UNITED STATES
DEPARTMENT OF THE INTERIOR
GEOLOGICAL SURVEY

PRODUCTION AND DECOMPOSITION OF FOREST LITTER FALL ON THE APALACHICOLA RIVER FLOOD PLAIN, FLORIDA

OPEN-FILE REPORT 82-252

March 3, 1849

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By John F. Elder and Duncan J. Cairns

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CONVERSION FACTORS

For use of those readers who may prefer to use inch- pound units rather than metric units, the conversion factors for the terms used in this report are listed below:

Multiply metric unit	By	To obtain inch-pound unit
	Length	
micrometer (um)	0.00003937	inch (in.)
millimeter (mm)	0.03937	inch (in.)
meter (m)	3.281	foot (ft)
	1.094	yard (yd)
kilometer (km)	0.6214	mile (mi)
meter per second (m/s)	3.281	foot per second (ft/s)

CONVERSION FACTORS--Continued

Multiply metric unit	By	To obtain inch-pound unit
	Area	
square meter (m^2)	10.76	square foot (ft^2)
	1.196	square yard (yd^2)
	0.0002471	acre
hectare (ha)	2.471	acre
square kilometer (km^2)	0.3961	square mile (mi^2)
square meter per hectare (m^2/ha)	4.3545	square foot per acre ($ft^2/acre$)
	Volume	
cubic meter (m^3)	35.31	cubic foot (ft^3)
	1.308	cubic yard (yd^3)
	0.0008107	acre-foot (acre-ft)
	264.2	gallon (gal)
liter (L)	1.0567	quart (qt)
cubic meter per second (m^3/s)	35.3145	cubic foot per second (ft^3/s)
	Mass	
milligram (mg)	0.00353	ounce (oz)
gram (g)	0.0353	ounce (oz)
	0.0022	pound (lb)
kilogram (kg)	2.2046	pound (lb)
metric ton (t)	2,204.6	pound (lb)
	1.1023	ton (short)
metric ton per hectare (t/ha)	892.18	pound per acre (lb/acre)
	0.4461	ton per acre
gram per square meter (g/m^2)	8.9218	pound per acre (lb/acre)
gram per square meter per day [$(g/m^2)/day$]	8.9218	pound per acre per day [(lb/acre)/day]
gram per square meter per year [$(g/m^2)/yr$]	8.9218	pound per acre per year [(lb/acre)/yr]
	Temperature	
degree Celsius (°C)	1.8 (+32°)	degree Fahrenheit (°F)
	Concentration	
milligram per liter (mg/L)	1.0	parts per million (ppm)

PRODUCTION AND DECOMPOSITION OF FOREST LITTER FALL ON THE APALACHICOLA RIVER FLOOD PLAIN, FLORIDA

By John F. Elder and Duncan J. Cairns

ABSTRACT

Measurements of litter fall (leaves and other particulate organic material) and leaf decomposition were made on the bottom-land hardwood swamp of the Apalachicola River flood plain in 1979-80. Litter fall was collected monthly from nets located in 16 study plots. The plots represented five forest types in the swamp and levee areas of the Apalachicola River flood plain. Forty-three species of trees, vines, and other plants contributed to the total litter fall, but over 90 percent of the leaf material originated from 12 species. Nonleaf material comprised 42 percent of the total litter fall. Average litter fall was determined to be 800 grams per square meter per year, resulting in an annual deposition of 360,000 metric tons of organic material in the 454-square-kilometer flood plain.

The levee communities have lower tree biomass but higher tree diversity than swamp communities. The levee vegetation, with lower tree biomass, produces slightly more litter fall per ground surface area than the swamp vegetation. The swamps are dominated by three genera: tupelo (*Nyssa*), cypress (*Taxodium*), and ash (*Fraxinus*). These genera account for over 50 percent of the total leaf fall in the flood plain but they are the least productive, on a weight-per-biomass basis, of any of the 12 major leaf producers.

Decomposition rates of leaves from five common flood-plain tree species were measured using a standard leaf-bag technique. Leaf decomposition was highly species-dependent. Tupelo (*Nyssa* spp.) and sweetgum (*Liquidambar styraciflua*) leaves decomposed completely in 6 months when flooded by river water. Leaves of baldcypress (*Taxodium distichum*) and diamond-leaf oak (*Quercus laurifolia*) were much more resistant. Water hickory (*Carya aquatica*) leaves showed intermediate decomposition rates. Decomposition of all species was greatly reduced in dry environments. Carbon and biomass loss rates from the leaves were nearly linear over a 6-month period, but nitrogen and phosphorus leaching was nearly complete within 1 month. Much of the organic substance may be recycled in the forest ecosystem, but annual flooding of the river provides an important mechanism for mobilization of the litter-fall products.

INTRODUCTION

Background

Forested ecosystems continue to occupy large land areas in many parts of the United States and the world. Worldwide, the combined area of various forest types is 39 million km^2, or about 29 percent of the area of terrestrial ecosystems (Odum, 1971, p. 51). These forests account for 38 percent of the total gross production of the biosphere. Trees dominate the biota of such systems and much of the biomass and production is associated with leaf material. In a young oak-pine forest, for example, 5 percent of the biomass and 50 percent of the net production were associated with leaves (Whittaker and Woodwell, 1969). Although these ratios may vary considerably with location and type of forest, there is no question that in any forested ecosystem leaves represent a substantial bulk of organic material. More important in terms of food web relations and interaction among different communities, the organic matter associated with leaves is relatively mobile. The continual cycle of leaf production, abscission, decay, and replacement can result in substantial accumulation of leaf litter which may be transported within and out of a forested ecosystem. In addition to the biomass of the leaf material itself, a large number of micro-organisms thrive in the system because of the substrate and food source provided by the leaves (Kaushik and Hynes, 1971; Cummins, 1974).

The Apalachicola River in northwest Florida is the principal stream in a river-wetland system in which annual leaf production is potentially a major source of nutrients and organic matter (fig. 1). The watershed is heavily forested with bottom-land hardwoods on the flood plain and pines mixed with other species of trees and shrubs in upland areas. This vegetation annually produces tons of leaf litter and other organic matter which must either be reincorporated into the system or transported out of it. Once litter fall reaches the flood-plain floor, annual flooding of the bottom-land hardwood forest provides a mechanism for transport of materials from the flood plain to the main stream channels.

The Apalachicola River-wetland system terminates in an estuary, and the amount of organic material produced and transported is critical to the river-estuary relation (Livingston and others, 1977; Naiman and Sibert, 1978). Estuaries, where river water mixes with and dilutes seawater in a semienclosed basin, are characteristically more productive on an areal basis than either the river on one side or the sea on the other (Odum, 1971, p. 357). Estuarine productivity depends largely on inflow of nutrients from the freshwater drainage. The estuary acts as a "nutrient trap" for such inflowing substances (Hobbie and others, 1975). Therefore, perturbations or natural changes in the river system which alter the form or the amount of substances transported to the estuary are likely to affect estuarine productivity.

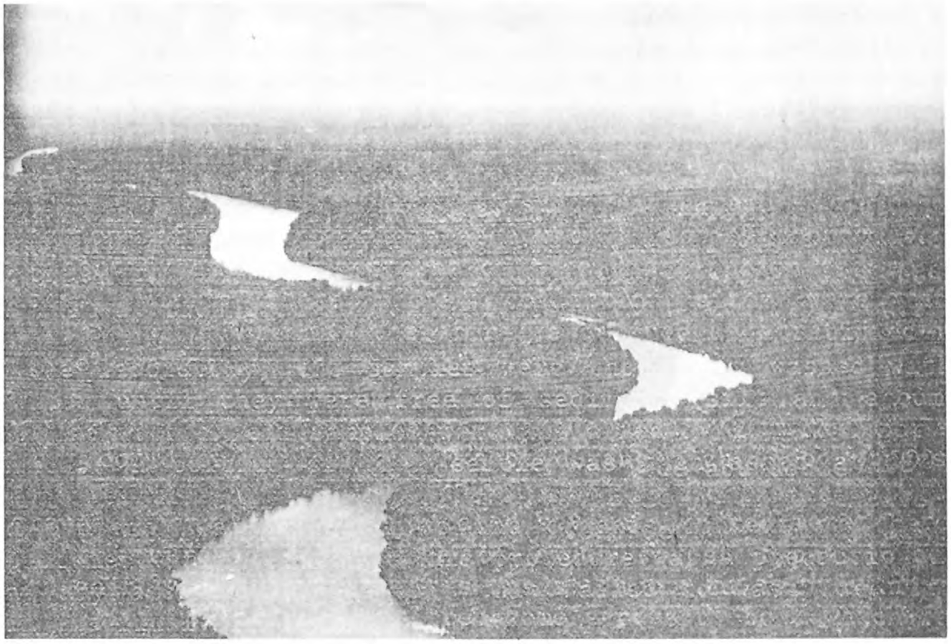

Figure 1.--Aerial view of the Apalachicola River, Florida looking south.

As a food source for estuarine biota, riverine substances may be evaluated by their content of nitrogen, phosphorus, and organic carbon. Nitrogen and phosphorus are the two major nutrients which are most often in limited supply for aquatic primary production (Ryther and Dunstan, 1971; Schindler and others, 1971; Taft and Taylor, 1976). Organic carbon, the principal constituent in all organic material, is transported in large quantities in river systems and continually cycles through complex pathways within the riverine and estuarine food webs (Brock, 1966, p. 233). The study of nutrient and detritus flow in the Apalachicola system focused on various forms of these three elements.

Substances which feed the biological productivity of Apalachicola Bay are transported by the river in two basic forms, dissolved and particulate. The particulate fraction includes suspended particles as well as large debris floating on the surface or rolled along the river bottom. Although total flux of dissolved nutrients may far exceed that of suspended organic particulate matter (detritus), the latter plays an important role in sustaining estuarine productivity. Detrital feeders are abundant in estuarine ecosystems (Odum and Heald, 1975). In the Apalachicola Bay, detritivores occupy key positions in the food web (Livingston and others, 1974). The blue crab (Callinectes sapidus Rathbun), shrimp (Palaemonetes pugio and Penaeus setiferus), and the American oyster (Crassostrea virginica Gmelin) form the basis of an economically important shellfish industry.

In view of the significant role of riverine nutrients and detritus in sustaining the estuarine food web, identification of their sources assumes considerable importance. Most freshwater-watershed systems may be compartmentalized into two components or subsystems: (1) the aquatic subsystem, including all channels and tributaries, impoundments, and ground-water, and (2) the terrestrial subsystem, principally soils and vegetation. The sources of nutrients and organic material in the system may be similarly classified. Autochthonous substances result from fixation by aquatic micro-organisms or other processes within the aquatic subsystem. Allochthonous substances are those which are transported into the aquatic subsystem from the outside.

The Apalachicola River system, like many other river-wetland associations, does not fit the simple conceptualization of a two-component system. In addition to the aquatic and terrestrial subsystems, a major portion of the basin is occupied by a third component, the wetland or flood plain, which has features characteristic of both terrestrial and aquatic environments. The role of the flood plain in nutrient cycling is determined primarily by hydrologic forces operating in a basically terrestrial habitat. Nutrients and detritus transported from the flood plain are technically neither autochthonous nor allochthonous. Because they are derived and processed in a periodically flooded wetland environment, they are more susceptible to transport than allochthonous matter from upland areas of the watershed. Annual production of litter fall from flood-plain vegetation is consequently a major potential contributor of nutrient and detritus to the river and, ultimately, to the estuary. Quantification of this potential contribution is a central purpose of this investigation.

Terminology

Certain terms which appear frequently in the following discussion require clarification to avoid confusion with similar terms used elsewhere in the literature. The definitions that follow apply specifically to the meanings of the terms as used in this report.

"Litter" and "litter fall" are used to refer to all organic material which falls from forest vegetation greater than 2 meters in height. This includes leaves, woody debris, fruits, berries, lichens, flowers, and other organic matter. "Leaves," "leaf litter," and "leaf-litter fall" refer only to the leaf portion of litter, excluding all nonleaf material. "Production" (or "productivity") refers specifically to litter or leaf litter; it is that component of primary production which actually results in substance which falls from the vegetation to the forest floor. Production which is incorporated in growth or otherwise resorbed or grazed before it is released as litter fall is not included in this component.

Leaf "decomposition" is used for simplicity to denote losses of biomass, carbon, nitrogen, or phosphorus from leaves. The actual measurements were of weight or substance loss, not decomposition which is purely a biological process. The term "nutrients" refers to soluble or leachable nitrogen, phosphorus, and organic carbon. "Detritus" refers to organic particulate matter which contains leachable nutrients as well as numerous other elements associated with biological tissues.

The terms "swamp" and "levee" are used for comparing the two basic environmental types in the flood plain. In the swamp areas, the ground is almost permanently saturated and the vegetation is dominated by two swamp-adapted trees, tupelo and cypress. The levee areas occur on somewhat higher ground, usually not saturated, and they are characterized by a variety of bottom-land hardwood species. Tree "density" refers to the number of trees per unit area, regardless of size. "Basal area" is a measurement of trunk diameter, hence an index of "stem biomass," regardless of density.

Purpose and Scope

The Apalachicola River Quality Assessment was initiated in 1978 as part of a national river quality assessment program of the U.S. Geological Survey. The broad objectives and development of the national program were (Greeson, 1978):

1. To define the character, interrelationships, and apparent cause of existing river-quality problems,
2. To devise and demonstrate the analytical approaches and the tools and methodologies needed for developing water-quality information that will provide a sound technical basis for planners and managers to use in assessing river-quality problems and evaluating management alternatives.

The specific goals of the Apalachicola River Quality Assessment conformed to these overall program objectives with the modification that the investigation was process oriented rather than problem oriented. Its primary purpose was to investigate river-wetland relations and controlling factors which influence the yield of nutrients and detritus to the bay. Emphasis was given to processes which influence nutrient and detritus flow rather than to problems involving environmental disturbance or pollution. Special attention was given to methods development because ecological studies of large river-wetland systems have been rare and few methods particularly applicable to this type of study have been described. The specific objectives of the Apalachicola River Quality Assessment were:

1. To determine the extent that potentially toxic trace elements and organic substances accumulate in benthic organisms and sediments.
2. To describe how tree distribution on the flood plain is related to the pattern of inundation (duration, level, and frequency).
3. To assess the importance of leaf production and decomposition on the flood plain to detritus and nutrient yields.

4. To identify major sources of nutrients to the river system and quantify transport of nutrients and organic detritus in various parts of the system.

The last three objectives address the processes whose net effect is the export of nutrients and organic detritus to Apalachicola Bay. Direct measurement of nutrient recycling within the flood plain was not included in the assessment objectives. Such an analysis would be helpful for thorough understanding of the processes which affect nutrient yield, but it would require several phases of data collection which were beyond the scope of the present study.

The approaches and results of the investigation of the production and decomposition of leaf litter are presented in this report. The overall objective of investigating leaf production and decomposition had four major thrusts:

1. To determine production rates of forest litter fall, including leaf and nonleaf material.

2. To determine decomposition rates relating to loss of total biomass, carbon, nitrogen, and phosphorus.

3. To measure the leaf-fall production rates of individual tree species on the flood plain.

4. To estimate overall potential nutrient and detrital yield from flood-plain litter fall to the river system.

Measurements of litter-production and leaf-decomposition rates, combined with information about tree community distribution obtained from other elements of the assessment (Leitman and others, 1982), resulted in a multifaceted investigation of the wetland system. Extrapolating the data to the entire flood plain provided a means of assessing potential nutrient and detritus yield from the flood plain as a whole.

Geographically, the Apalachicola River Quality Assessment is limited to the Apalachicola River and its flood plain from Jim Woodruff Dam, which impounds Lake Seminole, downstream to the northernmost extent of tidal influence, some 32 kilometers from Apalachicola Bay (fig. 2). This broad areal scope was achieved by collecting data at representative locations and extrapolating results to describe the entire basin south of Jim Woodruff Dam. Two detailed vegetative transects were supplemented with eight tree-survey transects across the flood plain distributed throughout the length of the river.

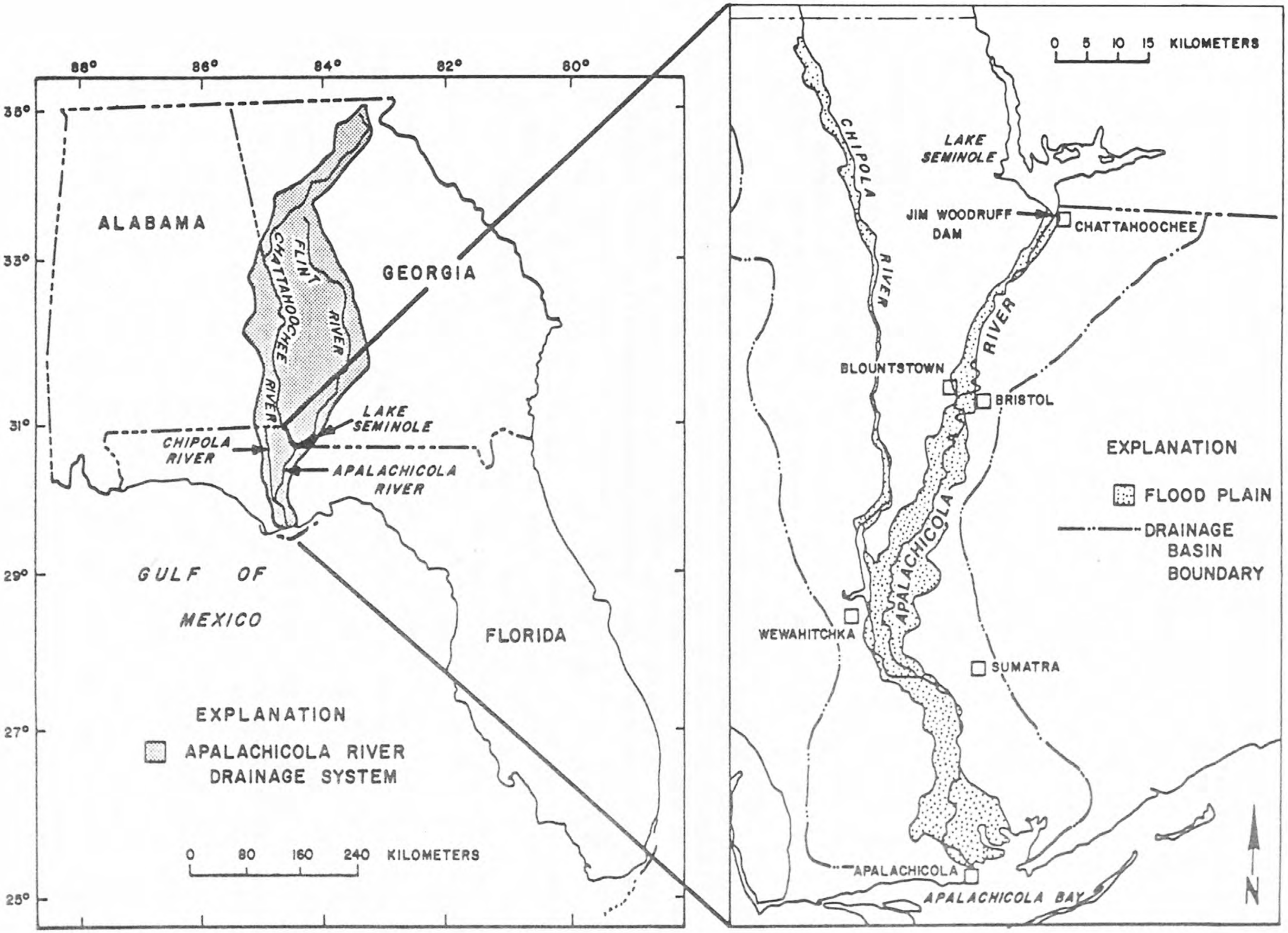

Figure 2.--(a) The drainage basin of the Apalachicola, Chattahoochee, and Flint Rivers in Florida, Georgia, and Alabama; and (b) the drainage basins of the Apalachicola and Chipola Rivers.

The data collection and experimentation dealing with leaf production and decomposition began in August 1979 and continued through November 1980. Regular monthly leaf collections during that period provided coverage of a complete annual cycle, with some overlap into the following autumn.

Description of Study Area

The Apalachicola River in northwest Florida is formed by the confluence of the Chattahoochee and Flint Rivers and has a 50,800-km^2 drainage system encompassing parts of three states (fig. 2). Approximately 12 percent of this area (6,200 km^2) is the watershed of the Apalachicola and Chipola Rivers. With an average discharge of 870 m^3/s at Chattahoochee, the Apalachicola is the largest river in Florida. The river falls 12 meters in its 171-km course from Lake Seminole, at the Florida-Georgia State line, to Apalachicola Bay in the Gulf of Mexico. Each winter and spring its rising waters flood the adjacent wetlands for 3 to 5 months. The flood plain occupies 454 km^2 and broadens downstream from 2 km wide just below Lake Seminole to over 10 km wide near the mouth. It is thickly forested with cypress, tupelo, and mixed hardwood trees which are well suited to periodic inundation. At its mouth, the river empties into Apalachicola Bay, one of the most productive shellfish areas in the United States.

The Apalachicola River basin south of Lake Seminole, excluding the Chipola River basin (fig. 2), has a drainage area of 3,100 km^2, of which nearly 15 percent is inundated during all or part of the year. The Chipola River drainage adds 3,100 km^2 to the total watershed and joins the Apalachicola near the town of Wewahitchka (fig. 2). Unlike the rivers upstream from Jim Woodruff Dam, the Apalachicola-Chipola basin is relatively undeveloped. A few towns are located near the rivers but there are no large urban centers and very little industrialization. The greatest disturbance to the river system is dredging and snagging to maintain a navigable channel for barge traffic. Deposition of dredging spoils also disturbs the natural flood-plain habitats (Clewell and McAninch, 1977).

The flood plain of the Apalachicola River is densely forested with a mixture of bottom-land hardwood tree species. Of the more than 40 species, a few thrive in flooded and saturated areas, more are limited to levees and other areas of high ground, and some with a wider tolerance range for moisture are found in both wet and relatively dry areas. All species in the flood plain are subject to at least some degree of flooding.

A typical view of the flood-plain community is pictured in figure 3. In January, after the period of heavy leaf fall and before the spring flood, a substantial accumulation of leaves was seen on the ground. The area was flooded during the succeeding months; and two days before the maximum flood peak (April 3) water depth had reached 2.4 meters with a velocity of 0.15-0.20 m/s. Among the potential impacts of flooding is transport of the accumulated leaf litter out of the forest. The sequence of leaf fall and inundation is essential to maintain flow of nutrients and detritus from the flood plain to the aquatic system.

Acknowledgments

The authors are indebted to many people whose assistance made this report possible. Critical reviews of the manuscript were furnished by Armando de la Cruz of Mississippi State University, Laurence R. Jahn of the Wildlife Management Institute, Robert J. Livingston of Florida State University, William E. Odum of the University of Virginia, and Frank J. Triska of the U.S. Geological Survey. Laboratory space and facilities for measurements of leaf decomposition and litter sample weights were provided at Florida State University by Livingston and David C. White. Numerous employees of the U.S. Geological Survey made valuable contributions to project planning and administration, field work, data interpretation, manuscript preparation, drafting, and editing.

METHODS

Overview

Three types of data were collected to evaluate the production and decomposition of litter fall on the Apalachicola flood plain: (1) Litter fall from the tree species on the flood plain was collected monthly for more than a year to estimate annual production. Litter-fall samples were separated by species, forest type, and month. (2) Nutrient analyses were made to evaluate leaves as a potential source of carbon, nitrogen, and phosphorus. (3) Decomposition rates were measured to quantify actual leaf breakdown rates as a function of saturation and temperature.

A number of difficulties arose in collecting the data. These were associated with variability of the flood-plain vegetation, the vast area of the basin, and poor accessibility of the interior flood plain where most data collection was needed.

Community variability of bottom-land hardwoods is reflected by the heterogeneous mixture of tree and undergrowth species. Although approximately half of the total forest biomass consists of two species of tupelo (Nyssa) and one species of cypress (Taxodium), a mixture of at least 44 species comprises the other half and contributes substantially to leaf-litter fall. Undergrowth is inhibited considerably by inundation and shading, but in some areas, particularly on the levees, undergrowth is quite abundant. Distribution of vegetation is so variable and intermixed that identification of distinct forest-type boundaries is difficult.

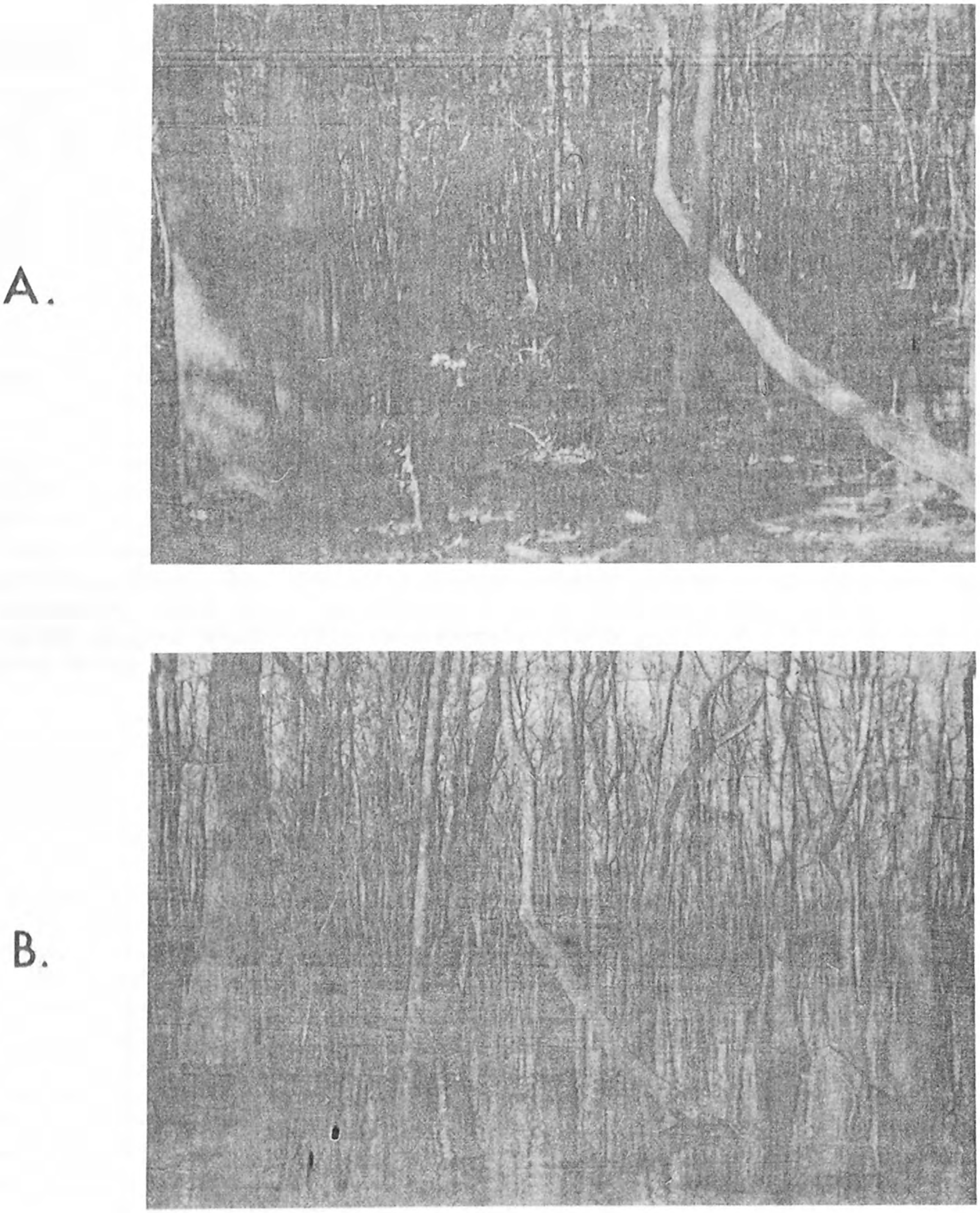

Figure 3.--Interior of flood-plain forest (a) dry and (b) flooded.

A. Flood plain near Sumatra, October 30, 1979. Site is plot 18, 200 feet west of Brothers River. Some of autumn litter fall is visible on ground surface.

B. Same site, February 4, 1980. Flood waters provide a mechanism of transport of litter fall from this area into main channels.

The flood-plain area (454 km^2) is approximately one-seventh of the total Apalachicola drainage area. In view of the variability of vegetation, there was no obvious sampling scheme which would adequately represent the entire area. The forest community structure of the region had not been described by previous studies. Aerial photography was used to select some sites for intensive data collection and others for rapid inventory of tree species. Data from all study sites were used to characterize functions of the flood plain as a whole. Aerial photography also helped to identify apparent patterns of tree distribution and to locate study plots. Within these plots, collection sites were randomly selected. This procedure may therefore be defined as stratified-random sampling (Mueller-Dombois and Ellenberg, 1974, p. 39).

Poor accessibility of the forest-swamp community limited the amount of data that could be collected. Except during high flood stages, the flood-plain interior was accessible only by walking over saturated or flooded ground. Many sites were located several hundred meters from the river bank to represent the range of swamp forest types. The time required to gain access to such sites was an important factor in project planning. Periodic flooding permitted some access by boat which facilitated gage installation and servicing. However, the wide range in water levels also required installation of sampling structures high enough to be above maximum flood stage.

Procedure Descriptions

Litter-Fall Sampling at Study Plots

Litter fall was sampled by using 32 nets located at 16 study plots in the flood plain. The nets (fig. 4) were made of nylon fishing netting with 1-mm mesh size. The use of netting material prevented accumulation of moisture yet provided a mesh size fine enough to entrap small particles of litter fall. Some decomposition of leaves could occur in the nets between monthly collections but breakdown into very fine particles which could be lost from the nets was unlikely. The upper opening, formed by a wooden frame, was 1 m^2 in area. A zipper in the bottom of the net facilitated monthly collection of accumulated organic material. The nets were mounted on wooden supports at heights ranging from 1.5 to 3 m to be above flood stage.

The study plots were selected on the basis of apparent differences in tree communities recognized by aerial photography. The plots, each containing a pair of litter-collection nets, were located along two transects across the flood plain (fig. 5). These transects, termed "intensive transects" because they were the sites of concentrated data-collection efforts, characterized the upper and lower parts of the river flood plain. Brickyard transect, near Brickyard Landing, 11 kilometers southwest of Sumatra, contained nine plots (18 nets) (fig. 6). All nine plots were west of the river since there is no flood plain east of the river in this region. Sweetwater transect, located 8 kilometers upstream of the town of Bristol, contained seven plots (14 nets) (fig. 7), four on the east side of the river and three on the west side.

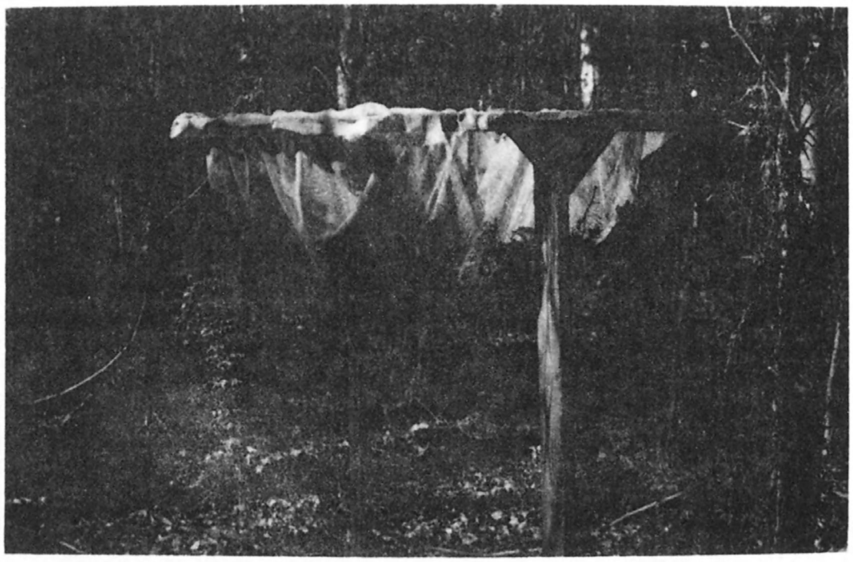

Figure 4.--Net used for collecting litter fall.

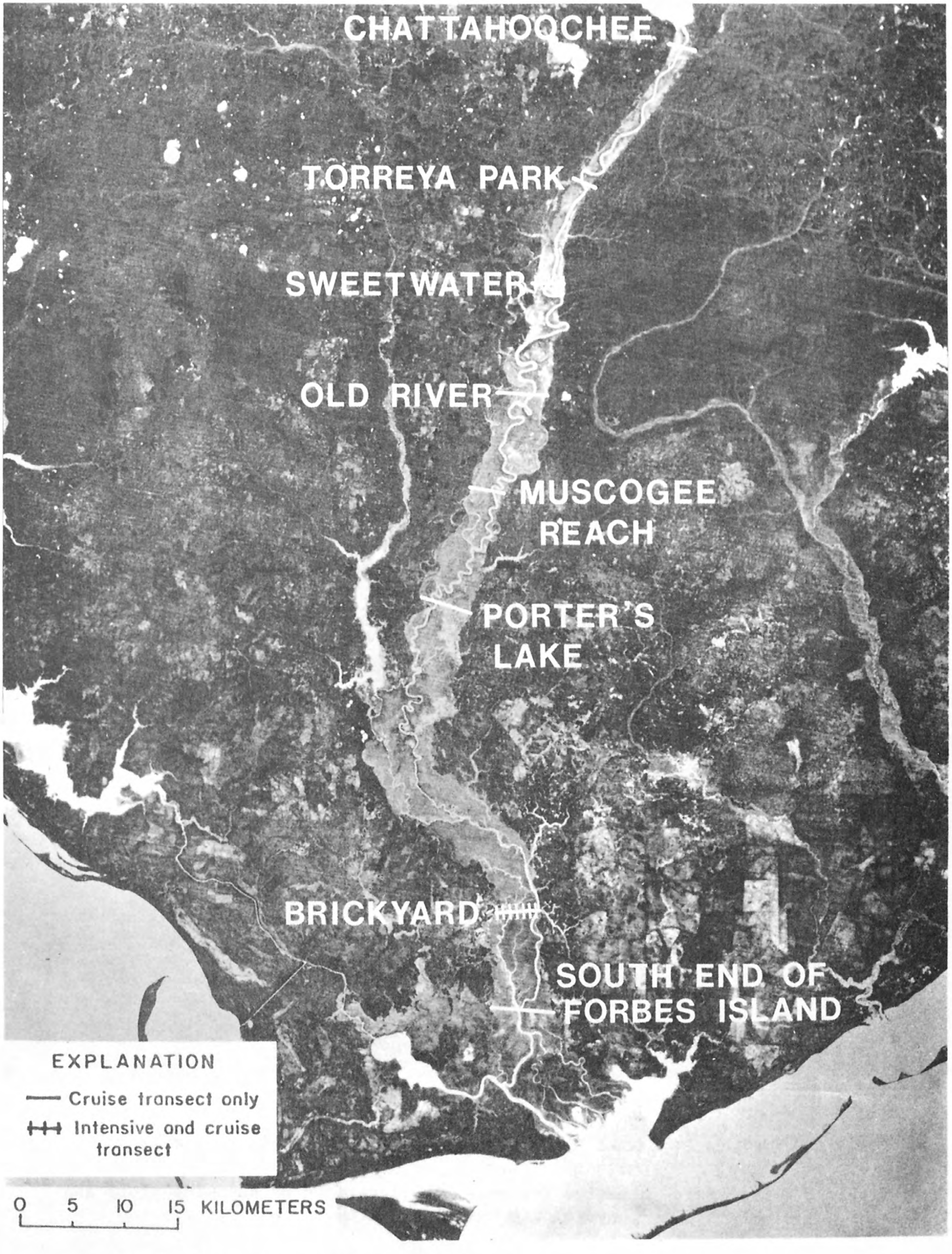

Figure 5.--Apalachicola River basin showing locations of transects.

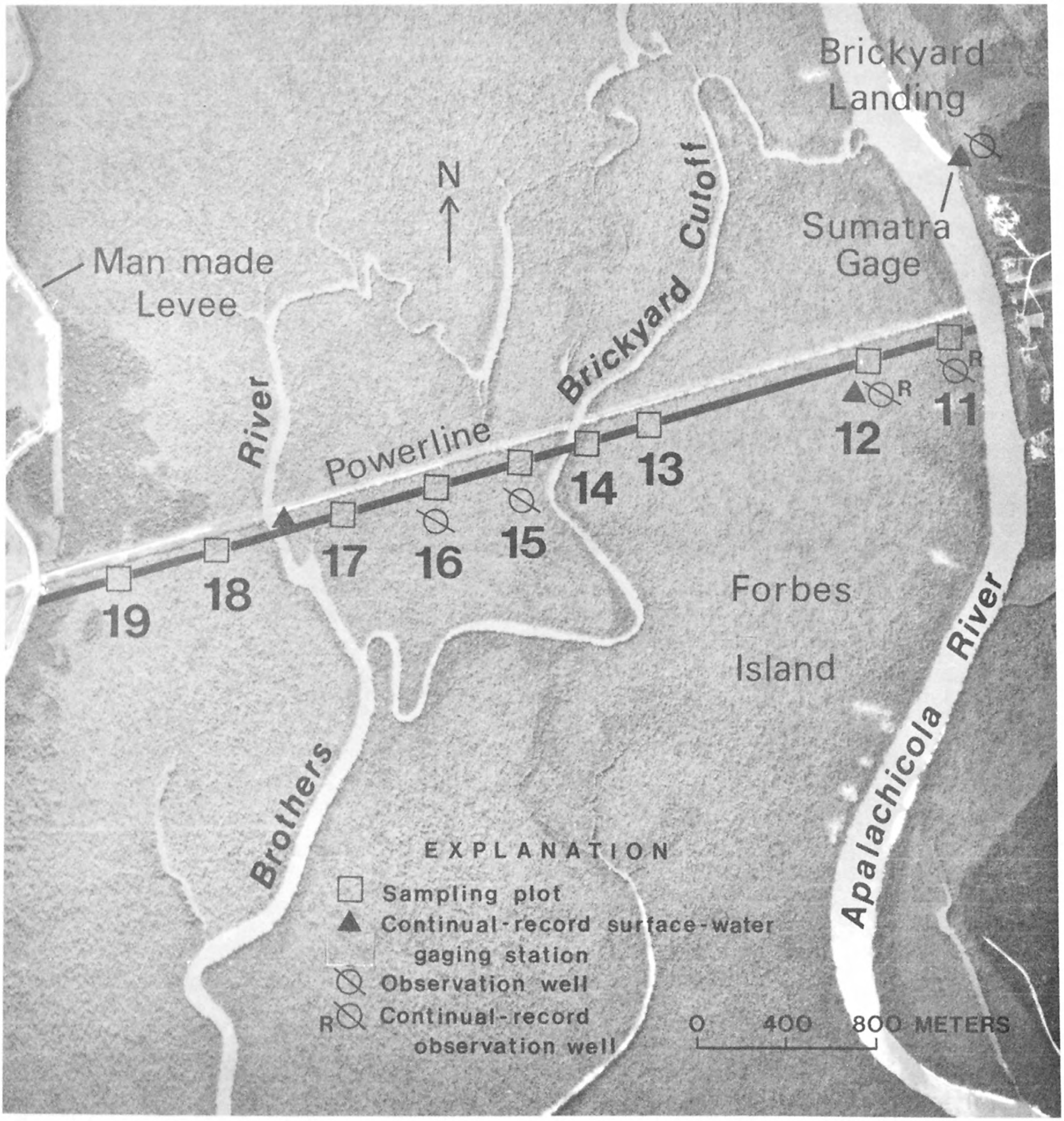

Figure 6.--Brickyard intensive transect with locations of sampling plots and hydrologic measuring sites.

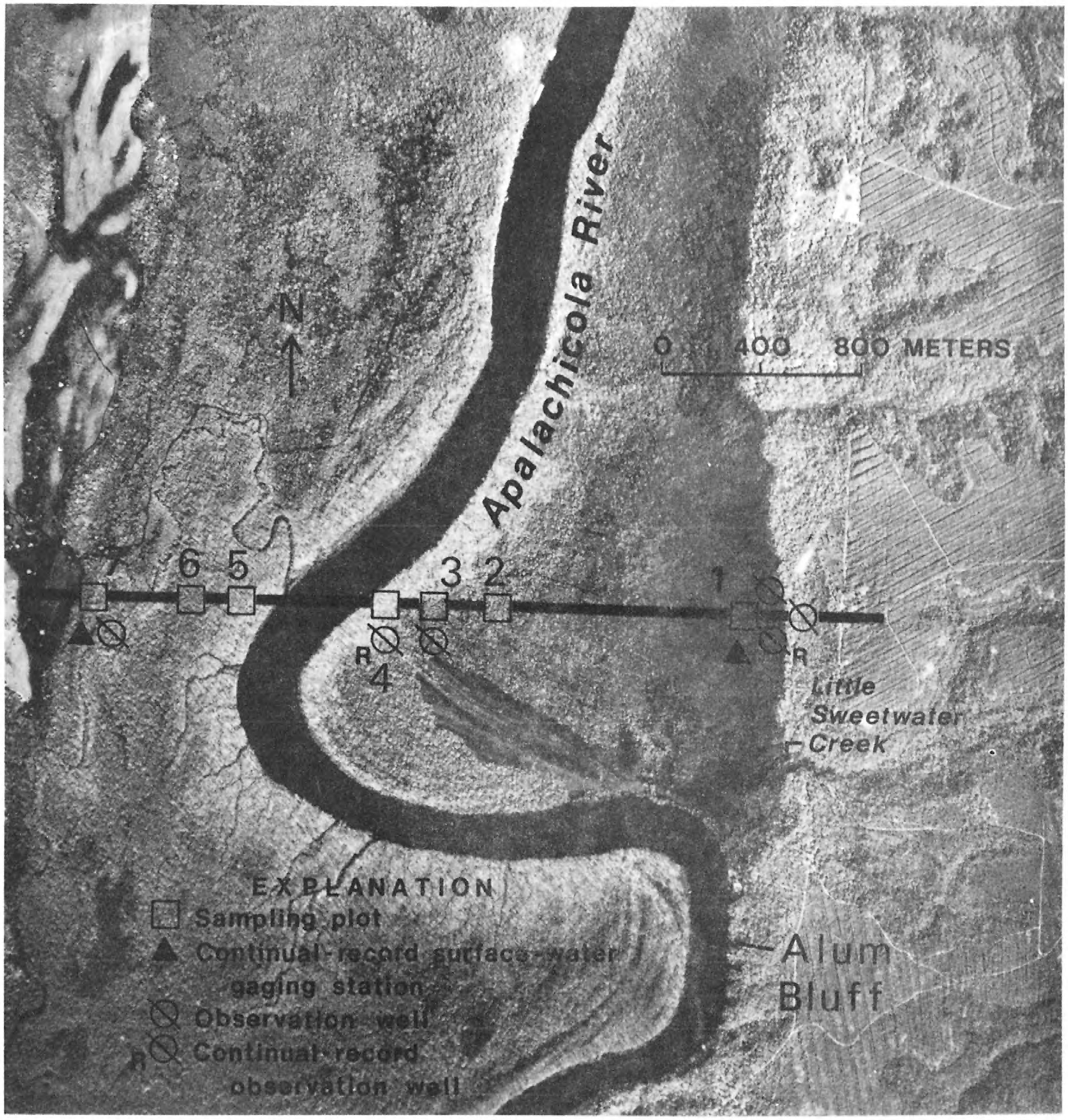

Figure 7.--Sweetwater intensive transect with locations of sampling plots and hydrologic measuring sites.

Each study plot area was 22.5 by 22.5 m (506 m^2) in area. A nested plot analysis (Mueller-Dombois and Ellenberg, 1974, p. 47-50; Leitman and others, 1982), which compared species counts in several successively larger plots, was used to determine representative plot size. The results of this test indicated that 500 m^2 was an optimum plot size. A table of random numbers was used to select grid squares within each plot for installation of two collection nets. The only restriction to random location was that the two nets were required to be at least 6 meters apart. The use of two nets per plot, and the 6-meter separation, prevented oversampling of litter fall from a single tree at any particular plot. The aim of the sampling design was to maximize sampling efficiency, in terms of data yield per unit effort. A distribution of 32 nets among 16 plots was judged more efficient than either more concentrated sampling (many nets per plot and few plots) or broader areal coverage (only one net per plot and more plots). The data collected were later used for evaluation of this sampling design.

Other Data from Study Plots

In addition to data on litter fall, other types of data were collected at each of the intensive-transect plots. Detailed views of the Brickyard transect (fig. 6) and Sweetwater transect (fig. 7) show the locations of plots and the hydrologic data-collection installations. Surface-water gages and ground-water wells were situated at some of the plots to provide data pertaining to hydrologic events. At the time of each leaf collection, a descriptive record was made of soil conditions, flooding (if any), leaf deposition and decomposition on the ground, and leaves remaining in the canopy. Photographs of the canopy, understory, and ground were also taken monthly at each site. Additional data were derived from three randomly located plastic sheets, 1 m^2 in area, affixed to the ground at the time of the installation of the leaf-collection nets and removed after the 1980 spring flood. Accumulated material on these sheets was separated into coarse and fine fractions (greater and less than 1 millimeter particle size) and analyzed for dry and ash weight. Results of the hydrologic measurements are available in the report by Leitman and others (1982). Deposition rates of sediment and organic material on plastic sheets have also been determined (H. C. Mattraw, Jr., written commun., 1981).

Analysis of Litter Fall

The litter-collection nets were installed in late August and early September 1979. Monthly collections began October 1, 1979, and ended September 2, 1980. Additional collections were made in October and December 1980 to provide data for comparing the autumn leaf-fall period of 1980 with the same period in 1979.

Material in nets was collected in plastic bags, brought to laboratory, and separated into five catagories, or subsamples. The first three subsamples were the three most common species. The fourth was a composite of all other leaf species, and the fifth was composed of all nonleaf material. Each species in the composite group was quantified by counting individual leaves. Individual leaf counting was not necessarily done on the first three species because they were quantified by weight. The five subsamples were placed in labeled, nylon-mesh bags and suspended in a dry environment for 1 week for air-drying. Each subsample was then weighed and the weight (minus tare) was recorded.

The individual species weights of the composite group were estimated by using the leaf numbers and composite weight. A weight factor, which varied among species according to leaf size, was used to correct leaf numbers to relative weights. These relative weights were converted to fractions of the total relative weight of the subsample. The fractions multiplied by the composite weight produced the estimated weight of the species in the subsample.

After all weights had been determined, data were stored in a computer data set for later analysis. The data categories stored included: plot, month, net, duration of collection period in days, species names, numbers of leaves (when available), and dry weight. Nonleaf material was considered collectively as one "species"; qualitative separations of the components of the nonleaf material were done but could not be used for quantitative analysis.

During the study, at least one subsample of each of the major species was analyzed for its content of moisture, carbon, nitrogen, and phosphorus. Analysis of total carbon was done with a total carbon analyzer. Subsamples of the leaves were combusted at 1600°C to convert carbon to carbon dioxide, which was measured by a thermistor detector. The inorganic carbon concentration, determined by a modified Van Slyke analysis, was subtracted from total carbon to give total organic carbon. For analysis of nitrogen (ammonia plus organic nitrogen) the sample was digested with sulfuric acid, mercuric sulfate, and potassium persulfate. The resulting ammonium ion was then determined by an indophenol salicylate-hypochlorite colorimetric analysis (Skougstad and others, 1979). For analysis of phosphorus, the sample was subjected to an acid persulfate digestion. Orthophosphate was then analyzed using the phosphomolybdate-ascorbic acid colorimetric reaction (Skougstad and others, 1979).

Leaf Decomposition

A standardized litter-bag method commonly used elsewhere (Witkamp and Olson, 1963; Mathews and Kowalczewski, 1969; Kaushik and Hynes, 1971; Paul and others, 1978; and de la Cruz, 1979) was employed to determine leaf decomposition rates. Preweighed samples (10 g) of freshly fallen leaves were placed in 200- by 200-mm bags of 2.5-mm-mesh nylon screen and subsequently placed in the flood plain, river, and bay (fig. 8). The leaves from five of the dominant tree species in the flood plain were chosen for the study. The species selected were water hickory, water tupelo, diamond-leaf oak, baldcypress, and sweetgum. Each mesh bag contained either (a) one of the selected species or (b) a mixture (composite) of species in weight proportions characteristic of samples from the nearest leaf-collection nets.

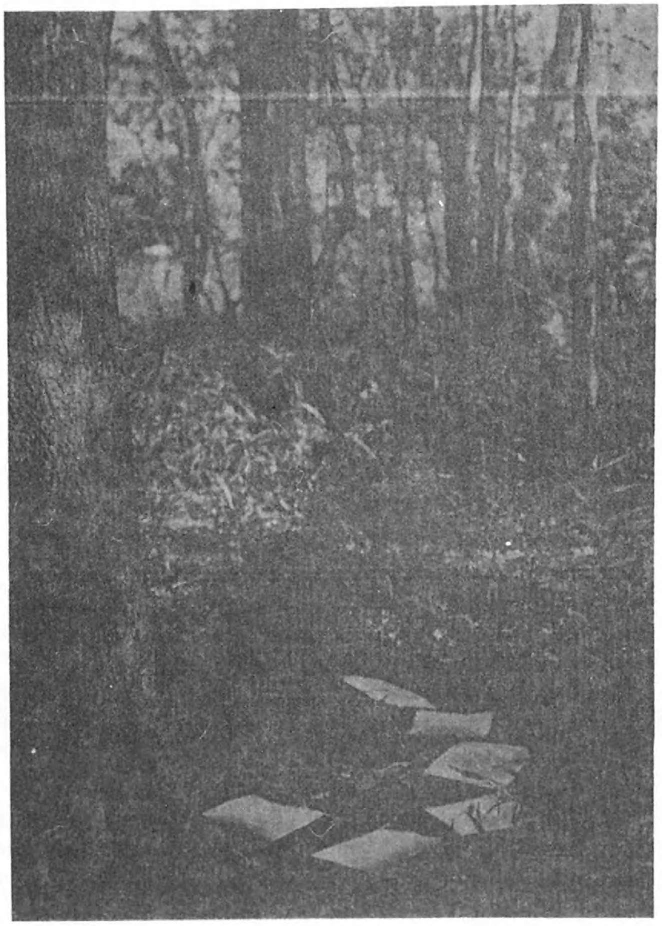

Figure 8.--Mesh bags containing leaf samples for leaf-decomposition study.

Mesh bags containing single-species samples were placed at four locations. The leaves were totally immersed in water at three sites, two in the river and one in the estuary. The two river sites, near the Sweetwater and Brickyard transects, represented the upper and lower river, respectively. The fourth site was at plot 14, a dry flood-plain site characteristic of levee areas. Because the water enhances decomposition (Mason, 1976, p. 18), most of the study focused on decomposition under flooded conditions.

The bags containing the mixed species were placed at six intensive-transect plots in the flood plain. Those were plots 1, 2, and 4 in the Sweetwater transect, and plots 12, 14, and 15 in the Brickyard transect.

This experimental design was chosen to provide information on how decomposition varies as a function of location and presence or absence of water. It also served as a comparison of monospecific decomposition with decomposition of a mixture of species combined as they would be in the natural environment.

Each sample of leaf material was air dried for 1 week prior to placement in the mesh bag. Samples were sealed and placed in the field sites as soon as possible after the estimated peak of leaf-litter fall. Since litter-fall peaks vary with species, the starting dates for the decomposition tests were different according to species. The species that decompose more rapidly (water tupelo and sweetgum) were sampled every 2 weeks for the first 2 months. The remaining collections were made monthly and all sampling was concluded after 6 months. Two single-species bags and one composite bag were collected at each sampling period.

In the laboratory, the samples were thoroughly washed with distilled water until they were free of sediment (silt and accumulated debris). The washed leaf samples were air dried at 20°-22°C for 1 week and weighed. A portion of each sample was then ashed at 500°C for 2 hours to determine the final ash-free dry weight. The ash weight lost (organic content) was compared to the organic content of the sample before placement in the field. This procedure was a precaution against including any accumulated sediment that failed to wash free from the sample in the final air dry weight.

After weighing and ashing, the remainder of each sample was finely ground in a mill, producing 125-micrometer particles, and split into subsamples for nutrient analyses. Carbon and nitrogen concentrations were determined on a carbon-hydrogen-nitrogen analyzer. The analysis is a total combustion to gaseous forms of carbon and nitrogen which are then separated in a chromatographic column and measured by thermal conductivity. Total phosphorus concentration was determined through digestion and acid molybdate analysis (Skougstad and others, 1979).

Extrapolation to the Entire Flood Plain

The 16 plots at the two intensive transects were selected to be as representative as possible of the forest types in the flood plain. Information on a much greater areal scale was needed in order to extrapolate the production and decomposition measurements to the entire system. Additional data were available by means of tree species identification at 223 points across eight "cruise transects" (fig. 5), two of which coincided closely with the intensive transects. Details of the method applied in the Apalachicola study are described by Leitman and others (1982). Each tree sampled was identified and its diameter at breast height (DBH) was measured to permit computation of relative basal area (RBA) by species. Tree measurement followed procedures described by Avery (1967).

Based on cruise-transect results, distribution of tree species over the entire flood plain was determined by Leitman and others (1982). Leaf-production rates at the plots were used to generally characterize production at species and community levels. Extrapolation of the data to the entire flood plain to provide estimates of nutrient and detritus production for the basin-wide flood plain was thereby accomplished.

RESULTS

Litter Fall

Species and Communities

During the 1979-80 sampling period, leaves from 43 species of woody plants (table 1) were collected from the litter nets. A number of vines and other nontree forms contributed to litter fall but understory species were excluded because they were below the level of the collection nets. Photographs of some of the most common leaf species from the collections of litter fall are shown in figure 9.

It was not always possible to distinguish different species of a single genus when sorting partially decomposed leaves. Notable examples of this were tupelo and ash, two of the most abundant leaf-litter genera. All water tupelo and Ogeechee tupelo leaves were grouped together for weighing, as were all species of ash. Swamp tupelo was distinguishable from the other *Nyssa* species but only with considerable difficulty. Two other genera whose leaves were usually indistinguishable by species were grape and greenbrier.

The Apalachicola flood-plain forest has been categorized into five forest types (Leitman and others, 1982). The forest types differ in tree species composition and hydrologic conditions (table 2). Each intensive-transect plot where leaves were collected represented only one forest type. All five forest types were represented by at least one plot.

Annual Litter Production

Litter-fall data are presented in most of the following discussions, tables, and illustrations as grams per square meter per unit time (year or day). These units were computed from means of all relevant data values. Individual species production, like total litter fall, was computed as the mean over all plots (or all plots representing a forest type), although no single species occurred at every plot. Hence, total production was divided by the total number of nets sampled to obtain a production rate on a square-meter basis. Daily litter production in any particular month was computed by dividing the production per square meter by the number of days in the sampling interval. Sampling intervals varied between 25 and 38 days.

Table 1.--Common and scientific names of all species of woody plants whose leaves appeared in leaf-collection nets in 1979-80

Common name	Form[1]	Scientific name
ash, Carolina	t	*Fraxinus caroliniana* Mill.
green	t	*Fraxinus pennsylvanica* Marsh.
pumpkin	t	*Fraxinus profunda* (Bush.) Bush.
baldcypress	t	*Taxodium distichum* (L.) Rich.
birch, river	t	*Betula nigra* L.
boxelder	t	see maple
chinaberry	t	*Melia azedarach* L.
coralbeads	v	*Cocculus carolinus* (L.) DC.
cypress		see baldcypress
dogwood, stiffcornel	t	*Cornus foemina* Mill.
elm, American	t	*Ulmus americana* L.
slippery	t	*Ulmus rubra* Muhl.
winged	t	*Ulmus alata* Michx.
grape	v	*Vitis* spp.
greenbrier	v	*Smilax* spp.
hickory, water	t	*Carya aquatica* (Michx. f.) Nutt.
holly, American	t	*Ilex opaca* Aiton
hornbeam, American	t	*Carpinus caroliniana* Walt.
Japanese climbing fern	f	*Lygodium japonicum* (Thunery) Swartz
locust, honey	t	*Gleditsia* triacanthos L.
locust, water	t	*Gleditsia aquatica* Marsh.
maple, red	t	*Acer rubrum* L.
(boxelder)		*Acer negundo* L.
mistletoe	ps	*Phoradendron serotinum* (Raf.) M. C. Johnston
mulberry, red	t	*Morus rubra* L.
oak, diamond-leaf	t	*Quercus laurifolia* Michx.
overcup	t	*Quercus lyrata* Walt.
swamp-chestnut	t	*Quercus prinus* L.
water	t	*Quercus nigra* L.
peppervine	v	*Ampelopsis arborea* (L.) Koehne
persimmon, common	t	*Diospyros virginiana* L.

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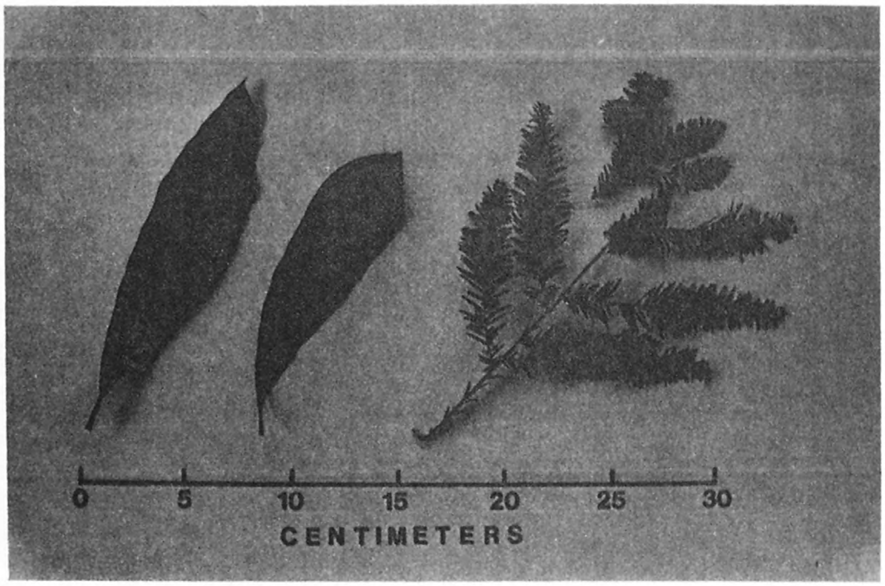
[1] t, tree; v, vine; ps, parasitic shrub; f, fern.

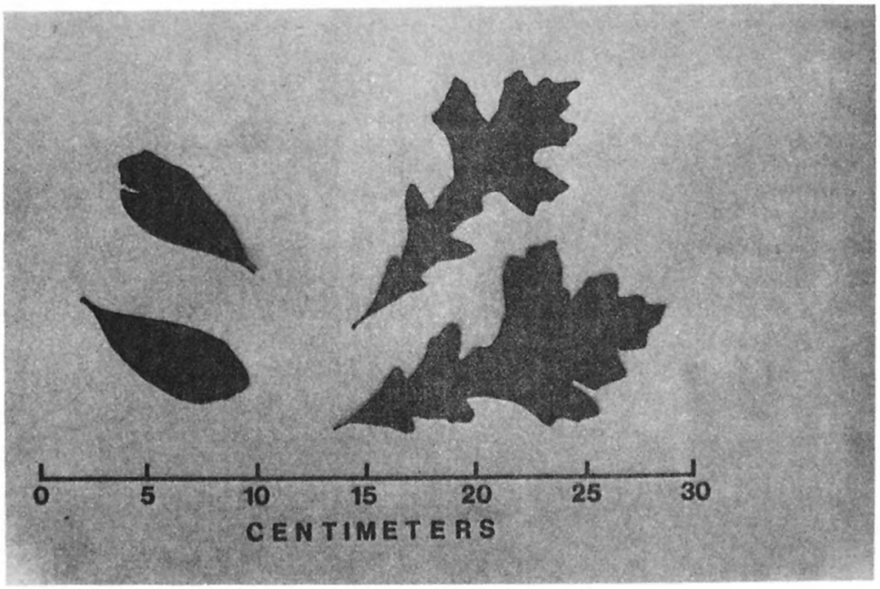
Table 1.--Common and scientific names of all species of woody plants whose leaves appeared in leaf-collection nets in 1979-80--Continued

Common name	Form[1/]	Scientific name
planer-tree	t	*Planera aquatica* Gmel.
poison ivy	v	*Rhus radicans* L.
possum-haw	t	*Ilex decidua* Walt.
rattan vine	v	*Berchemia scandens* (Hill) K. Koch
resurrection fern	f	*Polypodium polypodioides* (L.) Watt
sourgum		see tupelo
sugarberry	t	*Celtis laevigata* Willd.
sweetgum	t	*Liquidambar styraciflua* L.
sycamore, American	*t*	*Platanus occidentalis L.*
titi	t	*Cyrilla racemiflora* L.
trumpet vine	v	*Campsis radicans* (L.) Seeman
tupelo, Ogeechee	t	*Nyssa ogeche* Bartram ex Marsh
water	t	*Nyssa aquatica* L.
swamp	t	*Nyssa biflora* Walt.
virgin's bower	v	*Clematis virginiana* L.

[1/] t, tree; v, vine; ps, parasitic shrub; f, fern.

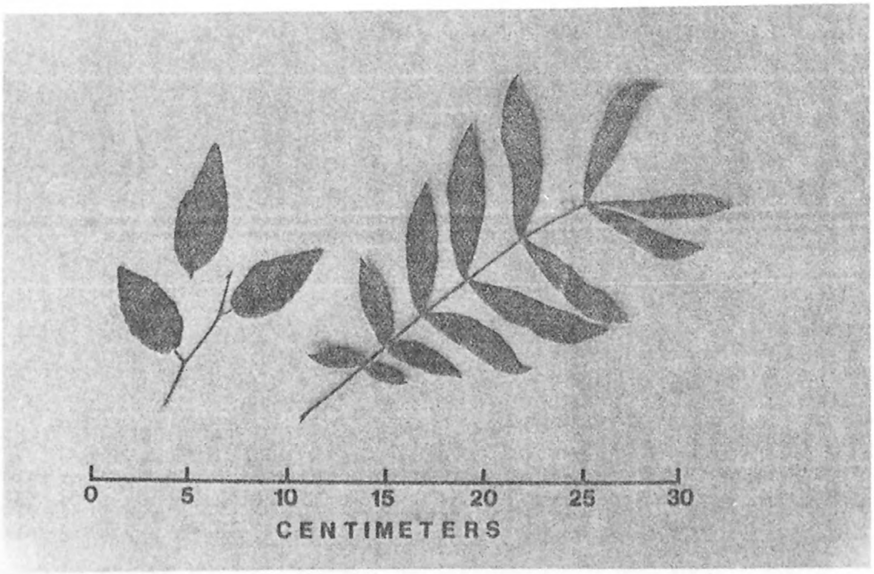


A. Tupelo (left and center), bald-cypress.

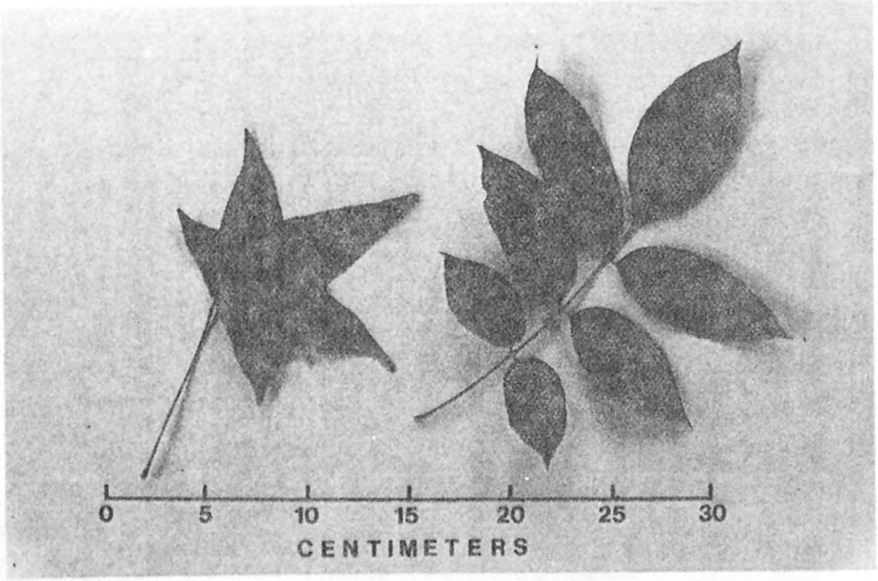


B. Diamond-leaf oak (left), overcup oak.

Figure 9.--Common leaves in the litter fall of the Apalachicola River flood plain.



C. Planer-tree (left), water hickory.



D. Sweetgum (left), ash leaf (complete leaf has 5-9 leaflets).

Figure 9.--Common leaves in the litter fall of the Apalachicola River flood plain--Continued.

Table 2.--Forest types, their species composition, distinguishing characteristics, and occurrence in intensive-transect plots

Forest type	Plots[1]	Predominant species	Associated species	Plot characteristics
A	4 5	Sweetgum Sugarberry Water oak American hornbeam Possum-haw	Diamond-leaf oak Green ash American elm American sycamore Water hickory	Located on levees and high ridges. Saturated only by high flooding. High tree species diversity.
B	3 6 11 14	Water hickory Green ash Overcup oak Diamond-leaf oak Sweetgum American elm	Sugarberry Red maple Water oak Possum-haw American hornbeam	Located on high flats and low ridges. Saturated by low to moderate flooding. High tree species diversity.
C	7 15 16 17 18	Water tupelo Ogeechee tupelo Baldcypress Swamp tupelo Carolina ash Planer-tree	Overcup oak Pumpkin ash Red maple Water hickory American elm Green ash Diamond-leaf oak Sweetbay	Located in low areas but with some ridges or hummocks which aid drainage. Usually saturated. High tree species diversity.
D	1	Water tupelo Swamp tupelo Ogeechee tupelo Baldcypress Carolina ash Pumpkin ash Planer-tree Sweetbay		Located in low, flat areas with poor drainage. Saturated almost continuously. Low tree species diversity.
E	2 12 13 19	Water tupelo Baldcypress Carolina ash Planer-tree		Located in low, flat areas with poor drainage. Saturated almost continuously. Low tree species diversity.

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[1] Plot numbers appear in figures 6 and 7.

Although the leaf litter represented 43 different species of woody plants, it was largely composed of leaves from a few dominant species. Twelve species contributed over 90 percent of the leaves collected (table 3). These twelve species were also the most abundant flood-plain tree species with the exception of grape. Grape is the only vine in the group. As a vine, supported by trees, its stem size is small and its foliage:DBH ratio is much higher than that of most tree species. It is very abundant in the flood plain, particularly in levee areas. In terms of density (numbers of plants per hectare, independent of basal area), grape was 10th among the species found in the cruise transects (Leitman and others, 1982). This ranking more closely corresponds to its leaf production. Swamp tupelo was the fourth most abundant species in the cruise transects, but not among the top 12 litter producers. Two factors are responsible for this: (1) difficulty in distinguishing swamp tupelo leaves from other tupelo leaves, and (2) under-representation of swamp tupelo in the intensive-transect plots relative to its abundance on the flood plain. Only plot 1 had a substantial stand of swamp tupelo trees.

The important component of the litter fall which is not shown in table 3 is nonleaf material, such as twigs, stems, bark, berries, and nuts. Some leaf parts were also included in this material because it was impossible to totally separate all small leaf parts from the conglomerate collected in the nets. Production of nonleaf material amounted to 330 $(g/m^2)/yr$ over the intensive-transect plots, or nearly twice that of the most abundant leaf species and over 40 percent of total litter fall. This material consisted of contributions from nearly every major tree species and a number of less common trees and other vegetation.

Table 3 also excludes a category of leaf material consisting of "miscellaneous and unidentified leaf material," principally leaf pieces from the major species. Because it contained a diversity of leaf parts, it was considered to come from several species. It accounted for 10 $(g/m^2)/yr$ of the litter fall.

Table 3 shows that tree-species ranking with respect to leaf-litter production corresponds closely with tree abundance in cruise transects. It also shows similar agreement between leaf-litter production and tree abundance in the intensive transects. Whereas the first relation is an indicator of good representation of the entire flood plain, the second is a measure of sampling accuracy within the plots themselves. Vines were not included in basal area measurements in the intensive-transect plots, hence no such data are available for grape. In the intensive transects, tree abundance rank numbers 5 and 10 were occupied by swamp tupelo and red maple, respectively. Leaf productivity of these two species was slightly lower than the 9.7 $(g/m^2)/yr$ of American hornbeam.

Table 3.--Major leaf-litter producers, and their abundance, in the Apalachicola flood plain

[Leaves of some genera (tupelo, ash, and grape) could not be distinquished by species; hence, leaves were grouped together. Although tree abundance by species was available for these genera, it was combined for this comparison to correspond to the leaf species groupings. Leaf production data represents means of all plots.]

	Leaf production (excluding nonleaf material)			Tree abundance			
				Cruise transects		Intensive transects	
Species	$(g/m^2)/yr$	Percent of total	Rank	Percent[1/]	Rank	Percent[1/]	Rank
Tupelo	172.5	33.0	1	40.9	1	49.8	1
Baldcypress	58.7	11.2	2	10.6	2	12.3	2
Sweetgum	48.8	9.3	3	4.8	5	5.7	4
Ash	39.3	7.5	4	10.2	3	9.6	3
Diamond-leaf oak	31.1	5.9	5	2.5	10	3.6	6
Overcup oak	28.1	5.4	6	3.2	6	2.0	8
Water hickory	26.8	5.1	7	2.9	8	3.2	7
Grape	24.3	4.7	8	0.1	28	--	--
Planer-tree	15.4	2.9	9	2.9	7	1.7	9
Sugarberry	15.2	2.9	10	2.8	9	1.0	12
American elm	13.5	2.6	11	2.4	11	1.3	11
American hornbeam	9.7	1.9	12	2.0	12	0.9	13

[1/] As relative basal area (from Leitman and others, 1982).

Leaf Fall per Stem Biomass

The data of table 3 suggest that leaf fall per stem biomass is greater among those species which have lower abundance. This is confirmed by the relation shown in figure 10. Leaf-litter productivity data were transformed from productivity per unit ground surface to productivity per tree biomass unit (leaf fall in grams per square meter basal area). Because the biomass unit is basal area, computed from a trunk diameter, this index may also be termed leaf-litter productivity per stem biomass. Only the 11 most common species are plotted. Grape is excluded because of the lack of basal area data. All other species had such low total basal areas that small differences in basal area would produce spurious fluctuations in the productivity calcualtion. Tupelo, which comprised half of the tree biomass in the test plots, produced only a third of the leaf litter. It was lowest in leaf-litter productivity per unit basal area. The less abundant species were sometimes three to four times more productive than tupelo. A power curve was fitted to the data to suggest the type of relation that exists between tree abundance and leaf-fall productivity in this system. A cause-effect relation should not be inferred from this association.

Forest-Type Differences

Forest-type differences in leaf production and tree abundance within plots are presented in table 4. At this breakout level, the data base becomes relatively small and sampling error factors become larger. Sugarberry, for example, may have been overrepresented in forest type A because one of the four collection nets representing that forest type in the study plots was located by random placement directly beneath a large sugarberry tree. The tree, in fact, was the only sugarberry in that plot (plot 4) but because of its size it accounted for 29 percent of the total basal area in the plot. Despite this potential error factor, there was nominal discrepancy between percentage values found for basal area and leaf production of sugarberry in forest type A (table 4). Rank comparisons for all forest types indicate that the most abundant trees were generally the greatest contributors to leaf litter. The major exceptions to this occurred in forest types A and B because of the presence of abundant vines. Basal areas for the vines were not measured, but as indicated previously for grape (table 3), the productivity:basal area ratios tend to be high for these lianoid plants.

Seasonal Variability

Considerable seasonal variability in leaf-litter production was observed by transect plot sampling. The daily leaf-litter production rate by month (phenological data) is illustrated in figure 11. A characteristic pattern is evident, with maximum production in November and other high production rates occurring in the other autumn months. Minimum leaf-litter production [<0.2 (g/m^2)/d] occurred from February to May. By June, there was a slight but perceptible increase in leaf fall as the canopy of the new season became established. Leaf-fall rates continued to increase during the summer.

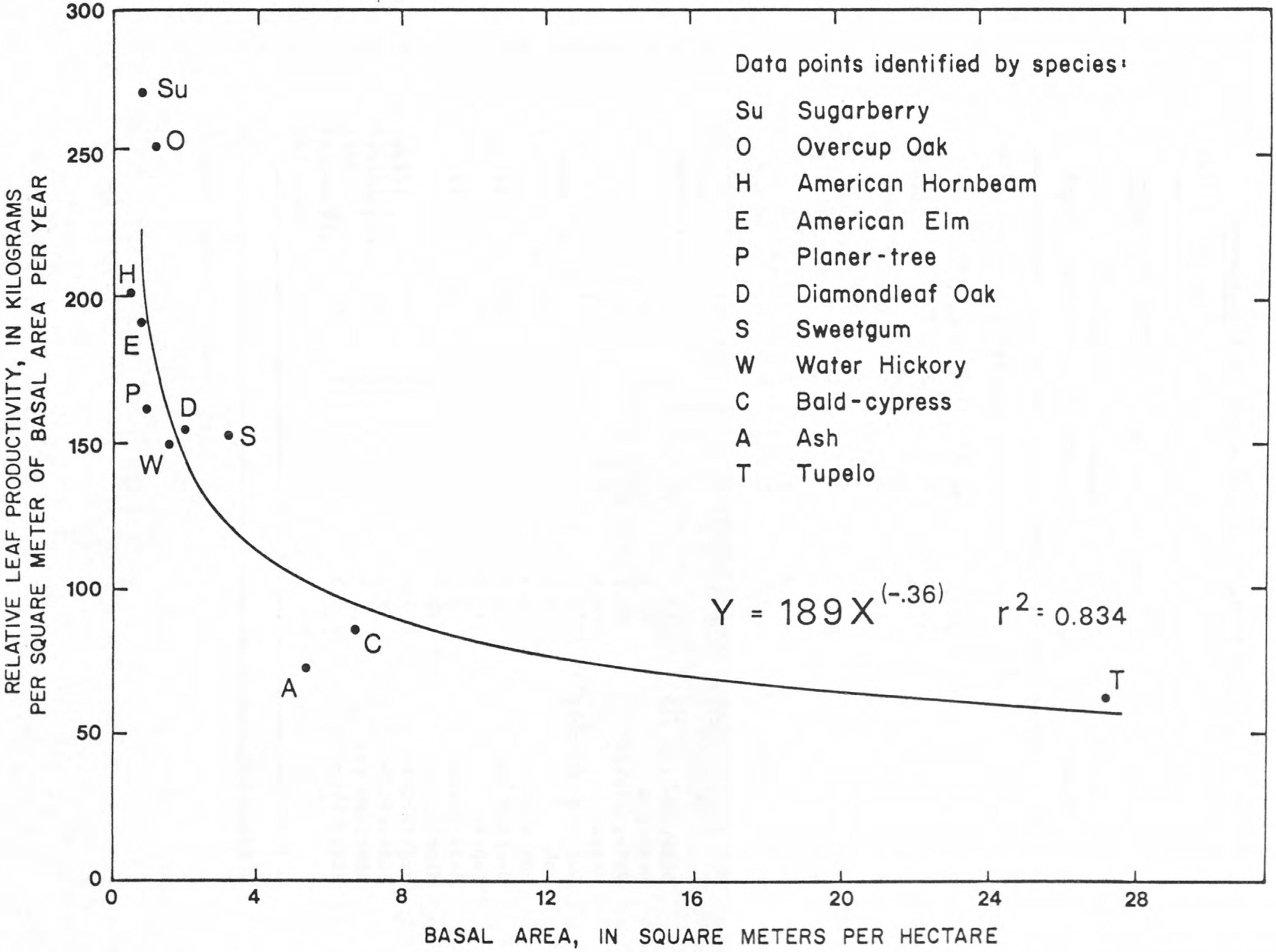


Figure 10.--Relative leaf productivity per stem biomass of 11 major leaf-fall producers (trees) in the Apalachicola River flood plain.

Table 4.--Leaf-litter production and tree abundance

	Leaf production			Tree abundance	
Species	$(g/m^2)/yr$	Percent of total	Rank	RBA,[1/] percent	Rank
		Forest type A (plots 4 and 5)			
Sweetgum	203.4	39.4	1	64.0	1
Sugarberry	102.8	19.9	2	15.1	2
Grape	96.9	18.8	3	--	--
Ash	42.1	8.2	4	10.8	3
Sycamore	7.8	1.5	5	5.8	4
Poison ivy	6.0	1.2	6	--	--
Trumpet vine	5.6	1.1	7	--	--
Water oak	5.3	1.0	8	0.7	8
Water hickory	2.7	0.5	9	0.4	10 tie
		Forest type B (plots 3, 6, 11, and 14)			
Diamond-leaf oak	117.7	21.7	1	30.1	1
Sweetgum	92.8	17.1	2	14.5	3
Water hickory	82.8	15.3	3	20.3	2
Grape	46.6	8.6	4	--	--
American hornbeam	37.9	7.0	5	7.3	6
Ash	31.7	5.8	6	8.1	5
Box elder	21.4	4.0	7	1.5	9
Overcup oak	16.4	3.0	8	0.2	17 tie
Tupelo	15.9	2.9	9	10.2	4
Baldcypress	10.8	2.0	10	0.4	13 tie
Mistletoe	10.5	1.9	11	--	--
Sugarberry	9.0	1.7	12	0.4	13 tie
Planer-tree	8.5	1.6	13	0.4	13 tie
American elm	5.9	1.1	14	3.2	7
River birch	5.5	1.0	15	2.1	8

[1/] RBA: relative basal area.

Table 4.--Leaf-litter production and tree abundance--Continued

	Leaf production			Tree abundance	
Species	$(g/m^2)/yr$	Percent of total	Rank	RBA,[1/] percent	Rank
Forest type C (plots 7, 15, 16, 17, and 18)					
Tupelo	232.4	42.6	1	56.7	1
Overcup oak	77.1	14.1	2	5.2	4
Ash	58.3	10.7	3	13.3	2
Baldcypress	57.6	10.6	4	8.9	3
American elm	37.9	7.0	5	2.3	8
Planer-tree	28.8	5.3	6	2.4	7
Water hickory	18.3	3.4	7	1.8	9
River birch	5.8	1.1	8	0.8	10
Swamp tupelo	4.7	0.9	9	5.1	5
Red maple	4.6	0.8	10	2.4	6
Diamond-leaf oak	4.5	0.8	11	--	--
Forest type D (plot 1)					
Tupelo	403.3	83.7	1	65.6	1
Swamp tupelo	40.4	8.4	2	28.5	2
Baldcypress	30.1	6.3	3	5.8	3
Titi	4.9	1.0	4	0.2	4
Ash	2.0	0.4	5	--	--
Forest type E (plots 2, 12, 13, and 19)					
Tupelo	283.6	58.1	1	61.9	1
Baldcypress	142.5	29.2	2	25.6	2
Ash	31.2	6.4	3	9.1	3
Planer-tree	16.9	3.5	4	2.5	4
Red maple	1.5	0.3	5	0.6	5

[1/] RBA: relative basal area.

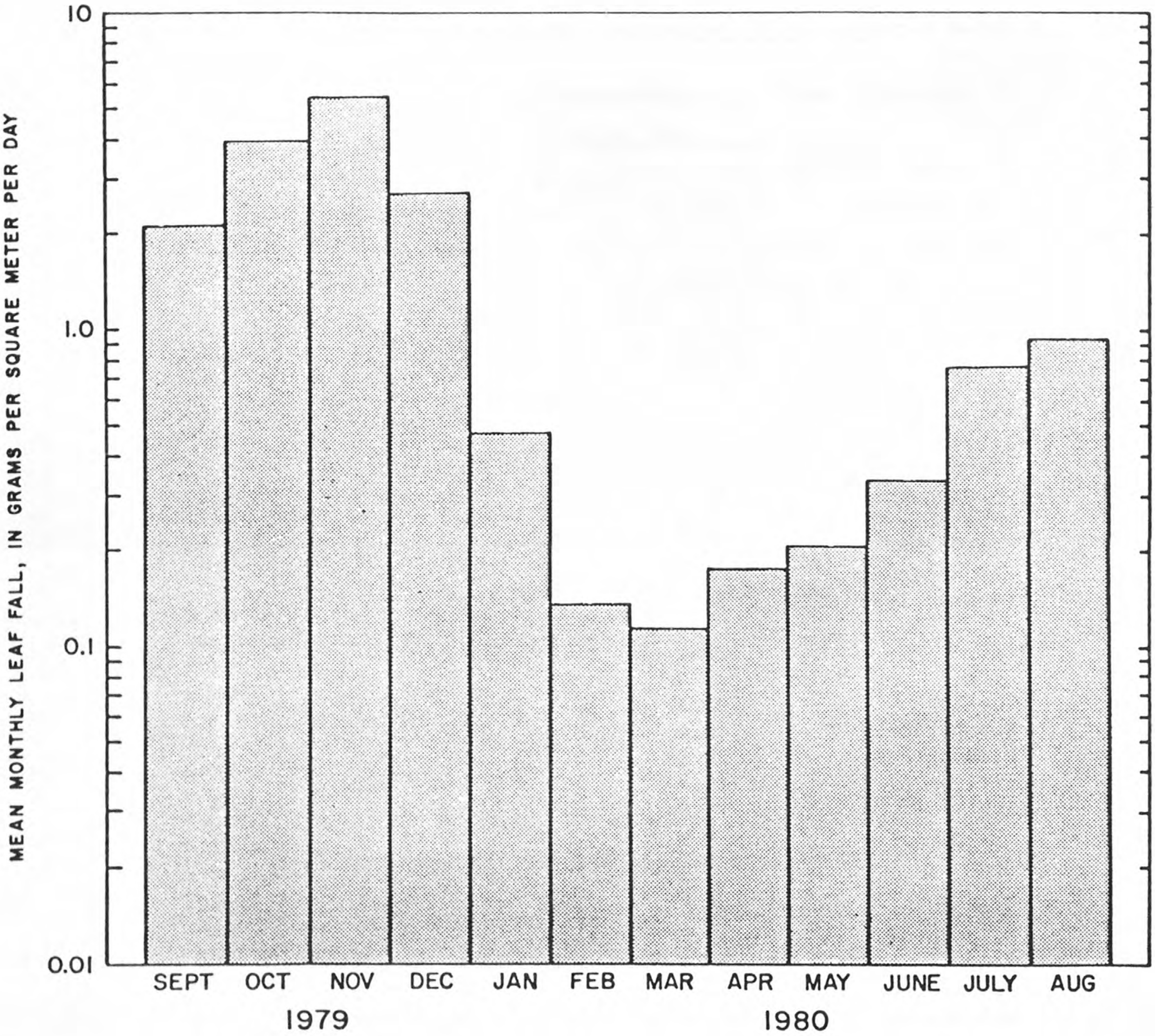


Figure 11.--Mean monthly leaf fall on intensive-transect plots.

Analysis of leaf fall from individual tree species revealed three distinct seasonal patterns represented in figure 12 by three common species. Water hickory represents the most common pattern, in which the maximum leaf fall occurred in November and the autumn peak was a sharp one. Summer leaf fall was only slightly greater than the minimum rates of spring. Other common species which exhibited similar seasonal patterns were baldcypress, ash, American elm, grape, and American hornbeam. A different seasonal pattern is represented by tupelo, which begins to drop appreciable quantities of leaves early in the summer and continues through the autumn at a high leaf-litter production rate. In 1980, its low-production period was quite short (January-March). Sweetgum was the only other major tree species to exhibit this seasonal leaf-fall pattern. A third pattern was characterized by diamond-leaf oak with a late and sustained leaf-fall production. Other major species with similar phenology were overcup oak and planer-tree.

Detailed monthly leaf-fall data for the 12 major leaf-litter species are available in the Supplementary Data.

In contrast to the quite consistent phenological patterns of leaf production, phenology of nonleaf litter fall showed no discernible pattern (fig. 13). Any month of the year was potentially a high-yield month for nonleaf material. Two of the highest yields in 1979-80 occurred in February and June when leaf fall was at minimum levels. The fact that the nonleaf material was composed of a diverse mixture of organic matter derived from various species partially accounted for its consistent occurrence in all seasons of the year. Storm events and wind variation may have accounted for some of the variability in the summer of 1980.

Annual Variability

Litter-fall measurements from the autumn months of 1979 are compared with corresponding data from the autumn of 1980 in table 5. The 1980 data were collected solely for the purpose of this comparison; there was no separation and weighing by species. The data showed some differences between the two years, but an analysis of variance indicated that the hypothesis of no difference should not be rejected at an alpha level of 0.05. Differences between the two years were somewhat greater in the October-November period than in September. The significance test applied at alpha = 0.10 did in fact suggest a difference between the two years when the Brickyard data are included. The null hypothesis was still valid at alpha = 0.05, however.

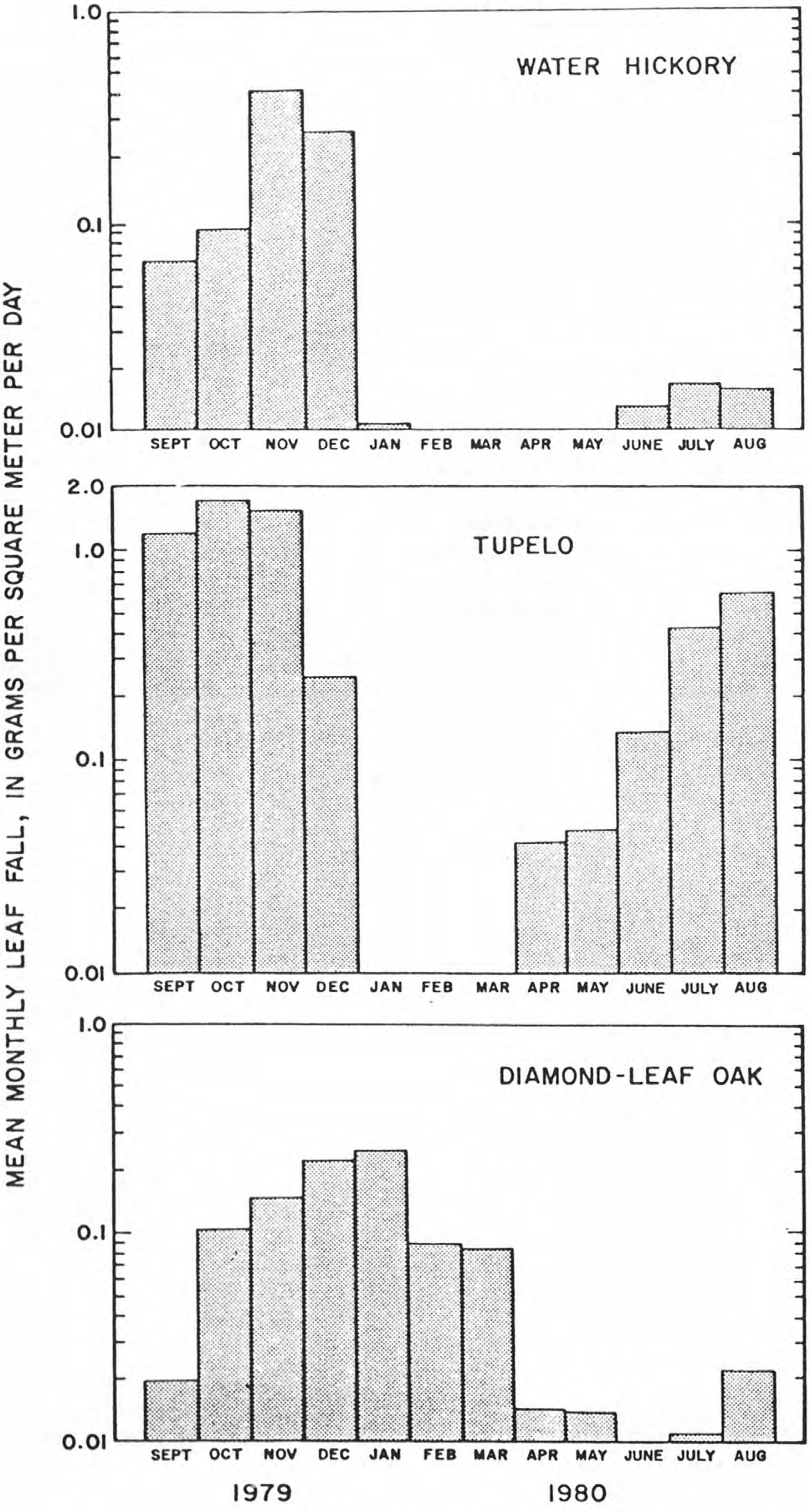


Figure 12.--Mean monthly leaf fall of three representative species on intensive-transect plots.

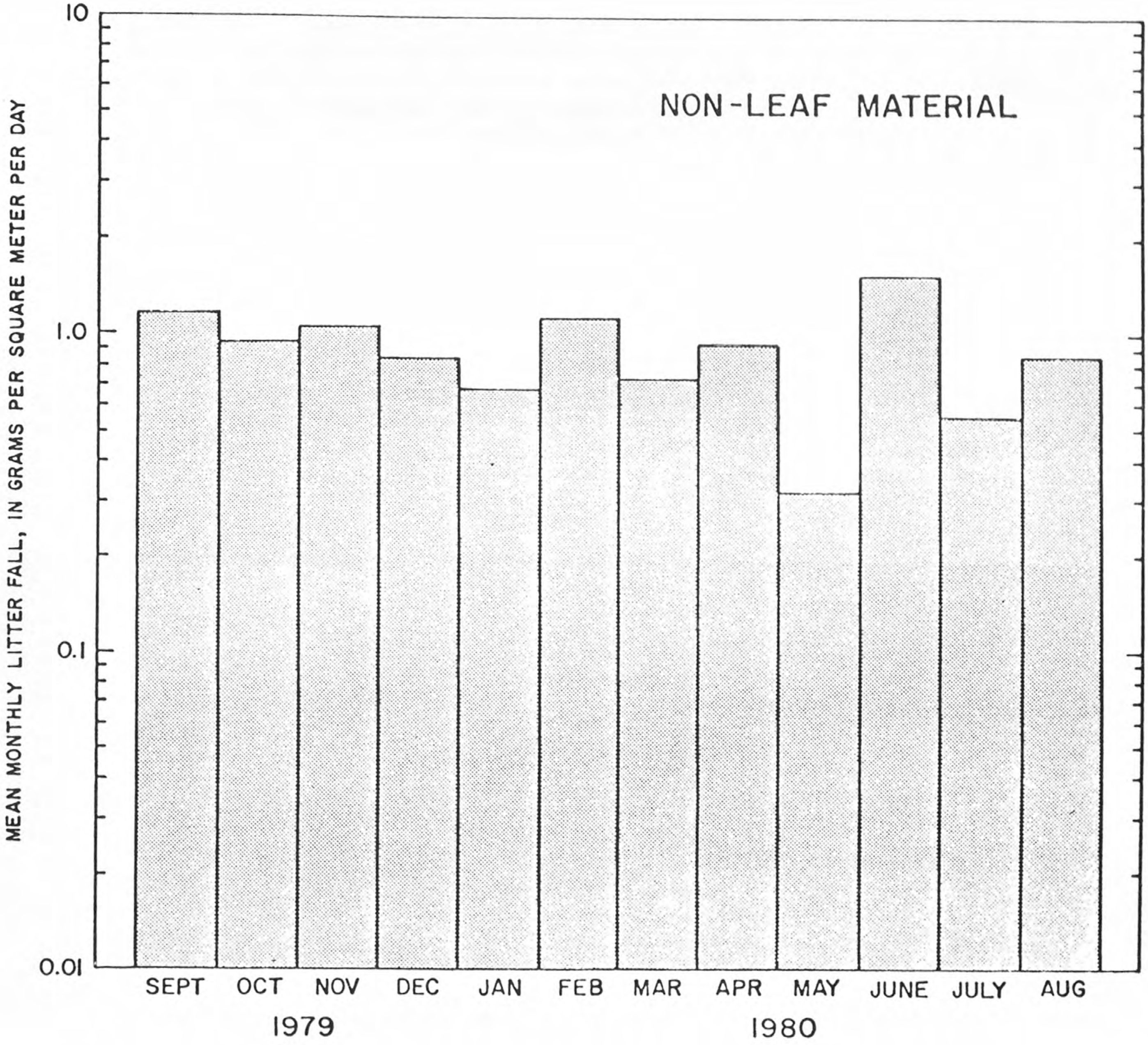


Figure 13.--Mean monthly litter fall, nonleaf material only.

Table 5.--Comparison of autumn litter fall between 1979 and 1980

[Litter fall in grams per day, summed over number of nets indicated]

[NS, not significant ($H = H_o$); S, significant ($H \neq H_o$)]

	Sweetwater transect (14 nets)	Brickyard transect (17 nets)	Total (31 nets)
September			
1979	40.9	58.6	99.5
1980	42.6	47.9	90.5
F-test ($\alpha = 0.10$	NS	NS	NS
October-November			
1979	82.8	91.4	174.2
1980	73.1	72.1	145.2
F-test ($\alpha = 0.10$)	NS	S	S
F-test ($\alpha = 0.05$	NS	NS	NS

Nutrient Content

Analyses of nutrient content of the leaves produced the results given in table 6. The carbon content of the leaves was found to be consistently between 40 and 60 percent, with a mean near 50 percent. There was less consistency in the nitrogen and phosphorus content. The nutrient ratios may be summarized by the general statement that there is approximately an order of magnitude increase from phosphorus to nitrogen, and again from nitrogen to carbon. The concentrations of nitrogen and phosphorus were higher by factors of 2 to 5, and the resulting C:N and C:P ratios lower, than those often reported for other systems (Carlisle and others, 1966; Triska and others, 1975). The data of table 6 represent pooled results of separate nutrient analyses of most of the major leaf-fall species. Differences among species were not detectable within the analytical level of precision.

Table 6.--Nutrient content of leaves collected in leaf-collection nets, autumn, 1979

[Leaf species included in the analyses were: tupelo, baldcypress, ash, swamp tupelo, overcup oak, sugarberry, sweetgum, grape, American elm, planer-tree, American hornbeam, and boxelder. Number of samples = 18]

Nutrients	Ratio	Mean leaf content, percent	Range, percent	Standard deviation	Percent standard deviation
		Nutrient content			
Carbon		50.3	40-60	5.3	11
Nitrogen		6.6	2.7-11.0	2.1	32
Phosphorus		0.65	0.1-1.4	0.32	49
		Nutrient pair ratios			
N:P	10.8		4.8-19.4	4.2	39
C:N	8.6		4.0-17.4	3.5	41
C:P	89.1		37-196	44.5	50

Evaluation of Sampling Design

The sampling design of two nets per study plot, each net of 1 m^2 opening and located at least 6 meters from the other net, proved valid, based on examination of the data. As an example, data from plots 3 and 6, which contain a high diversity of species, are shown on table 7. Both plots are classified as forest type B, and the species listed are those which are characteristic of that type (table 2). Within each plot, the second net added a considerable amount of information over that provided by only one net. Sugarberry, for example, did not appear in net 1 of plot 3, but did occur in net 2. At both plots, all characteristic leaves were collected with the two-net combination.

Table 7.--Annual litter-fall production in plots 3 and 6, with breakdown by individual nets and species characteristic of forest type B

[All units in grams per square meter per year]

	Plot 3			Plot 6		
Species	Net 1	Net 2	Mean	Net 1	Net 2	Mean
American elm	22.1	1.8	12.0	0.0	0.3	0.2
American hornbeam	19.5	10.6	15.1	2.1	66.5	34.3
Ash	93.1	8.6	50.9	33.7	60.0	46.9
Diamond-leaf oak	37.1	29.2	33.2	41.2	12.3	26.7
Grape	48.6	61.1	54.8	27.5	11.8	19.7
Overcup oak	15.5	2.7	9.1	0.4	5.3	2.9
Sugarberry	0.0	6.2	13.1	37.6	4.5	21.0
Sweetgum	78.0	258.7	168.3	196.5	7.7	102.1
Water hickory	41.4	5.2	23.3	199.6	109.4	154.5
Red maple	0.1	0.5	0.3	0.2	1.5	0.9
Other leaf species	247.3	272.6	259.9	257.1	273.9	265.5
Total leaf fall	602.7	677.2	640.0	795.9	553.2	674.7
Nonleaf material	282.9	114.6	198.7	409.3	529.4	469.3

Spearman's rank correlation coefficient

	r_s	Significance ($\alpha = 0.05$)
Between nets 1 and 2, plot 3	0.45	NS
Between nets 1 and 2, plot 6	0.61	NS
Between means, plots 3 and 6	0.67	S

The degree of similarity of nets in each of the two plots, and between the two plots, was tested by calculating Spearman's rank correlation coefficients, r_s (Snedecor and Cochran, 1967, p. 194). The higher the value of r_s, the greater the similarity between the two data sets being tested. In both plots the collections from the two nets were found to be dissimilar. A significant similarity was found, however, between the mean values of the plot 3 nets and those of plot 6. The similarity between the means of the two nets, which occurred although the plots were distant from each other, suggests that outlying values were compensated considerably by the addition of a second net in each plot. It should be noted that these data represents the worst case comparison to be expected. The two plots in question have a wide variety of vegetative species; other plots with lower diversity are less likely to contain species which are not characteristic of their forest types. Furthermore, the data interpretation throughout this report is based on cumulative results from forest types or transects rather than individual plots.

Leaf Decomposition

Results of leaf decomposition experiments are shown in figures 14-21.

The ratios of total weight loss for each of the five tested species are illustrated in figures 14 and 15. For the exponential loss curves (nitrogen and phosphorus, figs. 18-19), a "k factor" (Petersen and Cummins, 1974) was calculated using the formula

$$\frac{\ln Q}{t} = -k$$

where

Q = fraction of substance remaining after time t.

The k factor was translated to percent loss per day by the formula

$$(1 - e^{-k})\ 100 = \text{percent loss per day}$$

where

e = base of natural logarithms.

It should be noted that in the case of exponential curves, the "percent loss per day" is integrated over the entire 6-month period. Initially, the rate is faster; later it is slower.

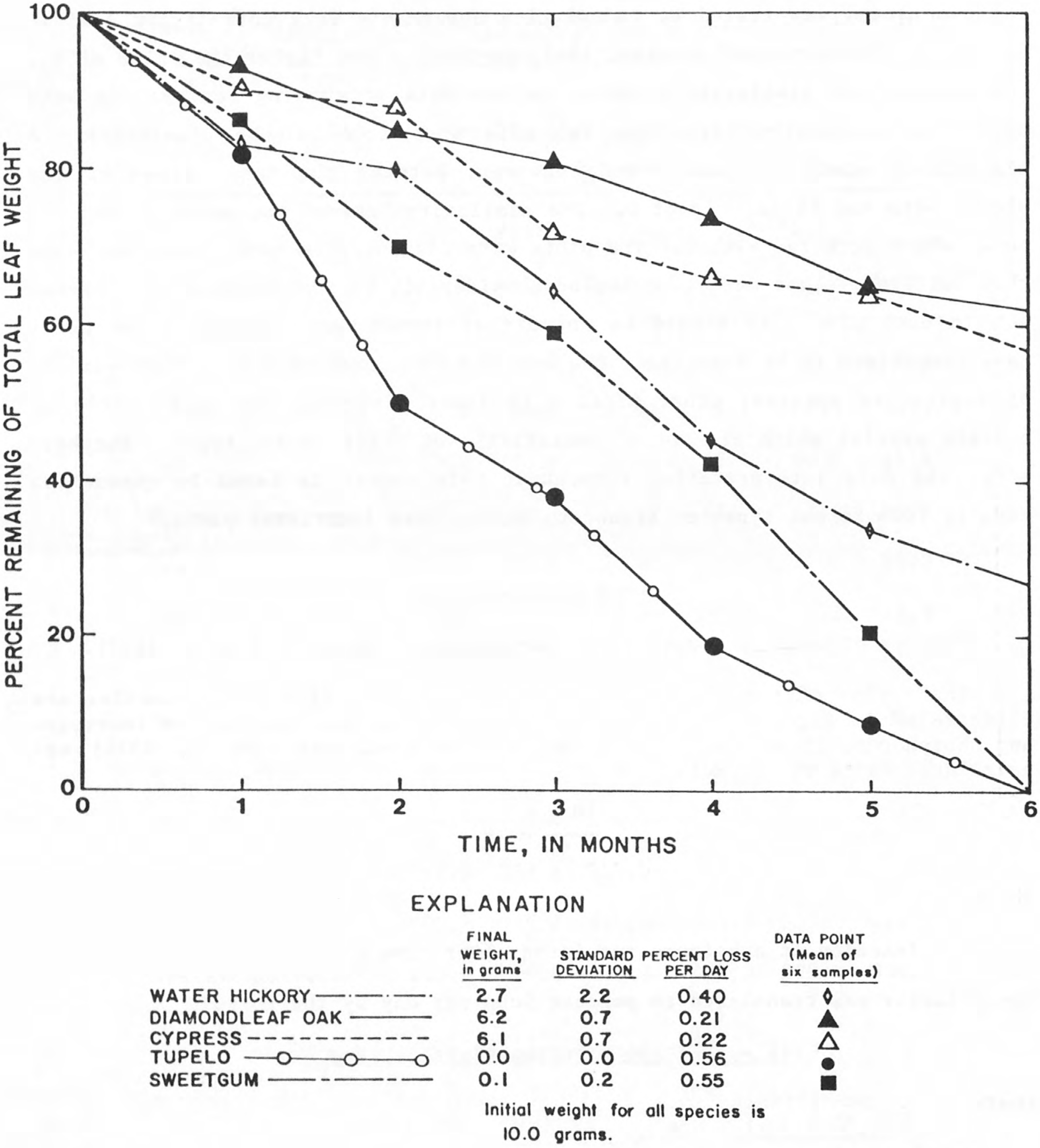
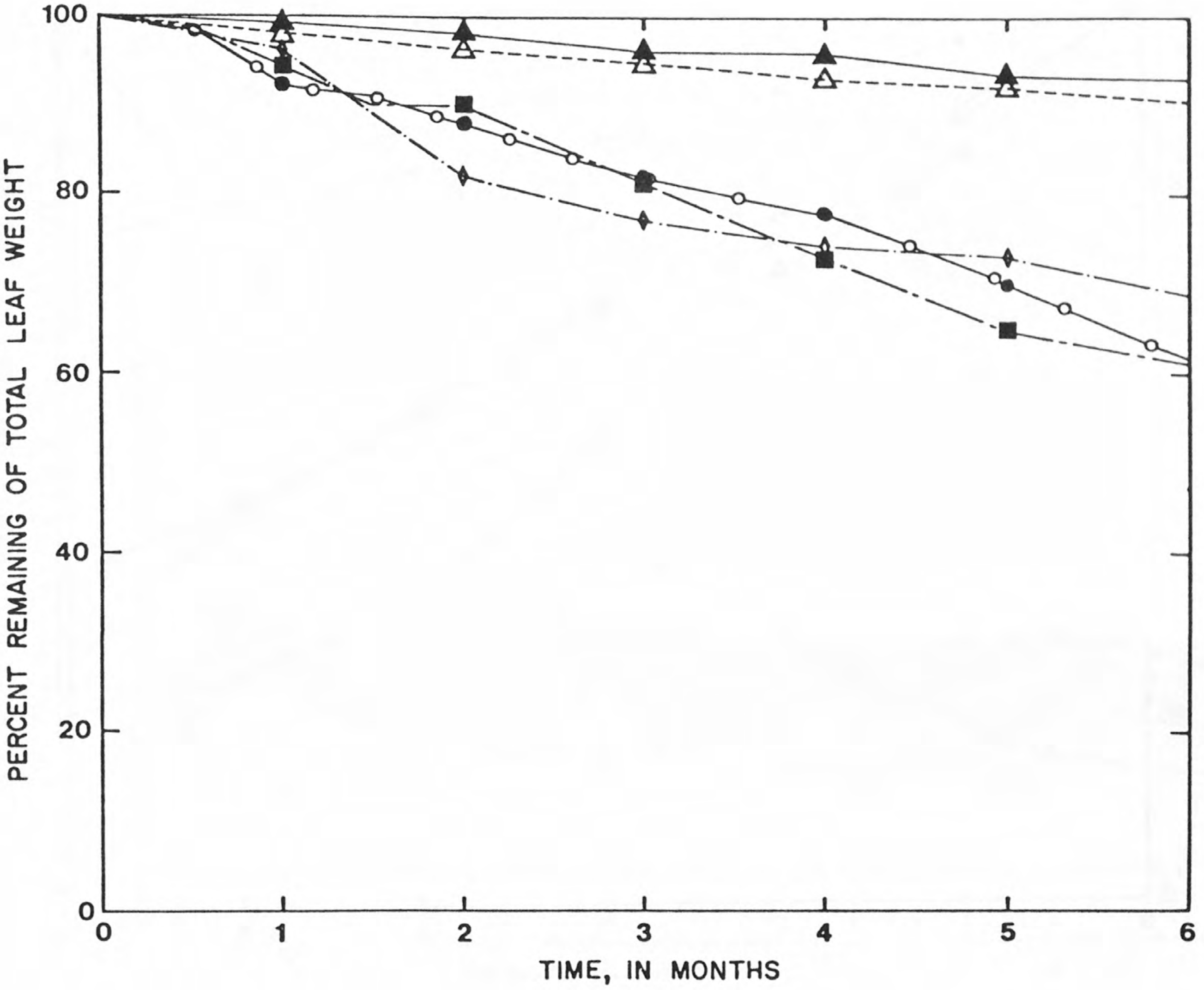


Figure 14.--Leaf decomposition: weight loss for five species in constantly flooded sites.



EXPLANATION

	FINAL WEIGHT, in grams	STANDARD DEVIATION	PERCENT LOSS PER DAY	DATA POINT (Mean of two samples)
WATER HICKORY —·—·—	6.9	0.2	0.17	◊
DIAMONDLEAF OAK ———	9.3	<0.1	0.04	▲
CYPRESS - - - - - -	9.0	<0.1	0.05	△
TUPELO —○—○—○—○	6.2	0.2	0.21	●
SWEETGUM —·—·—	6.1	<0.1	0.22	■

Initial weight for all species is 10.0 grams.

Figure 15.--Leaf decomposition: weight loss for five species in dry leaf packs on flood-plain floor.

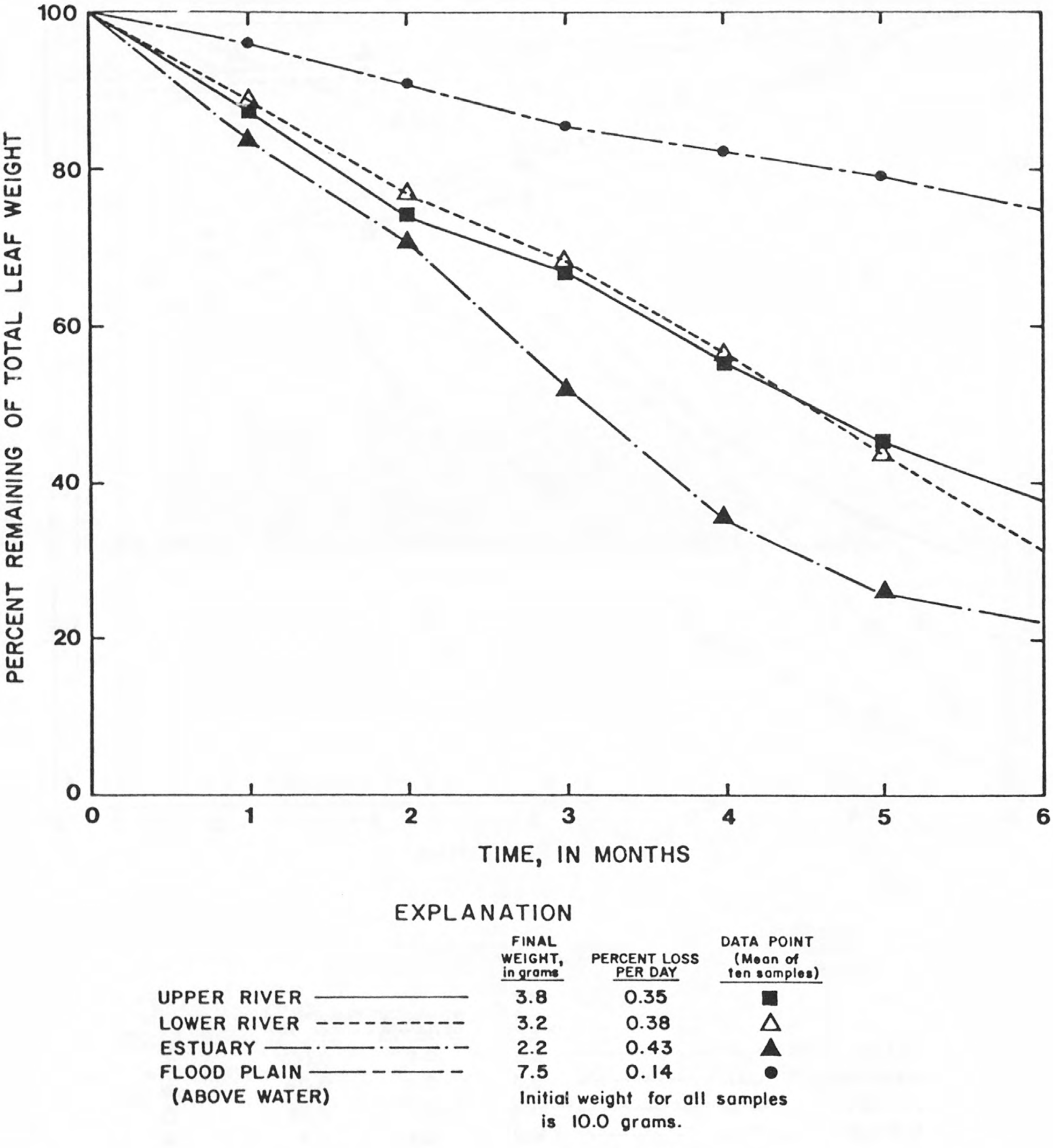


Figure 16.--Leaf decomposition: mean weight loss for all species at four sites.

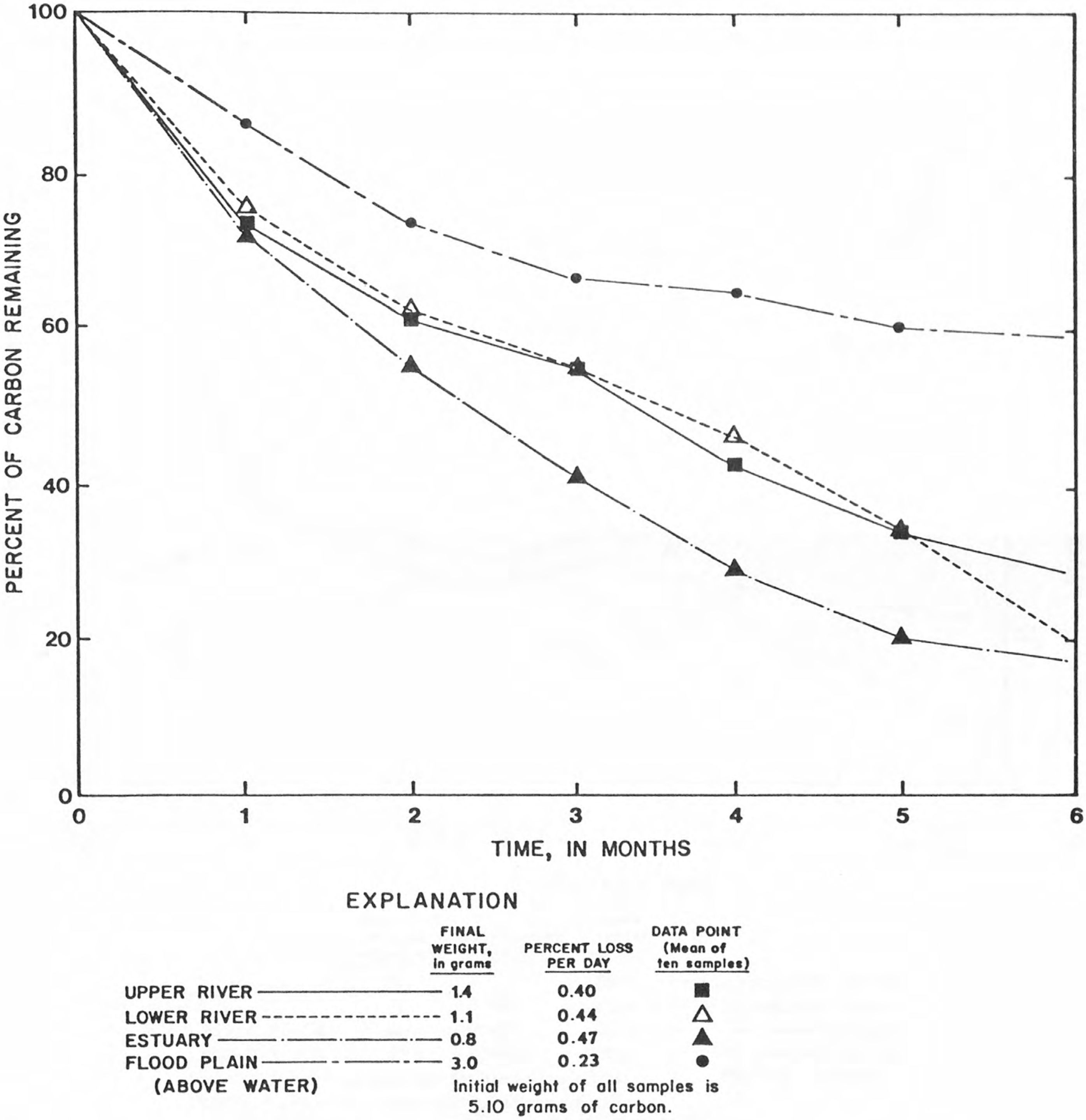


Figure 17.--Leaf decomposition: mean carbon loss for all species at four sites.

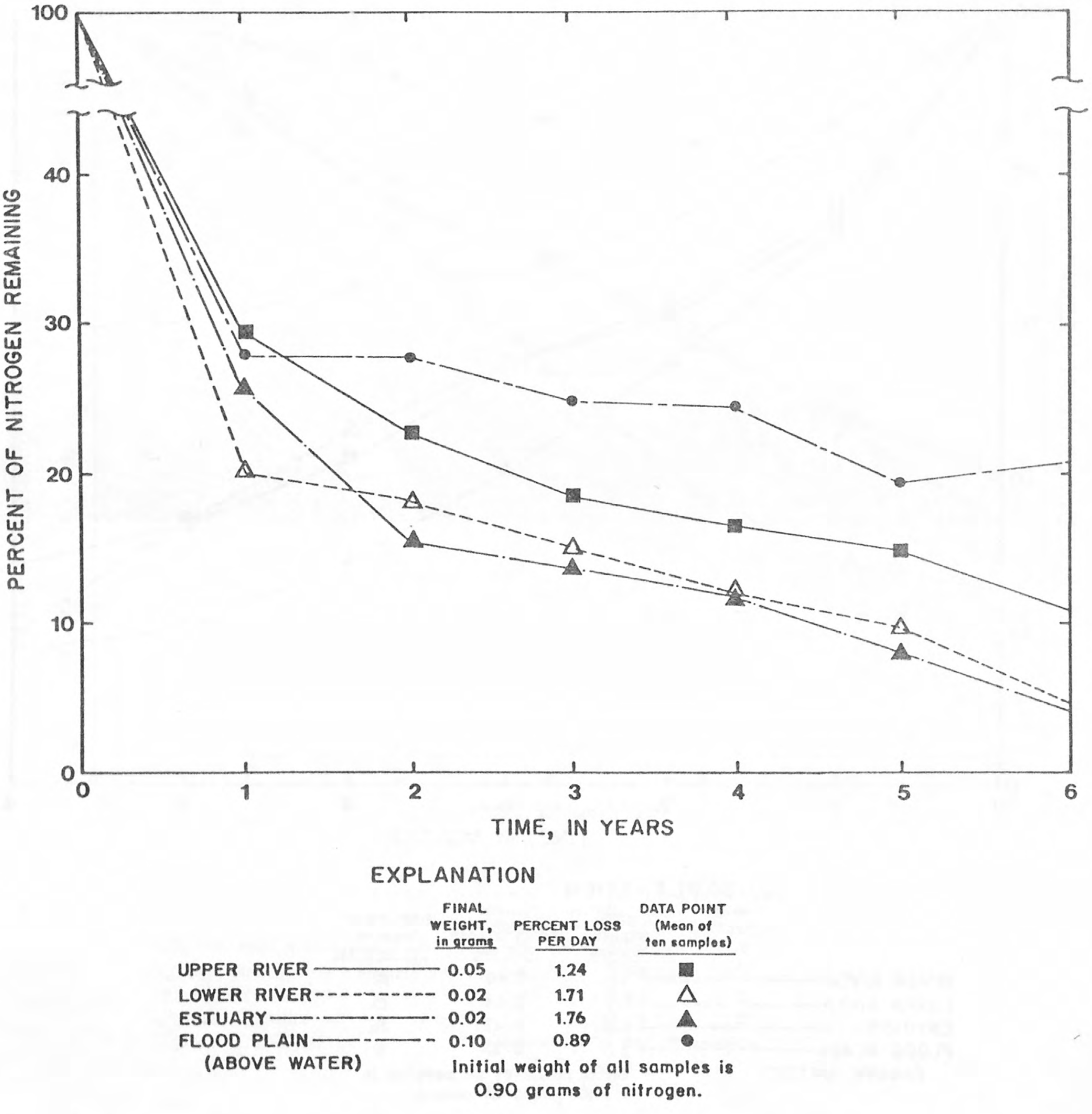


Figure 18.--Leaf decomposition: mean nitrogen loss for all species at four sites.

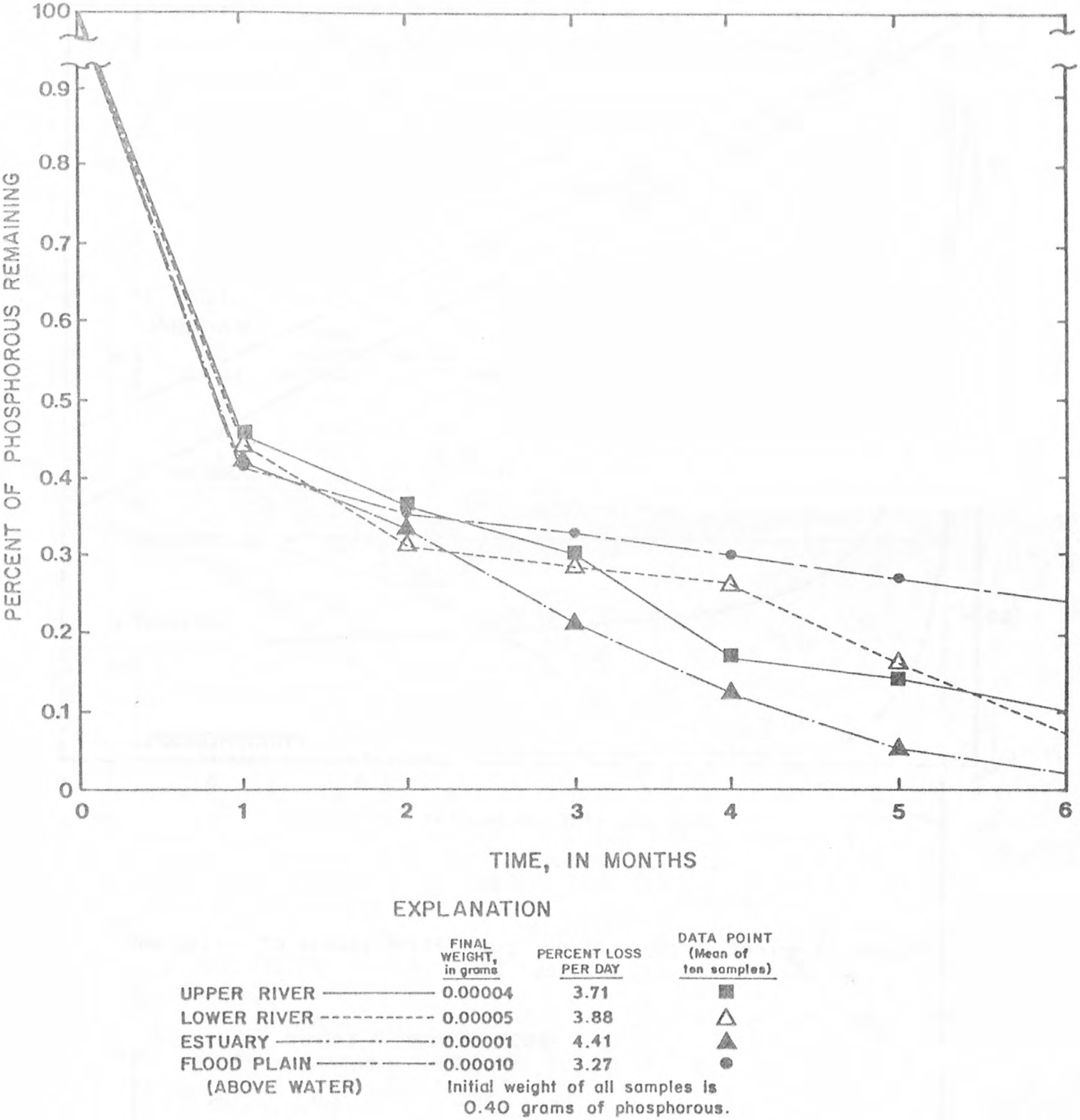


Figure 19.--Leaf decomposition: mean phosphorus loss for all species at four sites.

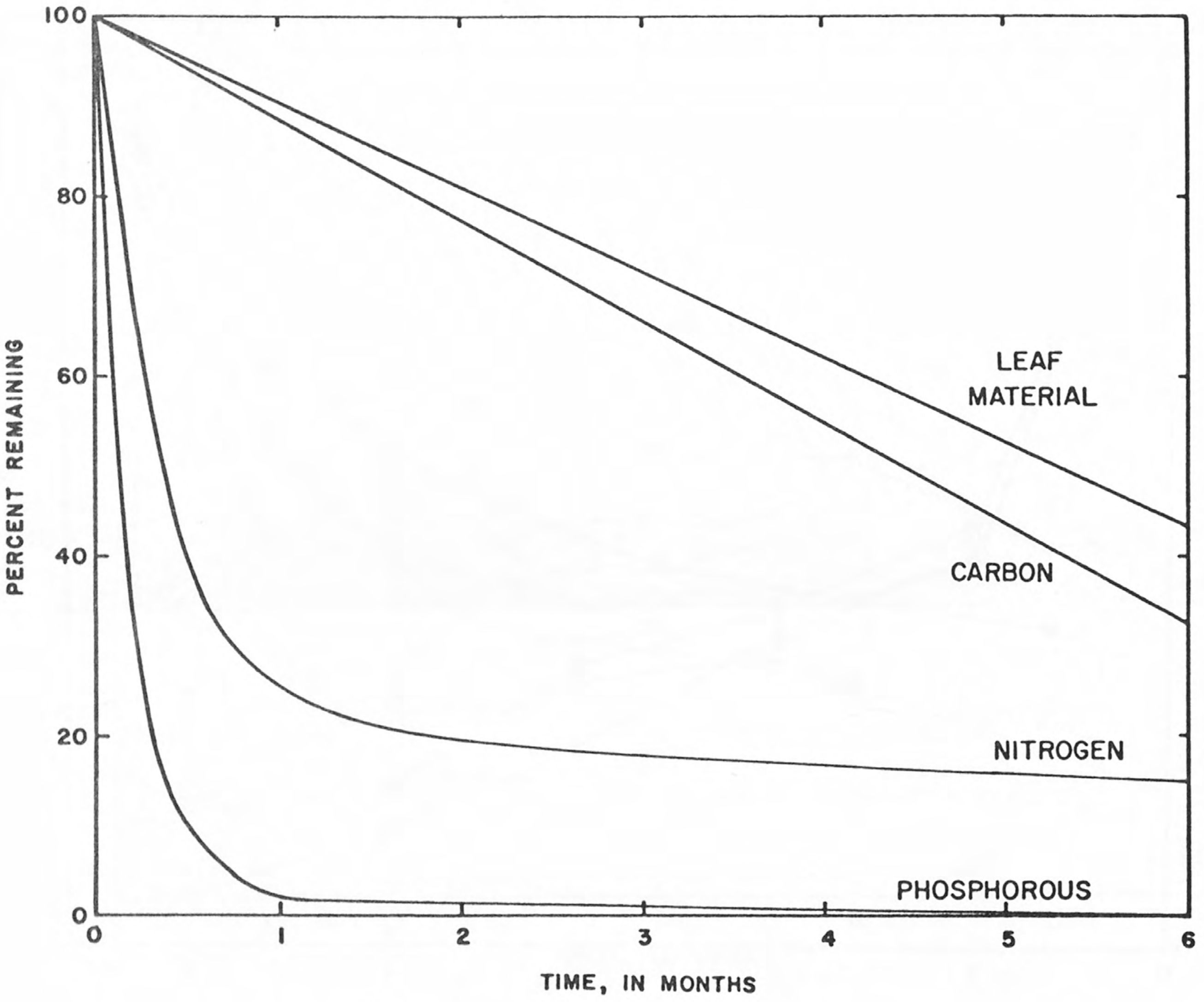
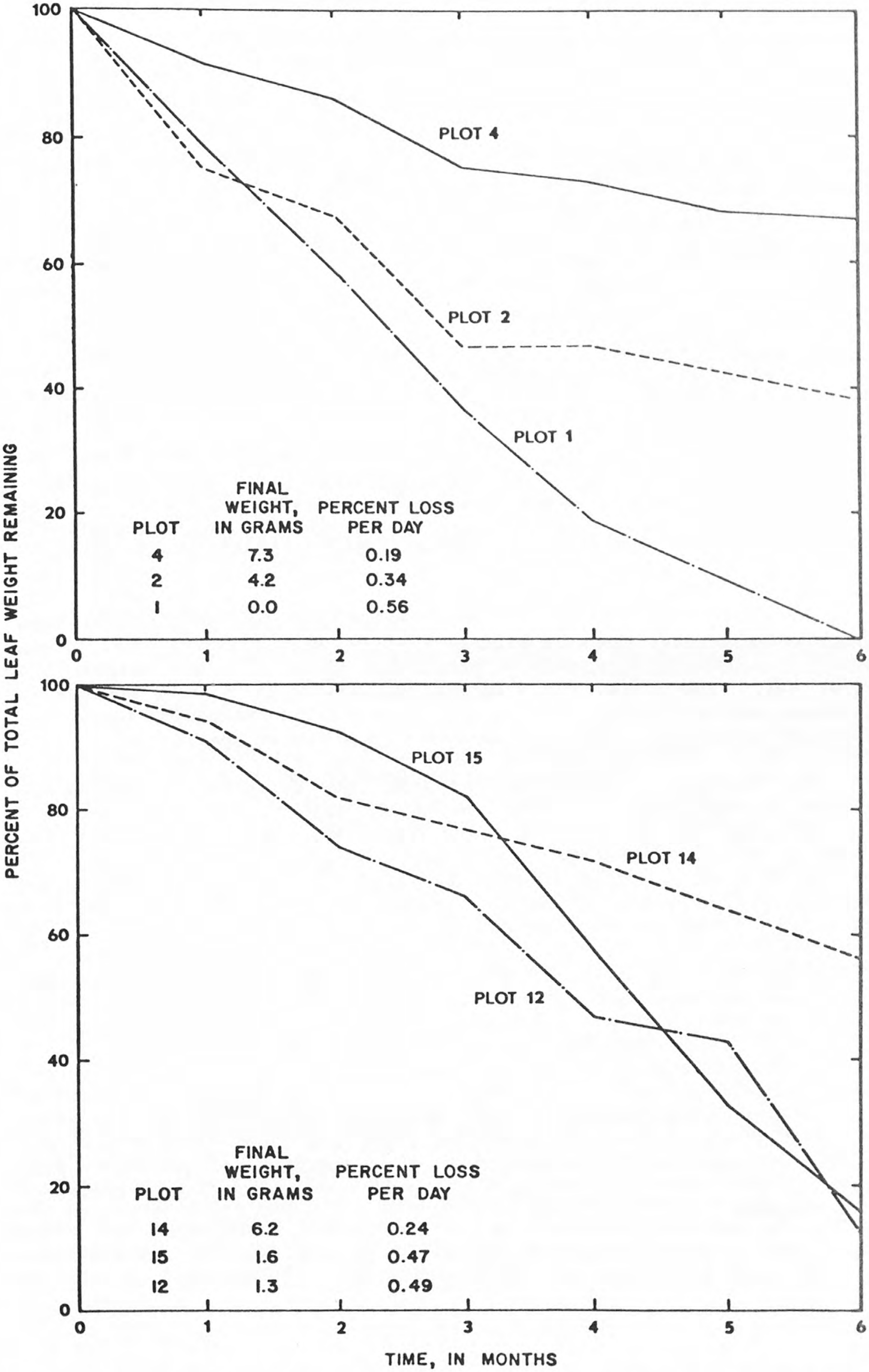


Figure 20.--Leaf decomposition: generalized trends of weight and nutrient loss.



PLOT	FINAL WEIGHT, IN GRAMS	PERCENT LOSS PER DAY
4	7.3	0.19
2	4.2	0.34
1	0.0	0.56

PLOT	FINAL WEIGHT, IN GRAMS	PERCENT LOSS PER DAY
14	6.2	0.24
15	1.6	0.47
12	1.3	0.49

Figure 21.--Leaf decomposition: weight loss of composite samples at six flood-plain plots.

Leaves from two species, tupelo and sweetgum, were broken down completely under saturated conditions and lost from the leaf bags within 6 months (fig. 14). Two others, diamond-leaf oak and baldcypress, lost less than half of their mass in the same time and conditions. Water hickory exhibited an intermediate weight loss rate. Under dry conditions (fig. 15), weight loss was much slower.

A more complete assessment of site differences is illustrated in figure 16. As previously noted, the nonaquatic site on the flood-plain forest floor was significantly less favorable for decomposition than the river or bay sites. Weight loss rates at the two river sites were indistinguishable. Somewhat higher rates were observed at the estuary site.

Loss rates of nutrients, carbon, nitrogen, and phosphorus are illustrated in figures 17-19. Site differences were somewhat diminished from those previously observed for weight loss, particularly for nitrogen and phosphorus. The flood-plain site, however, had consistently lower nutrient loss rates than the water locations. Unlike the gradual loss of organic carbon, most losses of nitrogen and phosphorus occurred during the first month.

Individual species results were pooled together to give the mean nutrient loss rates shown in figures 17-19. With respect to carbon loss, interspecific comparisons paralleled those of total weight loss (fig. 14). Carbon loss rates in oak and cypress were slow, whereas in sweetgum and tupelo they were rapid. Nitrogen and phosphorus loss rates were not appreciably different among the five tested species.

The results of weight and nutrient loss measurements are generalized in figure 20. Biomass and carbon loss occur relatively constantly over a 6-month period; hence their loss rate curves are linear. There is little difference between them, as expected, because approximately half of the leaf biomass is carbon. Nitrogen and phosphorus exhibit exponential loss curves. Phosphorus, in particular, is lost extremely rapidly and is virtually gone after 1 month.

Composite leaf packs, containing several species of leaves together in proportions simulating the litter fall of the plot, were placed at six study plots. Major differences in weight loss rates were observed (fig. 21). These differences were predictable, however, on the basis of plot characteristics and species composition. The most rapid decomposition rate was at plot 1, which is constantly flooded and dominated by the rapidly decomposing tupelo species. Plots 4 and 14 are relatively dry areas where decomposition rates are slow. Plot 2 was constantly flooded but its leaves consisted primarily of cypress, a slow decomposer. Its resulting decomposition rate was therefore intermediate.

Flood-Plain Litter-Fall Estimates

Litter-fall data from the intensive-transect plots, coupled with basal area estimates from the cruise transects (Leitman and others, 1982), were used to estimate litter production in the entire flood plain (table 8). The data indicate that litter fall in the Apalachicola flood plain is composed of 58 percent leaves and 42 percent other material. Tupelo and baldcypress account for 35 percent of the leaf material. The 11 species listed account for 86 percent of the leaf total.

Extrapolation of leaf-litter data to the entire flood plain can be evaluated on the basis of comparisons of data from cruise transects and intensive transects. Forest type identification in all transects indicated that the intensive-transect study plots contained a representative mix of forest types. This is shown by the following comparison of cruise-transect and intensive-transect community distribution.

	Percentage of all points	
Forest type	Cruise-transect points	Intensive-transect points
A	21	13
B	16	25
C	21	31
D	11	6
E	24	25
Unidentified	6	0

In addition, most flood-plain tree species were represented in the litter-fall collections. Of the 47 tree species identified in the cruise transects, 33 were positively identified in the litter samples. All of the remaining 14 species were minor, having relative basal areas in the flood plain of 1 percent or less. As previously illustrated (fig. 5), the cruise transects crossed the flood plain at eight sites throughout the basin, providing good representation of the entire system. The intensive transects also crossed the flood plain and represented the upper and lower parts of the basin. A sound data base was thus provided for extrapolation of litter-fall data to the entire system, with the estimates of overall flood-plain production reported in table 8.

Estimates of nutrient content of the litter fall may be obtained by factoring in the results of leaf nutrient analysis (table 6). Using concentration factors of 50 percent organic carbon, 7 percent nitrogen, and 0.7 percent phosphorus, annual nutrient deposition in the leaf matter only is estimated to be 240 g/m^2 organic carbon, 33 g/m^2 nitrogen, and 3 g/m^2 phosphorus (table 9). The total litter fall, including nonleaf material, was 800 $g/m^2/yr$. Chemical analysis of total nonleaf material was not feasible because its contents were so heterogeneous and variable. Carbon and phosphorous concentrations in the woody portion of nonleaf material are nearly the same as in leaves, whereas nitrogen concentrations are lower by a factor of two (Brinson, 1977; Post and de la Cruz, 1977).

Table 8.--Annual litter fall in the Apalachicola flood plain

[Flood-plain area is 454 square kilometers. Estimates are based on litter fall measured in intensive transects and basal areas measured in cruise transects]

Species	Flood-plain litter fall thousands of metric tons	Flood-plain litter fall $(g/m^2)/yr$	Leaf fall (Nonleaf material excluded) (percent)	Total litter fall (percent)
Leaves				
Tupelo	55.0	121	26.1	15.2
Baldcypress	19.6	43	9.3	5.4
Overcup oak	17.0	37	8.1	4.7
Sugarberry	16.2	36	7.7	4.5
Sweetgum	15.6	34	7.4	4.3
Ash	12.9	28	6.1	3.6
Planer-tree	9.9	22	4.7	2.7
American elm	9.9	22	4.7	2.7
Water hickory	9.4	21	4.5	2.6
American hornbeam	8.6	19	4.1	2.4
Diamond-leaf oak	8.2	18	3.9	2.3
All other species	24.2	53	11.5	6.7
Miscellaneous and unknown leaves	4.7	10	2.2	1.3
Total leaf fall	211	464	100	58.4
Total nonleaf material	150	331	--	41.6
Total litter fall	361	795	--	100

Table 9.--Nutrient content of organic litter fall, Apalachicola flood plain (area = 454 square kilometers)

	Leaves		All litter	
	Metric tons	g/m²	Metric tons	g/m²
Biomass	2.1×10^5	470	3.6×10^5	800
Organic carbon	1.1×10^5	240	1.8×10^5	400
Nitrogen	1.5×10^4	33	2.0×10^4	45
Phosphorus	1.5×10^3	3.3	2.5×10^3	5.6

DISCUSSION

Methodology

Leaf-litter measurements have been conducted in numerous studies in a variety of forest types. Leaves and other organic matter produced by the forest vegetation are unquestionably a major nutrient and energy source within such systems. Investigations of the pathways of energy flow have been hampered by the problems of measuring litter processing and transport in the field. Biomass accumulation measurements alone, as performed in this study, are more feasible; but their design must be suited to the system.

In any study of an extremely large and diverse ecosystem, such as the Apalachicola river-wetland system, a primary consideration is representing the entire system in the experimental design. Without such reliability, conclusions about the functions of the system as a unit are likely to be in error. Sampling on a large scale, however, generally requires some sacrifice of small-scale, detailed investigations of components of the system and particular pathways of energy and material cycles. The emphasis in the Apalachicola River Quality Assessment was on the large-scale viewpoint. Further study which would incorporate detailed investigations of processes would supplement this assessment.

One of the most critical elements of this study was selection of sampling locations for the litter-collection apparatus. Totally random placement would result in misleading characterization of the flood plain as a whole since the flood-plain forest is divided into at least five forest types. Two of these are limited to relatively narrow levee areas which might be missed entirely by random plot selection. This would have been a serious sampling error since the levee communities, although relatively small in area, are major contributors of organic material in the basin. The aim of plot selection, therefore, was to assure representation of all five forest types. The use of stratified random sampling, as previously described in Methods, was the most effective means of achieving accurate flood-plain characterization. Some overrepresentation or underrepresentation of certain types was inevitable, but complete absence of representation was to be avoided. Unbiased sampling of each community type was assured by random location of the two nets within each plot.

Various methods have been employed in other systems for the collection of litter fall. Many were infeasible in the Apalachicola forest because of flooding. Any procedure involving collection of litter fall from marked quadrats on the ground (Bray and Gorham, 1964; Carlisle and others 1966; Gaur and Pandey, 1978), or the use of traps or baskets (Post and de la Cruz, 1977), was excluded for this reason. Above-ground net collection has the additional advantage of eliminating infiltration by sediment and other nonlitter debris. The flooding problem was overcome by Bell and others (1978) by mounting floats on collection baskets and securing them with ropes. This procedure might be usable in the Apalachicola forest, although the range in flood stage at some plots is such that it would be difficult to continually maintain both flotation and position. The harvest method of measuring litter production (Monk and others, 1970), where all individuals within certain quadrats were harvested and weighed, was entirely impractical due to the size of the trees. Furthermore, this method precludes phenological analysis of litter fall. For similar reasons, the "limb-count" technique employed by Heald (1971) in mangrove swamps was rejected for the Apalachicola study.

Species identification of abscised and partially decomposed leaves is a problem associated with any litter-fall determination. Most of the Apalachicola species, however, have distinctive leaves which can be identified even when in poor condition, provided they are not broken into small parts. Tupelo leaves were the greatest problem because of the similarity of the the three tupelo species and the difficulty of distinguishing them from ash leaflets (fig. 9). The species identifications, especially with respect to tupelo and ash leaves, were subject to some error. Questionable identifications were not common, however, and errors tended to balance each other; tupelo leaves mistaken for ash were likely compensated by ash leaves mistaken for tupelo. On a large-scale analysis, such compensation presumably resulted in relatively little error. The only area where error compensation may have been incomplete was in the identification of swamp tupelo leaves at plot 1. Because of the apparent low productivity of swamp tupelo (percentage of leaf production is much smaller than percentage of basal area) (table 4), there was probably a significant bias in favor of Ogeechee and water tupelo identification in separating them from swamp tupelo leaves. The total litter fall of the three tupelo species is accurately represented. At plot 1, the total percentage of the leaf production of the three species, 92.1 percent, relates closely with their combined relative basal area (94.1 percent).

Annual Variability

Comparative litter-fall data for the autumn seasons of 1979 and 1980 (table 5) indicated that year-to-year variation was less than expected random variation. The 2 years of study happened to be very different with respect to weather (U.S. Department of Commerce, 1980) and hydrology (Leitman and others, 1982) in the Apalachicola basin. In September and early October 1979, rainfall was much greater than normal, producing unseasonal flooding in the lower river basin. Throughout autumn, wetter-than-normal conditions prevailed. Temperatures were at or slightly below normal. In 1980, the spring flood was somewhat higher and of longer duration than normal, producing wet conditions early in the year; but summer and autumn were unusually dry. The river stage fell to very low levels and the flood-plain soils became unsaturated in most areas. Mean monthly temperatures were 0.3° to 3°C above normal. There were no major storms in either year, other than heavy rains in September 1979.

For the 3 months in which litter-fall data were obtained, 1979 appeared to be a more productive year than 1980, although this distinction was not statistically significant (table 5). The hydrologic patterns and weather doubtlessly influenced rates and timing of litter fall, although the specific effects of particular weather and hydrologic events are not known. Because of the drier, warmer summer in 1980, leaf fall probably occurred earlier than in 1979.

Sample Loss

The comparisons for the October-November period, as well as total litter-fall estimates, were slightly hampered by some loss of data due to theft of five collection nets in November 1979. The nets were replaced, but 1 month of data for each net was lost. For the 1979-80 comparison, only data from nets which provided collections in both years were used; a matched-pairs analysis of variance was employed. For calculations of total litter fall from each plot, it was necessary to account for the lost data in some manner since November was the peak litter-fall month. For each plot in which only one net was missing, the sample weights from the other net were doubled to estimate the 2-square-meter collection from the plot. A greater problem existed at plot 5, where both nets were missing. In this case, the October-November-December data from plot 4 were used to estimate relative changes during those months. Plot 4 contained similar vegetation to that of plot 5. A correction factor was derived from the plot 4 data by dividing the litter-fall rate of November by that of October. This correction factor was applied to plot 5, using its October litter-fall rate as a basis for estimating the November rate.

Some nets were also lost in March and April 1980 because of inundation. This occurred although the nets were placed on high supports to put them above flood stage. That period, however, was one of minimum leaf fall. Examination of data from plots similar to those which were flooded showed negligible production relative to the annual total. These losses were therefore ignored in calculations of annual litter-fall.

Seasonal Patterns

The overall seasonal pattern of leaf fall (fig. 11) was quite predictable for this region. It was generally comparable to seasonal cycles seen elsewhere in the northern hemisphere (Bray and Gorham, 1964; Bell and others, 1978). Litter fall in a Louisiana freshwater swamp showed very nearly the same seasonal pattern, with a major peak occurring only in autumn (Conner and Day, 1976). In more tropical regions, and in a number of southern-hemisphere forests, a different seasonal pattern is often observed. There may be very little seasonal variation or it may be shifted toward a spring peak, associated with development of new leaves (Bray and Gorham, 1964). The dry season (January-April) was identified as the period of greatest leaf-fall rate in a tropical moist forest in Panama (Golley and others, 1975, p. 69).

Post and de la Cruz (1977) found a bimodal seasonal cycle for litter fall in a Mississippi coastal plain stream, with a spring peak and an autumn peak. The spring litter was composed mostly of woody twigs, whereas the autumn litter consisted mostly of deciduous leaves. Results from the Apalachicola system also show a relatively high proportion of nonleaf material in the spring, but no detectable increase in nonleaf litter which might produce a spring peak in total litter fall. In 1979-80, the total litter-fall rate in the September through November period was 4.8 $(g/m^2)/d$, nearly six times greater than the rate from March through May [0.8 $(g/m^2)/d$]. Nonleaf material comprised 80 percent of the spring litter but was only 22 percent of the autumn litter. This is similar to results reported by Post and de la Cruz (1977) in comparing litter-fall peaks of April and November.

The Apalachicola forest litter contains enough diversity of species that the autumn peak is not as sharp as it might be in a low-diversity system such as a pine forest (Kendrick, 1959). The breadth of the peak is attributable, in part, to the continual supply of nonleaf material, but it is also partially due to variations of seasonal patterns of litter fall among different species (fig. 12). Despite this effect of species diversity, a distinct seasonal pattern of autumn maximum and spring minimum exists in the overall litter production.

The timing of two annual events (litter fall and flood-plain inundation) is critical to detritus and nutrient transport through the river system. Usually, as in 1979-80, the peak litter fall occurs well before the flood, allowing leaves to settle on the ground and partially decompose before being inundated. It is possible that the two events may occur simultaneously, however, in which case much of the litter fall would be deposited directly on the water surface and be transported in a relatively fresh condition. The result would be transport of an increased volume of large, poorly decomposed particles.

Factors Influencing Litter-Fall Production

Species

Among the major litter producers in the Apalachicola flood plain, tupelo is clearly dominant. Dominance of tupelo is due primarily to its abundance in the flood-plain forest rather than its individual productivity. Nevertheless, it contributes one-third of the leaf litter in the system and accounts for a major portion of nonleaf litter fall. Tupelo berries were very common and at times constituted a large proportion of nonleaf litter fall. The tupelo leaves were derived principally from two species, water tupelo and Ogeechee tupelo. Water tupelo is more common and presumably contributed more to litter fall than Ogeechee tupelo.

Baldcypress is the third most common species in the flood-plain forest. Its litter fall, as a percentage of the total, approximates its relative abundance (table 3). Like tupelo, it is strictly swamp-adapted; hence it is rarely found on levees or other areas where the ground is frequently unsaturated. Cypress leaves are unique in form and texture (fig. 9), but indistinguishable in carbon, nitrogen, and phosphorus content from other leaves. The form and small size of the cypress leaves made sample drying and weighing difficult because they tended to slip through the mesh of the drying bags. The results of measurements of cypress leaves may be as much as 10 percent low due to handling loss.

Sweetgum is the third major contributor to leaf litter in the Apalachicola system and first among the levee species. It is restricted to high-ground areas where soil is saturated only during flood season (2 to 4 months annually). In forest type A, which is characteristic of such high-ground areas, sweetgum is dominant both in abundance and litter production (table 4). High-ground areas occupy a relatively small part of the flood plain, however, and the overall abundance of sweetgum is limited. Its high productivity, rather than abundance, is responsible for its prominence among the litter producers.

Diamond-leaf oak ranks first in leaf-litter production in forest type B (table 4), reflecting its relatively wide saturation tolerance. Forest type B is intermediate between the high-ground forest (A) and the swamp forest (C, D, and E). Oaks were generally abundant in swamp forest type C as well as in the levee areas. The other major oak species in the flood plain, overcup oak, was found in somewhat wetter environments than diamond-leaf oak. Overcup oak productivity was exceptionally high, which resulted in its high ranking among the contributors to leaf litter in forest type C (table 4).

Ash, whose leaflets consisted primarily of two species, Carolina ash and green ash, is a major contributor to leaf litter but not to the extent that might be expected from its abundance in the flood plain. Like baldcypress and tupelo, it is swamp adapted, which allows it to be widespread in the Apalachicola system; however, its productivity is relatively low.

Grape is a major leaf producer in forest types A and B (table 4). Since 6 of the 16 study plots represented these forest types, grape was a major leaf contributor in the two intensive transects. The basal area of grape was not measured in the intensive-transect plots, but cruise-transect data (table 3) indicated that its productivity per stem biomass was very high. The appearance of other vines, such as trumpet vine and poison ivy, among the major producers in forest types A and B, reflected the high foliage to stem ratio of the lianoid plants.

Canopy Cover

Canopy cover, or that part of the area overtopped by foliage, is presumably important in affecting litter fall. The Apalachicola forest has a relatively heavy canopy, but as illustrated in figure 22, sizable openings do occur. Although canopy measurements are not available, qualitative observations suggested that plot 7 had low canopy cover relative to its stem biomass and relative to other plots in the study. This may account for low litter-fall measurements at plot 7.

Tree Abundance and Density

Leaf-litter fall expressed as weight of litter per unit basal area of trees is inversely correlated to tree basal area itself (fig. 10). Tupelo, cypress, and ash--the three most abundant genera--were the least productive. Because these are all swamp species, and some of the very productive species, such as sugarberry and sweetgum, are restricted to high ground, there was a marked difference in leaf-litter per unit basal area between swamp plots and levee plots. There was also a remarkable difference in tree biomass, as measured by basal area, between the swamp and levee plots. The comparison is shown below:

Community type	Annual litter fall (g/m^2)	Basal area (m^2/ha)	Annual litter fall per square meter basal area (Kg)
Swamp	760	72	106
Levee	874	28	312

The levee communities produced a higher litter-fall rate although their basal area was much lower than taht of the swamp communities. As a result, the leaf-litter fall per unit of stem biomass was higher in the levees by a factor of three.

One plant ecological principle states that as density of vegetation increases, mean biomass of individual plants decreases (Harper, 1967). It has also been observed (Bray and Gorham, 1964) that in closed-canopy forests, litter production on an areal basis is independent of tree density. In the Apalachicola forest, the transition from levee to swamp forest types is accompanied by substantial increases in both tree density and total biomass. Total production of litter fall, however, is not appreciably different in the two regions. It follows, therefore, that litter productivity, relative to either tree biomass or density, is higher in the lower density levee areas.

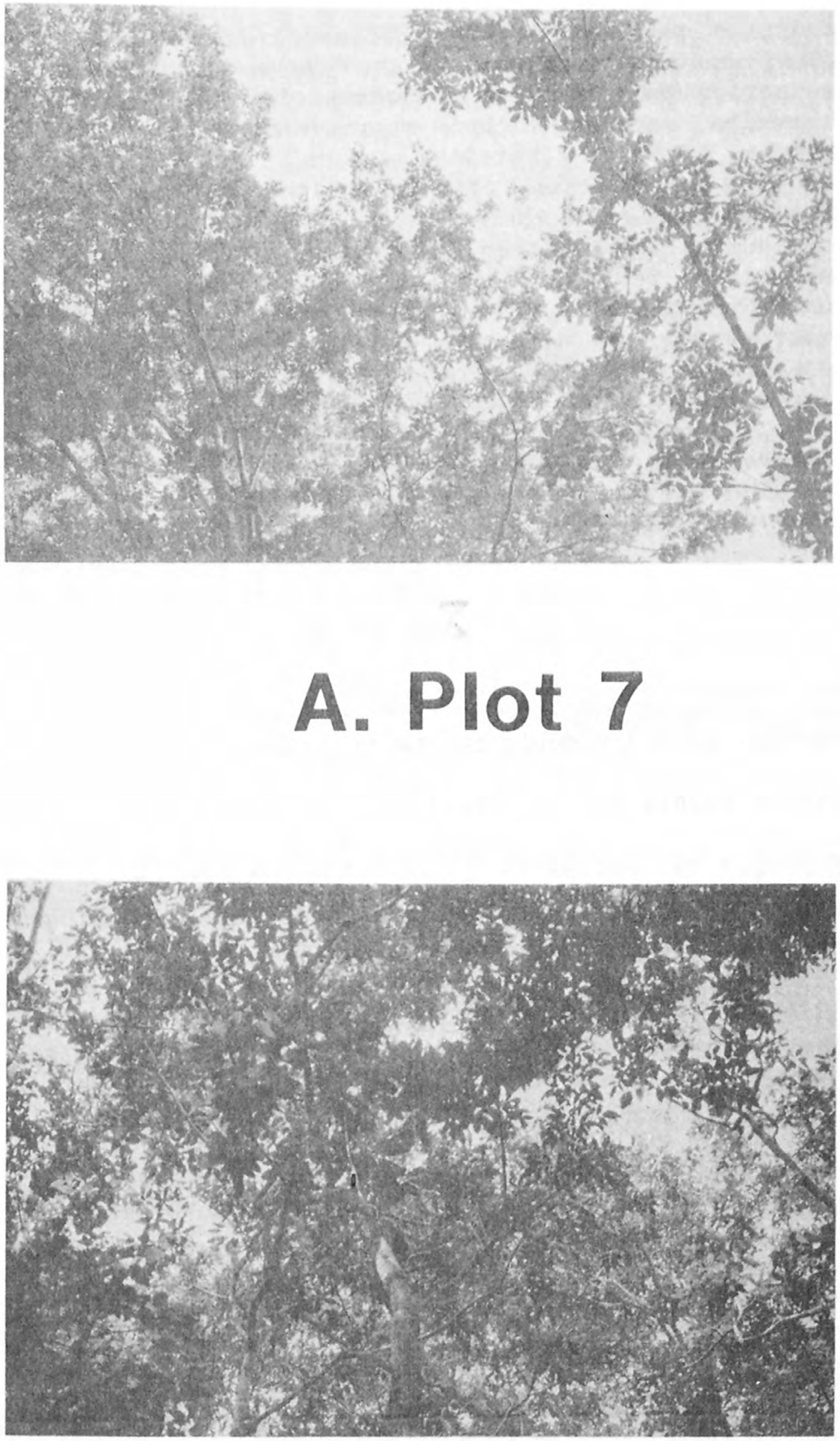


Figure 22.--Canopy cover in July at intensive plots 7 and 15.

Diversity

In addition to tree density, biomass, species composition, and canopy cover, another factor which may have an important effect on litter production is diversity. Communities which contain a large number of species, each of which is represented by about the same number of individuals, are high-diversity systems. Conversely, low-diversity communities have few species, or associations of rare species together with abundant species. In the Apalachicola flood plain, forest types D and E are by definition (Leitman and others, 1982) nearly pure stands of a few species; the few associated species are very rare. Hence, they tend to have low diversity. The levee forest types A and B contain a mix of numerous species and show relatively high diversity. Forest type C is also likely to be of high diversity, unlike the other two swamp forest types.

The diversity of the 16 study plots was quantified by applying the Shannon equation (Wilhm, 1968) to tree-density data. The equation computes the diversity index H', in "bits per individual".

$$H' = -\sum \frac{n_i}{N} \log_2 \frac{n_i}{N} \qquad (1)$$

where

n_i = number of individuals in the ith species, and

N = total number of individuals.

The n_i are sample values; hence H' is a maximum-likelihood estimator of the true community diversity. The index expresses a combination of two effects: species richness (number of species) and equitability (how equitably the individuals are distributed among species). A separate equitability coefficient, e', may be calculated as follows (Peet, 1974):

$$e' = \frac{H'}{\log_2 N} \qquad (2)$$

The two indices were matched with litter-fall data to determine what, if any, relation exists between them.

No correlation between litter fall and the diversity index, H', was found. The interaction of the two diversity components, species richness and equitability, was such that diversity was a poor indicator of leaf production. For example, plot 12 had low diversity ($H' = 1.73$) as compared with plot 17 with high diversity ($H' = 2.98$). The two sites had nearly the same litter-fall production rates.

A better indicator of litter-fall rates was the equitability coefficient, _e'_. A plot of leaf productivity per square-meter basal area versus _e'_ is shown in figure 23. Nonleaf material is excluded from the analysis because it was not identified by species. A least-squares regression line is fitted to the data. Among the observed data points which deviate from the prediction curve are plots 4, 7, and 11. Plots 4 and 11 are both levee plots which support large amounts of vine growth. Since the vines contributed a considerable amount of leaf litter without adding to basal area or species count, the productivity rates were especially high. As already noted, litter productivity at plot 7 may be low because of incomplete canopy cover.

A clustering trend of the forest types is also illustrated in figure 23. A clear distinction between swamp and levee plots is apparent. The "pure stand" plots of forest types D and E (plots 1, 2, 12, 13, and 19) are of low equitability and low litter productivity per unit biomass. Mixed-species swamp plots of forest type C (plots 7, 15, 16, 17, and 18) are intermediate. On the levees, plots of forest type B (plots 3, 6, 11, and 14) show somewhat higher equitability, but not higher productivity than type A plots (4 and 5).

Leaf Decomposition

Decomposition of leaf material after it has reached the forest floor is a critical link between leaf litter production and its transport through the river system. The Apalachicola River wetland, as a biologically rich, subtropical system, may be expected to be an environment favorable to rapid and complete leaf decomposition. Results of the decomposition experiments conducted here confirm that at least some species, including tupelo, may undergo complete decomposition, but others are quite resistant. Nitrogen and phosphorus are leached out of leaf material within a few days or weeks after leaf deposition.

Decomposition rates as reported by this study and others (Kaushik and Hynes, 1971; Petersen and Cummins, 1974) were highly species dependent. Such species dependence is evident among the Apalachicola species used for leaf decomposition experiments. In a flooded condition (fig. 14), the decomposition rates of the five species varied by a factor of 2.7 (0.21 to 0.56); in a dry environment (fig. 15), they varied by a factor of 5.5 (0.04 to 0.22). These rates are comparable to the "medium" and "slow" decomposition rates reported by Petersen and Cummins (1974) for a woodland stream. The rates were faster, in wet environments, than those observed by Bell and others (1978) for oak, maple, and hackberry leaves. In a dry environment the weight loss rate for tupelo was very close to results of Brinson (1977) who also measured decomposition of tupelo (_Nyssa aquatica_) leaves in a southeastern swamp forest.

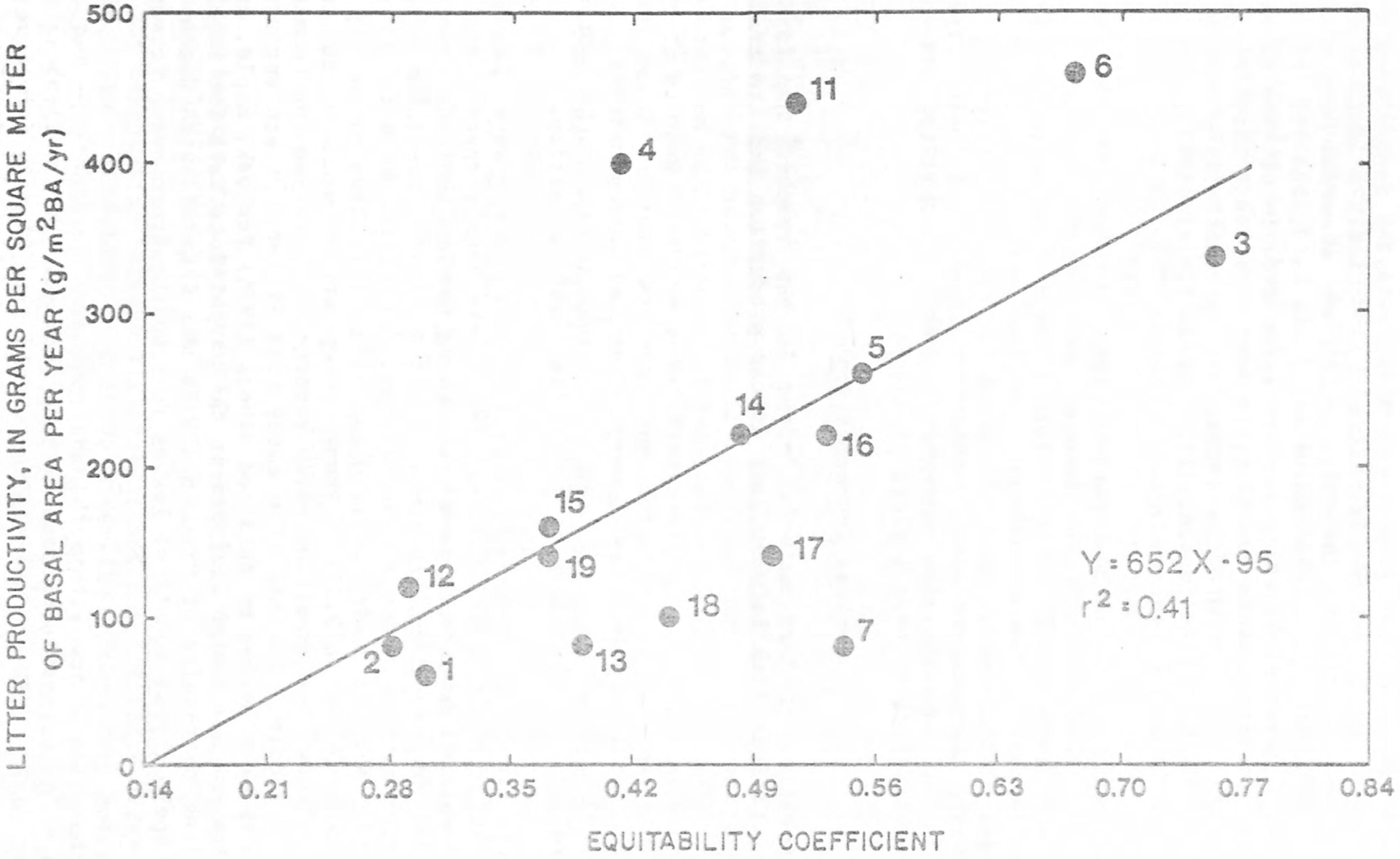


Figure 23.--Leaf-litter productivity (nonleaf material excluded) versus the Shannon equitability coefficient, e, at intensive-transect plots.

Maximum leaf fall normally precedes peak inundation by 3 to 4 months. During that time, most leaves deposited on the flood-plain floor are relatively dry and intact. During flooding itself, whose duration is generally from 30 to 90 days (Leitman and others, 1982), increased decomposition and transport may take place. The sequence is favorable, perhaps ideal, for maximizing detrital transport to the estuary.

Nitrogen and phosphorus losses are exponential (fig. 20). Most of the loss takes place during the first month, even in dry environments, and normally results in nearly total leaching of nitrogen and phosphorus prior to major flooding. As water-soluble leachates, however, nitrogen species and orthophosphate, if available, are mobilized by even minor flooding. In the 1980 water year, minor flooding occurred in the lower river basin as early as December, although major flooding did not begin until early March. It is possible that early flooding mobilized substantial amounts of the leachates from the recently deposited leaf litter. Early floods lacked the velocity of the later inundations but certainly saturated the forest floor and possibly accelerated material decomposition, resulting in rapid formation of small detritus particles.

Reversals of nutrient loss, such as those observed elsewhere by Triska and Buckley (1978) and Triska and Sedell (1976), were not in evidence with the Apalachicola leaves. Triska and coworkers reported increases of nitrogen, following initial loss, to the extent that the nitrogen concentrations eventually exceeded initial levels. Such reversal is attributed to microbial colonization. Although these changes were not observed in the Apalachicola leaf-pack samples, high concentrations of nitrogen were found in partially decomposed leaf material transported in the river channels.

The experiments showed definitively that decomposition in a dry environment is slower than in a wet or flooded one. Water in contact with the leaves expedites leaching and enhances microbial activity. The two river sites were equally favorable for decomposition. The estuary produced slightly faster decomposition, probably due in part to higher temperatures (Kaushik and Hynes, 1971; Iversen, 1975; Paul and others, 1978). Other features of the estuary which may favor decomposition are wave and tidal action and a large number of decomposer organisms.

There is no evidence from the leaf-bag experiments to suggest that decomposition rates of Apalachicola leaf species are dependent on association with other species (fig. 21). Virtually all variability among composite samples could be explained by location and species composition differences. Comparisons with single-species decomposition rates were hampered by the fact that composite sample species compositions were determined by local leaf species abundance, which resulted in a number of species being included which were not tested as single species. For those species that had been tested, no significant effect of combination with other species was observed.

Few other studies of leaf decomposition have taken place on large rivers such as the Apalachicola (Mathews and Kowalczewski, 1969; Paul and others, 1978). The Apalachicola River, like most other large rivers, provides a very different environment for leaf decomposition than small woodland streams, which are frequently the sites of such experiments (Kaushik and Hynes, 1971; Petersen and Cummins, 1974; Triska and others, 1975; Triska and Sedell, 1976; Triska and Buckley, 1978). Current velocity, turbulence, and sediment loads are some important differences between large rivers and small streams.

Litter-Fall Comparisons with Other Systems

Litter-fall mass varies with the type of forest, its locality, climate, tree density, and net productivity. Deciduous forests in tropical and subtropical regions generally have a higher biomass to production ratio, hence a lower net primary production to gross primary production ratio than immature temperate forests (Odum, 1971, p. 46). When compared with litter fall reported for other forest ecosystems (Bray and Gorham, 1964), the Apalachicola rate of nearly 800 $(g/m^2)/yr$ [8 (metric tons/ha)/yr] is similar to rates observed in equatorial forests. It is higher than some but lower than most. It is higher than litter fall rates reported for all cool temperate forests and nearly all warm temperate forests.

Freshwater wetlands are among the most productive of natural ecosystems (de la Cruz, 1978). Water flow, by circulating nutrients and materials, enhances productivity. As a result most wetlands are more productive than adjacent upland systems (Odum, 1979). We cannot compare the Apalachicola wetland with adjacent unsampled uplands, but comparison with other forests indicates that it is exceptionally productive for a nontropical environment. Very few of the forest studies reviewed by Bray and Gorham (1964) were done on wetland systems. The Apalachicola litter-fall production data, when compared with data from other forests, corroborate the assumption that wetlands are exceptionally productive.

The Apalachicola forest produced considerably more litter fall than most other comparable systems (table 10), including those in Mississippi, Louisiana, and Georgia, which have many features similar to those of the Apalachicola system. Again, these comparisons might support the deduction that wetlands are more productive than uplands. Some evidence to the contrary appeared in the results of Bell and others (1978), however. They found the highest litter fall [977 $(g/m^2)/yr$] in uplands, followed by the transition zone. The flood plain produced the lowest litter-fall rate [521 $(g/m^2)/yr$] in their study site. The authors suggested an elevational gradient to explain these differences. The amount of litter on the ground was quite variable as a function of very small changes in elevation. This appears to be analogous to the increased litter fall found in the Apalachicola levee communities relative to the flooded areas. If the "flood-plain-upland" gradient described by Bell and others (1978) is analogous to the "swamp-levee" gradient of this study, the results from the two studies are quite consistent.

Table 10.--Summary of litter-fall results of the Apalachicola study and other studies

[Parentheses designate estimates derived from diverse data]

Forest description and location	Litter fall in $(g/m^2)/yr$	Leaf material (percent)[1]	Nutrients (percent)			Reference
			C	N	P	
Oak woodland, England	386	55	51	1.1	0.6	Carlisle and others, 1966
Oak-hickory, Georgia	600	74				Monk and others, 1970
Freshwater swamp, Louisiana	574-620					Conner and Day, 1976
Coastal-plain stream, Mississippi	386	75	(47)	(0.5)	(0.02)	Post and de la Cruz, 1977
Tropical deciduous, India	153-183	70				Gaur and Pandey, 1978
Stream side (upland, transition, flood plain), Illinois	521-977	58-80				Bell and others, 1978
Apalachicola flood plain, Florida	800	58	50	7	0.7	This study

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[1] In autumn or peak litter-fall period, if overall annual average is not specified.

One discrepancy between the Apalachicola results and those of other studies is seen in the reported nitrogen and phosphorus concentrations of the litter-fall material. The reasons for higher concentrations found in Apalachicola litter are not known. There is a possibility that because the leaves were suspended well above ground level, and were in relatively dry conditions during the entire time from deposition to analysis, there was little opportunity for microbial attack or leaching. The carbon to nitrogen ratios in the Apalachicola leaves are close to the 10 to 1 ratio considered optimum for decomposition processes (Alexander, 1977, p. 139-140).

Litter Fall as a Nutrient and Detritus Source

A primary purpose of the Apalachicola River Quality Assessment litter-fall determinations was to ascertain the role of the flood plain as a potential source of nutrients and detritus transported through the river system and ultimately into the estuarine food web. An annual deposition of 3.6×10^5 metric tons of organic material is indeed a large potential source. Assuming 50-percent carbon content, this material, if totally flushed into the river system, would account for a mean organic concentration in the river water of 7 mg/L. The carbon cycle is far more complex than that, of course, and it is certain that a substantial part of the litter-fall material is recycled within the flood-plain community itself, rather than being transported through the aquatic system. Nevertheless, annual floods constitute a powerful catalyst for mobilization of substances out of the flood plain. The floods immerse the litter material, increasing decomposition rates, and provide a medium by which the litter material and its breakdown products--nutrients and detritus--can be transported.

Other sources of nutrients and detritus in the Apalachicola River system include (a) headwater inflow, which is the net outflow of the Chattahoochee and Flint River drainage area after passage through Lake Seminole and Jim Woodruff Dam; (b) tributary and ground-water inflow; (c) upland productivity; (d) atmospheric fallout; (e) point-source or nonpoint-source pollution; and (f) autochthonous substances resulting from productivity and fixation in the aquatic system itself. The first four of these sources were monitored as part of the Apalachicola River Quality Assessment (Mattraw and Elder, 1980). Headwater inflow brings a substantial load of dissolved nutrients to the river but very little detritus. Tributary inflow is attributable primarily to the Chipola River; it is a substantial quantity relative to total flow only during low-flow periods.

The quantity of litter-fall-generated nutrients is higher than that from any other source except the upstream drainage basin. It is difficult to determine the actual contribution of nutrients to the aquatic system because of recycling within the flood-plain community. The high productivity of flood-plain vegetation creates a high demand for nutrient uptake as well as a high potential for nutrient release. The flood plain may function as either a source or a sink for nutrients.

Many previous investigations of similar systems suggested that most wetlands function both ways at different times, depending on their hydrological and biological characteristics and the variability of numerous controlling factors (de la Cruz, 1979). The Apalachicola wetland is no exception. Dissolved nutrients are consumed at approximately the same rate that they are released. Where detritus is involved, however, the export function of the Apalachicola wetland appears to dominate over its role as a consumer. Detritus is of special importance to the detrital-based food web in the estuary (Livingston and others, 1974; Livingston and Loucks, 1979). The overall effect of the flood plain on nutrient and detritus yield to the estuary is therefore not to substantially increase the yield, but to favor relatively high proportions of particulate material.

SUMMARY

Litter-fall measurements were made from September 1979 through August 1980 in the Apalachicola River flood plain of northwest Florida. The estimated litter-fall rate is 800 $(g/m^2)/yr$. This rate would produce $3.6x10^5$ metric tons of organic material annually as litter fall in the 454-km^2 flood plain. Decomposition and leaching processes break down leaf litter shortly after deposition. Inundation provides a potential transport mechanism for mobilization of large quantities of litter fall before the cycle repeats itself the following year. Principal conclusions resulting from the study of litter production and decomposition on the Apalachicola flood plain are as follows:

1. The methodology for litter-fall study on a large river-wetland system such as the Apalachicola need not be drastically different from that used in other forests. The principal modification requirement is to allow for extreme changes in water levels in the flood plain. Sampling locations should be selected so as to represent major characteristic species associations, particularly the levee and swamp communities which are profoundly different from each other.

2. The accuracy of the estimate for litter fall may be judged partially on the basis of the comparison of data from the autumns of 1979 and 1980. The measured September-November litter fall in 1979 was 16 percent greater than that of the comparable period in 1980, but this difference was not statistically significant. The weather and hydrology were very different during the 2 years, so the variation in litter fall between them was probably higher than the usual year-to-year variation.

3. Some phenological (seasonal) differences between species were apparent but the cumulative seasonal cycle of litter fall is characterized by a single sharp peak in late autumn. Production of nonleaf material is not season-dependent, and no spring or summer peaks were observed in the Apalachicola River flood plain.

4. Eleven tree species and one vine (grape) account for over 90 percent of the leaf litter produced by 43 species in the flood plain. The leaf material comprises 58 percent of the total litter fall; the remainder is composed of nonleaf material. This proportion varied with season, ranging from 20 percent in spring to 78 percent in autumn.

5. The three most abundant trees in the flood plain, tupelo, cypress, and ash, account for over 50 percent of the leaf-fall total. However, they were found to be the least productive of all species, on a mass-per-stem biomass basis.

6. The levee areas produce more litter fall per unit area than the swamp areas, despite having substantially lower tree stem biomass. They are approximately three times more productive on a mass-per-stem biomass basis. This is partially attributable to the production by abundant vines in the levee areas. It is also associated with higher diversity in the levees, especially higher equitability of species (a component of diversity).

7. Leaf decomposition is complete within 6 months for some species of leaves when immersed in water. These species include tupelo species and sweetgum, two of the most common trees in the basin. Other species, including diamond-leaf oak and baldcypress, decompose much more slowly. In a dry environment, decomposition rates are much slower, such that even the fast decomposers lose less than half their mass within 6 months. Carbon loss, like total biomass loss, continues at a nearly constant rate. Losses of nitrogen and phosphorus from the leaves follow exponential decay curves, and these elements are largely leached out within the first month. This applies to all species, even in a dry environment.

8. Litter fall represents a major potential source of nutrients and detritus to the Apalachicola River system and estuary. If the annual litter fall were totally flushed into the channels, it could produce a mean concentration increase of 7 mg/L organic carbon. This is not likely to be the case, of course, because of natural recycling within the flood-plain communities. One variable which is likely to bear heavily upon mobilization of litter-fall material is the timing of the annual flood relative to the peak autumn leaf fall. If the flood occurs very early, much more material is directly deposited on the water surface and there is less opportunity for decomposition and recycling before flooding.

9. Compared with other systems worldwide, the Apalachicola forest litter-fall production rate of 800 $(g/m^2)/yr$ is high. It is higher than those of many tropical systems and almost all warm temperate systems. Because most other systems which have been studied are not wetland systems, this comparison adds credence to the suggestion that wetlands are more productive than uplands in comparable latitudes. Leaf decomposition rates in the Apalachicola environment appear very similar to comparable studies in other systems.

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SUPPLEMENTARY DATA

DAILY LITTER PRODUCTION RATE OF MAJOR SPECIES, IN GRAMS PER SQUARE METER. VALUES ARE MONTHLY MEANS OF PLOTS INDICATED.

I. LEVEE COMMUNITIES: PLOTS 3, 4, 5, 6, 11, 14

MONTH	TUPELO	BALD-CYPRESS	OVERCUP OAK	SUGAR-BERRY	SWEET-GUM	ASH
SEP	0.0282	0.0056	0.1775	0.0970	0.4596	0.1732
OCT	0.0842	0.0140	0.0068	0.3214	1.1439	0.7905
NOV	0.2300	0.1637	0.0336	0.4852	1.4610	0.1455
DEC	0.0265	0.0879	0.0868	0.1356	0.9767	0.0059
JAN	0.0000	0.0002	0.0074	0.0045	0.0528	0.0000
FEB	0.0000	0.0004	0.0000	0.0012	0.0229	0.0024
MAR	0.0039	0.0007	0.0000	0.0000	0.0122	0.0003
APR	0.0051	0.0000	0.0044	0.0053	0.0541	0.0003
MAY	0.0037	0.0000	0.0036	0.0106	0.0193	0.0088
JUN	0.0068	0.0001	0.0077	0.0650	0.1311	0.0157
JUL	0.0190	0.0001	0.0132	0.3331	0.0596	0.0071
AUG	0.0269	0.0007	0.0010	0.0507	0.1122	0.0344

MONTH	PLANER TREE	AMER. ELM	WATER HICKORY	AMER. HORNBM.	DIA-LF. OAK	GRAPE	NON-LEAF
SEP	0.0063	0.0076	0.1648	0.0730	0.0521	0.2609	0.9095
OCT	0.0132	0.0252	0.2125	0.1267	0.1700	0.6035	0.9540
NOV	0.1056	0.0323	1.1583	0.2489	0.5587	1.4661	1.1123
DEC	0.0401	0.0658	0.4933	0.2580	0.5946	0.0206	0.7155
JAN	0.0310	0.0084	0.0271	0.0057	0.6513	0.0010	0.3836
FEB	0.0021	0.0000	0.0040	0.0020	0.2368	0.0005	2.4680
MAR	0.0012	0.0000	0.0007	0.0000	0.1860	0.0002	0.7094
APR	0.0000	0.0000	0.0002	0.0038	0.0326	0.0039	1.2405
MAY	0.0007	0.0014	0.0095	0.0269	0.0374	0.0106	0.3010
JUN	0.0040	0.0017	0.0266	0.0404	0.0264	0.0452	1.2275
JUL	0.0044	0.0023	0.0441	0.0266	0.0278	0.0600	0.6742
AUG	0.0070	0.0022	0.0405	0.0335	0.0626	0.1523	0.4612

II. SWAMP COMMUNITIES: PLOTS 1, 2, 7, 12, 13, 15, 16, 17, 18, 19

MONTH	TUPELO	BALD- CYPRESS	OVERCUP OAK	SUGAR- BERRY	SWEET GUM	ASH
SEP	1.8063	0.1668	0.0322	0.0000	0.0000	0.0774
OCT	2.5709	0.5323	0.0674	0.0000	0.0000	0.2188
NOV	1.9033	1.1275	0.3366	0.0004	0.0000	0.6672
DEC	0.3604	0.7638	0.5505	0.0002	0.0000	0.1974
JAN	0.0092	0.0134	0.0598	0.0000	0.0000	0.0022
FEB	0.0122	0.0042	0.0010	0.0000	0.0000	0.0027
MAR	0.0157	0.0018	0.0013	0.0000	0.0004	0.0002
APR	0.0660	0.0098	0.0123	0.0000	0.0000	0.0103
MAY	0.0705	0.0113	0.0382	0.0000	0.0003	0.0280
JUN	0.1996	0.0122	0.0112	0.0000	0.0000	0.0065
JUL	0.6301	0.0286	0.0185	0.0000	0.0000	0.0122
AUG	0.9200	0.0228	0.0278	0.0000	0.0000	0.0106

MONTH	PLANER TREE	AMER. ELM	WATER HICKORY	AMER. HORNBM.	DIA-LF. OAK	GRAPE	NON- LEAF
SEP	0.0333	0.0847	0.0043	0.0000	0.0000	0.0036	1.2711
OCT	0.0491	0.1421	0.0210	0.0000	0.0669	0.0068	0.9473
NOV	0.1958	0.1719	0.1275	0.0082	0.0023	0.0036	1.0032
DEC	0.1901	0.0943	0.1090	0.0013	0.0034	0.0001	0.9148
JAN	0.1233	0.0000	0.0008	0.0003	0.0055	0.0000	0.8262
FEB	0.0127	0.0000	0.0002	0.0000	0.0025	0.0000	0.2856
MAR	0.0000	0.0000	0.0000	0.0000	0.0006	0.0000	0.7702
APR	0.0006	0.0063	0.0021	0.0000	0.0005	0.0000	0.7250
MAY	0.0039	0.0152	0.0012	0.0002	0.0000	0.0000	0.3272
JUN	0.0046	0.0127	0.0051	0.0001	0.0006	0.0005	1.7263
JUL	0.0054	0.0135	0.0012	0.0000	0.0010	0.0049	0.4791
AUG	0.0128	0.0278	0.0019	0.0007	0.0000	0.0054	1.1073

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