cedar stand exhibiting the greatest amount (43.72 g/m^2). Statistical tests indicated significant differences between this community and the other three. The cedar stand again exhibited the highest value for the

Table 2. Mean annual leaf deposition by species from December 11, 1977 to December 19, 1978. Values are in g m^{-2} yr^{-1}; standard errors are in parentheses.

	Maple-gum	%		Cypress	%
Nyssa aquatica	262.52 (26.12)	49.2	*Taxodium distichum*	209.48 (25.52)	38.9
Acer rubrum	126.40 (13.96)	23.7	*Nyssa aquatica*	126.84 (17.80)	23.6
Nyssa sylvatica	26.32 (8.16)	4.9	*Acer rubrum*	64.04 (16.36)	11.9
Liquidambar styraciflua	23.80 (7.16)	3.9	*Nyssa sylvatica*	30.16 (5.80)	7.5
Other	97.36 (9.48)	18.3	*Liquidambar styraciflua*	13.48 (5.20)	2.5
TOTAL	536.40 (20.28)	100.0	*Quercus laurifolia*	6.88 (2.40)	1.3
			Other	77.44 (13.20)	14.3
			TOTAL	528.32 (22.68)	100.0

	Cedar	%		Mixed Hardwood	%
Chamaecyparis thyoides	250.44 (22.92)	49.4	*Quercus* spp.	199.04 (29.24)	43.7
Acer rubrum	128.92 (15.96)	25.4	*Acer rubrum*	53.36 (13.30)	11.7
Nyssa sylvatica	35.40 (8.20)	7.0	*Nyssa sylvatica*	38.16 (13.64)	8.4
Clethra alnifolia	11.64 (4.04)	2.7	*Liquidambar styraciflua*	35.46 (10.00)	7.8
Magnolia virginiana	5.16 (0.96)	1.0	*Fagus grandifolia*	7.56 (2.36)	1.7
Persea borbonea	1.52 (0.68)	0.3	*Ilex opaca*	1.84 (1.16)	0.4
Other	73.48 (10.60)	14.2	Other	120.12 (16.20)	26.3
TOTAL	506.56 (10.76)	100.0	TOTAL	455.56 (22.52)	100.0

Table 3. Seasonal input of leaf litter. Estimates are in g/m^2; standard errors are in parentheses.

	11/12/77 - 30/1/78	4/4/78 - 26/7/78	27/7/78 - 18/11/78	TOTAL
Maple-gum	3.36 (1.32)	39.40 (3.76)	487.92 (18.12)	530.68
%	0.6	7.4	92.0	100.0
Cypress	5.32 (0.72)	23.68 (1.68)	452.60 (21.92)	481.60
%	1.1	4.9	94.0	100.0
Mixed Hardwood	18.88 (3.04)	43.72 (7.24)	363.00 (21.00)	425.60
%	4.4	10.3	85.3	100.0
Cedar	43.72 (5.28)	49.52 (1.84)	302.76 (14.32)	396.00
%	11.0	12.5	76.5	100.0

growth period (49.52 g/m^2), while the cypress community was lowest (23.68 g/m^2). The Duncan test showed that the mixed hardwood, maple-gum and cedar communities were similar to each other and significantly different from the cypress community. Greatest amounts of leaf deposition occurred during the leaf fall period and at the maple-gum stand, followed by cypress, mixed hardwood and cedar. This sequence is similar to the one for annual leaf deposition except for the reversal of the mixed hardwood and cedar communities. Results from ANOVA tests indicated a significant difference between stands. Differences were observed between all communities except between mixed hardwood and cypress.

Autumn leaf fall. Communities ranked in order of decreasing leaf fall for the autumn of 1977 were maple-gum, cypress, cedar and mixed hardwood (Table 4). The same sequence was observed for the 1978 peak except for the reversal of the cedar and mixed hardwood communities. A oneway ANOVA indicated a significant difference between the stands for both 1977 and 1978. Duncan multiple range tests showed that leaf fall at the maple-gum stand was significantly different from the other three stands for both autumns.

Total leaf deposition was greater during fall of 1978 than 1977 at all stands except cedar, which was lower in 1978. Results from ANOVA tests indicated amounts of total leaf deposition between the two autumn periods were significantly different only at the cypress and cedar communities, while leaf litter deposition of oak at the mixed hardwood stand, water gum at the cypress community and *N.aquatica* and the category of Other at the maple-gum community were also significantly different. Red maple in the cedar stand exhibited highest percent contribution to total leaf fall, followed by red maple in the maple-gum, cypress

Table 4. Leaf fall estimates for the major plant species during comparable periods (October and November) in 1977 and 1978. Values are in g/m^2; standard errors are in parentheses. (*Species included in category Other in 1977).

	Species	1977	%	1978	%
Maple-gum	*Nyssa aquatica*	86.12 (22.16)	37.4	142.84 (12.04)	51.4
	Acer rubrum	53.96 (8.20)	23.4	82.12 (12.84)	29.5
	Nyssa sylvatica	*		5.24 (1.84)	1.9
	Other	90.08 (16.04)	39.2	47.80 (7.24)	17.2
	TOTAL	230.16 (13.44)	100.0	278.00 (10.60)	100.0
Cypress	*Taxodium distichum*	69.28 (9.36)	35.0	59.84 (9.68)	28.4
	Nyssa aquatica	10.96 (4.88)	5.5	57.56 (10.00)	27.3
	Acer rubrum	35.80 (11.68)	18.1	40.88 (13.44)	19.4
	Nyssa sylvatica	*		15.68 (3.56)	7.4
	Other	81.92 (10.48)	41.4	36.92 (8.76)	17.5
	TOTAL	197.96 (16.80)	100.0	210.88 (12.32)	100.0
Cedar	*Chamaecyparis thyoides*	83.84 (10.48)	44.4	38.04 (4.92)	22.0
	Acer rubrum	83.32 (18.48)	44.1	97.80 (12.76)	56.6
	Nyssa sylvatica	*		11.36 (2.68)	6.6
	Other	21.64 (6.84)	11.5	25.68 (5.28)	14.8
	TOTAL	188.80 (26.72)	100.0	172.88 (12.32)	100.0
Mixed Hardwood	*Quercus* spp.	36.28 (6.00)	26.3	59.08 (10.68)	35.8
	Acer rubrum	32.08 (11.84)	23.2	36.92 (10.32)	21.1
	Nyssa sylvatica	*		11.64 (4.44)	6.7
	Other	69.68 (17.20)	50.5	66.96 (8.76)	38.4
	TOTAL	138.04 (18.04)	100.0	174.60 (12.76)	100.0

and mixed hardwood communities. The sequence was the same for both years.

Nutrient concentrations in litter fall

Leaf. Nutrient concentrations in leaf fall for 1977 and 1978 are reported in tables 5 and 6. Observations of standard errors indicated P was the least variable element, while N and Ca were most variable. In general, during the 1977 peak, leaf fall of species at the cypress stand exhibited highest nutrient concentrations except for Ca, while species at the cedar community consistently exhibited lowest concentrations, except for having highest Ca concentrations.

The nutrient concentrations of leaf fall in the more flooded communities showed a distinct pattern different from the two less flooded and more acidic communities. Leaf fall of dominant species at the maple-gum and cypress communities were higher in nutrient concentration than other species in these communities. Water gum in these two stands was consistently low in Ca. At the mixed hardwood and cedar communities however, leaf fall of dominant species was lower in the elements analyzed, while nutrient concentrations of red maple were greatest. Results from ANOVA tests indicated a significant difference between the communities in concentrations of P and K. Duncan multiple range tests showed that cypress differed significantly from the other three stands in P, while K was significantly different between all communities except maple-gum and cypress.

Red maple leaf fall in the cedar stand exhibited highest N, Mg and Ca and lowest K concentrations. Phosphorus concentrations were equal at the mixed hardwood, cypress and cedar communities, all greater than

Table 5. Mean nutrient concentrations in peak leaf fall of major species for 1977. Values are expressed as % dry mass; standard errors are in parentheses.

	Species	N	P	K	Ca	Mg
Maple-gum	*Nyssa aquatica*	1.60 (0.05)	0.08 (0.00)	0.36 (0.02)	0.99 (0.03)	0.34 (0.01)
	Acer rubrum	1.28 (0.08)	0.06 (0.00)	0.33 (0.02)	1.57 (0.21)	0.25 (0.02)
Cypress	*Taxodium distichum*	1.83 (0.02)	0.11 (0.00)	0.32 (0.04)	1.31 (0.02)	0.19 (0.00)
	Nyssa aquatica	1.56 (0.07)	0.09 (0.00)	0.34 (0.01)	0.94 (0.08)	0.32 (0.00)
	Acer rubrum	1.31 (0.04)	0.07 (0.00)	0.40 (0.05)	1.16 (0.03)	0.25 (0.01)
Cedar	*Chamaecyparis thyoides*	0.97 (0.02)	0.05 (0.00)	0.22 (0.00)	1.38 (0.06)	0.15 (0.00)
	Acer rubrum	1.71 (0.06)	0.07 (0.00)	0.29 (0.02)	1.83 (0.05)	0.26 (0.01)
Mixed Hardwood	*Quercus* spp.	1.00 (0.11)	0.05 (0.00)	0.23 (0.01)	1.26 (0.11)	0.24 (0.01)
	Acer rubrum	1.48 (0.13)	0.07 (0.01)	0.31 (0.03)	1.34 (0.14)	0.24 (0.01)

Table 6. Mean nutrient concentrations in peak leaf fall of major species for 1978. Values are expressed as % dry mass; standard errors are in parentheses.

	Species	N	P	K	Ca	Mg
Maple-gum	*Nyssa aquatica*	1.30 (0.07)	0.07 (0.00)	0.37 (0.02)	1.00 (0.04)	0.35 (0.01)
	Acer rubrum	1.06 (0.05)	0.06 (0.00)	0.32 (0.03)	1.23 (0.09)	0.23 (0.01)
	Nyssa sylvatica	1.09 (0.08)	0.06 (0.00)	0.25 (0.01)	1.05 (0.01)	0.38 (0.01)
Cypress	*Taxodium distichum*	1.40 (0.03)	0.10 (0.01)	0.24 (0.01)	1.36 (0.05)	0.21 (0.00)
	Nyssa aquatica	1.36 (0.06)	0.09 (0.00)	0.38 (0.01)	1.03 (0.04)	0.38 (0.01)
	Acer rubrum	1.03 (0.02)	0.07 (0.00)	0.35 (0.02)	1.25 (0.11)	0.26 (0.02)
	Nyssa sylvatica	1.20 (0.04)	0.08 (0.00)	0.24 (0.01)	0.98 (0.03)	0.41 (0.01)
Cedar	*Chamaecyparis thyoides*	1.20 (0.08)	0.07 (0.00)	0.18 (0.01)	1.51 (0.07)	0.14 (0.00)
	Acer rubrum	1.21 (0.08)	0.07 (0.00)	0.18 (0.02)	1.58 (0.12)	0.24 (0.01)
	Nyssa sylvatica	1.29 (0.04)	0.06 (0.00)	0.15 (0.02)	1.06 (0.01)	0.40 (0.01)
Mixed Hardwood	*Quercus* spp.	1.25 (0.04)	0.06 (0.00)	0.24 (0.01)	1.09 (0.05)	0.21 (0.02)
	Acer rubrum	1.00 (0.01)	0.06 (0.00)	0.30 (0.02)	1.46 (0.08)	0.30 (0.02)
	Nyssa sylvatica	1.21 (0.08)	0.05 (0.01)	0.22 (0.04)	1.38 (0.23)	0.38 (0.04)

at the maple-gum community. Red maple leaf litter at the two more flooded stands was greater in K concentrations than at the two less flooded communities. A oneway ANOVA showed a significant difference between the communities only in N concentrations, with cedar differing significantly from the other three communities.

Nutrient concentrations of leaf litter in the four communities showed similarities between 1977 and 1978. Leaf fall of species at the cypress community again exhibited highest N, P and K and lowest Ca concentrations during the 1978 peak (Table 6). High Ca and low K and Mg concentrations in the cedar stand leaf fall were also similar to the 1977 peak.

During 1978, dominant species at the mixed hardwood, maple-gum and cypress communities exhibited highest concentrations of N and P, with cypress being highest in Ca and water gum at the maple-gum stand exhibiting highest K concentrations. Leaf fall of dominant species at the mixed hardwood, cypress and cedar exhibited low Mg values, while black gum litter exhibited highest Mg concentrations in the four stands. Calcium concentrations was greatest in red maple leaf fall at the mixed hardwood, maple-gum and cedar communities. ANOVA tests indicated significant differences between communities in P and K concentrations, similar to the 1977 data. The Duncan tests again showed a significant difference between the cypress and the other three stands for P, and between all the communities, except cypress and maple-gum for K.

Red maple N and Ca concentrations were high at the cedar stand, while Mg and Ca were relatively high at the cypress stand. Phosphorus concentrations were equal at these two stands and greater than P at the mixed hardwood and maple-gum communities, which were also equal to each other. Variations between stands were significant for concentrations of K, Mg and P. Significant differences were observed between cedar and the other three communities in K, between the mixed hardwood and maple-gum stands in Mg and between the mixed hardwood and cypress stands in P.

Black gum leaf fall was highest in nutrient concentrations at the cedar community, except for K. Leaf fall at the cypress stand was relatively high in K, Mg and P, while concentrations of the other elements were relatively high at the mixed hardwood community. Differences between stands were significant for P and K concentrations. Phosphorus was significantly different between cedar and the other three communities.

Nutrient concentrations of peak leaf fall for 1977 and 1978 were highly variable. However, trends in nutrient concentrations were indicative of an early leaf fall for the 1977 autumn. Species at the more flooded communities exhibited higher N and P and lower Mg and Ca concentrations in 1977. Nutrient concentrations in leaf fall of dominant species at the cypress, maple-gum and cedar communities were significantly different between the two peak periods. N concentrations were significantly different at all three communities, Mg only at the cypress stand, while K and P differed significantly at the cedar community. Red maple leaf litter at all stands was higher in concentrations of N, P and K during the 1977 peak, while Mg and Ca were greater at the mixed hardwood and cypress communities during 1978. Statistical analyses indicated differences between the two years were significant in N at the mixed hardwood, cypress and cedar communities,and in K concentrations at the latter community.

Non-leaf.__In general, concentrations in small woody litter were more variable than in leaf litter (Table 7). Estimates reported are for bark and twigs combined. Small woody litter deposition at the maple-gum stand consistently exhibited greatest nutrient concentrations except for Ca, which was highest at the mixed hardwood community. The mixed hardwood and cedar communities were lowest in P and K concentrations. ANOVA tests showed that only K concentrations differed significantly between the stands. The Duncan tests showed concentrations of K and Mg in small woody litter fall at the maple-gum stand were significantly different from the other three stands.

Nutrient analyses were also performed on peak deposition of flower (cones), fruit and miscellaneous litter fall in each community. Maximum deposition of inflorescences occurred between April and May and consisted mostly of red maple flowers. Peak deposition of fruit and miscellaneous litter were recorded between May and July. In general, nutrient concentrations of reproductive tissues were greater than concentrations in leaf or woody litter fall. The maple-gum and cedar communities exhibited higher concentrations in flower litter except for Ca and K concentrations.

Nutrient concentrations in fruit litter were generally higher than in flower litter (especially N) except for Ca. Fruit deposition at the mixed hardwood stand exhibited highest concentrations except for Ca, which was highest at the cedar community. Fruit litter at the maple-gum stand was consistently low in nutrients. A oneway ANOVA showed significant differences between communities for all nutrients except N and Mg. The Duncan test showed all communities differed significantly in Ca, while P and K were similar at cedar and maple-gum and signifi-

Table 7. Mean nutrient concentrations in non-leaf litter fall during peak deposition periods in 1978. Values are expressed as % dry mass; standard errors are in parentheses.

		Maple-gum	Cypress	Cedar	Mixed Hardwood
Wood					
	N	1.22 (0.14)	0.97 (0.03)	1.17 (0.00)	0.99 (0.06)
	P	0.08 (0.01)	0.08 (0.00)	0.07 (0.01)	0.06 (0.00)
	K	0.37 (0.08)	0.26 (0.02)	0.16 (0.02)	0.21 (0.01)
	Ca	1.64 (0.16)	2.10 (0.22)	1.54 (0.11)	2.39 (0.18)
	Mg	0.16 (0.01)	0.11 (0.01)	0.11 (0.02)	0.11 (0.03)
Flower					
	N	2.70 (0.04)	2.58 (0.02)	2.71 (0.03)	2.45 (0.07)
	P	0.30 (0.01)	0.28 (0.01)	0.29 (0.00)	0.29 (0.01)
	K	0.70 (0.03)	0.69 (0.04)	0.75 (0.01)	0.79 (0.03)
	Ca	1.16 (0.03)	1.11 (0.08)	1.06 (0.02)	0.95 (0.06)
	Mg	0.16 (0.01)	0.13 (0.01)	0.14 (0.00)	0.13 (0.01)
Fruit					
	N	4.29 (0.06)	4.31 (0.08)	4.50 (0.12)	4.58 (0.05)
	P	0.41 (0.01)	0.47 (0.01)	0.40 (0.02)	0.53 (0.01)
	K	0.65 (0.00)	0.80 (0.00)	0.66 (0.03)	0.94 (0.04)
	Ca	0.51 (0.01)	0.47 (0.00)	0.58 (0.01)	0.57 (0.01)
	Mg	0.17 (0.01)	0.19 (0.00)	0.18 (0.00)	0.22 (0.00)
Miscellaneous					
	N	2.90 (0.03)	3.29 (0.08)	2.36 (0.05)	2.13 (0.37)
	P	0.18 (0.01)	0.19 (0.00)	0.13 (0.00)	0.17 (0.00)
	K	0.19 (0.03)	0.23 (0.02)	0.17 (0.01)	0.27 (0.01)
	Ca	0.88 (0.06)	0.83 (0.02)	0.91 (0.01)	0.84 (0.05)
	Mg	0.13 (0.01)	0.14 (0.01)	0.10 (0.01)	0.15 (0.01)

cantly different from the mixed hardwood and cypress stands.

Nitrogen concentrations of miscellaneous litter fall were relatively high and greater than N in leaf fall. The cypress stand exhibited highest values for N and P and lowest for Ca. The mixed hardwood community, on the other hand, exhibited highest K and Mg concentrations and lowest N. Miscellaneous litter fall at the cedar stand was consistenly lower in nutrient content except Ca, which was highest at this community. Results from ANOVA tests indicated significant differences between the communities for all nutrients, except Ca. The Duncan test showed that differences were significant between all stands for N and K, while cedar differed significantly from the other three communities in P and Mg.

Nutrient content of litter fall

*Leaf.*__Deposition of nutrients via leaf fall during the peak period for 1977 is shown in table 8. Estimates are the product of mean biomass and nutrient concentration. The category of Other was included in order to obtain a more complete picture of nutrient deposition through leaf fall at the four communities. The sequence for relative abundance of elements at the two more flooded stands was N>Ca>K>Mg>P. In the remaining stands, the sequence was Ca>N>K>Mg>P for the cedar stand and Ca>N>Mg>K>P for the mixed hardwood community.

Variabilities in nutrient deposition at each community reflected differences in plant species between communities. Greatest contributions to K and Mg deposition at the maple-gum stand were from water gum, while N, P and Ca deposition were highest for the category of Other. This category at the cypress community accounted for over 40% of leaf deposition and also contributed most to deposition of K, Mg and Ca. Cypress

Table 8. Deposition of leaf litter and nutrients for the period October 8 - October 31 1977. Estimates are in kg/ha; percentages are in parentheses.

Species	Litter mass	N	P
		Maple-gum	
Nyssa aquatica	861.2 (37.4)	13.78 (39.5)	0.69 (39.7)
Acer rubrum	539.6 (23.4)	6.91 (19.8)	0.32 (18.7)
Other	900.8 (39.2)	14.23 (40.7)	0.72 (41.6)
TOTAL	2301.6 (100.0)	34.92 (100.0)	1.73 (100.0)
		Cypress	
Taxodium distichum	692.8 (35.0)	12.68 (40.2)	0.76 (41.2)
Nyssa aquatica	109.6 (5.5)	1.71 (5.4)	0.10 (5.4)
Acer rubrum	358.0 (18.1)	4.69 (14.9)	0.25 (13.6)
Other	819.2 (41.4)	12.45 (39.5)	0.74 (39.8)
TOTAL	1979.6 (100.0)	31.53 (100.0)	1.85 (100.0)
		Cedar	
Chamaecyparis thyoides	838.4 (44.4)	8.13 (31.1)	0.42 (35.7)
Acer rubrum	833.2 (44.1)	14.25 (54.5)	0.58 (49.6)
Other	216.4 (11.5)	3.77 (14.4)	0.17 (14.7)
TOTAL	1888.0 (100.0)	26.15 (100.0)	1.17 (100.0)
		Mixed Hardwood	
Quercus spp.	362.8 (26.3)	3.63 (20.9)	0.18 (20.2)
Acer rubrum	320.8 (23.2)	4.75 (27.3)	0.23 (25.2)
Other	696.8 (50.5)	8.99 (51.8)	0.49 (54.6)
TOTAL	1380.4 (100.0)	17.37 (100.0)	0.90 (100.0)

continued ...

Table 8. (continued)

Species	K	Ca	Mg
	Maple-gum		
Nyssa aquatica	3.10 (39.5)	8.53 (29.1)	2.93 (44.2)
Acer rubrum	1.78 (22.7)	8.47 (28.9)	1.35 (20.4)
Other	2.97 (37.8)	12.34 (42.0)	2.34 (35.6)
TOTAL	7.85 (100.0)	29.34 (100.0)	6.62 (100.0)
	Cypress		
Taxodium distichum	2.22 (33.0)	9.08 (37.0)	1.32 (25.8)
Nyssa aquatica	0.37 (5.5)	1.03 (4.2)	0.35 (6.9)
Acer rubrum	1.43 (21.3)	4.15 (17.0)	0.90 (17.5)
Other	2.70 (40.2)	10.24 (41.8)	2.54 (49.8)
TOTAL	6.72 (100.0)	24.50 (100.0)	5.11 (100.0)
	Cedar		
Chamaecyparis thyoides	1.84 (38.1)	11.57 (38.7)	1.26 (29.3)
Acer rubrum	2.42 (49.9)	15.25 (51.0)	2.17 (50.5)
Other	0.58 (12.0)	3.07 (10.3)	0.87 (20.2)
TOTAL	4.84 (100.0)	29.89 (100.0)	4.30 (100.0)
	Mixed Hardwood		
Quercus spp.	0.83 (24.3)	4.57 (25.5)	0.87 (23.8)
Acer rubrum	0.99 (29.0)	4.30 (24.0)	0.77 (21.0)
Other	1.60 (46.7)	9.06 (50.5)	2.02 (55.2)
TOTAL	3.42 (100.0)	17.93 (100.0)	3.66 (100.0)

leaf fall returned greatest amounts of N and P to the forest floor in this stand. Cedar and red maple at the cedar community exhibited similar percent contribution to total leaf fall. However, nutrient deposition was greater in red maple leaf fall, accounting for approximately 50% of P, K, Mg and Ca deposition and almost 55% of N deposition. The combined leaf fall of *Quercus* and *A. rubrum* at the mixed hardwood community accounted for almost 50% of total leaf fall, and between 45 and 50% of nutrient deposition except for K, which was higher.

Nutrient deposition in red maple leaf litter at the four stands was highest at the cedar community and second highest at the maple-gum community, for all nutrients. Lowest estimates were recorded for red maple at the mixed hardwood community in P, K and Mg deposition and at the cypress stand in N and Ca deposition. A comparison of percentages of leaf fall and nutrient deposition to the total at each community showed N and P were relatively low in red maple leaf fall at the most flooded communities and K was relatively high at the cypress and mixed hardwood communities. A similar comparison for the category of Other indicated that a species or combination of species was relatively high in Mg at the cypress, cedar and mixed hardwood communities.

Nutrient deposition via leaf fall during the peak period of 1978 included *N. sylvatica* (Table 9). Black gum sheds its leaves earlier than other plant species; therefore values reported here do not correspond to peak leaf fall of this species. The two wetter stands exhibited the same sequence for relative abundance of elements: N>Ca>K>Mg>P, which was similar to the sequence for 1977. The two drier stands also exhibited similar relative abundance of nutrients. However, compared to the more flooded communities, relative positions of N and

Table 9. Deposition of leaf litter and nutrients for the period October 21 - November 5, 1978. Estimates are in kg/ha; percentages are in parentheses.

Species	Litter mass	N	P
	Maple-gum		
Nyssa aquatica	1428.4 (51.4)	18.57 (55.6)	1.00 (52.5)
Acer rubrum	821.2 (29.5)	8.71 (26.1)	0.49 (25.9)
Nyssa sylvatica	52.4 (1.9)	0.57 (1.7)	0.03 (1.6)
Other	478.0 (17.2)	5.55 (16.6)	0.38 (20.0)
TOTAL	2780.0 (100.0)	33.40 (100.0)	1.90 (100.0)
	Cypress		
Taxodium distichum	598.4 (28.4)	8.38 (31.5)	0.60 (32.2)
Nyssa aquatica	575.6 (27.3)	7.83 (29.5)	0.52 (27.9)
Acer rubrum	408.8 (19.4)	4.21 (15.8)	0.29 (15.4)
Nyssa sylvatica	156.8 (7.4)	1.88 (7.1)	0.13 (6.7)
Other	369.2 (17.5)	4.28 (16.1)	0.33 (17.8)
TOTAL	2108.8 (100.0)	26.58 (100.0)	1.87 (100.0)
	Cedar		
Chamaecyparis thyoides	380.4 (22.0)	4.57 (20.9)	0.27 (22.2)
Acer rubrum	978.0 (56.6)	11.83 (54.2)	0.69 (57.1)
Nyssa sylvatica	113.6 (6.6)	1.47 (6.7)	0.07 (5.7)
Other	256.8 (14.8)	3.98 (18.2)	0.18 (15.0)
TOTAL	1728.8 (100.0)	21.85 (100.0)	1.21 (100.0)
	Mixed Hardwood		
Quercus spp.	590.8 (33.8)	7.39 (35.5)	0.35 (32.1)
Acer rubrum	369.2 (21.2)	3.69 (17.8)	0.22 (20.1)
Nyssa sylvatica	116.4 (6.7)	1.41 (6.8)	0.06 (5.3)
Other	669.6 (38.3)	8.30 (39.9)	0.47 (42.5)
TOTAL	1746.0 (100.0)	20.79 (100.0)	1.10 (100.0)

Table 9. (continued)

Species	K	Ca	Mg
		Maple-gum	
Nyssa aquatica	5.29 (55.2)	14.28 (43.9)	5.00 (59.3)
Acer rubrum	2.83 (29.5)	10.10 (31.1)	1.89 (22.4)
Nyssa sylvatica	0.13 (1.4)	0.55 (1.7)	0.20 (2.4)
Other	1.34 (13.9)	7.60 (23.3)	1.34 (15.9)
TOTAL	9.59 (100.0)	32.53 (100.0)	8.43 (100.0)
		Cypress	
Taxodium distichum	1.40 (21.8)	8.14 (31.4)	1.26 (20.1)
Nyssa aquatica	2.19 (33.3)	5.93 (22.8)	2.19 (34.9)
Acer rubrum	1.43 (21.8)	5.11 (19.7)	1.06 (17.0)
Nyssa sylvatica	0.38 (5.7)	1.54 (5.9)	0.64 (10.3)
Other	1.15 (17.4)	5.24 (20.2)	1.11 (17.7)
TOTAL	6.59 (100.0)	25.96 (100.0)	6.26 (100.0)
		Cedar	
Chamaecyparis thyoides	0.69 (21.4)	5.74 (22.1)	0.53 (11.4)
Acer rubrum	1.76 (54.9)	15.45 (59.4)	2.35 (50.3)
Nyssa sylvatica	0.17 (5.3)	1.20 (4.6)	0.45 (9.7)
Other	0.59 (18.4)	3.62 (13.9)	1.34 (28.6)
TOTAL	3.21 (100.0)	26.01 (100.0)	4.67 (100.0)
		Mixed Hardwood	
Quercus spp.	1.42 (33.3)	6.44 (28.0)	1.24 (24.8)
Acer rubrum	1.11 (26.0)	5.39 (23.4)	1.11 (22.2)
Nyssa sylvatica	0.26 (6.0)	1.61 (7.0)	0.44 (8.8)
Other	1.47 (34.7)	9.58 (41.6)	2.21 (44.2)
TOTAL	4.26 (100.0)	23.02 (100.0)	5.00 (100.0)

Ca, and also K and Mg were reversed. In general, the more flooded communities cycled a greater amount of nutrients through leaf fall during both autumn periods.

The maple-gum stand was dominated by water gum and red maple, accounting for nearly 80% of leaf fall during the 1978 autumn maximum. Water gum accounted for over 50% of leaf fall and nutrient deposition except for Ca, which was relatively high in red maple leaf fall. At the cypress community, *T. distichum* and water gum exhibited similar percent contributions to total leaf deposition at this community. However, cypress accounted for over 30% of N, P and Ca deposition, while water gum accounted for over 30% of N, P and Ca deposition. *N. aquatica* again exhibited relatively low Ca, as did water gum in the maple-gum community. The several species of oak at the mixed hardwood community accounted for almost 34% of leaf fall and between 32 and 36% of N, P and K deposiiton. Percentages of Mg and Ca were lower, with Mg being only slightly higher than Mg for red maple, which accounted for slightly over 20% of leaf deposition. This stand had the highest species diversity and the category of Other contributed nearly 40% of total leaf fall and accounted for between 34 and 44% of nutrient deposition at this stand. Peak leaf fall at the cedar community was dominated by red maple, which was responsible for 55% of total leaf fall and between 50 and 60% of nutrient deposition. Cedar accounted for 22% of litter deposition and exhibited similar percentage values for nutrient deposition except for Mg, which was much lower. Black gum accounted for slightly over 6% of leaf fall, yet exhibited a Mg value similar to that of the cedar litter.

Red maple leaf fall and nutrient deposition were greatest in the cedar and maple-gum communities. Red maple at the cypress stand exhibited the lowest deposition of Mg and Ca, yet leaf fall rates were lowest at the mixed hardwood community. Black gum deposition of leaf litter and of N,P,K, and Mg were greatest at the cypress community, while Ca deposition was greatest at the mixed hardwood community. Lowest values were consistently recorded at the maple-gum stand.

Input of nutrients to the forest floor during periods of peak leaf fall in 1977 and 1978 showed some similarities between communities. Nutrient deposition was greater in 1978 at the mixed hardwood and maple-gum communities, except for N deposition at the maple-gum stand, which was greater in 1977. Nitrogen and K deposition, at both the cypress and cedar communities, were greater in 1977, while P and Mg deposition were greater in 1978. A ranking of the communities in order of decreasing nutrient deposition for 1977 showed that deposition of N, K and Mg followed the sequence of ranked stands for litter deposition (1977). However, P deposition at the cypress community was greater than at the maple-gum stand, while Ca deposition at the cedar stand was greater than at the maple-gum and cypress communities. A similarity between sequences of ranked stands for nutrient deposition and leaf fall in 1978 was only evident in K and Mg deposition. Also, the mixed hardwood community consistently exhibited lowest deposition, even though leaf fall was lowest at the cedar community. Contribution by red maple to total leaf and nutrient deposition at each stand showed more variability between the two autumns at the maple-gum and cedar communities. Trends were observed for both years that differentiate these two communities from the mixed hardwood and cypress communities. Relative contributions by red maple to total nutrient deposition at each community were highest for K at the mixed hardwood and cypress communities and for Ca at the maple-gum and cedar communities.

Deposition of nutrients in litter collected during peak periods for each category at the four communities in 1978 are reported in table 10. Wood estimates however do not correspond to peak deposition. All the communities, except cedar, exhibited the same sequence for relative abundance of elements: N>Ca>K>Mg>P. A similar sequence was observed at the cedar stand, except for the reversal of K and Mg. Again, more nutrients were cycled through litter fall at the two more flooded stands than at the two less flooded stands.

Leaf fall was the major contributor to total nutrient deposition in the four communities. Leaf litter fall cycled between 88 and 96% of the total Mg deposition and between 80 and 92% of the Ca deposition. Percentages of N and K deposition were more variable, ranging from 66% to 82% and 65% to 90%, respectively. Amounts of P cycled through leaf fall were lower and ranged from 51% at the mixed hardwood community to 76% at the maple-gum community.

In general, small woody litter contributed small amounts of nutrients to total deposition at each community. Deposition of woody litter and nutrients were greatest at the mixed hardwood stand and lowest at the cedar community. However, this is misleading since annual woody litter fall was greatest at the cedar stand. The two more flooded communities exhibited equal wood fall estimates, but only P deposition was equal among the nutrients. Deposition of N, K and Mg were greater at the maple-gum community, while Ca deposition was greater at the cypress community.

Contribution of nutrients by reproductive organs and miscellaneous

Table 10. Deposition of litter and nutrients in litter fall collected during peak deposition periods in 1978. Estimates are in kg/ha; percentages are in parentheses.

Tissue	Litter mass	N	P
	Maple-gum		
Leaf	2780.0 (91.1)	33.39 (81.5)	1.91 (75.9)
Wood	51.2 (1.7)	0.63 (1.5)	0.04 (1.6)
Flower	48.0 (1.6)	1.30 (3.2)	0.14 (5.7)
Fruit	47.6 (1.6)	2.04 (5.0)	0.20 (7.8)
Miscellaneous	124.8 (4.0)	3.62 (8.8)	0.23 (9.0)
TOTAL	3051.6 (100.0)	40.98 (100.0)	2.52 (100.0)
	Cypress		
Leaf	2108.8 (88.3)	26.58 (77.3)	1.86 (75.3)
Wood	51.2 (2.1)	0.50 (1.5)	0.04 (1.7)
Flower	70.4 (3.0)	1.82 (5.3)	0.20 (8.0)
Fruit	24.8 (1.0)	1.07 (3.1)	0.12 (4.7)
Miscellaneous	134.4 (5.6)	4.42 (12.8)	0.26 (10.3)
TOTAL	2389.6 (100.0)	34.39 (100.0)	2.48 (100.0)
	Cedar		
Leaf	1728.8 (85.6)	21.84 (70.2)	1.20 (60.9)
Wood	13.6 (0.7)	0.16 (0.5)	0.01 (0.5)
Flower	60.8 (3.0)	1.65 (5.3)	0.18 (8.9)
Fruit	112.4 (5.6)	5.06 (16.3)	0.45 (22.9)
Miscellaneous	102.8 (5.1)	2.43 (7.7)	0.13 (6.8)
TOTAL	2018.4 (100.0)	31.14 (100.0)	1.97 (100.0)
	Mixed Hardwood		
Leaf	1746.0 (79.3)	20.79 (66.3)	1.10 (51.4)
Wood	107.2 (4.9)	1.06 (3.4)	0.06 (3.0)
Flower	111.6 (5.1)	2.73 (8.7)	0.32 (15.1)
Fruit	69/2 (3.1)	3.17 (10.1)	0.37 (17.1)
Miscellaneous	168.8 (7.6)	3.60 (11.5)	0.29 (13.4)
TOTAL	2202.8 (100.0)	31.35 (100.0)	2.14 (100.0)

Table 10. (continued)

Tissue	K	Ca	Mg
		Maple-gum	
Leaf	9.58 (90.0)	32.54 (92.2)	8.43 (95.5)
Wood	0.19 (1.8)	0.84 (2.4)	0.08 (0.9)
Flower	0.34 (3.1)	0.56 (1.6)	0.08 (0.9)
Fruit	0.31 (2.9)	0.24 (0.7)	0.08 (0.9)
Miscellaneous	0.24 (2.2)	1.10 (3.1)	0.16 (1.8)
TOTAL	10.66 (100.0)	35.28 (100.0)	8.83 (100.0)
		Cypress	
Leaf	6.58 (85.4)	25.96 (89.4)	6.26 (94.2)
Wood	0.13 (1.7)	1.08 (3.7)	0.06 (0.8)
Flower	0.49 (6.3)	0.78 (2.7)	0.09 (1.4)
Fruit	0.20 (2.6)	0.12 (0.4)	0.05 (0.7)
Miscellaneous	0.31 (4.0)	1.12 (3.8)	0.19 (2.9)
TOTAL	7.71 (100.0)	29.06 (100.0)	6.65 (100.0)
		Cedar	
Leaf	3.21 (69.7)	26.02 (91.4)	4.67 (92.0)
Wood	0.02 (0.5)	0.21 (0.7)	0.02 (0.3)
Flower	0.46 (9.9)	0.64 (2.3)	0.09 (1.7)
Fruit	0.74 (16.1)	0.65 (2.3)	0.20 (4.0)
Miscellaneous	0.18 (3.8)	0.94 (3.3)	0.10 (2.0)
TOTAL	4.61 (100.0)	28.46 (100.0)	5.08 (100.0)
		Mixed Hardwood	
Leaf	4.26 (65.8)	23.01 (80.9)	5.00 (88.2)
Wood	0.23 (3.5)	2.56 (9.0)	0.12 (2.1)
Flower	0.88 (13.6)	1.06 (3.7)	0.15 (2.6)
Fruit	0.65 (10.1)	0.39 (1.4)	0.15 (2.7)
Miscellaneous	0.46 (7.0)	1.42 (5.0)	0.25 (4.4)
TOTAL	6.48 (100.0)	28.44 (100.0)	5.67 (100.0)

litter to toal nutrient deposition differed at each community. Contributions by these categories were generally higher for N, P and K than for the other two elements. Contribution to Mg deposition was relatively low for flower and miscellaneous litter, while fruit litter accounted for a relatively small percentage of total Ca deposition. Miscellaneous and reproductive tissue litter seemed important contributors to total nutrient deposition at the mixed hardwood community (especially P). These categories appeared relatively less significant at the maple-gum community. Nutrient inputs to the forest floor in this stand were dominated by leaf litter. Deposition of nutrients in miscellaneous litter fall seemed relatively significant at the cypress community, while fruit fall at the cedar community accounted for approximately 16% of total N and K and almost 23% of total P deposition.

Macrolitter. Deposition of macrolitter, i.e. tree boles and large branches (greater than four cm in diameter) was investigated at the mixed hardwood, maple-gum and cypress communities. Deposition of large woody litter was greatest at the maple-gum community, followed by cypress and mixed hardwood (Table 11). The cypress community exhibited highest nutrient concentrations except for Mg, which was highest at the maple-gum stand. Large litter fall at this community was lowest in concentrations of N, P and K, while Mg and Ca were lowest at the mixed hardwood community. Nutrient deposition was greater in the more flooded communities as a result of the greater litter fall rates and higher nutrient concentrations. Nutrient deposition followed the sequence for litter deposition except for K deposition, which was greatest at the cypress community. T-tests indicated differences between communities were not significant.

Table 11. Mean annual deposition of tree boles and large branches, nutrient concentrations and nutrient deposition in the macrolitter. Estimates are in kg/ha; standard errors are in parentheses. Data were not collected for the cedar site.

	Maple-gum	Cypress	Mixed Hardwood
Litter mass	186.24 (27.00)	160.56 (31.44)	109.68 (41.28)
% N	0.65 (0.08)	0.67 (0.05)	0.66 (0.08)
N deposition	1.21	1.08	0.72
% P	0.06 (0.00)	0.09 (0.02)	0.07 (0.01)
P deposition	0.11	0.14	0.08
% K	0.02 (0.01)	0.07 (0.04)	0.03 (0.02)
K depostion	0.04	0.11	0.03
% Ca	0.50 (0.12)	0.53 (0.13)	0.42 (0.13)
Ca deposition	0.93	0.85	0.46
% Mg	0.07 (0.02)	0.05 (0.01)	0.04 (0.00)
Mg deposition	0.13	0.08	0.04

DISCUSSION

Annual litter production

The deposition of organic matter in forest can be used as a guide to minimum levels of net above-ground production. Lang (1974) calculated that annual detrital input, as a percentage of net above-ground production, ranged from 30 to 94% (65% $\bar{X}$) for 12 deciduous forests over a range of ages and types, and from 39 to 80% (67% $\bar{X}$) for 12 coniferous forests. He also indicated that the detrital input increased as a percentage of net production with age, and that the remaining net production was disproportionately divided between the grazing pathway (5-10%) and tree biomass accumulation. Ricklefs (1973), reporting on the relationship between litter fall and net above-ground productivity (NAP) in several North American habitats, indicated that litter production accounted for approximately 40% of NAP in temperate forests. Therefore above-ground production is equal to about 2.5 times the amounts of litter fall. On the basis of this information, the four plant communities in the Great Dismal Swamp appear to be relatively productive.

In the Great Dismal Swamp, the cedar stand had the greatest amount of total litter deposition. Litter fall in mixed coniferous-deciduous forests has been reported to be greater than in a pure deciduous or coniferous system (Rodin and Bazilevich 1967). Total litter production in the Dismal Swamp communities was in the upper range reported by Rodin and Bazilevich (1967) for deciduous and broad-leaved forests, and for coniferous and mixed forests. Litter fall in the four stands was also greater than estimates reported by Bray and Gorham (1964) for total litter production in the Warm Temperate Zone.

The relatively high litter production of the Dismal Swamp stands was also apparent from comparisons with other systems (Table 12). The mixed hardwood community exhibited greater litter production than a mixed deciduous woodland in England (Sykes and Bunce 1970), a mature northern hardwood forest in New Hampshire (Gosz *et al* 1972) and oak forests in Minnesota.(Reiners and Reiners 1970) and Oklahoma (Johnson and Risser 1974). Differences in litter production between the Dismal Swamp stand and the more northern forests are probably due to colder climates and shorter growing seasons of northern regions. The Oklahoma study was conducted in an upland forest characterized by lower precipitation than the Dismal Swamp. Annual litter fall in a New Jersey mixed oak forest (Lang 1974) was greater than in the Dismal Swamp mixed hardwood forest; however, this estimate included shrubby and herbaceous litter. The cedar community exhibited a much higher value than those reported by Reiners (1972) and Reiners and Reiners (1970) for a northern white cedar (*Thuja occidentalis* L.) swamp in Minnesota. Variation between these two systems can also be explained by climate differences. Litter production in the cypress stand was greater than a Louisiana baldcypress-water tupelo stand (Conner and Day 1976) and was twice that of a cypress forest in the Okefenokee Swamp (Schlesinger 1978). This Georgia swamp differs from the seasonally flooded Great Dismal Swamp in that it is characterized by slow moving surface waters for most of the year. Brinson *et al* (1980) suggest that water movement and periodic flooding may result in higher net primary production and higher litter fall. Deposition of litter in

Table 12. Annual litter fall for wetland and upland temperate forests. Estimates are expressed as g dry mass m^{-2} yr^{-1}

Forest type and locality	Litter fall (dry mass)	Source
Wetland forests		
Cedar stand, Virginia	757	This study
Cypress stand, Virginia	678	This study
Maple-gum forest, Virginia	658	This study
Mixed hardwood, Virginia	652	This study
Floodplain swamp, North Carolina	638	Kuenzler *et al* 1980
Alluvial swamp, North Carolina	642	Brinson *et al* 1980
Cypress-tupelo stand, Louisiana	620	Conner and Day, 1976
Bottomland hardwood, Louisiana	574	Conner and Day, 1976
Cypress forest, Georgia	328	Schlesinger, 1978
Cypress swamp, Florida	756	Carter *et al*,
Cedar swamp, Minnesota	488	Reiners, 1972
Upland forests		
Hardwood watershed, North Carolina	436	Cromack and Monk, 1975
Mixed oak forest, New Jersey	715	Lang, 1974
Hardwood forest, New Hampshire	570	Gosz *et al* 1972
Oak forest, Minnesota	457	Reiners and Reiners, 1970
Oak-pine forest, New York	439	Woodwell and Marples, 1968
Oak forest, Oklahoma	513	Johnson and Risser, 1974
Deciduous woodland, England	272	Hughes, 1971
Sweet chestnut coppice, England	356	Anderson, 1973
Beech coppice, England	466	Anderson, 1973
Sessile oak woodland, England	385	Carlisle *et al* 1966
Mixed deciduous woodland, England	524	Sykes and Bunce, 1970

a cypress stand in Florida (Carter *et al*1973) was greater than in the Dismal Swamp, probably because of the more southern location of the Florida swamp. Litter fall in the maple-gum community was comparable to a North Carolina floodplain swamp (Kuentzler *et al* 1980) and alluvial swamp (Brinson *et al* 1980), but was greater than a Louisiana bottomland hardwood stand (Conner and Day 1976).

Bray and Gorham (1964) reported that environmental parameters exerted the greatest influence on litter production. Factors such as climate, latitude, altitude, exposure, soil fertility and soil moisture affected litter fall rates, while age and density of the stands, after closure of the canopy did not. Anderson (1973) concluded that once the canopy was closed, differences in stand structure and species composition did not significantly affect litter production. Litter fall rates among the Dismal Swamp communities did differ, apparently because of differences in species composition and the extent of flooding.

Leaf fall in the Swamp communities, as a percentage of total litter fall, ranged from 66.9% to 81.5%. Rodin and Bazilevich (1967) reported leaf fall in temperate deciduous forests accounts for between 40 and 65% of total litter deposition in a mature stand, and between 75 and 85% in a young stand. The maple-gum community exhibited the highest percentage of leaf deposition. The area in which this stand is located was selectively logged for cypress approximately 30 years ago (P. Gammon, USGS, GDSNWR, personal communication), however, the water gum trees were not removed. Previous research (Train and Day, unpublished) indicated that the average age of the water gum was 51.8 ($\pm$ 5.5) years, thus they are younger than dominant species in the other stands. In a coniferous forest, leaf fall represents 30 to 60% of total litter fall; the lower value occurring in mature stands due to increased contribution of dead timber (Rodin and Bazilevich 1967). The cedar community exhibited the lowest percentage of leaf deposition and highest estimate for wood deposition. The Atlantic white cedar were dying due to natural senescence and the forest floor was characterized by a large amount of woody litter.

Production of leaf litter can be used as an estimate of net aboveground production. However, leaf litter represents an underestimate of leaf production due to weight losses prior to and following abscission of the leaf (Bray and Gorham 1964). Leaf deposition in the four communities was greater than ranges reported by Rodin and Bazilevich (1967) for deciduous and coniferous forests. Leaf fall rates were also greater than most systems reported in table 13, except the oak hickory forest in New Jersey (Lang 1974). The cypress and maple-gum communities had greater leaf deposition than the mixed hardwood and cedar communities, possibly as a result of differences in flooding conditions. Broadfoot and Williston (1973) and Conner and Day (1976) have shown that periodic increases in water supply result in increased stand productivity for bottomland forests.

Seasonality of leaf fall in forests is quite obvious, with maximum input to the forest floor occurring in autumn. This was observed in the four Dismal Swamp communities. Leaf deposition in the cedar community was greater than in the deciduous communities during the other seasons. This was expected since the natural, progressive mortality that takes place from leaf initiation until senescence occurs in varying degrees throughout the year for evergreen conifers (Gosz *et al* 1972). Leaf fall of most deciduous angiosperms occurs within a short

Table 13. Annual leaf litter production for wetland and upland temperate forests. Estimates are expressed as g dry mass m^{-2} yr^{-1}.

Forest type and locality	Litter fall (dry mass)	Source
Maple-gum stand, Virginia	536	This study
Cypress forest, Virginia	528	This study
Cedar stand, Virginia	506	This study
Mixed hardwood, Virginia	455	This study
Alluvial swamp, North Carolina	422	Brinson *et al*, 1980
Cypress forest, Georgia	233	Schlesinger, 1978
Mixed hardwood watershed, North Carolina	277	Cromack and Monk, 1975
Oak-pine forest, New York	281	Woodwell and Marples, 1968
Hardwood forest, New Hampshire	280	Gosz *et al*, 1972
Oak-hickory forest, Missouri	349	Rochow, 1974
Mixed oak forest New Jersey	493	Lang, 1974
Sweet chestnut coppice, England	330	Anderson, 1973
Beech coppice, England	385	Anderson, 1973
Sessile oak woodland, England	212	Carlisle *et al*, 1966
Mixed deciduous woodland, England	344	Sykes and Bunce, 1970

period of time following formation of the abscission layer (Wilson *et al* 1971); however, the time involved differs between species. Autumn leaf fall was complete within a short period of time at the two more flooded communities, while the process was prolonged at the two drier stands. The latter pattern results in a more continuous deposition of litter, possibly contributing to a more tightly closed mineral cycle in these communities.

Leaf deposition was greater during the autumn of 1978 than 1977 at all stands except cedar. Climatological data (National Oceanographic and Atmospheric Adminsitration, U.S. Dept. of Commerce 1977 and 1978) indicated precipitation was greater during the growing season of 1978 (52% of total annual precipitation) compared to 1977 (35%). Increased rainfall in 1978 may have resulted in greater leaf production and subsequently greater leaf deposition the following autumn. On the other hand, a dry growing season would have the opposite effect, i.e. lower leaf fall rates. Therefore, more accurate values may actually lie between the estimates reported here for the two autumns.

The Atlantic white cedar exhibited greater deposition during the 1977 autumn, reflecting the extremely dry conditions of this period. Since longetivity of evergreen needles is dependent upon internal and external conditions, it was expected that the 1977 drought would affect litter deposition of this species more than deciduous species. That is, during a drought, several years of needle accumulation may drop off at one time (Spurr and Barnes 1980). Litter production is affected by annual fluctuations in weather conditions and species often react very differently to the same weather abnormality (Bray and Gorham 1964). In general, annual variation in leaf fall rates is to be expected (Bray and Gorham 1964; Lang 1974; Sykes and Bunce 1970) and differences could be attributed to differences in weather, stem growth rates and seed production (Dixon 1976).

Leaf phytomass budgets estimated from regression equations by Day and Dabel (1978) were comparable to the leaf fall estimates. Deposition values were similar to phytomass estimates at the four communities except cedar. However, Day and Dabel cautioned that the cedar stand value was an overestimate due to difficulty in measuring foliage production by members of the Cupressaceae.

Wood fall was continuous throughout the year and showed marked variation. The fall of branches is a local phenomenon of great weight when it occurs and therefore wide annual variation is to be expected. A comparison of wood fall with other systems is difficult since this category varies among studies due to differences in diameter and length of woody litter collected. However, wood deposition in the cedar stand was relatively high, higher than in a northern white cedar swamp in Minnesota (Reiners 1974). Wood fall at the cypress community was much greater than in the Okefenokee Swamp (Schlesinger 1978). Deposition of wood at the mixed hardwood stand was comparable to that of a mixed oak forest in New Jersey (Lang 1974). Woodfall was lowest at the maple-gum community and comparable to a Danish oak forest (Christensen 1975).

Peaks in wood fall occurring in winter and late spring coincide with storm activity reported for the southeastern portion of Virginia (NOAA, U.S. Dept. of Commerce 1978). Bray and Gorham (1964), Gosz *et al* (1972) and Rochow (1974) observed a relationship between maximum wind speed and peak values of wood fall. They concluded seasonal dynamics of wood fall can almost be explained by wind factor alone.

Christensen (1975) observed that the effect of wind on rate of wood fall depended on the season. That is, in autumn, wind had a direct effect on amount and timing of wood litter fall, while there was no relationship between wind factor and wood fall for the rest of the year.

A slight increase in wood deposition corresponding with autumn leaf fall was observed at the mixed hardwood, cypress and maple-gum communities. Autumnal peaks have also been observed by Christensen (1975) and Rochow (1974). Others have shown wood fall to be sporadic (Lang 1974; Sykes and Bunce 1970) and cause skewness of seasonal patterns of total litter fall.

Fruits and flowers were minor contributors to total litter production in the communities. However, Ovington (1963) demonstrated that annual production studies which excluded the production of tree reproductive organs result in underestimates for the system. Although flower and fruit litter fall represented a small amount, these organs are nutrient rich and may possibly be important nutrient inputs to the forest floor. Miscellaneous litter fall consisted mostly of insect frass, which may indicate higher herbivory rates in this stand. The cedar community exhibited the lowest deposition, indicating reduced herbivory, which could be attributed to the evergreen schlerophyllous nature of cedar needles. Schlerophyllous tissue mechanically impedes digestion and reduces the mineral reward per gram of tissue consumed (Schlesinger and Chabot 1977).

Nutrient concentrations of litter fall

Leaf litter.—The elements analyzed (N,P,K, Ca and Mg) are the most widely investigated nutrients in terrestrial systems. Previous studies of acid bogs (Small 1972) have indicated that N and P are the most limiting elements in nutrient deficient habitats. The mineral element composition of leaf litter is generally lower than live material due to translocation of some nutrients (Epstein 1972; Hoyle 1965; Rodin and Bazilevich 1967; Tilton 1977). Reabsorption of elements into perennial portions prior to abscission is well documented. Nitrogen, P and K are mobile elements and are retranslocated, while Ca increases in concentration throughout the growing season and Mg remains relatively constant (Duvingneaud and Denaeyer-DeSmet 1970; Devlin 1974; Epstein 1972; Rodin and Bazilevich 1967). A severe drought occurred during 1977 and was reflected in the leaf fall nutrient concentrations. The two more flooded communities exhibited greater N and P and lower Mg and Ca concentrations, which is indicative of early leaf fall with less translocation of nutrients. Gosz *et al* (1972) also observed that senescent leaves falling early in autumn had higher concentrations of more mobile elements and lower concentrations of immobile elements relative to leaves falling late in autumn.

Nutrient concentrations were generally higher in leaf fall at the two more flooded communities, indicating greater nutrient availability and uptake than at the two drier stands. Hoyle (1965) also observed greater nutrient concentrations in litter of yellow birch (*Betula lutea* Michaux F.) on poorly drained soils than on well drained soils. Tilton (1977) found that moisture, aeration conditions, and nutrient supply had fundamental effects upon nutrient concentrations in wetland species. Availability of nutrients in soil is influenced by soil moisture, with a decrease in soil moisture affecting nutrient availaibility by slowing down cation movement (Hosner *et al* 1965; Reich and Hinckley 1980).

Poor aeration under stagnant conditions impedes nutrient uptake (Schlesinger 1978), while seasonal flooding, on the other hand, allows for periodic inputs of water and nutrients and penetration of gaseous O_2 to the ground litter and upper soil layers (Kuenzler *et al* 1980).

Lower concentrations in leaf litter at the two less flooded communities indicated lower nutrient availability and uptake. These two stands are also characterized by more acidic conditions. An indirect effect of acid soils is impaired absorption of Ca, Mg, K and P (Lund 1970). Also, decay rates were lower in these two communities (Day, unpublished), resulting in slower nutrient release.

Nutrient concentrations in forest tree leaves is highly variable, since plant species have different nutrient requirements and differ in their ability to extract nutrients from the soil (Collander 1941; Daubenmire 1953; Devlin 1974; Garten *et al* 1977; Van Camp 1948). Also, nutrients occur in varying amounts in different soils. However, trends at the species level and at the community level can be observed. In general, the nutrient content of leaf fall can be used as an indicator of a community's nutrient status.

Cypress leaf fall, in the cypress stand, consistently exhibited high N, P and Ca and low K and Mg concentrations. Schlesinger (1978) also reported low K concentrations in cypress foliage. He also observed great K reabsorption prior to abscission and comparatively low losses by leaching from the cypress canopy, indicating that K may be conserved by cypress trees. Nutrient concentrations of cypress leaf fall in the Dismal Swamp community were comparable to that of a cypress forest in the Okefenokee Swamp (Schlesinger 1978). However, K and Mg concentrations were lower in the Dismal Swamp. Potassium concentrations were lower in the Dismal Swamp compared with a deciduous bog system in Canada (Small 1972), while N and P estimates were comparable.

The cedar stand, dominated by the evergreen conifer, *Chamaecyparis thyoides*, generally exhibited lower concentrations in litter deposition than the deciduous stands. Coniferous species are known to be poorer in elements (Cromack and Monk 1975; Hoyle 1965; Van Camp 1948), with a marked difference in N and Ca concentrations (Rodin and Bazilevich 1967). However, Ca in cedar needle deposition in the Swamp was relatively high. Lutz and Chandler (1947) indicated that the K, Mg and Ca concentrations of conifer needles in the temperate zone of the United States may reach very high levels. Previous studies (Loveless 1961; Monk 1966; Schlesinger and Chabot 1977) indicated that the occurrence of evergreenness (schlerophylly) may be correlated with soil infertility. Monk (1966) hypothesized that the evergreen nature was significant as a nutrient conservation mechanism in nutrient deficient substrates. The Dismal Swamp exhibited greater Ca, lower P and K and comparable Mg concentrations compared with a coniferous swamp in Minnesota (Tilton 1977). Compared to a northern white cedar swamp (Reiners and Reiners 1970), concentrations were lower in the Dismal Swamp community except for N. Nutrient concentrations in the cedar stand leaf fall were comparable to an evergreen bog (Small 1972) except for K, which was lower in the Dismal Swamp stand.

Oak species at the mixed hardwood community consistently exhibited relatively low leaf fall nutrient concentrations. Oaks are marcarescent species, which allows for greater retranslocation of nutrients by delayed leaf abscission. This could be a nutrient conservation mechanism, since Duvingneaud and Denaeyer-DeSmet (1970) concluded that nutrient requirements of oak forests are much greater than those of other temperate forest ecosystems. Nutrient concentrations in the Dismal Swamp mixed hardwood stand were lower than a non-bog deciduous system in Canada (Small 1972) and were comparable to a hardwood forest in North Carolina (Cotrufo 1977) except for Ca, which was higher in the swamp community.

N. aquatica, in both flooded communities, exhibited relatively high N and P and low Ca concentrations. Low Ca content may be an inherent species characteristic. Decomposition studies (Day, unpublished) have demonstrated higher decay rates in the two more flooded communities. Since N and P are usually limiting nutrients in decomposition, high values in leaf fall may enhance decay relative to the other two stands.

Highest nutrient concentrations for red maple leaf litter were obtained at the cedar community. Potassium concentrations, however, were greater for red maple in the two more flooded communities and lowest at the cedar community. Red maple may be uptaking and returning greater quantities of nutrients because of the expanding population, which is rapidly growing.

Black gum leaf fall in the four communities was relatively high in Mg. The category of Other during 1977 included this species and also exhibted high Mg concentrations. The consistently high values may indicate selective absorption of Mg by this species. The nutrient content of black gum in the Great Dismal Swamp was lower than in the Okefenokee Swamp (Schlesinger 1978) except for Ca.

In general, nutrient concentrations of leaf fall in the Dismal Swamp communities were lower than ranges reported by Rodin and Bazilevich (1967), while Mg values were comparable. Compared with other systems, N, P and K appeared relatively low, especially K. The high leachability of this element perhaps explains the lower concentrations. Eaton (1973) reported approximately 20 kg/ha of K was leached from the Hubbard Brook Forest canopy during June to August (1969). A study of the throughfall and stem flow chemistry in the Great Dismal Swamp stands would contribute valuable information to the study of nutrient recycling in these communities.

Non-leaf litter. In general, nutrient concentrations of small woody litter are usually lower than leaf litter (Cromack and Monk, 1975; Gosz *et al* 1972; Schlesinger 1978). However, N and Mg in wood fall in the Dismal Swamp communities were lower, P and K were comparable, while Ca was greater. The Dismal Swamp estimates appeared relatively high compared with other systems, possibly due to a large proportion of bark in the samples. Rodin and Bazilevich (1967) reported that mineral element concentrations in bark were similar to those in leaf litter and were greatest in branch bark. High Ca in bark has also been reported by Day and Monk (1977), Cromack and Monk (1975), Johnson and Risser (1974) and Schlesinger (1978).

Deposition of fruit, flower and miscellaneous litter was generally much higher in nutrient concentrations than leaf litter, except Ca. High nutrient concentrations, in non-leaf litter, except for Ca, were also observed by Cromack and Monk (1975). The infloresence litter, however, was relatively high in Ca. Bayly and O'Neill (1972) showed that cat tail (*Typha glauca* Godron) floral stalks were high in Ca upon first appearance, then they experienced a rapid decline. High Ca was attributed to the presence of both soluble Ca being translocated to the infloresence and structural Ca bound within the floral stalk. Infloresence litter collected in the Dismal Swamp communities consisted mostly of young red maple floral stalks. Miscellaneous material collected was mostly insect frass, which is mainly undigested green plant tissue. Therefore, it is logical that concentrations would be greater in green tissue than senescent leaf litter.

Nutrient deposition in litter fall

Leaf.__The two more flooded communities apparently cycled a greater amount of nutrients via leaf fall than the two less flooded communities, as a result of higher leaf fall rates and nutrient concentrations in the litter. These two stands also exhibited similar relative abundance of elements, which differed from the sequence at the two less flooded and more acidic communities. The two latter communities may possibly be characterized by a decreased availability of N and K. Decomposition studies (Day, unpublished) showed greater C:N ratios and thus lower decay rates in the more acidic communities. This slower nutrient release plus the immobilization of N result in smaller amounts of nutrients available for plant uptake.

Nutrient deposition data indicated that red maple was perhaps more significant to nutrient cycling through leaf fall at the cedar and maple-gum communities. Although nutrient deposition was generally greater in the two more flooded communities, Ca deposition in the cedar stand was relatively high due to the great contribution by red maple leaf litter. Observations of relative contributions by red maple to total nutrient deposition at each community, suggested a more important contribution to Ca deposition at the maple-gum and cedar stands and to K deposition at the mixed hardwood and cypress stands.

Since nutrient deposition data reported for the Dismal Swamp communities represented only peak leaf fall, meaningful comparisons with other systems are difficult. Also, the great year to year variation in amount of litter deposition and nutrient concentrations of the litter results in high nutrient fall variation. However, a comparison of nutrient deposition in peak leaf fall at the mixed hardwood stand with nutrient deposition during October in the Hubbard Brook Forest indicated higher estimates for the Dismal Swamp stand. Phosphorus and K deposition in the Dismal Swamp cypress community, compared to deposition in a cypress forest of the Okefenokee Swamp was greater. Although nutrient concentrations in leaf fall were similar between these two stands, deposition of leaf litter was much greater in the Great Dismal Swamp. Lower production and nutrient availability in the Okefenokee is explained to some degree by the acidic and anaerobic conditions that prevail there most of the year. It appears that higher leaf fall rates in the seasonally flooded Great Dismal Swamp compensate for low nutrient concentrations in leaf fall.

Table 10 showed that the greatest input of nutrients to the forest floor was in leaf litter. However, deposition of reproductive structures and miscellaneous litter appeared to be relatively important nutrient sources at a time when leaf fall is at a minumum. The two more flooded communities again cycled the greatest amount of total nutrients. The maple-gum and cedar communities appeared to differ most in amounts of total nutrient deposition. The two communities also appeared to exhibit the greatest difference between proportions of N, K, Mg and Ca relative to total nutrient deposition in each community. This probably resulted from differences in species composition between the stands. The maple-gum community represents the more common altered vegetation that predominates in the Great Dismal Swamp today, while the cedar stand vegetation is more representative of formerly undisturbed Swamp.

Macrolitter. Large woody litter fall was greatest in the cypress and maple-gum communities. Deposition of tree boles in these stands was more frequent, possibly as a result of soft, water-logged soils. The anaerobic conditions associated with flooded soils possibly retards root production in these stands (Montague and Day 1979) and thus may facilitate wind throw of trees.

Although data were not collected for the cedar stand, deposition of macrolitter is probably highest in this stand. Previous research on litter accumulation (Day 1979) indicated greater standing crops of woody litter (large and small) in this community.

In a relatively young stand, leaf litter represents the most important source of recycled nutrients in the forest floor. However, as the stand matures, the role played by large woody litter increases (Spurr and Barnes 1980). Therefore, decaying macrolitter can be considered as a reservoir of nutrients slowly released over time. The nutrient content of large woody litter was generally lower than nutrient concentrations in other tissues except P, which was comparable. A large percentage of P contained in tree boles and large branches suggested a nutrient conservation mechanism, through storage of P in the perennial portion of the vegetation.

CONCLUSIONS

In general, litter fall rates in the four Dismal Swamp communities were high relative to other wetland and upland forest systems. There were differences in litter production between the stands, which were presumably due to differences in species composition and extent of flooding. The two more flooded communities, cypress and maple-gum, exhibited greater leaf fall rates and cycled more nutrients through litter fall than the two less flooded communities, mixed hardwood and cedar. These two stands, characterized by more acidic conditions, exhibited similar relative abundance of elements, differing from that at the maple-gum and cypress stands. Trends were observed distinguishing the more flooded from the less flooded stands, but differences in litter production between the stands are probably due to the difference in major species of each community. Variabilities in nutrient deposition at each community reflected differences in plant species between the communities. The stands appeared to have relatively high nutrient return to the forest floor due to high litter fall rates, despite low concentrations in the litter. Nutrient inputs to the forest floor were dominated by leaf litter; however, nutrient deposition through non-leaf litter also appeared relatively important.

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