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The Coosawhatchie Bottomland Ecosystem Study

A Report on the Development of a Reference Wetland

Marianne K. Burke and Mark H. Eisenbies, Editors

The Editors

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Cover photo: The floodplain of the Coosawhatchie River is vegetated by bottomland hardwood tree species. As a result of logging during the 20th century, only a small amount of baldcypress remains on the site.

Acknowledgments: The authors thank the Westvaco Corporation for the use of their property and assistance in this study. Also, thanks to Andy Harrison, Todd Thompkins, Cindy Bunton, Nitsa Dagan, Auerbach, Carl Phillips, Andrew Hulin, Michele Stevens, Kim Miller, Matt Eldridge, Margaret Bailey, Keshika Butler, Karen Johnson, Frederick James, and Jim Dixon for technical assistance.

List of Abbreviations

Length		Land area		Weight	
km	kilometer	ha	hectare	kg	kilogram
m	meter			g	gram
cm	centimeter			mg	milligram
mm	millimeter				
d.b.h.	diameter at breast height				
mt	metric ton (old abbreviation was t)				

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Abstract

Only 23 percent of the presettlement acreage of bottomland hardwood forests remains today, and the remaining forests have lost many of their original functions. To successfully manage these forests we must be able to compare their functional capacities with reference or model wetlands. This report contains the results of the Coosawhatchie Bottomland Ecosystem Study during Phase I, 1994 through 1999—the baseline calibration period for development of the reference wetland. Information about the physical and community characteristics and the ecosystem processes is presented in 15 individual reports. Where possible, results from this site are compared with results from other sites, both within the Southern Forested Wetlands Initiative and from other bottomland hardwood research sites. Those who use this information should consider these results preliminary and are invited to contact the authors of each chapter for more detailed information about the methods, results, interpretations, and plans for participation in Phase II.

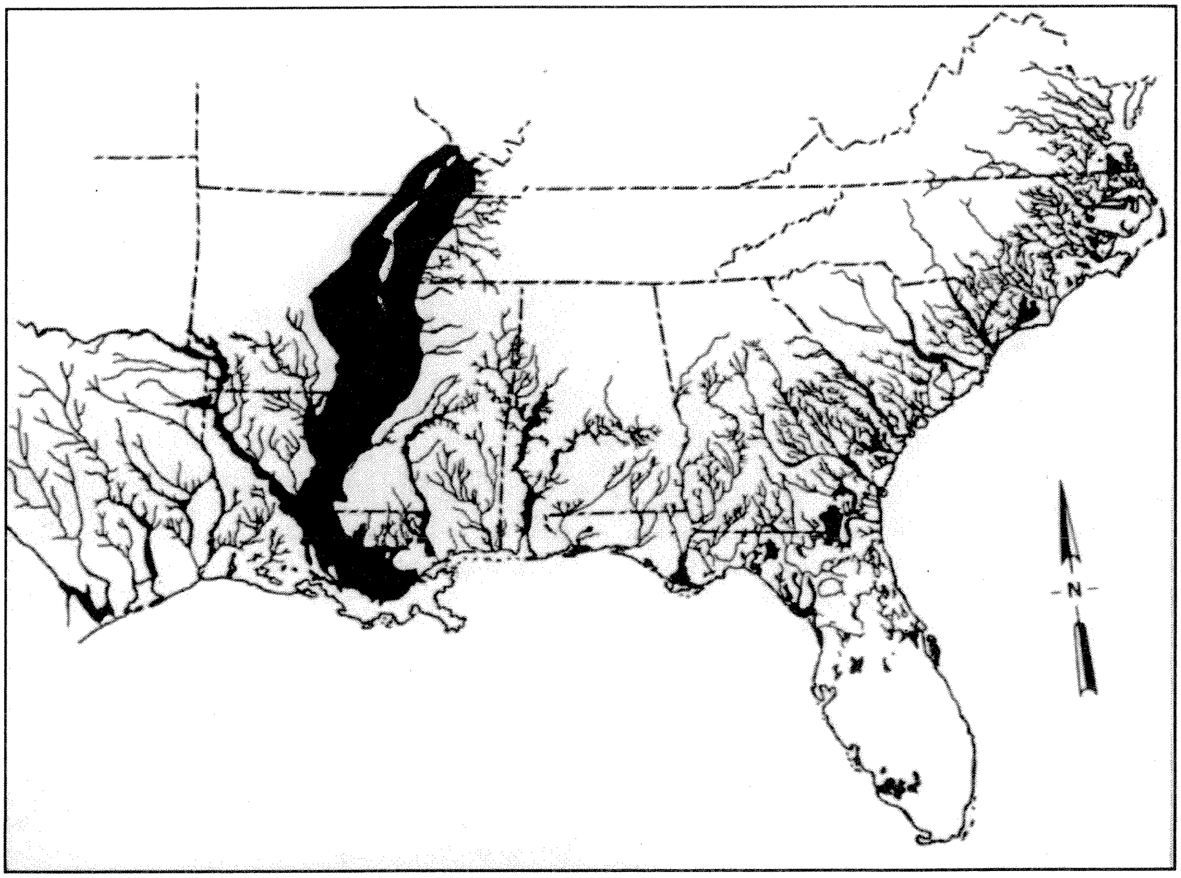
Keywords: Bottomland hardwood, Coosawhatchie River, ecological processes, ecosystem study, neotropical migratory birds, reference wetland, wetland hydrology.

Introduction

Marianne K. Burke[1]

When Europeans colonized the area that is now the United States, wetlands comprised 9 percent of the landscape (Dahl 1990). Since then, one-half of this wetland area has been lost, primarily by draining for agriculture. Of the bottomland hardwood forest component, only 23 percent of the presettlement acreage remains. Most of the remaining areas are "seriously fragmented and may have lost many of their original functions" (Mitch and Gosselink 1993).

At the initiation of Phase I of the Coosawhatchie Bottomland Ecosystem Study, we had only just begun to understand how these remaining bottomland hardwood ecosystems functioned and how they should be managed (Stanturf and Messina 1997). We understood that hydroperiod is the driving influence behind all ecological processes, and that over the long term, timber harvesting alone has little influence on hydroperiod. We also knew that natural regeneration after clearcutting does not threaten water quality if best management practices are followed; that decomposition rates appear to be mostly influenced by site wetness; and that vegetation productivity should be sustainable at preharvest levels although harvest method can influence tree species composition (Lockaby and others 1997). In addition, we knew that selective timber harvesting has little influence on bird communities (Hamel 1989). However, many of the studies on which these conclusions were based were conducted on relatively small cut units, much smaller than would be used in an operational harvest, and preharvest information to help assess harvesting impacts was seldom available.



Wetland areas of the Southeastern United States.

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[1] Research Ecologist, USDA Forest Service, Southern Research Station, Center for Forested Wetland Research, Charleston, SC.

As a result of our limited understanding of the functional capacity of these ecosystems, our attempts to mitigate their losses by creating and restoring bottomland hardwood forests had been met with mixed success, in part because no reliable assessment techniques or indicators of successful creation or restoration had been developed. We needed a better understanding of how undisturbed forested wetlands were structured and an assessment of their functional capacity for reference, or a model for comparison.

The Southern Forested Wetlands Initiative was formed to establish a series of reference wetlands and to quantify their structural and functional capacities. By obtaining quantitative knowledge of the structure and functions of bottomland hardwood ecosystems, we can meet the two objectives of the initiative.[2] This information will be used to analyze and assess the impacts of alternative management actions on ecosystem integrity. It will also provide guidelines for evaluating the success of wetland restoration efforts. This initiative consists of a group of researchers from three Federal agencies: the USDA Forest Service, Southern Research Station; the U.S. Geological Survey, Biological Resources Division and Water Resources Division; and the U.S. Army Corps of Engineers. The researchers obtained funding from their respective agencies and worked together to establish a series of reference bottomland hardwood forests that could be used as long-term research sites for the quantification of relatively undisturbed ecosystem characteristics. They recognized that these sites had to be representative of the present and historic bottomland hardwood forests in the southern region, and that the structural and functional capacity of these sites had to be quantified in ways that would allow comparison among them.

A multiagency technical committee was formed to guide the process of selecting and establishing studies on the reference sites. The committee identified candidate sites based on five selection factors: (1) the sites had to be large (at least 300 contiguous ha), (2) the canopies could not have been disturbed during the last 40 years, (3) the sites could not be tidally influenced, (4) the hydroperiods could not have been altered by humans, and (5) the sites had to be accessible. Finally, at least one of the sites had to be manipulatable, so current understanding of how these systems functioned could be tested. After visits to the six most promising candidate sites in Texas, Louisiana, Arkansas, Georgia, and South Carolina, and considering budget constraints, three sites were selected—one on the Cache River in Arkansas, one on the Iatt Creek in Louisiana, and one on the Coosawhatchie River in South Carolina (fig. 1).

The technical committee guided the process of establishing the reference wetlands by deciding on core (required) tasks that were to be replicated at each site. These core tasks characterized vegetation and soils, aboveground net primary production, nutrient cycling, sedimentation, coarse woody debris, hydrology, litter decomposition, breeding neotropical and wintering Nearctic migratory birds, microclimate, and topography. The researchers used a geographical information system to spatially represent the data. In addition, other studies were conducted on each site according to the interests and expertise of the researchers.

Of the three Southern Forested Wetland Initiative sites, the Coosawhatchie River site, owned and managed by Westvaco Corporation, is the only one that is on private land. In addition to being one of the study sites, Coosawhatchie is managed for forest products by Westvaco Corporation and is leased by a hunt club. The study provided a unique opportunity to determine the influence of timber harvesting on ecosystem processes. After extensive characterization of the site during the first 5 years of the study (Phase I), operational scale harvests were planned so that the impacts of harvesting could be assessed.

This report contains the results of the Coosawhatchie Bottomland Ecosystem Study during the baseline calibration period (Phase I) from summer 1994 through spring 1999. Where possible, results from this site are compared with results from other sites, both within the Southern Forested Wetlands Initiative and at other bottomland hardwood research sites. In addition to the Federal agencies mentioned above, participants in this phase of the study were: the U.S. Geological Survey's National Research Center in Reston, VA; the USDA Natural Resource Conservation Service in Walterboro, SC; Auburn University; Clemson University; Michigan Technological University; North Carolina State University; University of Georgia; and the Savannah River Ecology Laboratory. Westvaco Corporation's scientific staff, located at Summerville, SC, also collaborated in research on the site.

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[2] Harms, W.R.; Stanturf, J.A. 1994. A quantitative assessment of the structure and functions of forested wetlands in bottomland hardwood ecosystems in the Southern United States. Study Plans FS-SE-4103-207 and FS-SO-4152-110. [Not paged]. Available from: U.S. Department of Agriculture, Forest Service, Southern Research Station, P.O. Box 2680, Asheville, NC 28802.

Study participants hope these results will provide insight for continued research on forested wetlands and for the management and restoration of bottomland hardwood ecosystems. They also hope this information will encourage others to join in the study during the experimental manipulation planned for the fall of 1999, when Phase II begins. Those who use this information should consider the results preliminary; and they are invited to contact the authors of each paper for more detailed information on the methods, results, interpretation, and plans for participation in Phase II.

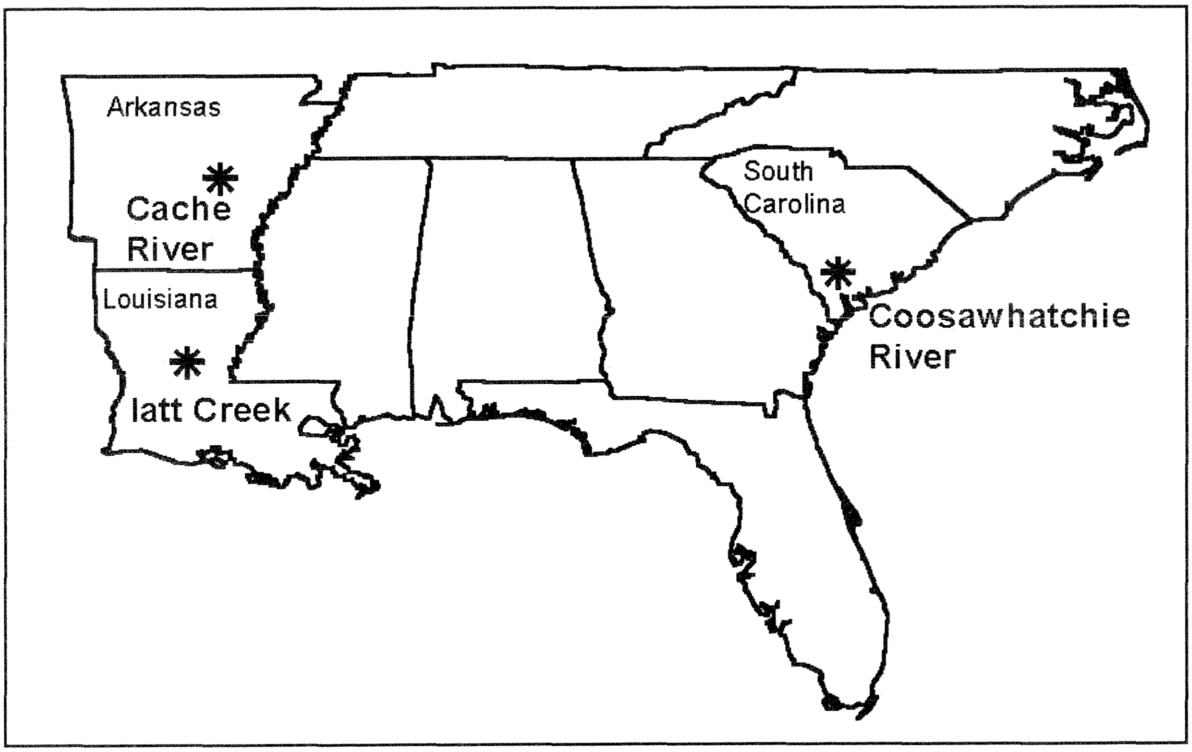


Figure 1—General location of the three field sites of the Southern Forested Wetlands Initiative Study of bottomland hardwood ecosystems.

Section 1—Physical Characterization

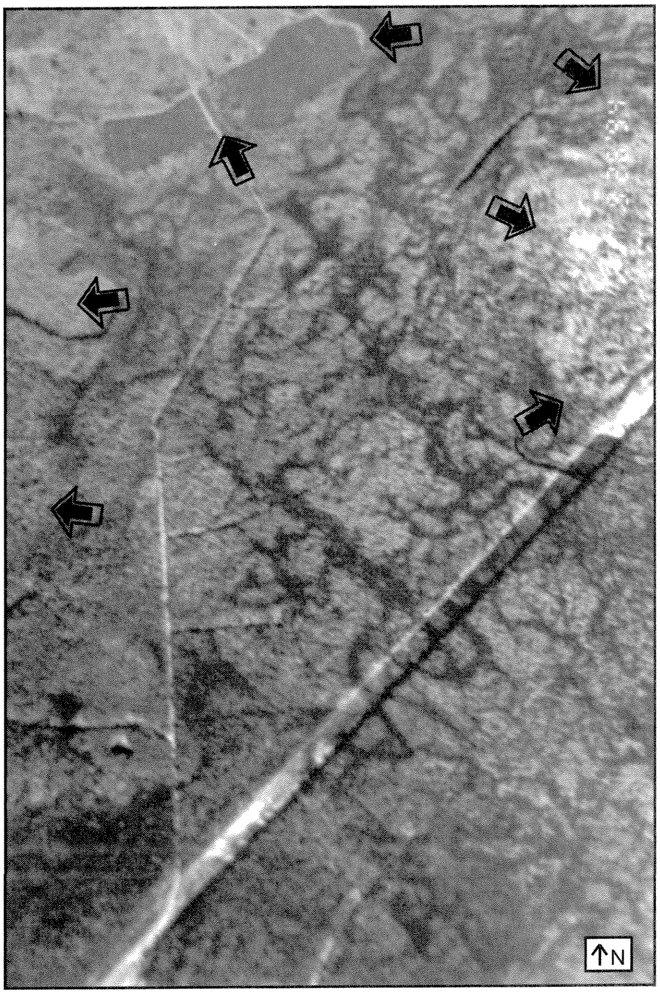
Geomorphology and Soil Survey

Laura A. Murray, Bob Eppinette, and John H. Thorp[1]

The Coosawhatchie River, through erosion and downcutting, carved a fluvial valley through the Wicomico and Pamlico marine terraces during the late Pleistocene-Holocene period. The floodplain is relatively small and immature compared to the major river systems of the South Carolina Lower Coastal Plain. Consequently, the classic geomorphic features of a larger fluvial system are subtly expressed. The study area is composed of two weakly developed terraces, distinguished primarily by flooding frequency and surface sand size. The soils of the lower terrace consist of highly variable loamy and clayey Pamlico and recent fluvial sediments over older sandy fluvial beds. The soils of the upper terrace along the western edge of the floodplain consist of clayey and loamy Pamlico sediments with an alluvial surface layer. Small amounts of sediment from sandy, upland Wicomico deposits are delivered via short, well-dissected drainageways. The underlying stratigraphy consists of unconsolidated Quaternary and Pliocene marine and fluvial sediments blanketing semilithified Miocene through Cretaceous marine sediments (Colquhoun 1965, 1974; Dubar 1971; Hughes and others 1989).

The floodplain's relief—approximately 2 m—is characterized by a distinct microtopography of convex hummocks and scoured swales. The fluvial geomorphology is the result of the low gradient, anastomosing river's inability to completely erode the residual Pamlico sediments and to move the coarse component of its sediment load. The sandy bed load is left behind as channel bars and small natural levees. These curvilinear, low ridges are composed primarily of siliceous, loamy, fine sands. The floodplain, exposed to temporal variations in discharge, experiences relatively short, intense flooding periods and an extensive period of lower discharge. The scoured branching channel networks are formed through avulsion, as main channel banks divert flood flows onto the floodplain surface and as the water table rises above the land surface. The sloughs' soils are composed of silts and clays, deposited by overbank flooding. Floodwaters tend to persist in swampy, shallow pools on the very poorly drained, low-permeability soils. On the Coosawhatchie River floodplain, generalized soil horizons and subsurface stratigraphy consist of a thick, loamy surface layer underlain by interbedded, silty, slackwater deposits and lenses of point bar and channel sands, surrounding reworked relict islands of Pamlico terrace material.

Soils on the study site were mapped during the 1970's as one unit—the Santee Association (U.S. Department of Agriculture, Soil Survey Staff 1980). A more detailed characterization of the floodplain was necessary to better understand the site history and hydrologic controls on surface and subsurface water, and to determine the distribution of elements in nutrient cycling studies. Samples collected from representative horizons at approximately 100 locations and analyzed for physical and chemical properties were used to generate a detailed soils map (fig. 1.1).



Aerial photo of study area showing the anastomosing channels dissecting the incompletely eroded marine terrace, the limits of which are marked with arrows.

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[1] Graduate Student/Research Assistant, Department of Environmental Sciences, University of Virginia, Charlottesville, VA; Resource Soil Scientist, USDA Natural Resource Conservation Service, Walterboro, SC; and Certified Soil Classifier, Silva-Soils Consulting, Silsbee, TX, respectively.

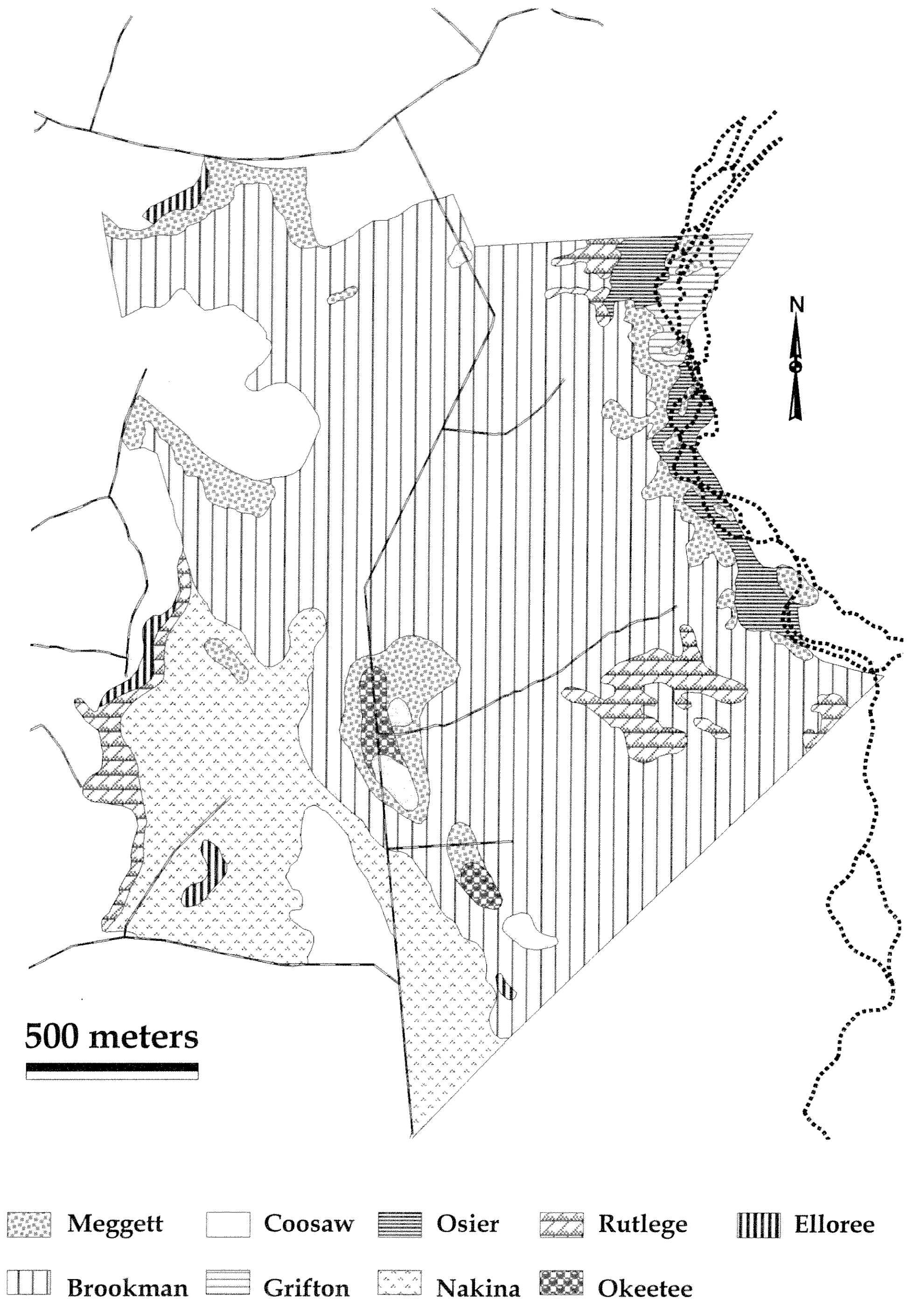

Figure 1.1—Soil series map of the Coosawhatchie Bottomland Ecosystem Study site, South Carolina.

Nine soil series were identified, with the most clayey subsoils thinning towards the river, where sandy lithologic discontinuities increase. The majority of the site was classified in the Brookman series—a fine, mixed, thermic, Typic Umbraqualf (fig. 1.2). These soils have thick, black, loamy surface layers and dark gray, clayey subsoils. Scoured areas have higher silt content. Less important was the Meggett series: a fine, mixed, thermic, Typic Albaqualf found on areas slightly higher in elevation (< 1 m) than the rest of the floodplain, located on large islands and adjacent to upland areas. Black or dark gray surface layers are < 25 cm thick in the Meggett series. The Nakina series is a fine-loamy, siliceous, thermic, Typic Umbraqualf in the western part of the study area, adjacent to the upland. Surface layers consist of black loam to approximately 50 cm in depth. Comprising a total of approximately 20 percent of the area is soils characteristic of the Okeetee, Coosaw, Elloree, Grifton, Osier, and Rutlege series. All are composed of siliceous, sandy, and sandy loam surface layers; however, the Osier and Rutlege series are devoid of leached E and argillic B horizons. This lack of profile development in the Osier and Rutlege series supports a recent fluvial origin, whereas the Okeetee, Coosaw, Elloree, and Grifton series exhibit well-developed horizons and are composed of older terrace sediments.

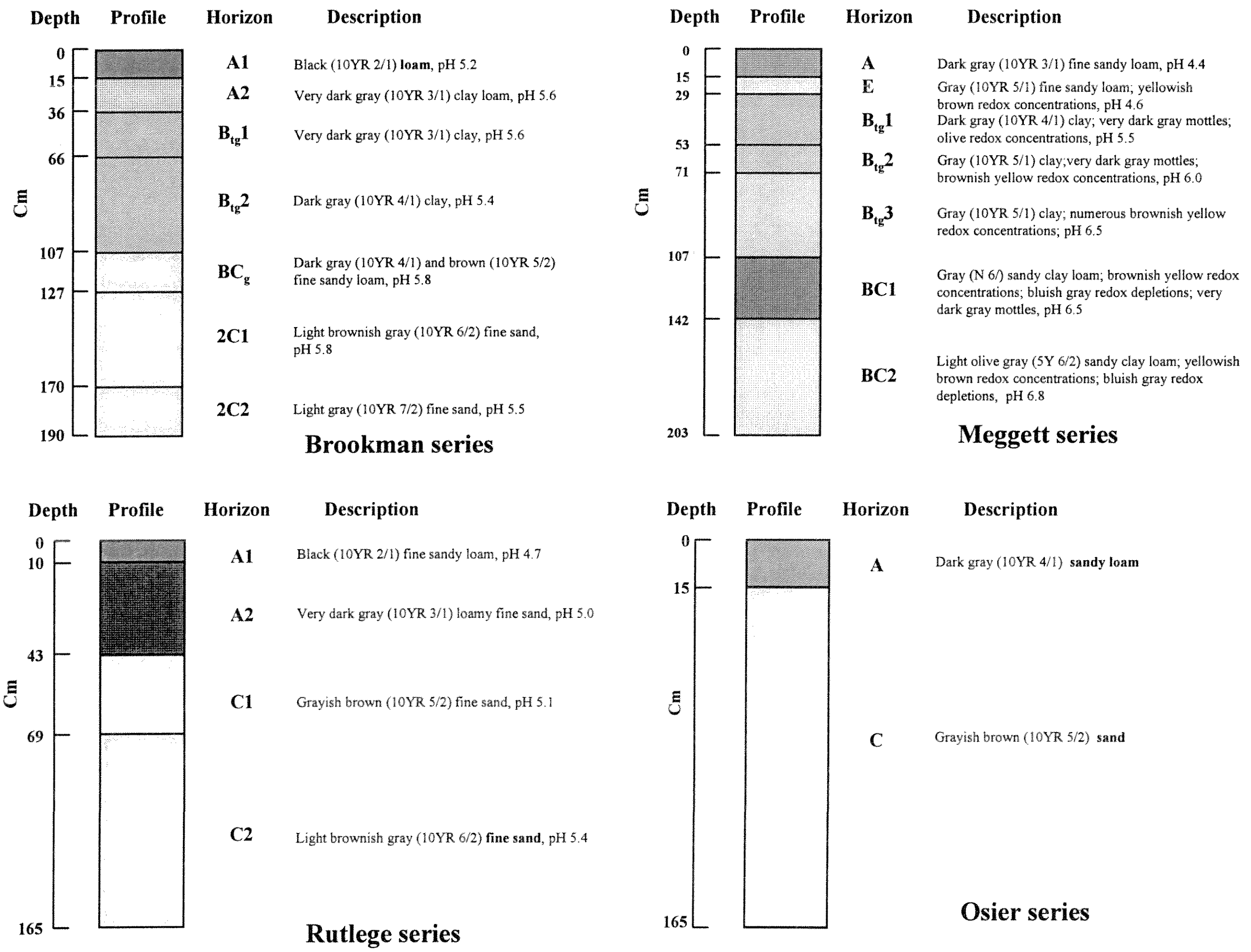

Figure 1.2—Four representative soil series illustrating the variety of horizon development in soils on the Coosawhatchie Bottomland Ecosystem Study site, South Carolina.

Hydrology

Mark H. Eisenbies and W. Brian Hughes[1]

Hydrologic processes are the main determinants of the type of wetland located on a site. Precipitation, groundwater, or flooding interact with soil properties and geomorphic setting to yield a complex matrix of conditions that control groundwater flux, water storage and discharge, water chemistry, biotic productivity, biodiversity, and biogeochemical cycling. Hydroperiod affects many abiotic factors that in turn determine plant and animal species composition, biodiversity, primary and secondary productivity, accumulation of organic matter, and nutrient cycling. Because the hydrologic regime has a major influence on wetland functioning, understanding how hydrologic changes influence ecosystem processes is essential, especially in light of the pressures placed on remaining wetlands by society's demands for water resources and by potential global changes in climate.

The Coosawhatchie is a fourth-order, anastomosing, blackwater river with a drainage area of approximately 1000 km^2. The floodplain surface is approximately 1.6 km wide and the relief on the surface is about 2 m. A surficial aquifer at the study site is about 9 m thick and consists of alluvial sand and clay, deposited by the Coosawhatchie River, and older Pleistocene sand and clay. These deposits are underlain by a 12-m-thick confining unit, which in turn overlies the Floridan aquifer.

Surface-water stage data from two gauging stations upstream and one downstream from the study site were used to predict the historical duration of flooding and inundation across the study site. Hampton Branch Station is located approximately 24 km upstream; Early Branch Station is approximately 8 km upstream; and Grays Station is immediately downstream of the site. At the study site, the river generally crests 3 to 4 days after rain events, and crests at Grays are 2 to 3 days after those at Hampton (figs. 1.3, 1.4) (Cooney and others 1996).

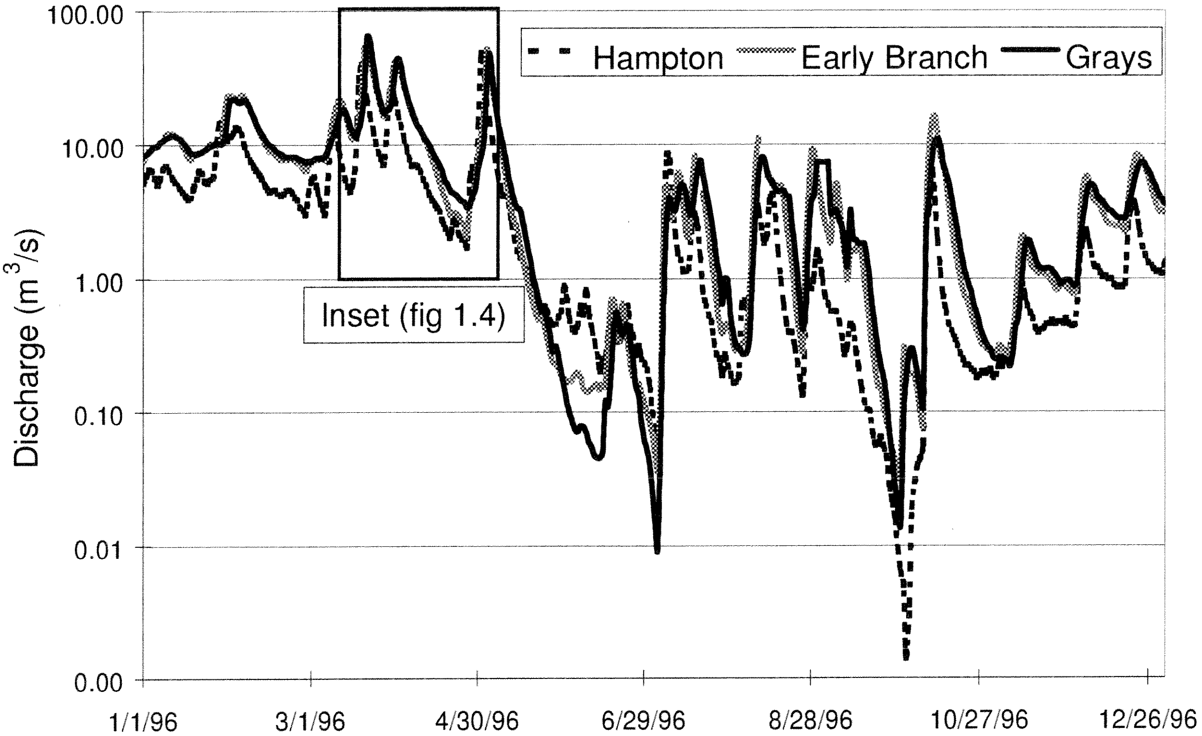

Figure 1.3—Discharge during 1996 for the three U.S. Geological Survey gauging stations located on the Coosawhatchie River (Cooney and others 1996).

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[1] Forestry Technician, USDA Forest Service, Southern Research Station, Center for Forested Wetland Research, Charleston, SC; and Hydrologist, U.S. Geological Survey, Columbia, SC, respectively.

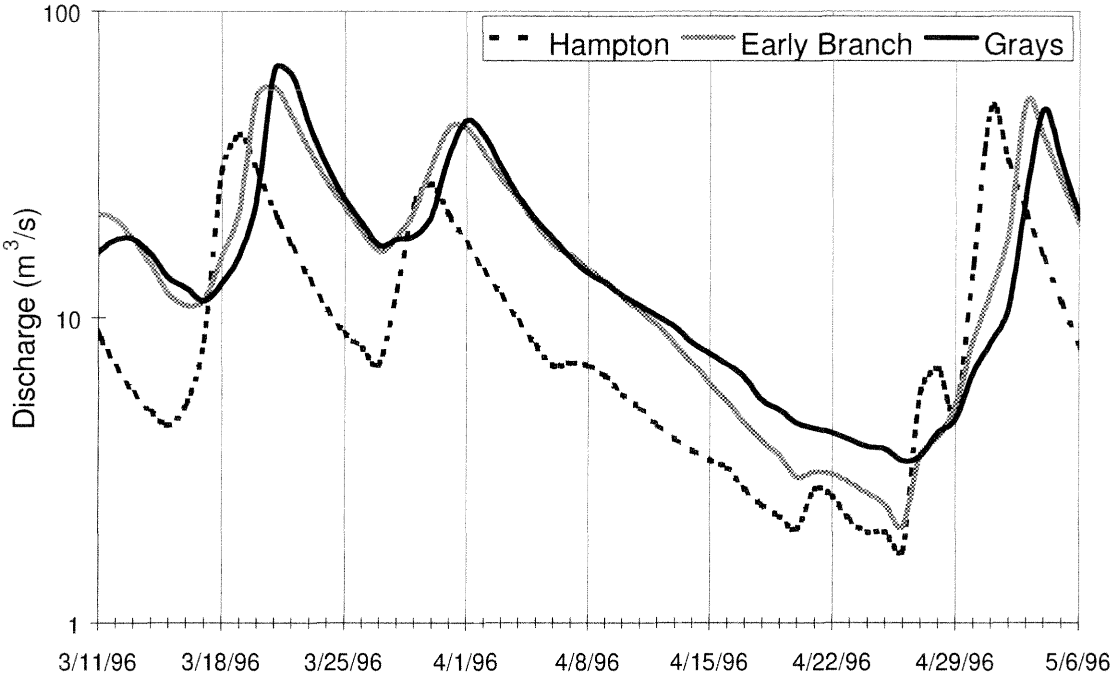


Figure 1.4—Stream response to storm events and lag between three U.S. Geological Survey gauging stations located on the Coosawhatchie River between March 11, 1996, and May 6, 1996 (Cooney and others).

Ground- and surface-water levels have been monitored since July 1996. Depth and duration of surface inundation and the elevation of the water table were used to examine the factors controlling hydrologic conditions across the site and the relationship between hydroperiod, plant community structure, and ecological processes. Wells and piezometers were installed in the surficial aquifer adjacent to and in the river channel at 22 locations (fig. 1.5) to monitor the elevation of the water table in association with the vegetation plots, and to determine the recharge-discharge relation between the ground water and surface water.

Regressions of water-table elevations on the floodplain at 18 polyvinyl chloride observation wells, using the river stage and 4 continuous recording wells as the independent variable, yielded correlation coefficients that ranged from 0.56 to 0.97. Water levels in wells closest to the river generally correlated best with river stage. The regression models predicted that the mixed oak (*Quercus* spp.), laurel oak (*Q. laurifolia* Michx.), swamp tupelo (*Nyssa sylvatica* var. *biflora* [Walt.] Sarg.), and water tupelo (*N. aquatica* L.) forest communities were inundated on average 0, 12, 39, and 52 percent of the year, respectively, and were saturated within 30 cm of the soil surface on average 24, 41, 77, and 88 percent, respectively, (fig. 1.6) during the October 1996 to September 1997 water year. Measurements of potentiometric surface indicated ground-water discharge is the dominant condition, but recharge can occur during extremely high flows.

The Floridan aquifer is about 21 m deep and currently has a potentiometric surface approximately 0.5 m above land surface at the study site. The potentiometric surface of the Floridan aquifer has declined approximately 5 m at the study site during the last century due to ground-water withdrawals for municipal and industrial water supplies (Hughes and others 1989). Historic decreases in ground- and surface-water flow at this site may have affected vegetation community dynamics, and may have resulted in long-term shifts from wetter to dryer species compositions. Only after the hydrologic functions and their influence on other ecosystems are determined, will it be possible to assess the potential influences of regional (aquifer drawdown) and global (climate) changes.

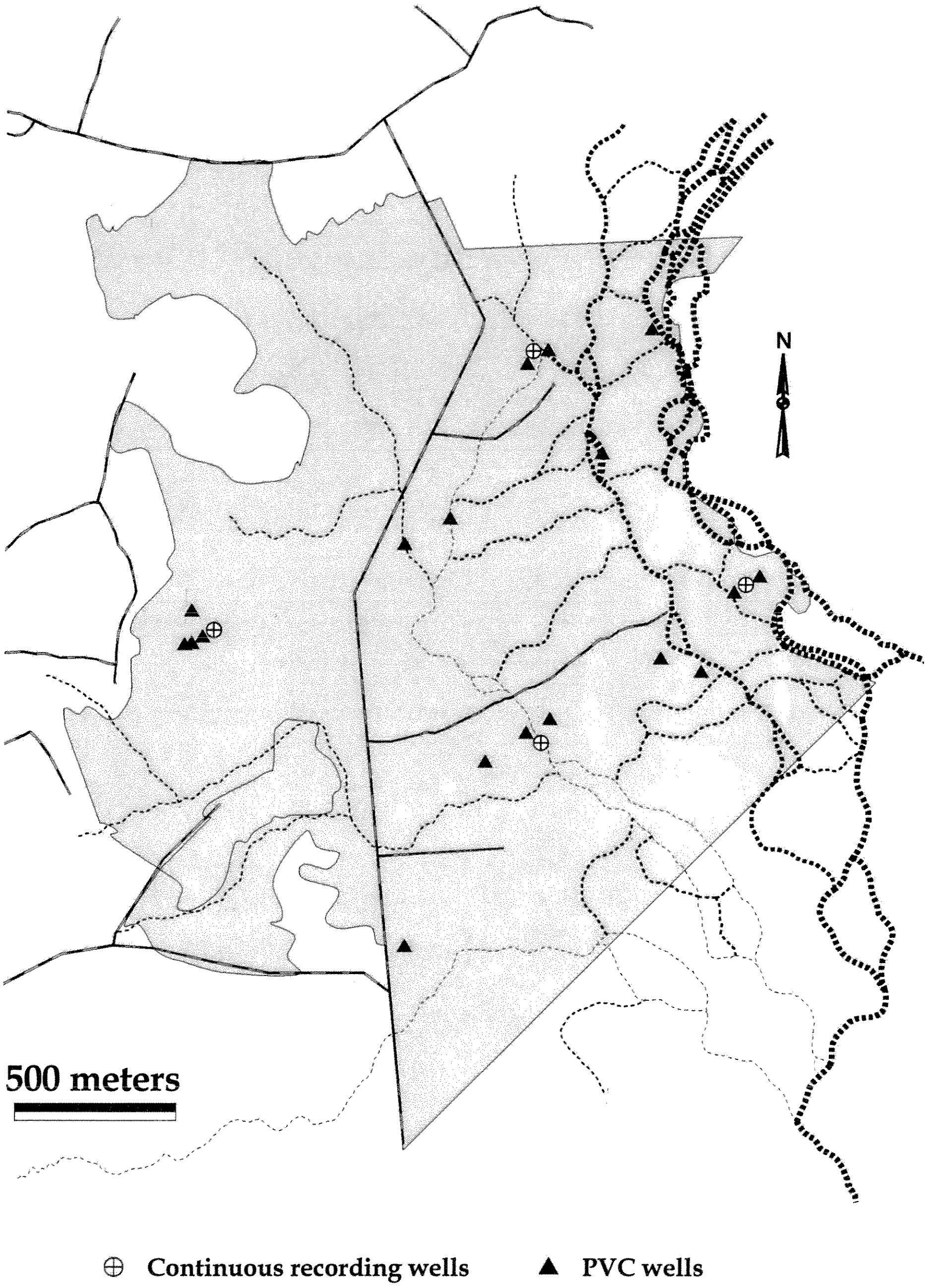


Figure 1.5—Map showing the shallow polyvinyl chloride (PVC) well locations, the continuous monitoring well locations, and the primary water-moving channels on the Coosawhatchie Bottomland Ecosystem Study site, South Carolina.

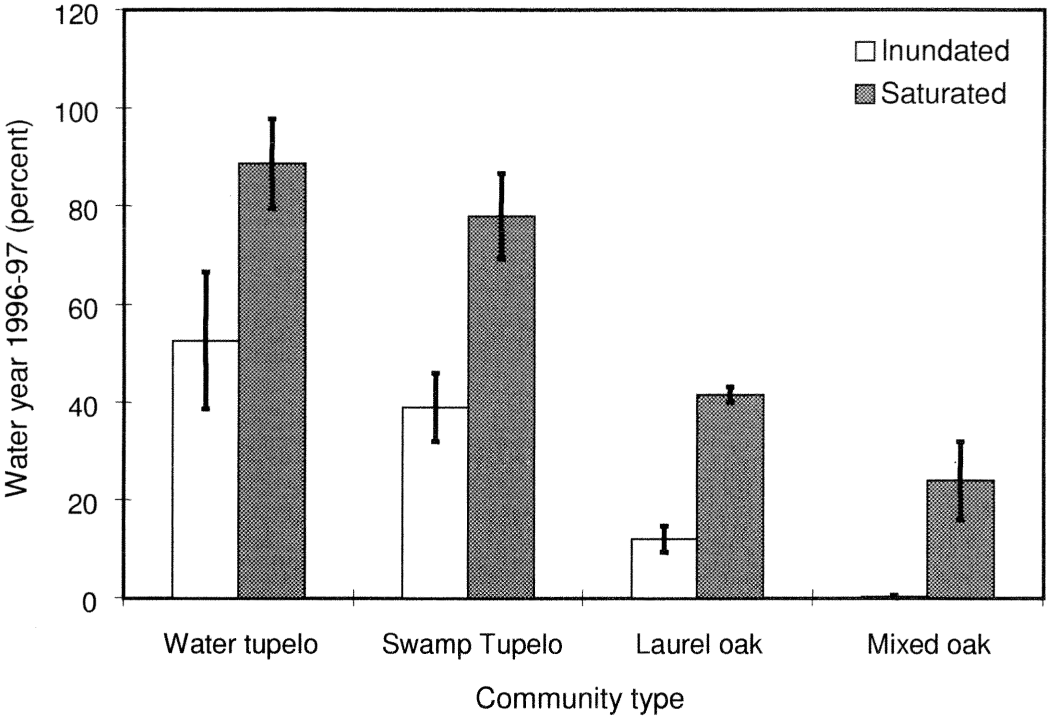


Figure 1.6—Duration (mean and standard error) of flooding (inundated) and saturation within 30 cm of the average soil surface elevation at the well for the 16 productivity plots located on the Coosawhatchie Bottomland Ecosystem Study site in water year 1996-97 (October through September).

Downloading data from continuously recording water well.

Sedimentation

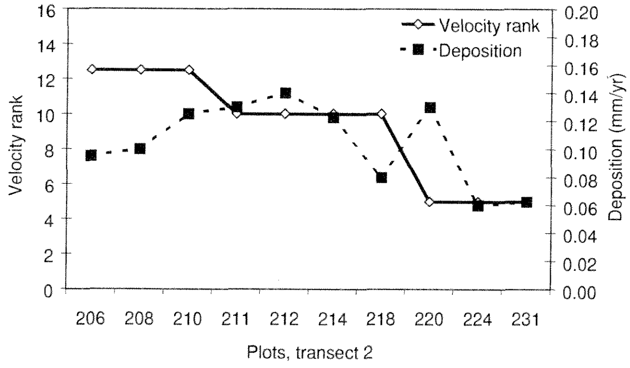
Cliff R. Hupp and Michael R. Schening[1]

Sedimentation is arguably the most important water-quality concern in the United States. Sediment trapping is cited frequently as a major function of riverine-forested wetlands, yet little is known about sedimentation rates at the landscape scale in relation to site parameters, including woody vegetation type, elevation, velocity, and hydraulic connection to the river. The Coosawhatchie River in coastal South Carolina, a blackwater stream, is compared to the Cache River on the Mississippi alluvial plain in Arkansas, a brownwater stream (Hupp and Schening 1997). Sedimentation rates along each river were estimated at sites along transects perpendicular to the channel by measuring the amount of deposition over the major root system of age-determined trees. These rates were related in turn to vegetation type, ground surface elevation relative to adjacent channel, hydroperiod, flow velocity, and hydraulic connection to river water. Additionally, short-term rates of deposition were estimated through the establishment of white, feldspar clay markers.

Mean deposition rates ranged from 0.02 to 0.20 cm per year on the Coosawhatchie site and from 0.20 to 0.36 cm per year on the Cache site. This result was expected because the brownwater Cache River carries an order-of-magnitude-greater suspended load—about 100 to 350 mg per liter—than the Coosawhatchie (about 5 to 25 mg per liter). Sedimentation patterns within both study areas varied strongly with elevation and thus vegetation patterns; sedimentation rates were greatest in sloughs and low elevations away from the main channel. Deposition varied inversely with velocity category on the Coosawhatchie site, while on the Cache site deposition varied directly (fig. 1.7). No sites along either stream experienced high velocities, which would have precluded most deposition of fine sediments. Low velocities facilitated deposition of fines, particularly organic material; however, relatively moderate velocities may have ensured a continuous supply of sediment-laden water available for deposition. On the Cache site, mild velocities may have increased mineral fines deposition whereas the lowest velocities may have had a poor connection to the river and were subject to stagnation.

Construction of white feldspar clay pad as a marker for determining short-term sedimentation rates.

(A) Coosawhatchie River



(B) Cache River

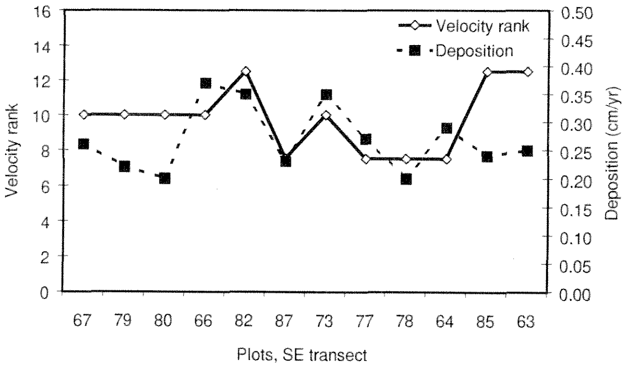


Figure 1.7—Deposition rates (dashed line) and velocity category rank (solid line, higher rank indicates higher velocity) along transect 2 of the (A) Coosawhatchie River and along the SE transect of the (B) Cache River.

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[1] Research Botanist and Project Chief, and Ecologist, respectively, National Research Program, U.S. Geological Survey, Water Resources Division, Reston, VA.

Hydraulic connectivity (degree of flow-path connections to the river) appeared to affect sedimentation rates on the Coosawhatchie site; greatest deposition occurs along sloughs with a direct flow path to the river (figs. 1.8, 1.9). A slough enters the Coosawhatchie study area upstream and away from the channel (top of fig. 1.9), bifurcates through the area, and reenters the main channel downstream. Sedimentation rates are highest in this slough (connected to the river upstream of study area). The most distal (away from river) end of transect 3, the central parts of transect 2, and the distal three sites on transect 1 are all affected (increased sedimentation) by this slough (fig. 1.10). Similar results could not be confirmed along the Cache River because high water has prevented sedimentation investigations along the central transect. Preliminary results from clay-pad analyses along the Coosawhatchie River suggest that sedimentation rates were generally greatest along tract 2 and near the river along all three transects (fig. 1.10). Hydraulic connectivity explained the increased deposition along transect 2 and the decreased deposition along transect 1, which is partially blocked by a road. Most clay pads west of the main forest road are largely separated from the river and have only trace amounts of deposition. Fines deposited over the clay pads contained substantial amounts of organic material, nearly 40 percent on the blackwater Coosawhatchie Bottomland Ecosystem Study area. This contrasts with 22 percent on the Cache River site. Subsequent decomposition and compaction may affect preliminary results of these highly organic deposits. Whether mineral fines and organic fines share the same deposition patterns is currently unknown.

Both streams annually trap substantial amounts of sediment, although deposition rates on the Cache site are twice those on the Coosawhatchie site. Soil chemistry investigations will allow estimation of the trapping of sediment-associated contaminants. Preliminary results suggested that sediment trapping patterns were most closely related to sediment supply, hydraulic connectivity to river water, and flow velocity. Additionally, vegetation patterns, largely controlled by hydroperiod, probably affected deposition rates though variation in surface roughness (stem size and density, coarse woody debris production) and thus the velocity of sediment-laden flows.

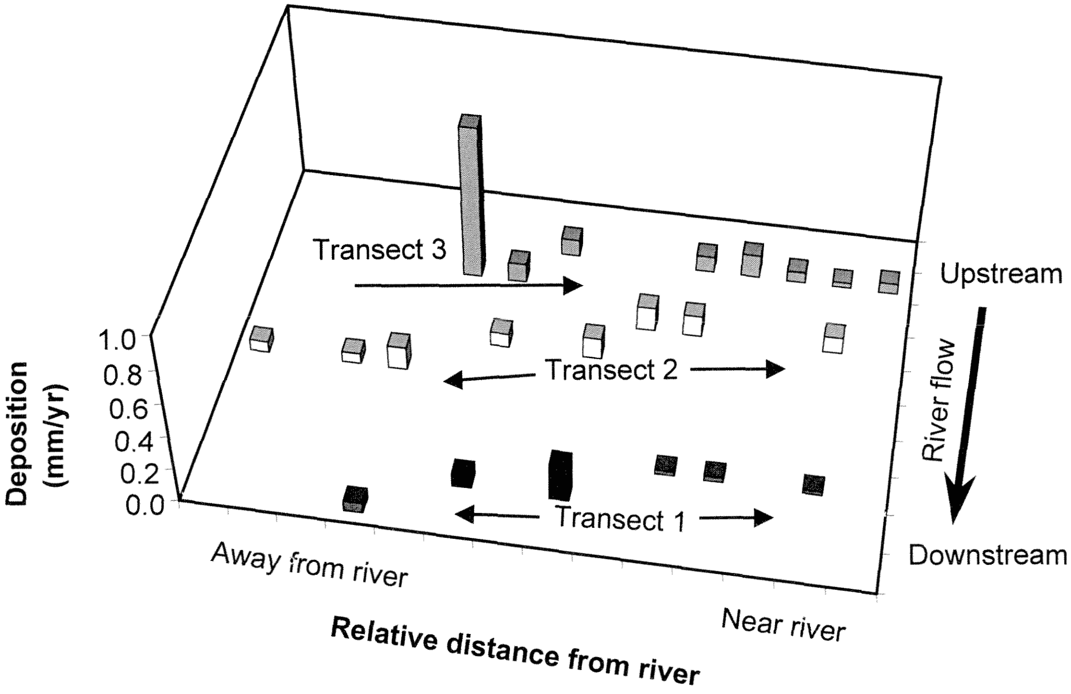

Figure 1.8—Sediment depostition along the three transects of the Coosawhatchie Bottomland Ecosystem Study site.

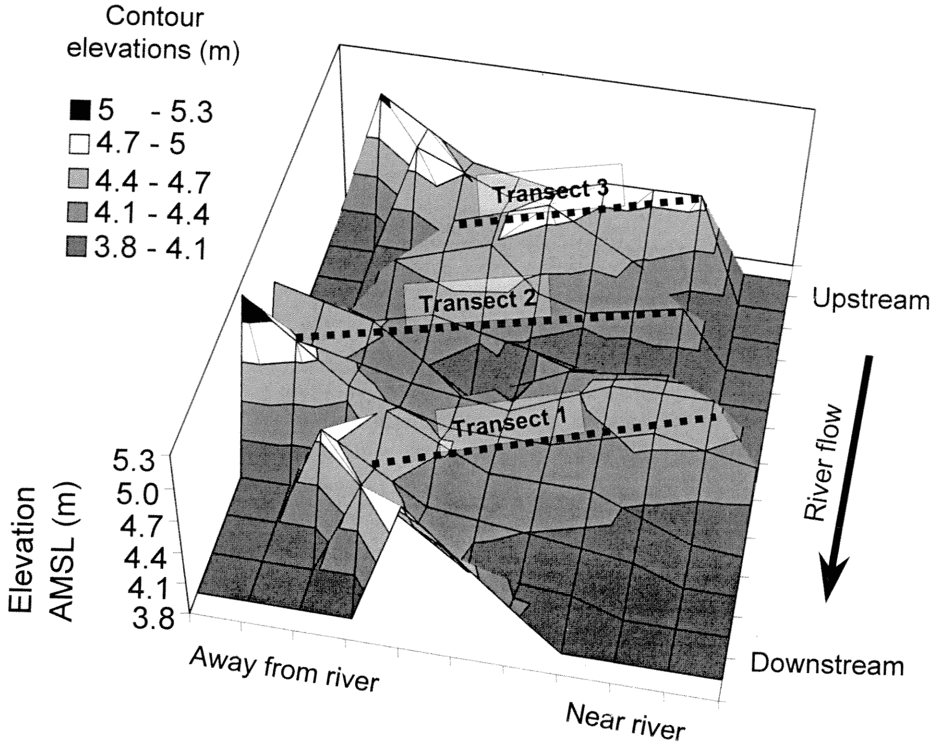

Figure 1.9—Grid point elevation on the Coosawhatchie Botomland Ecosystem Study site.

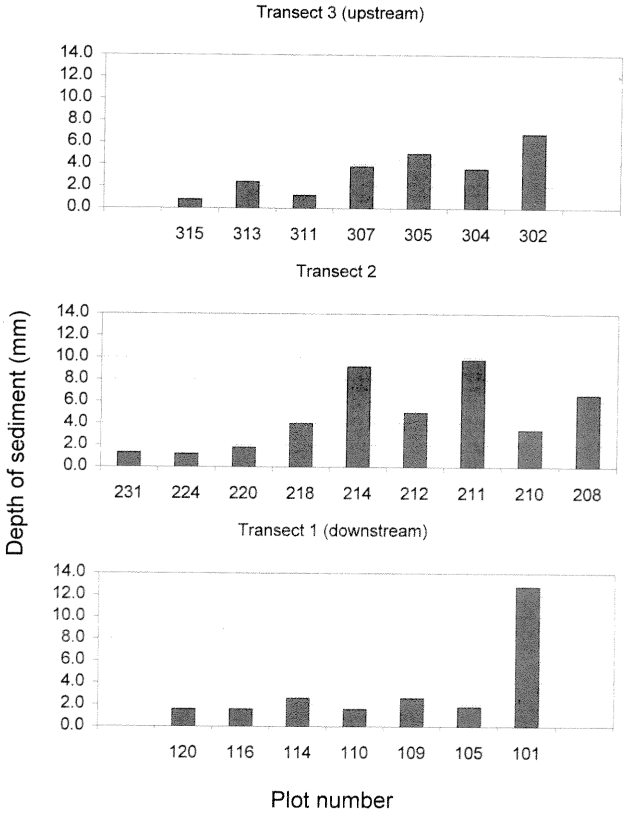

Figure 1.10—Short-term deposition above clay-pad markers (May 1996 to May 1997, preliminary data) along the three Coosawhatchie River transects.

Water Quality

Terry L. Maluk, Thomas A. Abrahamsen, and Richard H. Day[1]

The U.S. Geological Survey (USGS) began the National Water-Quality Assessment Program (NAWQA) in 1991 to describe the status of and long-term trends in the quality of the Nation's surface- and ground-water resources. The study of the Santee River Basin and Coastal Drainages began in 1994 and included about 60 800 km^2 in North Carolina and South Carolina. A network of data collection sites in the NAWQA study area was designed for ecological, surface-water, and ground-water sampling.

One of the sites in the network was the Coosawhatchie River near Early Branch, SC (USGS Station 02176517) (fig. 1.11). The drainage area of this blackwater river upstream of the site is approximately 1000 km^2. Land use in the basin has consisted almost entirely of agriculture (42 percent), forest (30 percent), and wetlands (24 percent). Water-quality samples were collected monthly at the Coosawhatchie River site from October 1995 through September 1997 as part of the NAWQA program.

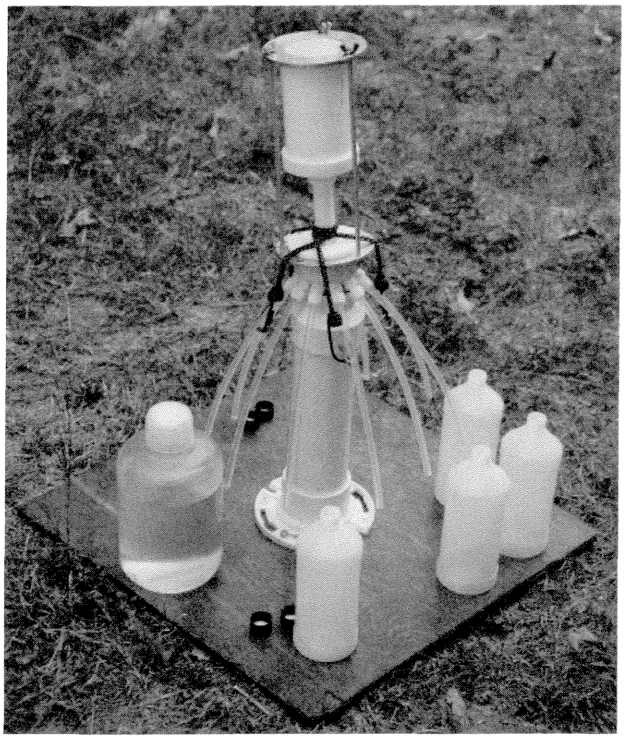

Photo by Brian Hughes

Each water sample was split into several bottles using a core splitter to ensure similar subsamples.

Seasonal patterns were observed in nutrients, suspended organic carbon, dissolved oxygen, and silica. Phosphorus concentrations were highest during low streamflows in the late spring and early summer, decreased through the fall, and were lowest during the winter (fig. 1.12). Ammonia-nitrogen concentrations were generally low, with a median of 0.015 mg per liter and a range from below detection (0.002 mg per liter) to 0.12 mg per liter. A comparison of total and dissolved ammonia-plus-organic-nitrogen and ammonia-nitrogen concentrations indicated that the majority of the nitrogen was in the dissolved, organic form. Nitrate-nitrogen concentrations ranged from below detection (0.005 mg per liter) to 0.12 mg per liter. The median suspended organic carbon concentration was 0.5 mg per liter with a range of 0.2 to 2.8 mg per liter. Dissolved oxygen saturation ranged from 25 to 84 percent and was highest in the winter. Silica concentrations ranged from 2.3 to 11 mg per liter and were highest in the winter.

In a 300-m reach of the river, specimens of algae, macroinvertebrates, and fish were collected and aquatic habitat was described. Bed sediment and native bivalve (*Elliptio insula*) tissue samples were collected and analyzed for organic constituents and trace elements. The sediment mercury concentration in this reach of the Coosawhatchie River was 0.26 mg per gram. Trace-element concentrations in the Coosawhatchie River native bivalves were similar to those in other streams in the NAWQA study area (data available at http://wwwsc.er.usgs.gov/nawqa/santhome.html).

Among the organic constituents in the sediment samples, p-cresol was present at the highest concentration, 810 mg per kilogram. The concentration of the next-most-abundant organic compound, di-n-butyl-phthalate, was < 100 mg per kilogram. A metabolite of the pesticide DDT, p, p'-DDE, was detected at a concentration of 8 mg per kilogram. No organic contaminants were detected in the *E. insula* tissue samples.

Fish were collected from the main channel of the Coosawhatchie River by using a boat-mounted electrofishing apparatus. In shallows and sloughs along the reach, a backpack-mounted electrofisher was used. Twenty-three species of fish were collected. The dominant species were the warmouth (*Lepomis gulosus*), comprising 20 percent of the total number of fish captured and 17 percent of the biomass; and the bluegill sunfish (*Lepomis macrochirus*), comprising 15 percent of the total number of fish and 7 percent of the biomass. Compared with 11 other streams in the NAWQA study area, the Coosawhatchie River ranked fifth in the number of fish species collected.

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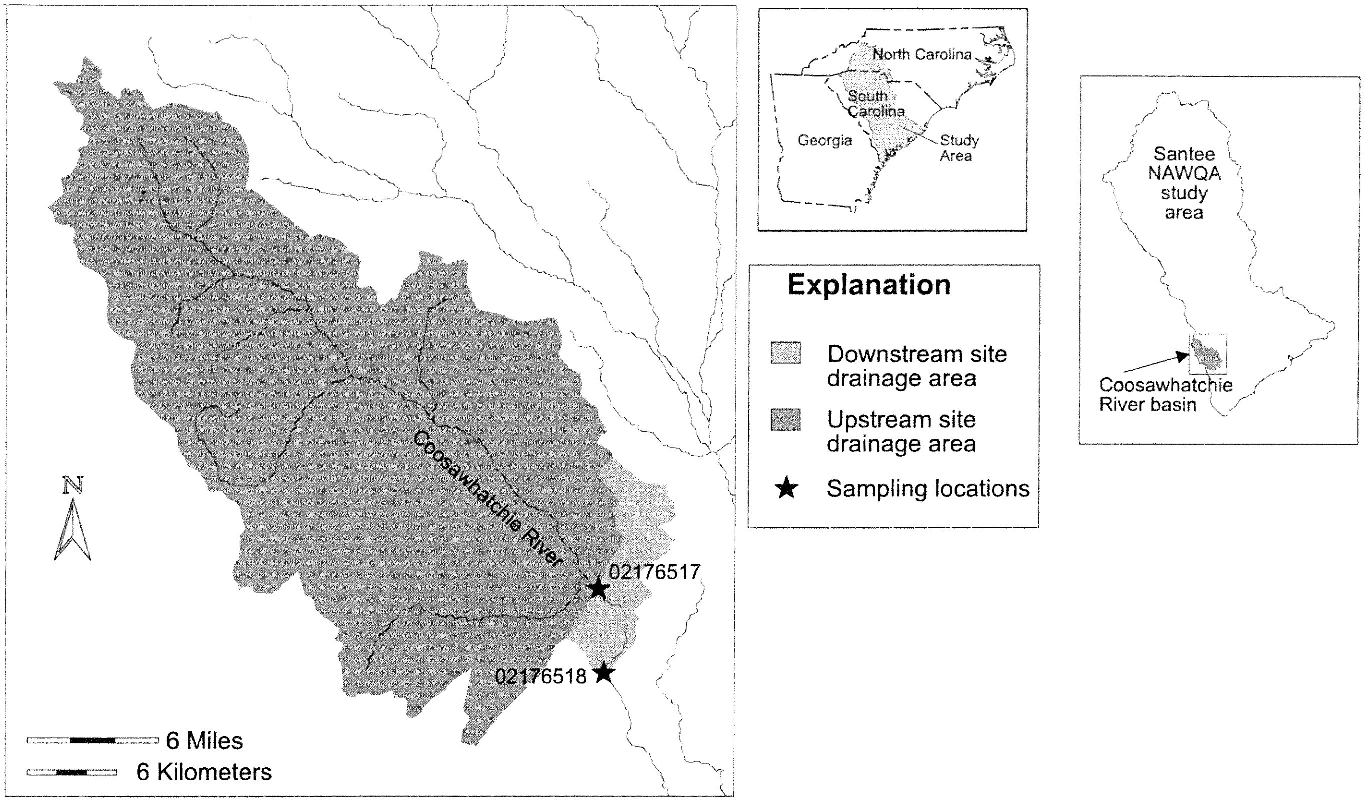

Figure 1.11—The extent of the Coosawhatchie River watershed and the Coosawhatchie Bottomland Ecosystem Study gauge locations at Early Branch, SC, (USGS Station 02176517) and Grays, SC (USGS Station 02176518).

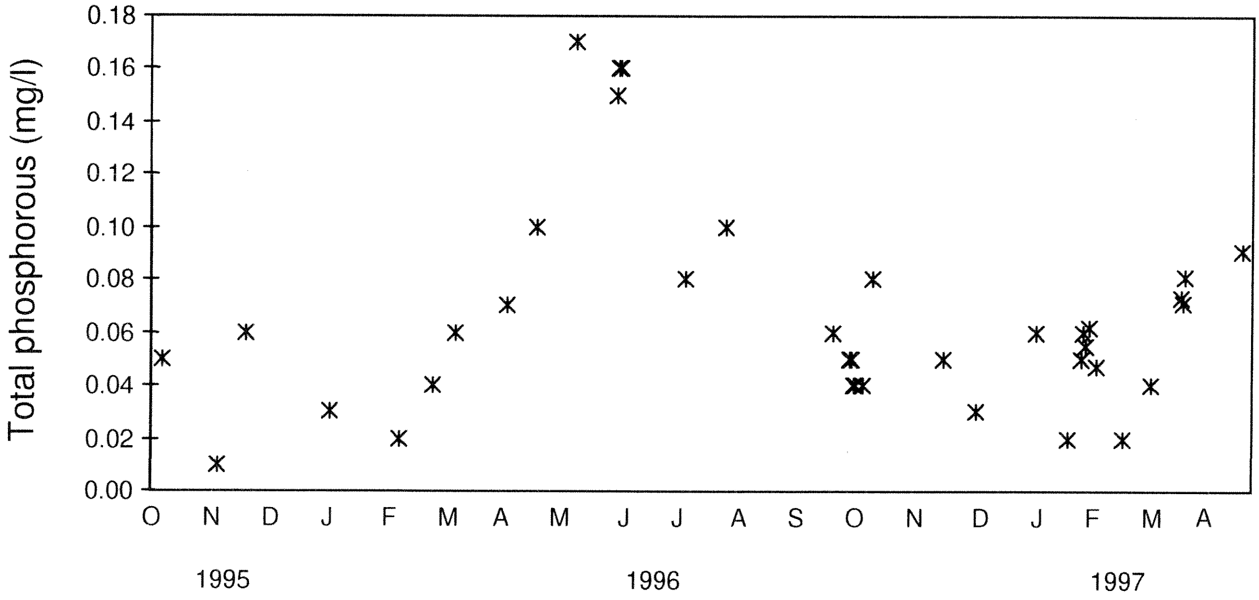

Figure 1.12—Seasonal patterns in total phosphorus concentrations in the Coosawhatchie River above the study site near Early Branch, SC, 1995–97.

Water-quality samples were analyzed and results compared between the Coosawhatchie River near Early Branch, SC (USGS Station 02176517), and a downstream site near Grays, SC (USGS Station 02176518) (fig. 1.11). Land use between these two sites is primarily forested wetlands. Samples were collected in the summer (low streamflows), winter (intermediate streamflows), and during storms (high streamflows). At low and intermediate streamflows, samples were collected daily at each of the two sites for 3 days. Storm-flow samples were collected daily on the rising limb of hydrographs and intermittently on the falling limb. Temperature, conductivity, dissolved oxygen, and acidity/alkalinity were measured in the field. Samples were collected and processed for analysis of nutrients, organic carbon, major ions, and suspended sediment. Stream stage was measured continuously at both sites. Streamflows during sampling ranged from 0.37 to 22.6 m^3 per second.

Some of the water-quality measurements were conducted in the field.

A comparison of the upstream and downstream sites indicated varying trends in water quality. Nutrient concentrations at both sites were highest during summer's low streamflows, and the downstream ammonia-nitrogen concentrations were higher than the upstream concentrations (fig. 1.13). Phosphorus concentrations were generally higher at the upstream site during intermediate and high streamflows and higher at the downstream site during low streamflows. Suspended organic carbon concentrations were higher downstream during low streamflows. Dissolved organic carbon concentrations were lowest at both sites during low streamflows. Dissolved oxygen saturation was lowest in the summer at both sites. As streamflow increased, iron, manganese, potassium, and magnesium concentrations decreased (data available at http://wwwsc.er.usgs.gov/nawqa/santhome.html).

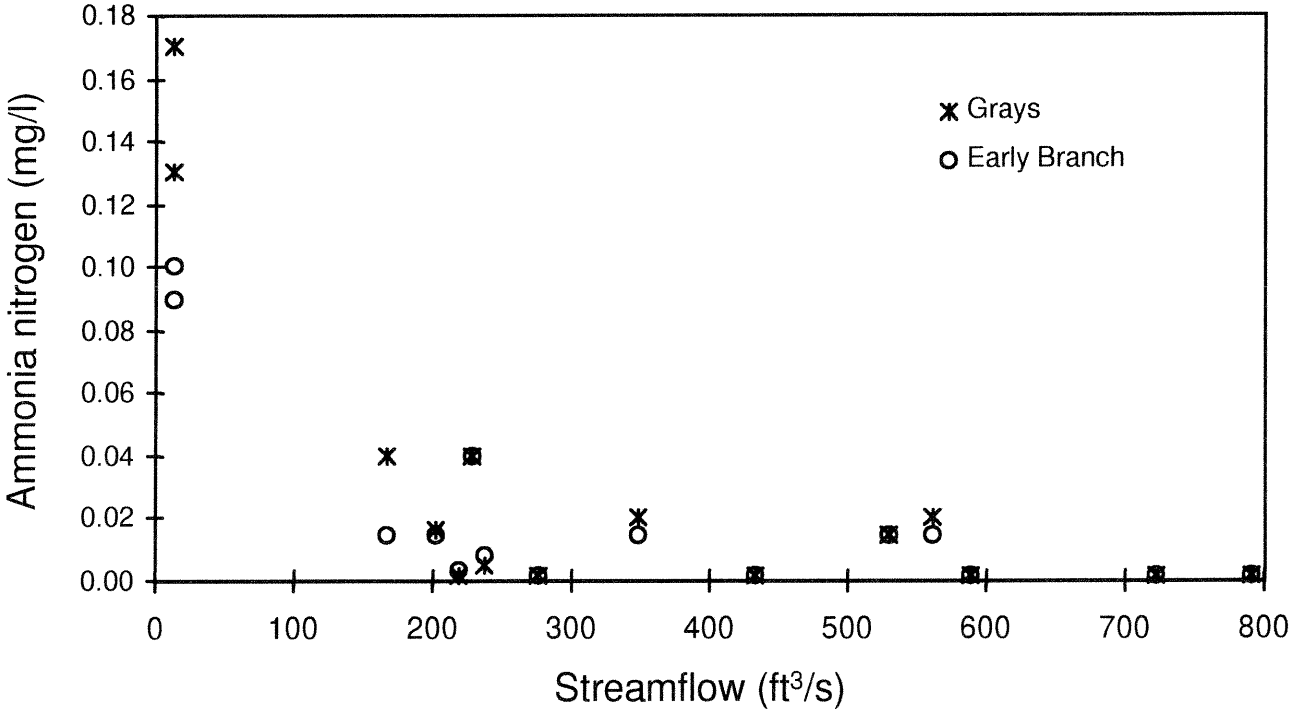

Figure 1.13—Ammonia nitrogen concentrations (individual data points) in the Coosawhatchie River above the study site near Early Branch, SC, and at Grays, SC, 1995–97 (multiply streamflow by 2.831 by 10^{-2} to obtain m^3 per second).

Section 2—Community Characterization

Vegetation and Soils

Marianne K. Burke, Sammy L. King, Mark H. Eisenbies, and David Gartner[1]

Characterization of bottomland hardwood vegetation in relatively undisturbed forests can provide critical information for developing effective wetland creation and restoration techniques and for assessing the impacts of management and development. Classification is a useful technique in characterizing vegetation because it summarizes complex data sets, assists in hypothesis generation about factors influencing community variation, and helps refine models of community structure. Hierarchical classification of communities is particularly useful for showing relationships among samples (Gauche 1982).

This study had three objectives: (1) to classify the bottomland hardwood vegetation, (2) to produce a vegetation map, and (3) to quantify the physical and chemical characteristics of soils in each of the vegetative communities. During the summer of 1995, 68 sampling plots (fig. 2.1) were established and basal area and density of overstory trees, shrubs, and saplings were measured. In addition species composition, total stem density, and percent coverage of all woody seedlings and herbs were measured within subplots. Elevation and soil physical and chemical parameters (texture of A and B horizons, depth to b layer, chroma, value, organic matter content, pH, and the entire suite of inductively coupled plasma emission spectrometer elements) were measured for each plot.

Standard cluster analysis was performed on the relative basal areas of woody plants. The cluster analysis (fig. 2.2) showed there were four major community types—water tupelo (*Nyssa aquatica* L.), swamp tupelo (*N. sylvatica* var. *biflora* [Walt.] Sarg.), laurel oak (*Quercus laurifolia* Michx.), and mixed oak (*Q.* spp.)—arrayed along an elevational gradient, and one minor community type—overcup oak (*Q. lyrata* Walt.). An analysis of the species compositions determined that clusters could be keyed based on the following hierarchical decision process:

1. Water tupelo when > 30 percent of the basal area is *Nyssa aquatica.*
2. Swamp tupelo when:
   a. more than 25 percent of the basal area is in *N. aquatica*, *N. sylvatica* var. *biflora*, and *Taxodium distichum* (L.) Rich. and the proportion of basal area in *N. aquatica*, *N. sylvatica* var. *biflora*, and *T. distichum* is greater that the proportion of basal area in *Q. laurifolia*; or
   b. more than 50 percent of the basal area is in *N. aquatica*, *N. sylvatica* var. *biflora*, *T. distichum*, *L. styraciflua*, and *Acer rubrum* L. with at least 9 percent of the basal area composed of *N. aquatica*, *N. sylvatica* var. *biflora*, and *T. distichum* and < 15 percent of the basal area is *Q. laurifolia.*
3. Overcup oak (*Q. lyrata* Walt.) when > 25 percent of the basal area is in *Q. lyrata.*
4. Laurel oak when a greater proportion of basal area is in *Q. laurifolia* than in *N. aquatica*, *N. sylvatica* var. *biflora*, and *T. distichum* and
   a. more than 20 percent of basal area is in *Q. laurifolia*; or
   b. the sum of *Q. laurifolia*, *L. styraciflua*, and *A. rubrum* is > 40 percent of basal area and at least 15 percent of the basal area is in *Q. laurifolia.*
5. Mixed oak when > 30 percent of the basal area is in *Q. phellos* L., *Q. nigra* L., and *Q. falcata* var. *pagodifolia* Ell. and
   a. *Magnolia grandiflora* L., or
   b. *Liriodendron tulipifera* L.
6. Loblolly (*Pinus taeda* L.) when > 50 percent of the basal area is *P. taeda.*

Photo by Marianne Burke

Water tupelo community.

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Using this information and vegetation surveys of numerous other points on the site, a vegetation map was produced (fig. 2.3) showing that flood-tolerant oaks with sweetgum and red maple were characteristic of the slightly higher elevations of the floodplain, and swamp tupelo, water tupelo, and sweetgum were characteristic of the shallow-to-deep swamps.

Soil analyses showed a difference among the soils of the main vegetation types. Soils in the water tupelo- and swamp tupelo-vegetated plots contained more clay in both soil horizons than the oak-dominated plots, which were sandier in both horizons (fig. 2.4). Extractable calcium, potassium, magnesium, cation exchange capacity, aluminum, organic matter, and pH were greatest in the water tupelo-vegetated sites and decreased up the flooding gradient. Bulk density, porosity, and depth to the B layer increased up the flooding gradient (table 2.1).

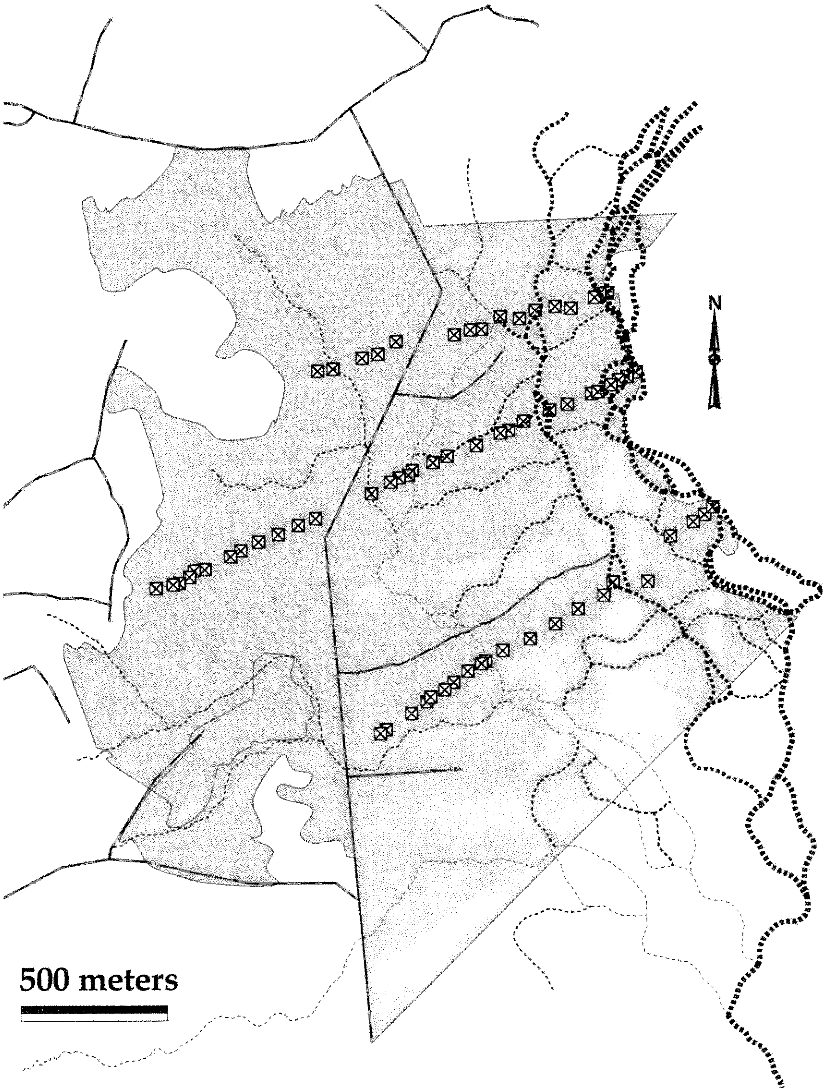

Figure 2.1—Ordination plot locations along transect 1 (southernmost), and 2 and 3 (northernmost).

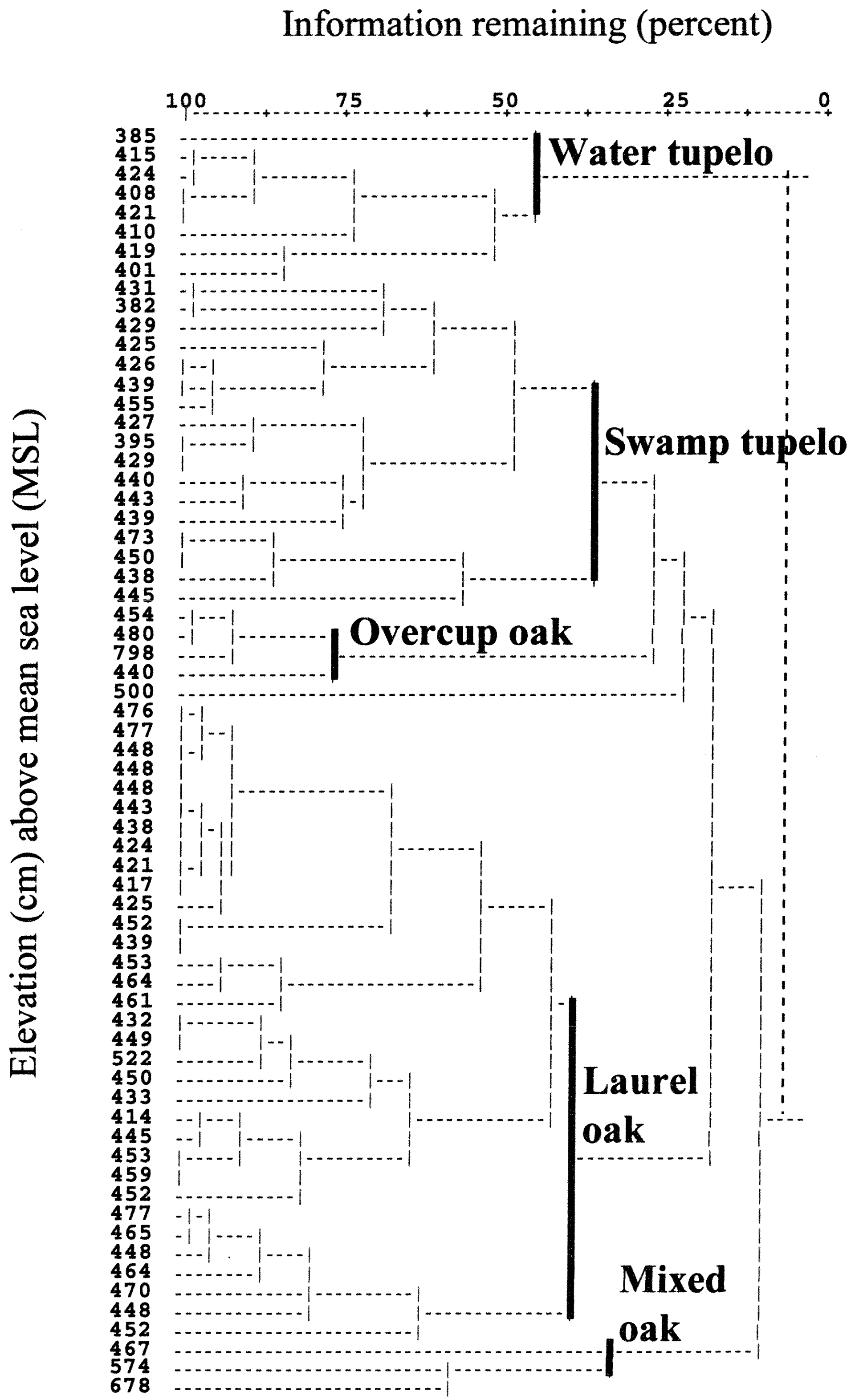

Figure 2.2—Results of standard cluster analysis performed on the relative basal areas of woody plants.

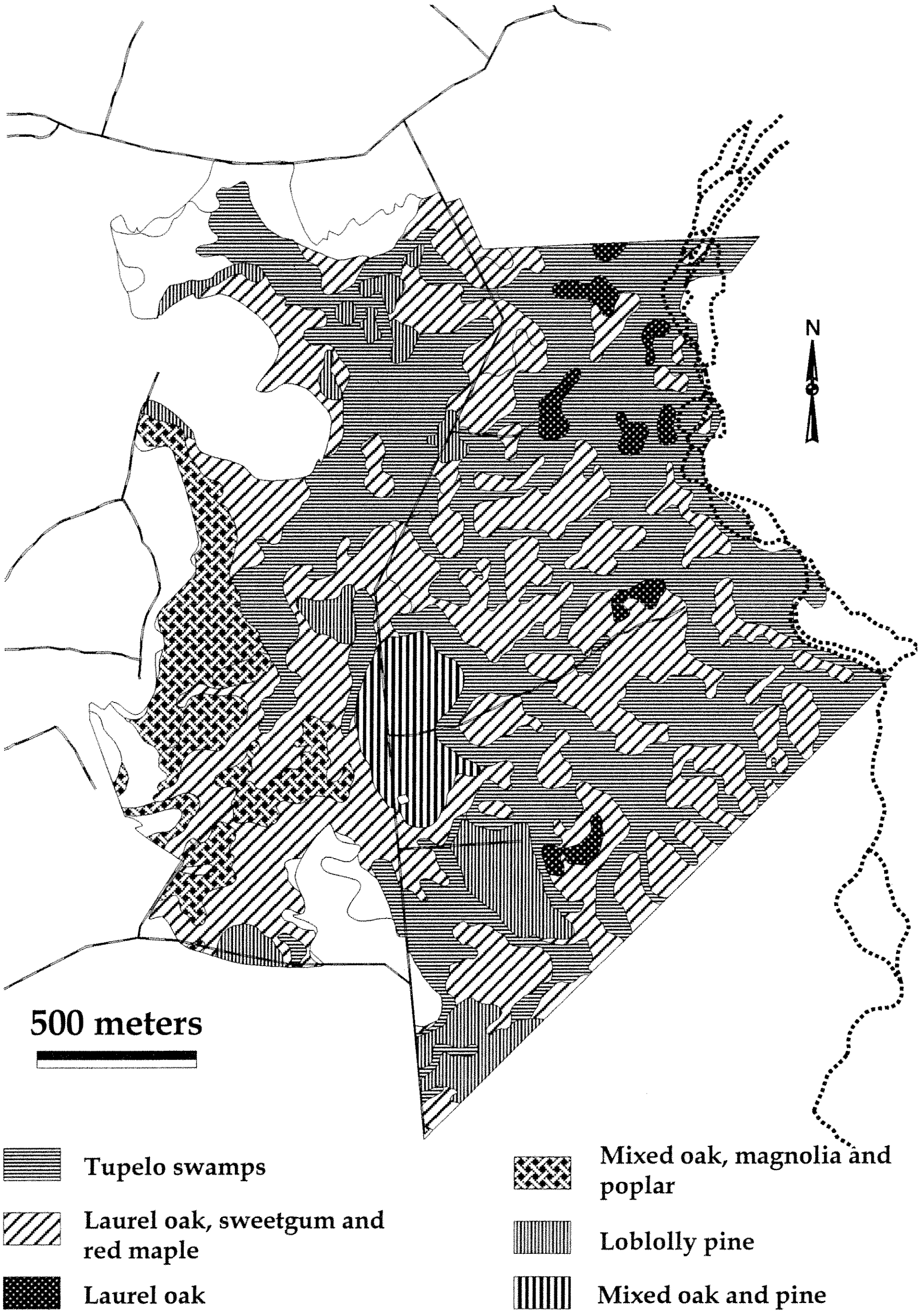

Figure 2.3—Vegetation types on the Coosawhatchie Bottomland Ecosystem Study site.

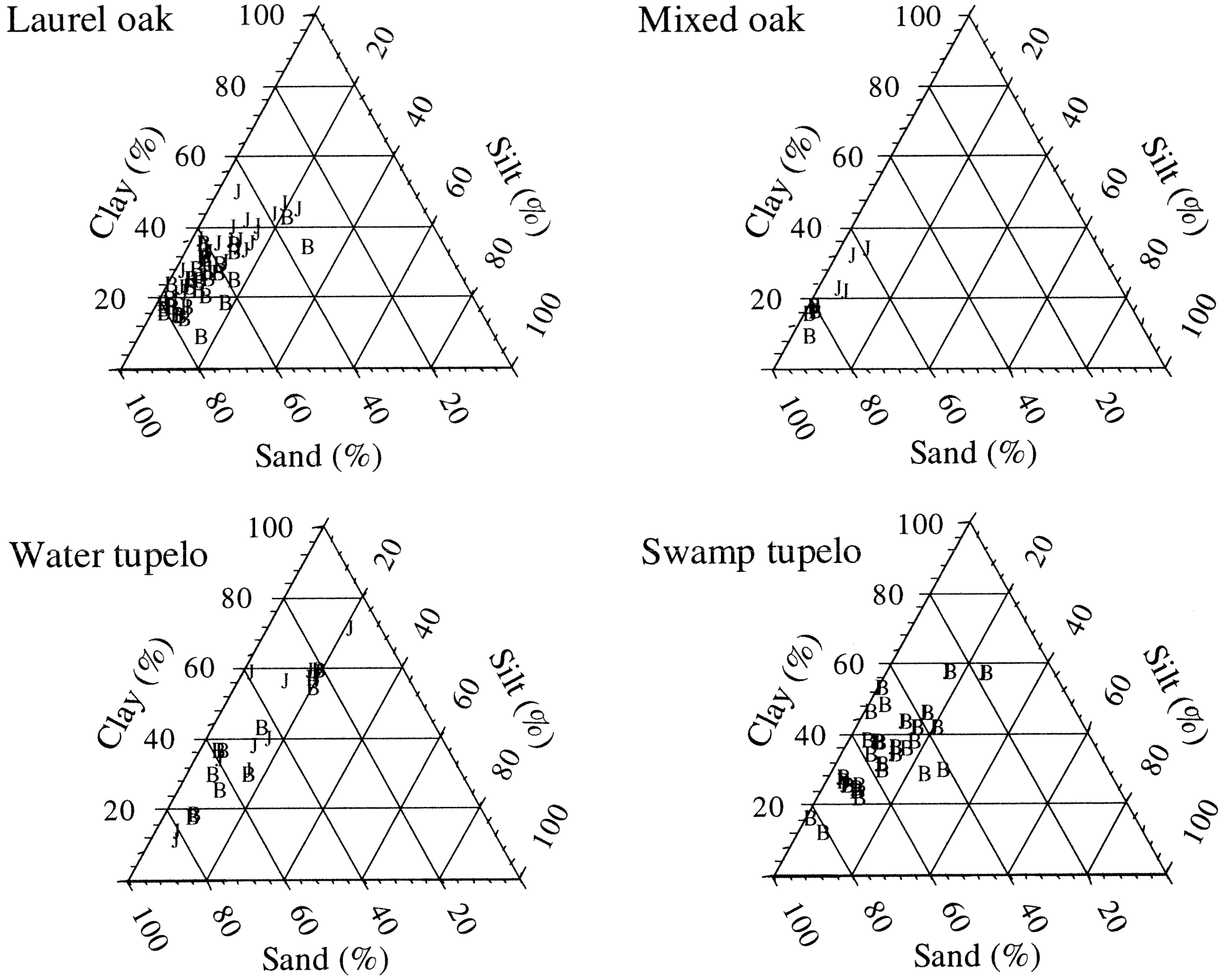

Figure 2.4—Texture triangles showing percent clay, silt, and sand in the A (uppercase B) and B (uppercase J) horizons for the four main plant communites.

Table 2.1—Soil characteristics[a] for the four main community types[b]

Soil characteristics	Water tupelo	Swamp tupelo	Laurel oak	Mixed oak
Ca_A (µg/g)	829.39 (175.18)a	460.17 (75.15)ab	482.52 (53.13)ab	195.37 (118.12)b
Ca_B (µg/g)	971.45 (168.81)a	533.20 (87.25)ab	725.55 (71.32)ab	259.58 (152.63)b
K_A (µg/g)	44.73 (6.44)	38.17 (4.79)	32.99 (2.43)	25.77 (2.62)
K_B (µg/g)	34.96 (6.55)a	22.58 (1.30)b	21.01 (.53)b	20.50 (.50)b
Mg_A (µg/g)	165.52 (28.45)a	105.61 (11.46)ab	95.25 (8.54)b	49.42 (23.64)b
Mg_B (µg/g)	162.13 (26.44)a	102.59 (10.06)ab	101.77 (8.80)b	78.75 (27.41)b
CEC_A (cmol/kg)	1039.64 (208.19)a	603.95 (89.44)ab	610.75 (63.08)b	270.56 (143.26)b
CEC_B (cmol/kg)	1168.54 (198.57)a	658.37 (94.21)ab	848.32 (77.36)ab	358.82 (175.68)b
P_A (µg/g)	52.36 (9.93)	48.03 (6.57)	32.16 (3.17)	41.92 (10.69)
P_B (µg/g)	39.44 (14.65)a	25.65 (6.12)a	9.57 (1.79)a	100.72 (64.70)b
Na_A (µg/g)	28.88 (3.89)	26.40 (1.39)	22.80 (1.47)	15.07 (7.23)
Na_B (µg/g)	35.45 (3.97)	40.10 (9.47)	47.28 (5.26)	27.77 (16.20)
Al_A (µg/g)	1478.86 (273.10)a	1230.59 (196.07)ab	797.78 (75.40)b	653.07 (74.74)ab
Al_B (µg/g)	1338.37 (327.64)a	1011.09 (209.35)a	411.93 (46.38)b	765.73 (322.92)ab
Bulk $density_A$ (g/cm^3)	.79 (.07)A	.95 (.06)AB	1.08 (.04)B	1.17 (.09)B
Bulk $density_B$ (g/cm^3)	.97 (.11)A	1.20 (.04)A	1.42 (.03)B	1.50 (.03)B
$Porosity_A$ (cm^3/cm^3)	.70 (.03)A	.64 (.02)AB	.59 (.01)B	.56 (.03)B
$Porosity_B$ (cm^3/cm^3)	.63 (.04)A	.55 (.02)A	.46 (.01)B	.43 (.01)B
SOM_A (percent)	8.12 (1.20)	7.84 (.83)	5.66 (.32)	4.86 (.31)
SOM_B (percent)	6.04 (1.29)a	4.14 (.70)ab	2.03 (.22)b	1.02 (.23)b
Elevation (MASL)	4.19 (.05)b	4.32 (.06)b	4.51 (.04)b	5.51 (1.25)a
Cm to B horizon	25.6 (3.5)A	29.2 (4.6)A	30.6 (3.1)A	55.7 (7.0)B
Chroma	.30 (.12)b	.67 (.23)b	.78 (.25)b	1.56 (.68)a
Value	2.18 (.10)	2.33 (.12)	2.19 (.07)	3.53 (.90)
pH_A	4.70a	4.50ab	4.59ab	4.35b
pH_B	4.76	4.61	4.68	4.78

Ca = Calcium, K = potassium, Mg = magnesium, CEC = cation exchange capacity, cmol = centimoles; P = phosphorus, Na = sodium, Al = aluminum, SOM = soil organic matter, MASL = meters above sea level.

[a] Results of multiple range tests (Sheffé's) on soil parameters. Nutrients are expressed in extractable (ammonium acetate) values. Variable subscripts indicate soil horizon. Different uppercase letters indicate significant differences ($p = 0.05$) within rows and different lowercase letters indicate significant differences ($p = 0.1$) within rows. All data were checked for homogeneity of variance before analysis, and variables with heteroscedastic variances were transformed before analysis.

[b] Standard error of the mean is in parentheses.

Vegetation Dynamics

Sammy L. King, Marianne K. Burke, Terry J. Antrobus, and Sarah Billups[1]

A disturbance can be defined as "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment" (Pickett and White 1985). Vegetation dynamics are a function of the temporal and spatial patterns of the disturbance regime. Natural disturbance regimes support the highest biological diversity; therefore, forest management practices that most closely mimic natural disturbances are expected to sustain the highest biological diversity within a given area (Denslow 1980). In southern forested wetlands, flooding is the dominant disturbance factor, thus plant species are usually distributed along a growing-season flood gradient (Franz and Bazzaz 1977).

Flooding is not, however, the sole factor affecting vegetation dynamics within these systems. Light availability can constrain regeneration of wetland plants (Brinson 1990). In general, plant species can be divided into light generalists, low-light specialists, and high-light specialists based upon their habitat requirements (Menges and Waller 1983). As a result, the frequency, size, and distribution of canopy disturbances can alter forest structure and composition because they affect the amount and quality of light available to plants (Streng and others 1989). Understanding the relationship between light availability and forest structure and composition is important to restoring and managing wetland ecosystems because forest structure and composition are correlated with wetland functions such as wildlife habitat and water quality (Dickson and Noble 1978). To date, no studies have been conducted on canopy disturbance patterns and their influence on plant regeneration in southern bottomland hardwood ecosystems.

Photo by Marianne Burke

Canopy gaps can influence ground vegetation through changes in light regime.

This study had two objectives: (1) to characterize and compare annual canopy disturbance rates in bottomland hardwood ecosystems in the Coosawhatchie River and Cache River floodplain forests, and (2) to determine the influence of canopy gaps and associated changes in light level on ground vegetation at the Coosawhatchie Site.

To determine annual canopy disturbance rates, we conducted complete censuses of a 119-ha section of the Coosawhatchie study area during May 1996 and May 1997. These results were compared with censuses of a 103-ha section of the Cache River study site completed during June 1995 and October 1996. All canopy gaps formed during the previous year were identified based upon the presence of leaves, the amount of soil on the roots, and other diagnostic characteristics.

A pole was placed in the center of each restricted gap, i.e., the actual area of the opening in the canopy projected onto the ground surface (Runckle 1981). The d.b.h. and species of trees forming the boundary of the expanded gap were determined, i.e., the area defined by the boles of the trees whose canopy defines the actual canopy opening (Runckle 1981). To determine the area and configuration of the restricted and expanded gaps, the distance and azimuth from the plot center pole to the edge of the restricted gap ($\geq$ 6 azimuths [0, 60, 120, 180, 240, 300]) and to the boundary trees were recorded and the gap area was calculated.

At the Coosawhatchie site, ground vegetation was inventoried in two habitats: nongap habitat in permanent ground vegetation plots described in Burke and others (2000a) and in gap habitat in plots established at gap centers during the summer of 1997 (fig. 2.5). In each plot the density and percent cover of each species of tree seedling, grass, and forb were determined, and species richness and the Shannon-Weiner diversity index were calculated. In addition, elevation was determined and light regimes, expressed as percent of incident light, were characterized. Relative density and cover were analyzed for each individual species and for groups of tree seedlings, grasses, and forbs. The effect of light and elevation served as covariates, while

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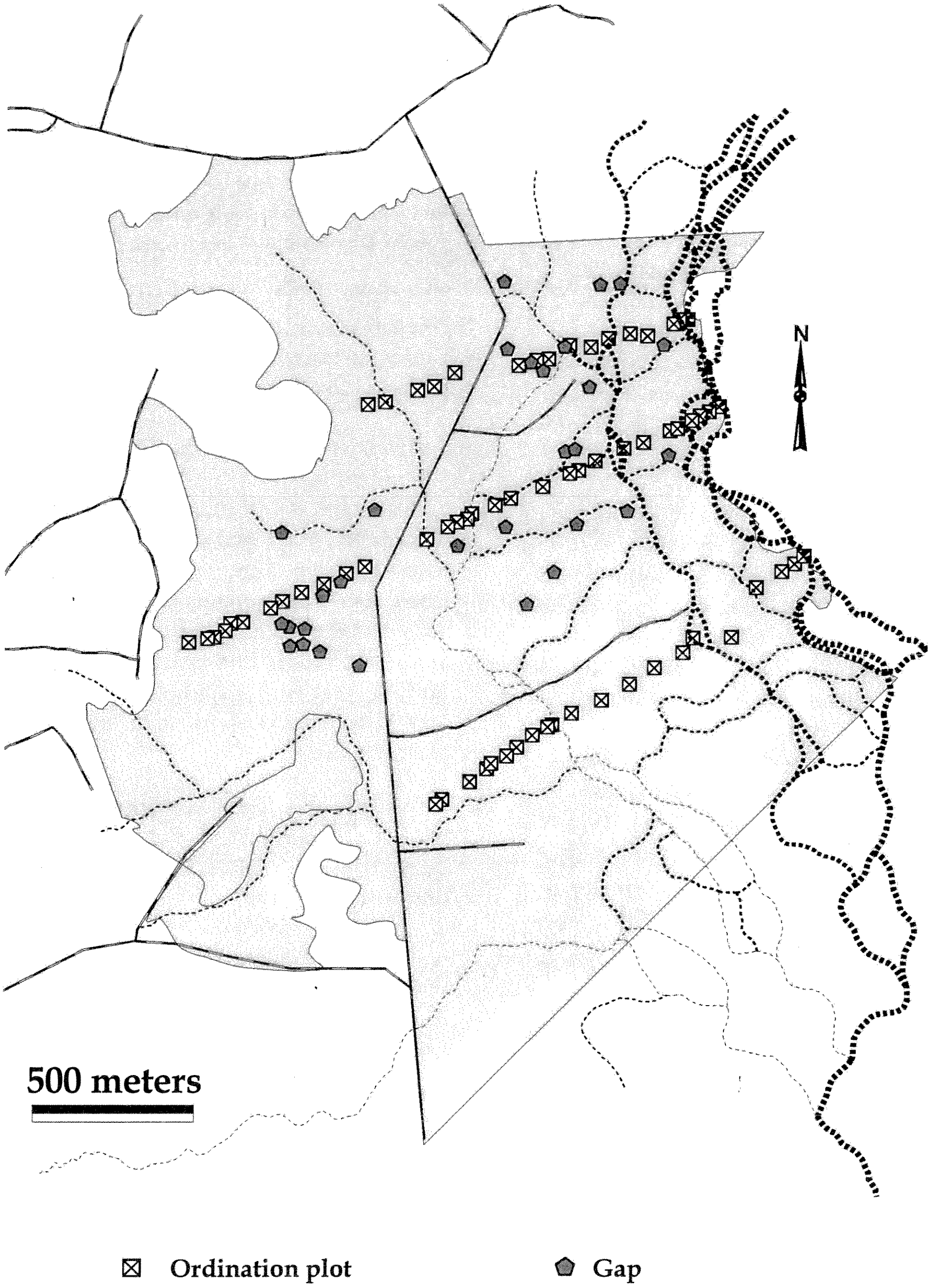

Figure 2.5—Locations of ordination plots and canopy gaps from the first census of the Coosawhatchie Bottomland Ecosystem Study site.

species richness, Shannon-Weiner diversity, and relative density and cover of trees, forbs, and grasses served as response variables.

A total of eight newly formed gaps were located on the Coosawhatchie site in May 1996. The mean gap size was 216.1 m^2 with a median gap size of 187.8 m^2; 0.02 percent of the total study site area was located within newly formed canopy gaps. The results from the Coosawhatchie site differed markedly from previous studies and from the Cache River study. At the Cache site, 47 newly formed canopy gaps were located in 1995 and 43 in 1996, and the mean size of the gaps was 366.4 m^2 and 234.3 m^2, respectively. The total area within newly formed gaps at the Cache site encompassed 1.3 percent of the study area. Previous studies estimated the gap formation rate at 0.5 to 1.3 percent of the area (Quinghong and Hytteborn 1991, Runckle 1985, Van der Meer and Bongers 1996).

Although these canopy gap dynamics results are preliminary, the data suggest that the Cache River site approximates the standard for percentage of forest canopy consisting of newly formed canopy gaps (1 to 3 percent: Pickett and White 1985). The much lower rate of disturbance at the Coosawhatchie site may be related to stand structure, age, soils, flooding, or a temporal anomaly. The Coosawhatchie site was logged as recently as 1950, and the site is affected by hurricanes more often than the Cache River site—the eye of Hurricane Gracie passed within 20 miles of the site in 1961.

The analysis of ground vegetation indicated an effect of gaps: tree seedlings were relatively more important in the nongap habitat, and grass was more important in the gap habitat ($p < 0.05$); but there was an elevation x habitat interaction for relative cover of tree seedlings ($p = 0.08$) and relative cover of grass ($p = 0.04$). There was also an elevation x habitat interaction for species richness (0.06), with more species occurring higher in the elevational gradient ($p = 0.02$) and in the nongap habitat ($p = 0.05$). Surprisingly, the light environment did not differ significantly between habitats; hence, light did not significantly affect any response variable. These findings suggest that the gaps were small enough to prevent significant changes in light regime, and that something besides elevation or light level is influencing the ground vegetation composition on the Coosawhatchie Bottomland Ecosystem Study site. Although the rate of canopy disturbance is low at the Coosawhatchie site, and gap formation may only subtly change the light regime at the forest floor, ground vegetation appears to respond to gap formation with lower relative cover of tree seedlings, greater relative cover of grasses, and lower species richness.

Bird Community Composition

T.J. Antrobus; M.P. Guilfoyle; W.C. Barrow, Jr.;
P.B. Hamel; and J.S. Wakeley[1]

Neotropical migrants are birds that breed in North America and winter primarily in Central and South America. Long-term population studies of birds in the Eastern United States indicated declines of some forest-dwelling birds, many of which winter in the Neotropics (Peterjohn and others 1995). These declines were attributed to loss of wintering and breeding habitat due to deforestation and fragmentation, respectively. Many species of Nearctic migrants—birds that breed in the northern regions of North America and winter in the Southern United States—are also experiencing population declines. Because large areas of undisturbed, older, bottomland hardwood forests often contain large numbers of habitat specialists, including forest-interior neotropical migrants and wintering Nearctic migrants, these forests may be critical in maintaining avian diversity.

This study had two primary objectives: (1) to create a baseline data set that can be used as a standard against which other bottomland hardwood forests can be compared, and (2) to establish long-term monitoring stations during both breeding and wintering seasons to discern population trends of avian species using bottomland hardwood forests.

The same methods were used on the Coosawhatchie, Cache, and Iatt Creek study sites. A grid system was established at each site with intersections at 250-m intervals (fig. 2.6), and bird surveys were conducted at each grid intersection. The number of sampling points varied among sites because site sizes differed: Coosawhatchie River (60), Cache River (47), and Iatt Creek (44). The intent was to saturate the sites with grid points. Surveys began in 1995 and continued through the spring of 1998; data for winter 1995–96 and spring 1996 are presented here. Breeding-bird counts were conducted during May and June, and winter surveys were conducted during December and January.

Overall, species richness was similar across sites (table 2.2). The Cache and Iatt sites had significantly higher average species richness for Nearctic migrants than did the Coosawhatchie River site, and the Coosawhatchie River had the highest number of species detected during the breeding season, followed by Iatt Creek and the Cache River site. The Cache and Coosawhatchie Rivers had significantly higher average species richness for breeding neotropical migrants than Iatt Creek. Initial avian/vegetation comparisons suggest that a diversity of habitats within a bottomland hardwood forest is important for increasing avian species richness. In addition, sightings of both the prothonotary and Swainson's warblers, priority species for conservation, occurred on the Coosawhatchie and Cache River sites. This database will assist in the design of research examining the effects of forest structure manipulations on bird communities, exploring patterns of vegetation-bird associations, and monitoring bottomland hardwood bird communities.

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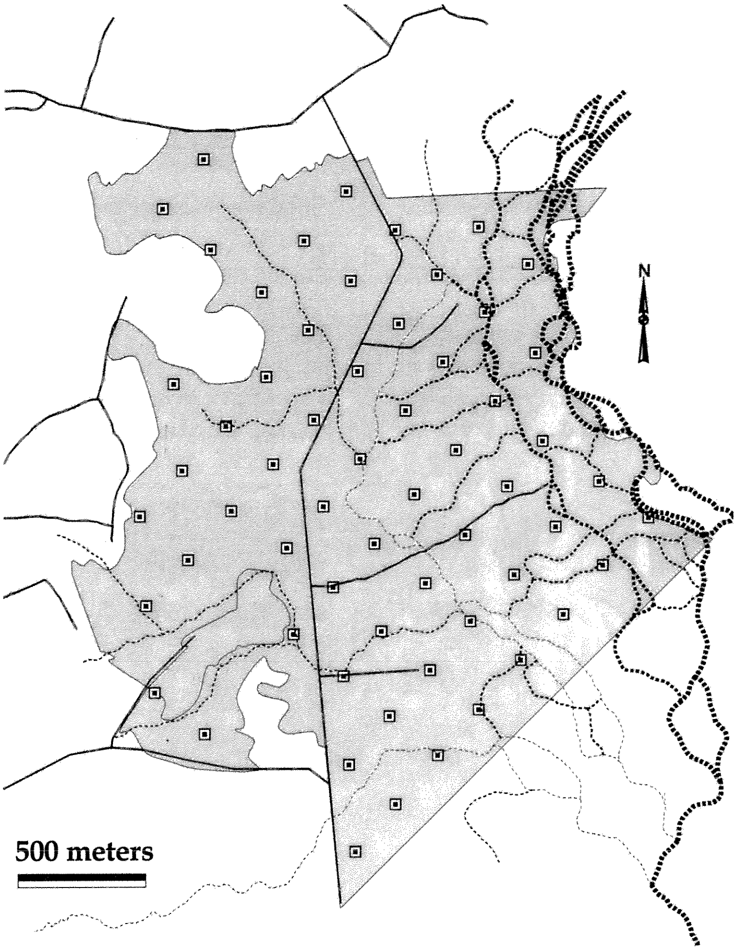

Figure 2.6—The 250-m-interval grid system established on the Coosawhatchie Bottomland Ecosystem Study site.

Table 2.2—Breeding and wintering birds detected on the Coosawhatchie Bottomland Ecosystem Study and two other Southern Forested Wetlands Initiative sites in 1996

Bird species	Coosawhatchie River, SC[a]	Cache River, AR[b]	Iatt Creek, LA[c]	Total observations
Wintering				
Nearctic, migrant	13[d] (452)	16 (111)	15 (307)	19 (870)
Resident	24 (831)	20 (1,413)	20 (757)	28 (3,001)
Total	37 (1,283)	36 (1,524)	35 (1,064)	47 (3,871)
Breeding				
Neotropical, migrant	19 (478)	16 (549)	19 (301)	23 (1,328)
Resident	21 (415)	19 (442)	19 (337)	26 (1,194)
Total	40 (893)	35 (991)	38 (638)	49 (2,522)
Total species	60 (2,176)	54 (2,515)	57 (1,702)	75 (6,393)

[a] 60 sampling points.
[b] 47 sampling points.
[c] 44 sampling points.
[d] Numbers represent total detections of species; numbers in parentheses represent total detections of individuals.

Response of Bird Communities to Natural Disturbance

Michael P. Guilfoyle; Wylie C. Barrow, Jr.; Paul B. Hamel;
James S. Wakeley; Sammy L. King; and Terry J. Antrobus[1]

In addition to providing numerous important ecological functions, bottomland hardwoods provide important habitat for many wildlife species (Harris 1989), particularly many forest interior birds (Hamel and others 1996). National monitoring efforts showed nationwide declines for many forest bird species, including forest-dependent neotropical migrants (Johnston and Hagan 1992). However, our understanding of how these birds respond to natural disturbance is limited.

In forested habitats, canopy gaps created by dying and down trees are conspicuous features that contribute to the natural heterogeneity of forested systems. Microhabitats found in canopy gaps may support greater insect abundance due to increased foliage density and temperature gradients created by higher light intensity (Blake and Hoppes 1986, Smith and Dallman 1996). Some studies have shown that canopy gaps support a higher diversity of bird species than nongap areas (Blake and Hoppes 1986, Levy 1988, Martin and Karr 1986, Schemske and Brokaw 1981). The combination of increased insect abundance (food resources), greater foliage density (increased foraging opportunities, nesting sites, cover from predators), and more extreme temperature regimes (may reduce thermoregulatory costs) (Smith and Dallman 1996) suggests that canopy gaps may be important features affecting avian community abundance, composition, and distribution in forested systems (Blake and Hoppes 1986, Levy 1988, Martin and Karr 1986, Schemske and Brokaw 1981, Smith and Dallman 1996). Yet, conversely, many forest species are sensitive to disturbance (Johnston and Hagan 1992, Martin and Finch 1995). Determining how birds respond to natural disturbance enables production of models of avian response to increased disturbance patterns, such as those created by human activity. These models may help provide management guidelines for timber production and restoration in bottomland hardwood systems.

This study focused on four basic questions about relationships between avian species and canopy gaps in bottomland hardwoods: (1) How does the distribution of canopy gaps affect the abundance, composition, and distribution of breeding and wintering birds on the three study areas for the Southern Forested Wetland Initiative? (2) How does the potential value of canopy gaps as resource patches differ among insectivorous birds that use different foraging strategies (foliage gleaners, aerial flycatchers, and trunk foragers)? (3) To what extent are differences in gap suitability for bird use explained by variations in gap size, age, or structure? and (4) How do avian responses to canopy gaps change seasonally?


Photo by Mark Eisenbies

Turkey nest in the mixed-oak community.

A sampling grid was established at each of the three Southern Forested Wetlands Initiative study sites, with point-count surveys done at 250-m intervals (Antrobus and others 2000). Repeated count surveys of bird communities were conducted in the breeding and wintering seasons during 1996 through 1998. At each grid point, other pertinent habitat information, e.g., tree species diversity, density and basal area of trees, and canopy cover, was also collected in 0.04-ha circular plots (James and Shugart 1970). Eventually, avian abundance and species diversity metrics will be correlated with the number and distribution of canopy gaps on all three sites.

Figure 2.7 represents a model of the research strategy being used to determine avian community/canopy gap relationships. Community level analyses (fig. 2.7A) are being performed on all three study areas and include correlation analyses of avian community metrics gathered from point-count surveys of canopy gap distribution. Population- (fig. 2.7B) and individual- (fig. 2.7C) level analyses are being performed only on the Cache River study area. The research strategy illustrated in figure 2.7 incorporates issues of scale and allows hypotheses to be tested at the three scales discussed. For example, if a positive correlation with canopy gaps is observed for a focal species based on point-count

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data, one can test the hypothesis that activity area distributions will be correlated with canopy gap distributions at the population level. Furthermore, one can hypothesize that if activity areas are distributed with canopy gaps, individual birds will spend proportionately more time in canopy gaps and will achieve a higher foraging success rate in canopy gap versus nongap areas. Such a research design can test the hypothesis that canopy gaps provide sources of prey refuges important for some bird species, and thus are important in predicting how these species are distributed throughout bottomland hardwood systems.

Community-wide relationships may show positive or negative correlations of avian community metrics with canopy gaps, providing insights into how communities and species respond to natural disturbance. However, positive or negative associations with canopy gaps do not show how birds use gaps or whether gaps are used at all. Using focal species, determining how these species are distributed, and quantifying use of gap and nongap areas can attain a more comprehensive view of avian community/canopy gap relationships. Preliminary analyses indicate that species utilizing a foliage-gleaning foraging strategy tend to use gaps more than nongap areas. Other focal species tend to avoid gap areas and may be sensitive to disturbance. The research design directly addresses issues of scale (*sensu* Wiens 1989) and may provide insights into why specific distribution patterns are observed.

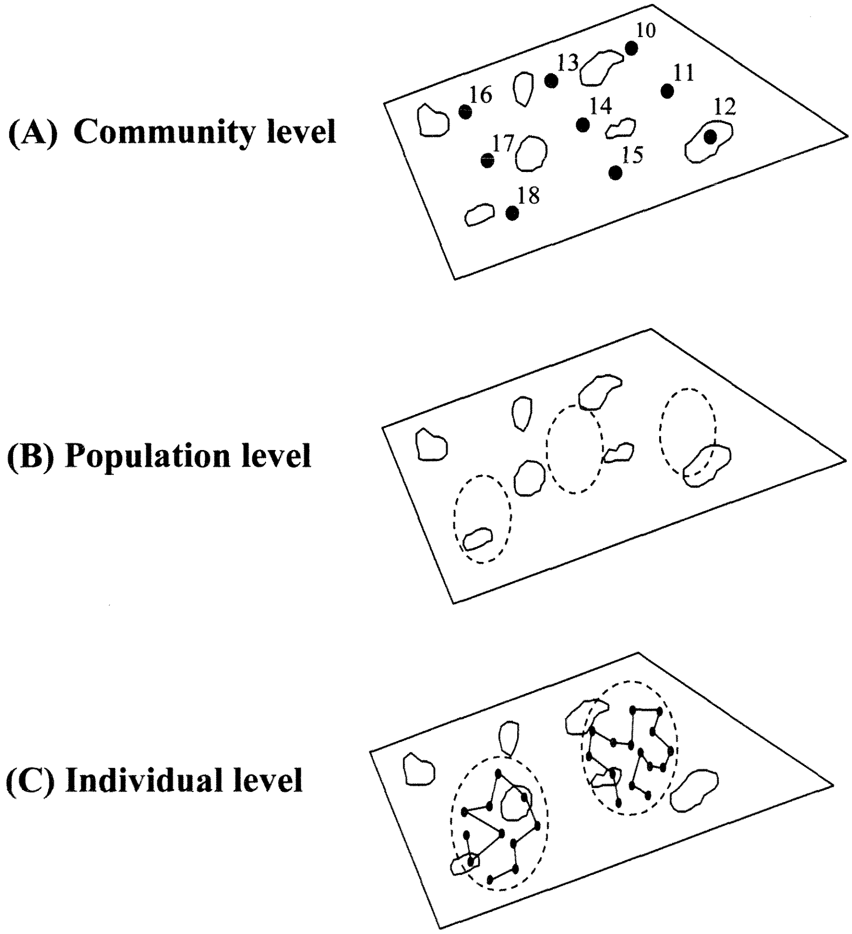

Figure 2.7—Model of the research strategy being used to determine avian community/canopy gap relationships in southern bottomland hardwood forests. In the (A) community level, a hypothetical distribution of gaps (irregular shapes), and site grid points (numbered). In the (B) population level, the hypothetical distribution of gaps is compared with the potential distribution of avian-use areas (dashed ovals). In the (C) individual level, the hypothetical movements of focal-avian species (connected solid lines) within activity-use areas distributed among canopy gaps are compared.

Section 3—Ecosystem Processes

Aboveground and Belowground Net Primary Production

Marianne K. Burke, Hal O. Liechty, and Mark H. Eisenbies[1]

The relationship among net primary productivity (NPP), hydroperiod, and fertility in forested wetlands is poorly understood (Burke and others 1999), particularly with respect to belowground NPP (Megonigal and others 1997). Although some researchers have studied aboveground and belowground primary production in depressional, forested wetland systems, e.g., Day and Megonigal (1993), there are no published studies of aboveground and belowground NPP in riverine systems in the Southeastern United States.

During the summer of 1995, a baseline study of NPP was initiated on the Coosawhatchie site. Sixteen of the 68 permanent vegetation plots (Burke and others 2000a) were randomly selected as representatives of each of the main vegetation types: water tupelo (*Nyssa aquatica* L.), swamp tupelo (*N. sylvatica* var. *biflora* [Walt.] Sarg.), laurel oak (*Quercus laurifolia* Michx.), and mixed oak (*Q.* spp.) (fig. 3.1). Each plot was expanded to 0.1 ha (15 by 66.6 m), and five litter traps were installed in each plot. During the winter of 1995–96, diameter and height were measured for all woody stems over 5 cm in d.b.h. Remeasurements of the d.b.h. during the following three winters and species-specific volumetric tables (Clark and others 1985, 1986; Clark and Taras 1976; McNab and others 1983; Phillips 1981; Schlaegel 1981, 1984a, 1984b; Taras and Clark 1974) were used in estimating stemwood production. Foliage, seed, and miscellaneous litterfall components were estimated between April 1996 and April 1999 from litter trap contents. Results up to April 1997 are presented here.

Stem basal area, tree height, tree diameter, and tree density declined up the flooding gradient (table 3.1). Total aboveground production for 1996–97 did not differ significantly among communities ($p > 0.1$) although stemwood production in the laurel oak community was greater than in the water tupelo community (fig. 3.2). Seed production was greater in the mixed oak than in both water tupelo and laurel oak communities ($p = 0.05$), but foliage and miscellaneous litterfall production were similar ($p > 0.10$).

Biomass, production, mortality, and turnover of fine roots (< 3 mm in diameter) were estimated along 200-m-long transects during 1996–97 for two of the communities: swamp tupelo and laurel oak. Sequential coring showed that root biomass was greater ($p = 0.05$) in the laurel oak community (5.7 Mg per hectare) than in the swamp tupelo community (2.4 Mg per hectare). There was no significant difference in necromass between the communities (2.4 and 1.3 Mg per hectare). Fine root production, estimated as the sum of significant ($p = 0.05$) increments in biomass, was 2.3 Mg per hectare per year for the laurel oak and 0.3 Mg per hectare per year for the swamp tupelo communities. Fine root mortality, estimated as the sum of significant increments in necromass, was 1.3 Mg per hectare per year for the laurel oak and 2.8 Mg per hectare per year for the swamp tupelo communities. Fine root turnover, calculated as production/biomass, was greater in the laurel oak community (26 percent per year) than in the swamp tupelo community (7 percent per year).

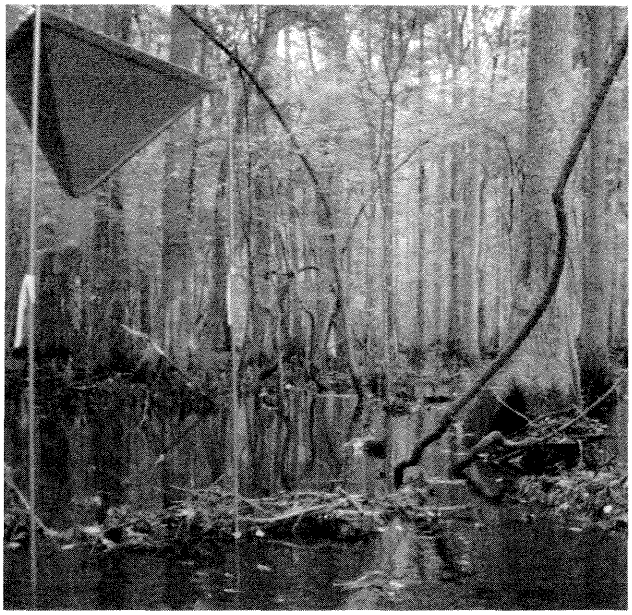

Photo by Marianne Burke

Litter traps were elevated above flood level.

Aboveground biomass partitioning was equal between stemwood and litterfall for all but the laurel oak community, where more was partitioned to the stemwood. This observation can be interpreted as greatest growth efficiency in the laurel oak community. More biomass was partitioned to root production in the laurel oak than in the swamp tupelo community (fig. 3.3), suggesting that either the tree species in the swamp tupelo community partitioned more biomass to aboveground production, or that the wetter sediments stimulated shoot growth relative to root growth in that community.

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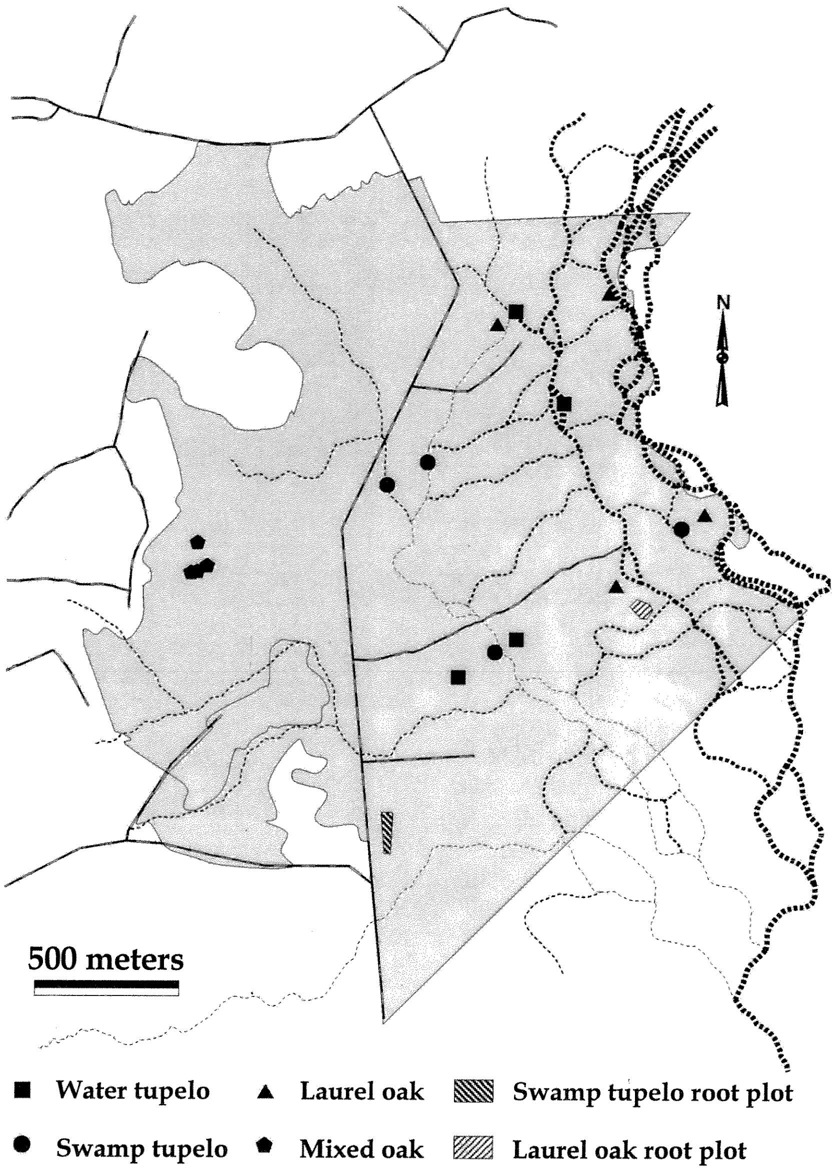

Figure 3.1—Locations of 16 aboveground and 2 belowground productivity plots on the Coosawhatchie Bottomland Ecosystem Study site.

Table 3.1—Statistics, shown as mean (standard error[a]), for woody plants (> 5 cm diameter) at the Coosawhatchie Bottomland Ecosystem Study site (winter of 1995–96)

			Tree		
Community	Basal area	Aboveground biomass	Height	Diameter	Density
	m^2/ha	*Mg/ha*	*m*	*D.b.h. in cm*	*No./ha*
Mixed oak	36.0 (1.7)	288 (11.5)	15.3 (0.4)	18.6 (0.6)	773 (55)
Laurel oak	40.7 (1.4)	334 (47.5)	16.3 (1.8)	20.7 (3.4)	885 (328)
Swamp tupelo	45.9 (1.5)	297 (16.9)	19.0 (1.0)	21.7 (1.4)	945 (241)
Water tupelo	58.3 (3.9)	306 (25.5)	20.1 (1.7)	22.6 (1.1)	1138 (46)

[a] Standard error of the mean is in parenthesis.

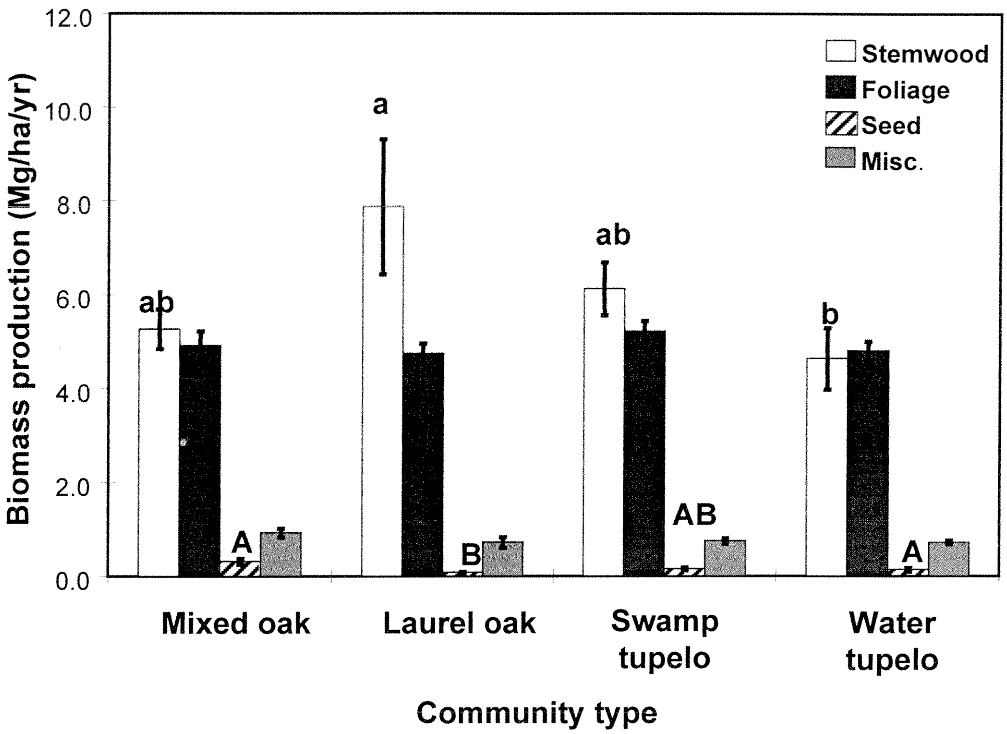

Figure 3.2—Aboveground biomass production between April 1996 and April 1997. Significant differences within component communities are indicated by different lowercase (p = 0.10) and uppercase (p = 0.05) letters. (The I indicates standard error.)

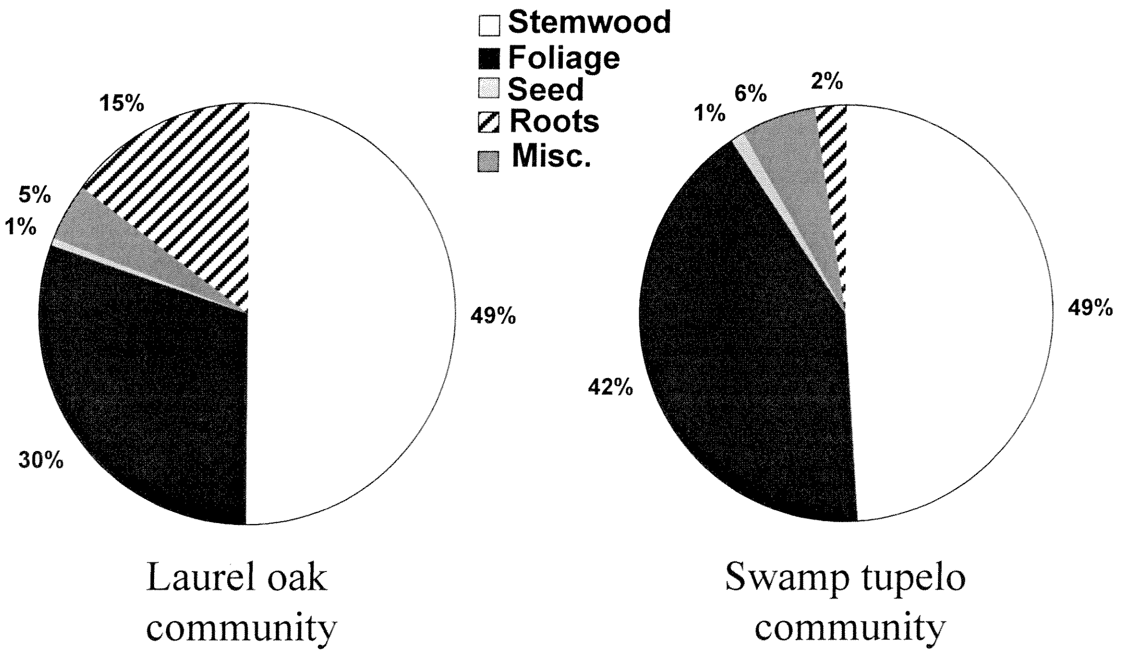

Figure 3.3—Biomass partitioning to stand components in the two most productive communities.

Root Growth

Terrell T. Baker III, William H. Conner, B. Graeme Lockaby,
Marianne K. Burke, and John A. Stanturf[1]

While vegetation dynamics of forested floodplains have received considerable attention (Megonigal and others 1997, Mitch and Gosselink 1993), the highly dynamic fine root component of these ecosystems has been primarily ignored. Characterizing fine root growth is a challenging endeavor in any system, but the difficulties are particularly evident in forested floodplains where frequent hydrologic changes may directly influence fine root growth.

Within the mixed-oak (*Quercus* spp.) community on the Coosawhatchie Bottomland Ecosystem Study site, three distinct soil series were identified (Murray and others 2000). The Coosaw, Meggett, and Brookman soil series were classified as well drained, intermediately drained, and poorly drained, respectively; and this drainage was confirmed by the depth of rusting on steel welding rods inserted into the soil for each soil series. In March 1995, fine root biomass distribution was estimated by collecting 12 soil cores along each of 3 transects that intersected the 3 soil series and did not extend beyond the perimeter of the mixed-oak community. In addition, six *in-situ* screens were installed in close proximity to each of the coring locations and sampled in May, June, July, August, and November 1995 and April 1996 to estimate fine root productivity. Nutrient contents (nitrogen [N] and phosphorus [P]) of fine roots intersecting the screens also were determined for all but the first of the six sample dates. Along each of two additional transects, six minirhizotron tubes were installed, and root lengths were measured monthly to a 30-cm depth for 1 year using a fiber-optic video camera (Bartz Technology, Inc., Santa Barbara, CA).

Photo by Marianne Burke

Root elongation was quantified using minirhizotron technology.

Within the surface to 45-cm depth, 74 percent of total fine root biomass was restricted to the surface 15 cm, 17 percent within the 15- to 30-cm depth, and 9 percent within the 30- to 45-cm depth. Comparison of fine root biomass among the three soil series revealed that biomass plus necromass was greatest in the well-drained soil and least in the poorly drained soil (p = 0.1). Both the *in-situ* screen and

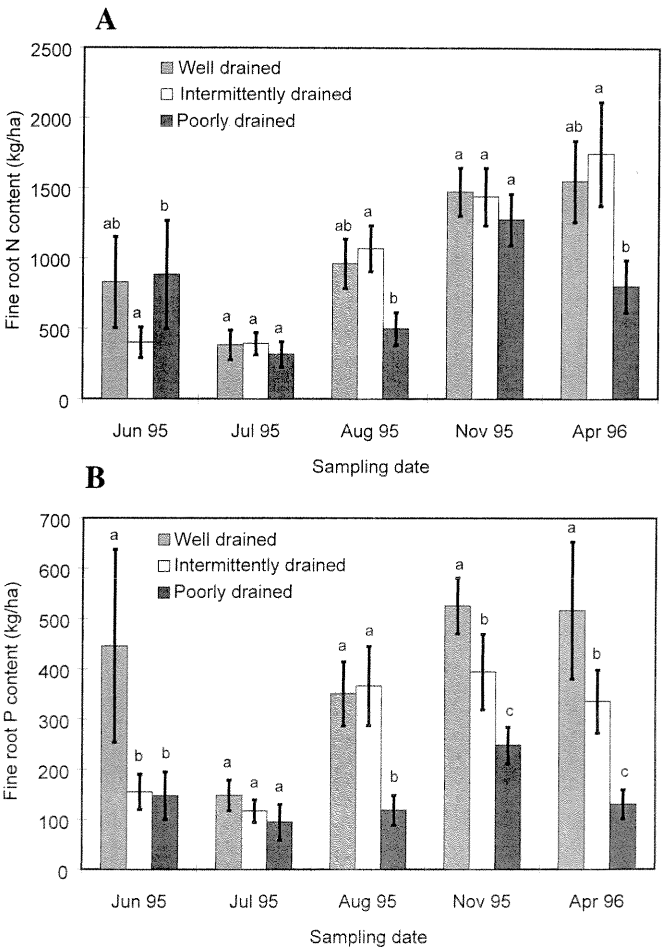

Figure 3.4—Temporal changes in fine root N (A) and P (B) among three drainage categories in the mixed-oak community. Different letters indicate significant differences (p = 0.1) among soil types at that sampling date. (The I indicates standard error.)

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minirhizotron methods showed that fine root length and densities changed with time of sampling, indicating that changes occur throughout the year, not just seasonally. The frequency of changes suggested that frequent sampling is needed to accurately assess fine root growth phenology and production. Fine root production, using measurements of significant ($p = 0.1$) increases in roots between sampling dates taken with *in-situ* screens, was estimated at 1.5, 1.8, and 0.9 Mg per hectare per year in the well-drained, intermediately drained, and poorly drained soils, respectively.

Figure 3.4 compares temporal changes in fine root N and P contents among the three drainage categories, indicating the pool of nutrients associated with fine roots at each sampling interval. Fine root N content tended to increase throughout the year and was generally greater in better-drained soils. Fine root P content exhibited a similar temporal pattern suggesting that nutrient cycling of both N and P through fine root turnover is greater in better-drained soils. Minirhizotron results (fig. 3.5) showed that fine root length density was consistently greater ($p = 0.1$) in both the 0- to 15- and 15- to 30-cm soil depths in the intermediately drained compared with the poorly drained soil. Results from the minirhizotrons also suggested that fine roots typically grow to greater depths in the intermediately drained soil relative to the poorly drained soil (data not shown). Root images collected in the minirhizotrons were classified according to morphological categories, e.g., very fine (< 0.5 mm) rootlike structures, white roots, and brown roots. In the intermediately drained and poorly drained soils, the majority of observations were of very fine rootlike structures. White and brown roots were proportionally more abundant in the intermediately drained than in the poorly drained soil.

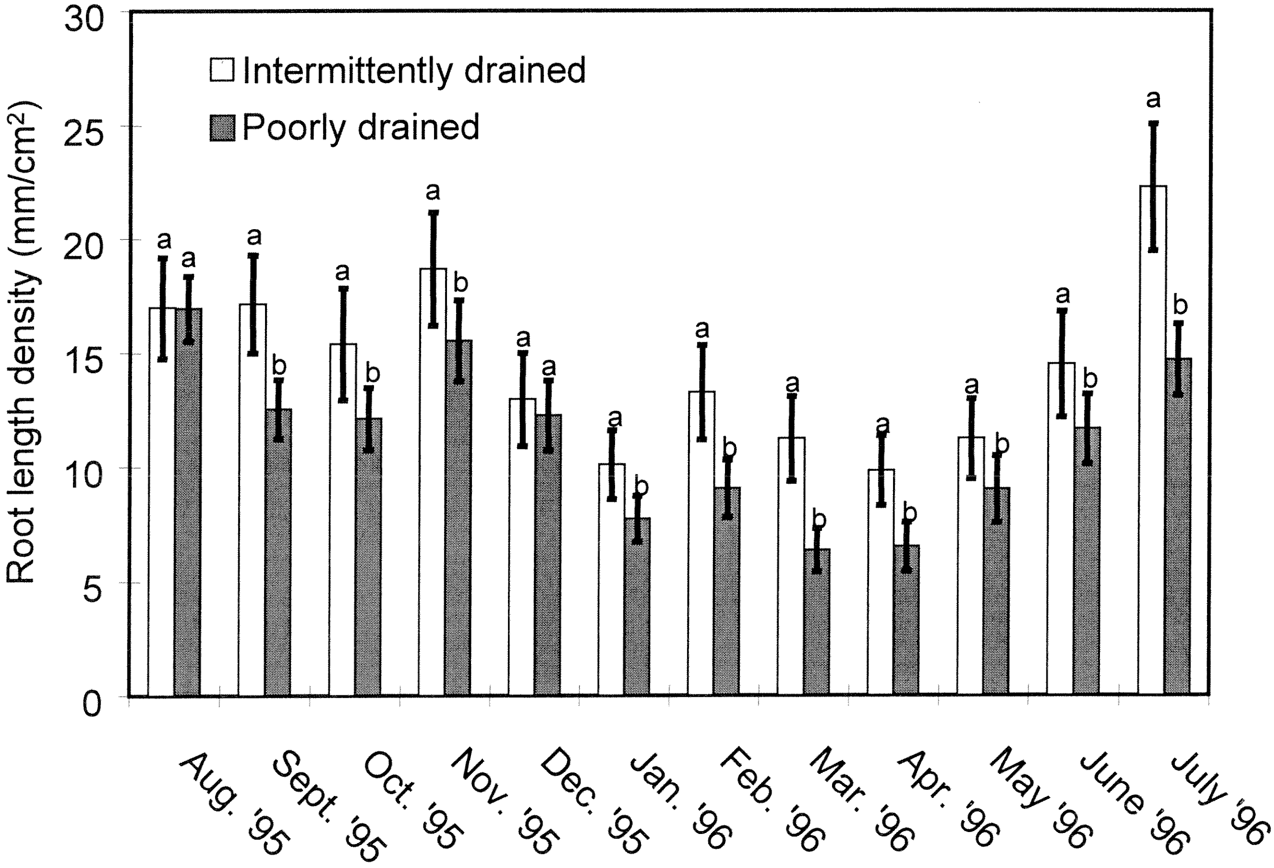

Figure 3.5—Temporal distribution of root length densities (determined using minirhizotrons) in two soil series found in the mixed-oak community. Different letters indicate significant differences ($p = 0.1$) among soil types at that sampling date. (The I indicates standard error.)

Mycorrhizae

Martin Jurgensen, Dana Richter, Carl C. Trettin, and Mary Davis[1]

Mycorrhizae, a mutual partnership between certain soil fungi and fine root tips, contribute to tree growth and vigor by increasing both water and nutrient uptake, especially nitrogen (N) and phosphorus (P). The fungal hyphae increase root surface contact with the soil, while the fungi are supplied with a reliable source of carbon (Allen 1991, George and Marschner 1995). Two types of mycorrhizae are found on most trees—ectomycorrhizae (EM) and endomycorrhizae—also called vesicular-arbuscular mycorrhizae (VAM). The EM fungi are mainly mushroom-forming basidiomycetes, while the VAM fungi are Zygomycetes, most of which form microscopic underground spores. The majority of plants, including many trees, are colonized by VAM fungi, while EM are almost exclusively limited to woody species (Allen 1991, Mosse and others 1981). Some plants can have both VAM and EM fungi (Safir 1987).

Most research on mycorrhizae/plant relationships has been conducted on agricultural soils, upland forests, dry grasslands, or desert sites (Allen 1991). In contrast, mycorrhizal dynamics in wetland ecosystems, and especially bottomland hardwood forests, have not been well studied. Jurgensen and others (1997) reported that bottomland hardwood mycorrhizae have been studied on 14 tree species, 5 of which have VAM, 2 have EM, and 7 can have both mycorrhizal types. The majority of these studies were on sweetgum (*Liquidambar styraciflua* L.) and green ash (*Fraxinus pennsylvanica* Marsh.), important forestry and horticultural species. However, considerable work was still needed to understand mycorrhizal relationships of bottomland hardwood trees and how they affect the development and productivity of these variable and complex ecosystems. Consequently, a study was conducted on two plant community types at the Coosawhatchie Bottomland Ecosystem Study site to determine: (1) the numbers of EM and VAM roots, (2) VAM spore populations in bottomland hardwood soil, and (3) the dominant EM fungi associated with representative bottomland hardwood tree species. Information on numbers of mycorrhizal roots is presented in this paper.


Photo by Hal Liechety

Mychorrhizae were identified from soil cores.

Root and soil sampling were conducted on June 12 and 13, 1995. One soil core (30 cm long by 7.5 cm in diameter) was taken 2 to 3 m from the base of three cherrybark oaks (*Quercus falcata* var. *pagodaefolia* Ell.) and three water oaks (*Q. nigra* L.) in the drained mixed-oak (*Q.* spp.) community type, and three green ash and three water hickories (*Carya aquatica* [Michx f.] Nutt.) in the wetter swamp tupelo (*Nyssa sylvatica* var. *biflora* [Walt.] Sarg.) community type. The soil cores were divided into the following depth sections: (1) surface to 10 cm, (2) 10 cm to 20 cm, and (3) 20 cm to 30 cm. Roots were removed from each core section and weighed. The number of root tips were counted under a dissecting microscope (10–40X) and categorized as ectomycorrhizal or endomycorrhizal.

Vesicular-arbuscular mycorrhizae spores were removed from the soil by wet-sieving and then separated by size class and color. Spore size was used to separate VAM fungal genera. Spore size class 0.25 to 0.5 mm is predominately the genus *Scutellospora*. This size class also includes the genus *Gigaspora*, although current taxonomy considers this group to be of the *Scutellospora* genus (Morton and Benny 1990). Spore size class 0.062 to 0.25 mm is predominantly the genus *Glomus*. Color was used for distinguishing species within genera. Black spores within the *Glomus* genus represent *G. fecundisporum;* white to yellow spores are *G. convolutum* or *G. gigantea* (Morton 1988).

Much higher numbers of VAM spores were found in the surface 10-cm mineral soil layer than in the deeper soil layers of both plant community types (fig. 3.6), and these values were higher than has been reported for other wetland soils (Janos 1992, Rickerl and others 1994). Soil spore populations were considerably higher in the swamp tupelo soil than in the mixed-oak soil, which probably reflects the predominance of VAM tree species in the forest community. As expected, VAM spore numbers decreased as soil depth increased. The number of VAM spores in soil is often used

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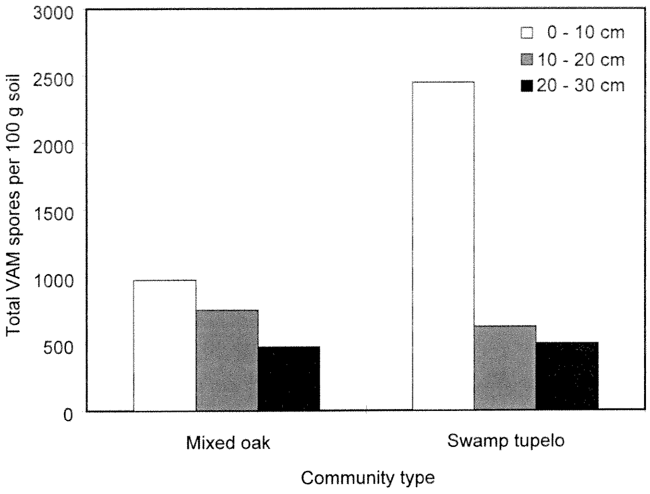

Figure 3.6—Number of endomycorrhizal (VAM) spores per 100 grams dry soil at three soil depth intervals in two community types.

as an indicator of root mycorrhizal infection (Daniels Hetrick 1984, Mosse and others 1981). However, VAM root infection may not always be reflected in spore numbers because (1) VAM spores may be dormant; (2) other infective propagules, e.g., hyphae may be present; and (3) counting spores in the soil is difficult (Abbott and Robson 1991). Also, VAM spore numbers may reflect seasonal variations and soil moisture levels at the time of sampling (Douds and Chaney 1986). Based on spore size differentiation, 90 percent of the VAM spores in both community types at the Coosawhatchie site were in the genus *Glomus*. Black spores (*G. fecundisporum*) made up between 20 to 30 percent of the total population at all soil depths. White to yellow VAM spore *(G. convolutum* or *G. gigantea)* numbers ranged from 10 to 20 percent.

Root biomass tended to be greater in the mixed-oak type than in the swamp tupelo (fig. 3.7), while the total number of root tips was higher in the swamp tupelo type (fig. 3.8). These results may reflect the rooting structure of the different plants growing in each community, or they may be anomalies from the low number of soil cores taken. The predominance of EM over VAM on roots (figs. 3.9, 3.10) was expected in the mixed-oak type, because oaks are predominately EM. However, dominant trees in the swamp tupelo type are primarily VAM (Jurgensen and others 1997), so the predominance of EM in this community suggested EM are important; again, however, this may be an artifact of a small sample size.

This preliminary investigation of mycorrhizae on the Coosawhatchie Bottomland Ecosystem Study site has indicated high levels of VAM spores in the soil of two of the community types. The occurrence of large numbers of EM in the swamp tupelo community raises questions about the significance of these mycorrhizal fungi in nutrient cycling and productivity in periodically flooded soil. Such high spore populations would seem beneficial for vegetation establishment after major site disturbance, such as harvesting or hurricane damage.

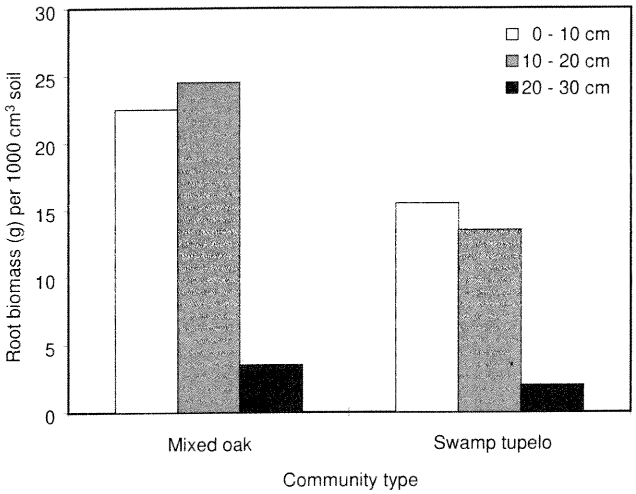

Figure 3.7—Average root biomass at three soil depth intervals in two plant community types.

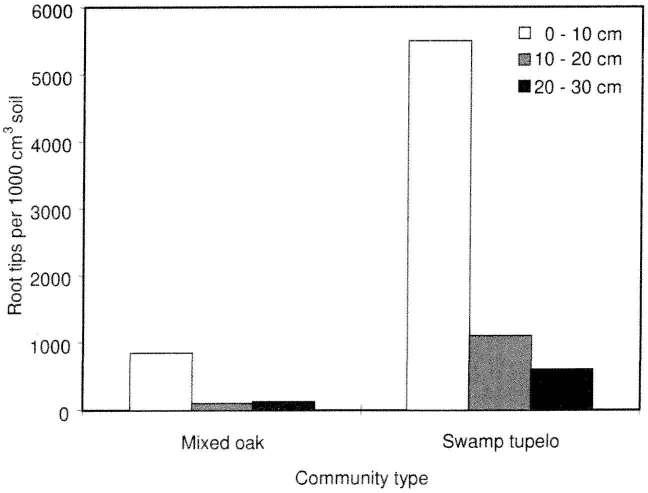

Figure 3.8—Average number of mycorrhizal root tips at three soil depth intervals in two bottomland hardwood community types.

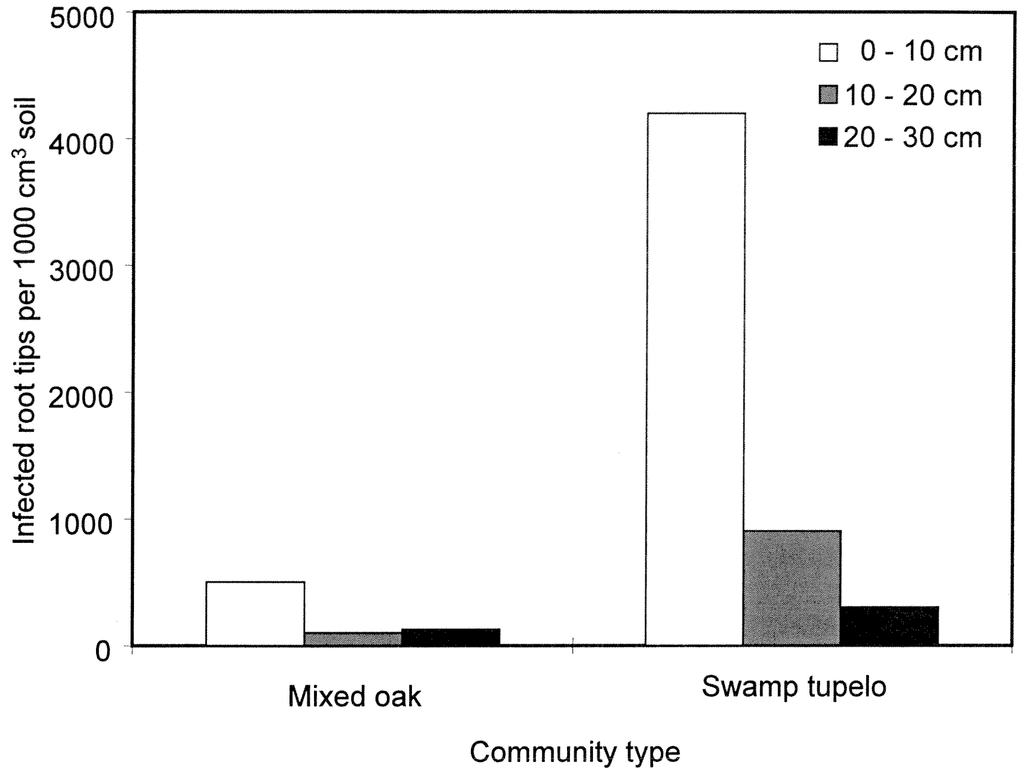

Figure 3.9—Number of ectomycorrhizal root tips at three soil depth intervals in two community types.

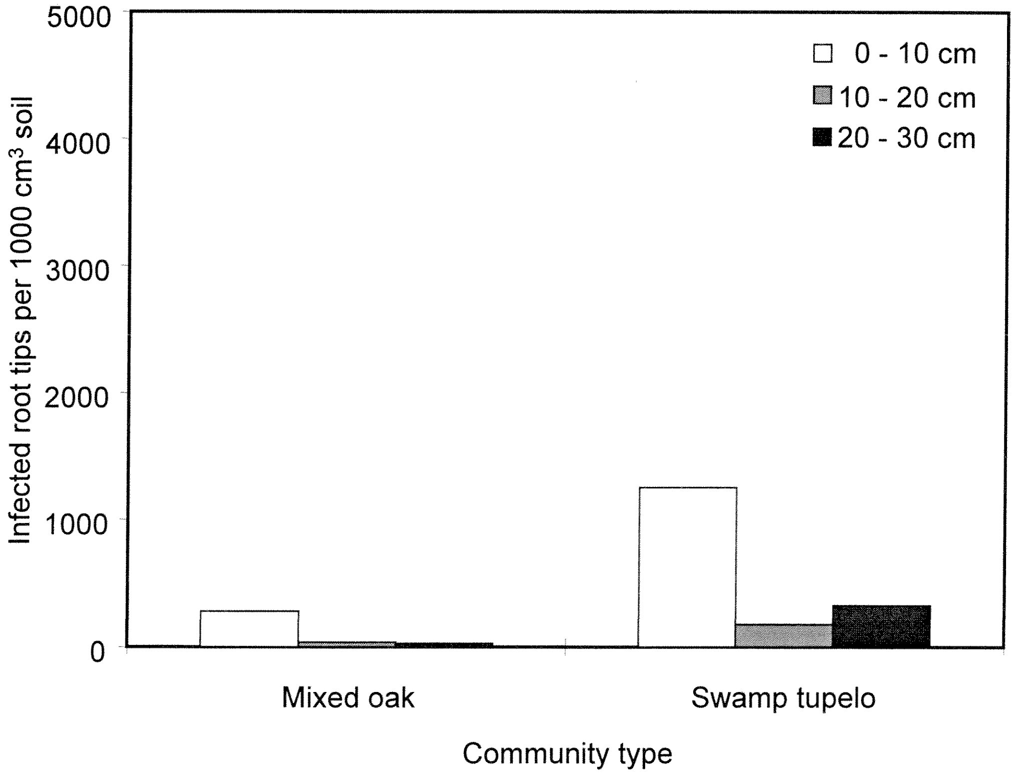

Figure 3.10—Number of endomycorrihizal root tips at three soil depth intervals in two community types.

Woody Debris

Donna B. Scheungrab, Carl C. Trettin, Russ Lea, and Martin F. Jurgensen[1]

Woody debris can be defined as any dead, woody plant material, including logs, branches, standing dead trees, and root wads. Woody debris is an important part of forest and stream ecosystems because it has a role in carbon budgets and nutrient cycling, is a source of energy for aquatic ecosystems, provides habitat for terrestrial and aquatic organisms, and contributes to structure and roughness, thereby influencing water flows and sediment transport (Harmon and others 1986). Few studies of woody debris in forested wetlands have been done in the Southeastern United States. To characterize this important ecosystem component, the influence of flooding and plant community type on woody debris must be understood.

The woody debris study has two primary objectives: (1) to quantify and characterize the distribution of woody debris in the bottomland hardwood forest, and (2) to determine the flux of woody debris through the forest. A fundamental first step was to develop and apply a woody debris classification system that can be used in forested wetlands in the Southern United States. All published woody debris classification systems (Brown 1974, Harmon and others 1986, Triska and Cromack 1980, Van Wagner 1968, Warren and Olsen 1964) consist of divisions by size class, decay class, and sometimes position class. Because no critical review of woody debris classification systems for the South existed, two initial objectives were to (1) examine existing classification systems and assess their appropriateness for use in a bottomland hardwood forest and (2) develop a data matrix that provided values of specific gravity of woody debris classified by decay and size classes for each tree genera present on the Coosawhatchie site. The classification system provided a way to more accurately inventory the amount of woody debris in the Coosawhatchie Bottomland Ecosystem Study site by producing values in volume, which could then be converted to values in mass using the specific gravity data matrix.

The classification system divided woody debris into three size classes: 1 to < 2.5 cm, 2.5 to 10 cm, and > 10 cm in diameter. According to the recommendations of Harmon and Sexton (1996), the breakpoint between fine woody debris and coarse woody debris is 10 cm. Woody debris < 1 cm, snags, and root wads were not addressed in this study. Fine woody debris was divided into the two smaller size classes using a go-no-go gauge (Brown 1974) and coarse woody debris was measured to the nearest centimeter diameter with calipers. Coarse woody debris was classified into shapes (fig. 3.11) to increase volume accuracy by accounting for missing parts of logs. Fine woody debris was divided into two decay classes: sound and decayed. Coarse woody debris was divided into three decay classes: sound, intermediate, and advanced decay.

The method used to divide coarse woody debris into decay classes was based on the penetration of a bluntly pointed steel rod pushed firmly into each piece of woody debris: penetration < 0.5 cm was sound, penetration 0.5 cm to the radius of the woody debris was intermediate, and penetration greater than the radius of the woody debris indicated advanced decay (Lambert and others 1980, Lang and Forman 1978). The penetration method was selected over visual criteria because achieving accuracy in southern bottomland hardwood forests using the latter method is difficult; these forests contain a vast number of genera that exhibit different decay patterns.

A pilot inventory was conducted in October 1997 on the lower floodplain portion of the site using the planar intersect method (Brown 1974). For each piece of woody debris inventoried, the following data were recorded: (1) size class, (2) penetrability, and (3) position on the ground (in contact

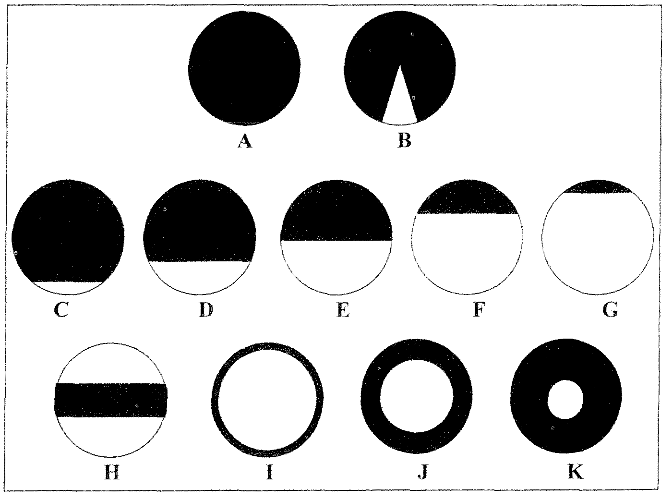

Figure 3.11—Idealized cross-sectional shapes of coarse woody debris. The shape that best matches the piece of woody debris was recorded to improve volume estimates. Shapes are not to scale.

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with ground, elevated, or in a debris dam). The diameter of coarse woody debris was measured, and the cross-sectional shape of each piece was recorded. The results from the pilot inventory are shown in table 3.2. Fine woody debris in the 2.5- to 10-cm diameter size class contributed almost as much to total volume, as did coarse woody debris.

Specific gravity values for woody debris were needed to transform estimates of volume to estimates of corresponding mass. Samples for specific gravity analysis were collected in July and August 1997, and the results of the specific gravity analyses will be incorporated with data from the complete inventory.

Input and flux of woody debris are being measured in a series of plots distributed among three elevation zones on the site. The plots consist of nested traps that permit the calculation of net woody debris input, net woody debris output, and direct deposition of woody debris. Transport distance is being assessed by tagging pieces of woody debris and tracing their movement through the bottomland.

A complete inventory of the bottomland portion of the site was conducted during September and November 1998. Results were similar to those of the pilot study (table 3.2). except that fine woody debris in the 2.5- to 10-cm diameter size class contributed only half as much to total volume, as did coarse woody debris. In any event, it appeared that fine woody debris constituted an important part of the total woody debris on the Coosawhatchie Bottomland Ecosystem Study site. Future investigations will include decomposition studies wherein the decay rate of different tree species and the influence of site conditions on decay processes will be compared.

Table 3.2—Results from a pilot inventory on the Coosawhatchie Ecosystem Study Site showing average woody debris volume, percent of total volume, and percent of total number of woody debris pieces per 100 linear meters by size class

Size class	Volume		Pieces per 100 linear m
Diameter	*m³/ha*	*%*	*% of total*
Fine woody debris			
1 to 2.5 cm	1	5	56
2.5 to 10 cm	12	46	38
Coarse woody debris			
> 10 cm	13	49	6
Total	26	100	100

Installation of drift fences for woody debris studies.

Litter Decomposition

Terrell T. Baker III, B. Graeme Lockaby, William H. Conner,
John A. Stanturf, and Marianne K. Burke[1]

While many factors regulate litter decomposition and nutrient flow in floodplain systems, litter quality and hydrologic influences are of primary importance (Belyea 1996, Heal and others 1997). To a large extent, these two driving forces determine the pattern and extent of nutrient immobilization and mineralization during the decomposition of leaf litter.

This study examined decomposition processes on the three Southern Forested Wetlands Initiative study sites. The Coosawhatchie River site represented a particularly valuable opportunity to examine decomposition processes within a floodplain system because it contains two distinct, but adjacent, vegetative communities that differ in terms of hydroperiod and litter quality. While both communities experienced seasonal flooding, the first, a laurel oak (*Quercus laurifolia* Michx.) community with drained soils, is typically drier than the second, a swamp tupelo (*Nyssa sylvatica* var. *biflora* [Walt.] Sarg.) community with poorly drained soils.

In fall of 1995, leaf litter from each Southern Forested Wetlands Initiative site and from two communities on the Coosawhatchie Bottomland Ecosystem Study site was collected with littertraps and tarps, returned to the lab, and sorted according to species. Litter from the five most important tree species (by air-dried weight) was combined into litterbags (30.5 by 45.7 cm with 6- and 2-mm openings on the upper and lower sides, respectively). The relative quantity of each species' litter in each bag represented the proportion of total litter collected from each community.

All litterbags contained approximately 20 g of leaf litter. On the Coosawhatchie site, litterbags in the laurel oak community contained small-leafed oaks—water (*Q. nigra* L.), willow (*Q. phellos* L.), and laurel (37 percent)—sweetgum (29 percent); large-leafed oaks—white (*Q. alba* L.) and red (*Q. falcata* Michx.) spp. (26 percent)—and red maple (*Acer rubrum* L.) (8 percent). Litterbags in the swamp tupelo community contained sweetgum (48 percent), large-leafed oaks (21 percent), swamp tupelo (16 percent), small-leafed oaks (12 percent), and red maple (3 percent). In addition, litterbags containing control litter (uniform litter quality), primarily cherrybark oak (*Q. falcata* var. *pagodifolia* Ell.) collected from the Iatt Creek site, were placed and sampled in a similar way to test the physiographic influences on decomposition processes in all but the swamp tupelo community. Litterbags were placed in the field in April 1996, and samples were collected (n = 3) at 0-, 2-, 4-, 6-, 8-, 12-, 16-, 22-, 28-, 38-, 48-, 64-, and 80-week intervals. Each sample was returned to Auburn University and material was washed of sediment, ovendried to a constant weight, weighed, and analyzed for nitrogen (N), phosphorus (P), and carbon (C). All values are expressed on an ash-free basis.

Figure 3.12 illustrates the temporal trend of mass loss for mixed- and single-species litter during an 80-week period. Table 3.3 provides descriptive statistics for mixed- and single-species litter through week 80 on the four floodplain sites. Although differences were not statistically significant,

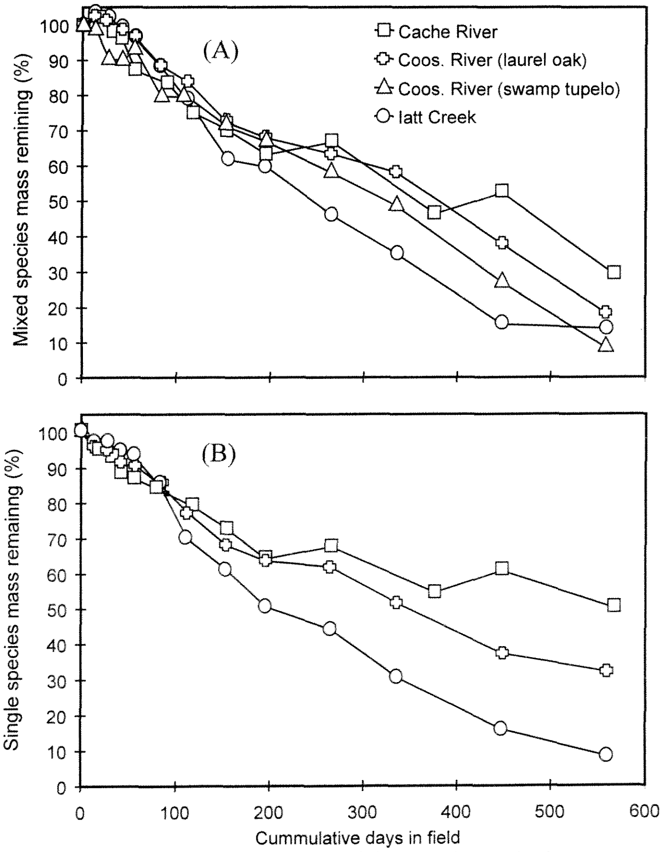

Figure 3.12—Average percent mass remaining (ash-free basis) for (A) mixed- and (B) single-species leaf litter in four and three, respectively, forested floodplain commmunities in the Southern United States.

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decomposition rates (k) were numerically greater for the mixed-species litter in the swamp tupelo community (0.96) than in the laurel oak community (0.82) on the Coosawhatchie Bottomland Ecosystem Study site. Similarly, the mixed-species litter in the swamp tupelo community contained numerically less of the original litter mass and P than the mixed-species litter in the laurel oak community. The decay rate for single-species litter on the Coosawhatchie River site was intermediate to that on the other two sites, being significantly greater than the Cache River but significantly less than the Iatt Creek sites. The dramatic separation of the Iatt Creek site in terms of decay rate, mass remaining, and P remaining is not surprising because this site is the least flooded. Although the data cannot explain the mechanisms behind this tendency, soil temperature and hydrologic data collected during this study are being analyzed to improve understanding of the decay and mineralization patterns on these four floodplain sites.


Photo by Marianne Burke

Installation of decomposition litter bags.

Table 3.3—Decomposition rates[a] and percentage of mass and phosphorus remaining in leaf litter of mixed and single species in four forested floodplain sites in the Southern United States after 80 weeks

	Decay coefficient		Mass		Phosphorus	
Site	Mixed	Single[b]	Mixed	Single	Mixed	Single
			Percent			
Cache River, AR	0.7095 (0.02)[c]A[d]a[e]	0.4667 (0.03)Ab	29.34 (2.82)Aa	50.14 (2.96)Ab	27.05 (1.80)Aa	65.00 (5.69)Ab
Coosawhatchie River, SC						
Laurel oak	.8210 (.04)ABa	.7557 (.07)Ba	18.20 (1.50)Ba	32.18 (5.34)Ba	23.98 (4.58)Aa	53.51 (4.81)Ab
Swamp tupelo	.9572 (.43)B	NA	8.32 (4.75)B	NA	18.54 (10.73)A	NA
Iatt Creek, LA	1.2499 (.06)Ca	1.3378 (.08)Ca	13.84 (2.25)Ba	8.23 (2.13)Ca	18.67 (2.50)Aa	10.82 (3.07)Ba

NA = Not applicable.

[a] Calculated as $\{X/X_0\} = e^{-xt}$.

[b] Control litter.

[c] Standard error of the mean is in parentheses.

[d] Means for each floodplain site within each litter type with the same uppercase letter do not differ significantly at the p = 0.05 level.

[e] Lowercase letters compare k, mass, and P among litter types; means with same lowercase letter do not differ significantly at the p = 0.05 level.

Nutrient Dynamics—Soil Microorganisms

Don Stoeckel and Mary Miller-Goodman[1]

Effective management of floodplain systems for purposes of ecosystem health, woody biomass production, or wild game habitat is dependent, in part, upon an understanding of nutrient partitioning between plants and soil microorganisms. Soil microorganisms convert organically bound nutrients, especially nitrogen and phosphorus, to inorganic forms that can be available for uptake by plants. Plants in turn transport organic molecules to the rhizosphere providing sources of carbon and energy to soil microorganisms (Cheng and others 1994). This interaction between plants and microorganisms is the basis for a complex nutritional web that is difficult to understand even in simple systems. The situation is further complicated on floodplains because periodic flooding causes the redox characteristics of the system to fluctuate (Jones and others 1996). Flooding events can disrupt otherwise-stable relationships between microorganisms and plants, because metabolic pathways of both microorganisms and plants are controlled by the environmental redox status.

Data were collected from soils of the Coosawhatchie River floodplain to evaluate microbial responses to indices of nutrient availability with season, depth, and hydrologic regime. Table 3.4 summarizes values for nutrient ratios observed in the soils during the first year of data collection. Observed $C:N_{org}$ ratios in this floodplain fell into expected ranges. Organic nitrogen accumulation occurred in the organic surface materials as the year progressed, while the $C:N_{org}$ ratio remained relatively constant in the mineral soils. Further accumulation of nitrogen in the organic matter over longer time scales was indicated by higher $C:N_{org}$ values in the organic layers than in the mineral soils ($p < 0.001$). Organic nitrogen accumulation was more prevalent in hydric plots than in mesic plots ($p < 0.05$), mirroring the finding of Shure and others (1986) that plots near the main channel (more frequently flooded) had lower organic C:N ratios than those at higher elevation (analogous to mesic plots). The $C:NH_3$ values remained relatively constant across the two seasons it was measured. The $C:N_{org}$ ratio values reflected a net accumulation of nitrogen in organic surface material over the course of the year ($p < 0.05$).

Phosphorus dynamics were more complicated. Because total phosphorus data were unavailable, the ratio presented is the organic carbon-to-exchangeable phosphate ratio. Inorganic phosphorus accumulated in the organic surface materials over time ($p < 0.01$) while ratios fluctuated in the mineral soils. In the mesic plots, the most biologically active soil layer (0 to 10 cm) had the highest $C:PO_4$ ratios, while at the hydric sites the $C:PO_4$ ratio indicated relatively lower phosphorus availability at the 20- to 30-cm depth. Carbon-to-available phosphate ratios did not consistently differ between hydric and mesic sites, and seasonal fluctuations in $C:PO_4$ may reflect changes in microbial activity.

Soil enzyme activities were measured on each soil sample in an attempt to infer nutritional deficits at measured nutrient ratios. Table 3.5 presents significance levels and signs of correlations between nutrient ratios and enzyme activities. Correlations within the entire data set were not always reflected in subdivisions of the data set, indicating that putative relationships between nutrient ratios and microbial activities were variable in different hydrologic regimes and depths.

Nutrient pool control over microbial activity was inferred from correlation of enzyme activities with nutrient ratios. The strong positive correlation of all enzyme activities with the index of substrate richness ($C:N_{org}$) indicated that the various populations of bacteria across the site responded to nutrient-poor substrates through increased enzyme activities to break down soil organic material and acquire nutrients.

An organic C:N ratio of 30 has been proposed as the critical substrate richness below which microorganisms are not nutritionally limited and function to produce a net mineralization of nutrients (Fog 1988). Organic surface materials exceeded this value in the autumn and winter at hydric plots and in all seasons at mesic plots, suggesting that the microbial populations should be actively working to immobilize organic nitrogen at these plots. This test of the critical $C:N_{org}$ ratio hypothesis was not supported by the data, which showed no correlation between organic C:N ratios and urease activity in the organic surface materials.

The carbon-to-mineral N ratio ($C:NH_3$) also failed to correlate with urease activity. This result indicated that microorganisms in the floodplain soils were not generally limited for nitrogen. The $C:PO_4$ ratio was correlated with enhanced phosphatase activity, an indication that microbial populations in hydric soils (0- to 10-cm depth) and mesic soils (to 30 cm) may have responded to relative shortages of free phosphate by releasing phosphatase enzymes. This response may be specific to those three combinations of depth and hydroperiod because the soil with the highest $C:PO_4$ ratio in the spring and summer (20 to 30 cm at the

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hydric plots) did not exhibit any correlation between the nutrient ratio and phosphatase activity. Glucosidase activity was correlated with $C:PO_4$ ratios in several of the microbial populations, implying some degree of phosphate feedback to that enzyme system. The negative relationship of phosphatase and glucosidase activity with the $C:PO_4$ ratio at the hydric plots in the organic surface material indicated that these microbial communities may slow litter degradation activities when phosphorus is in short supply, the inverse of the relationship observed in the mineral soils.

Organic material cycling by soil microorganisms on the Coosawhatchie floodplain appears to have been governed in part by the balance of organic carbon and exchangeable phosphate in the system. Low availabilities of exchangeable phosphate were correlated with enhanced enzyme activities, especially in the well-aerated surface mineral soils of both hydrologic regimes and the 20- to 30-cm depth of the mesic regime. The relationship was inverted in organic litter layers, possibly a statistical artifact resulting from high $C:PO_4$ ratios in autumn of 1996, a cold season when enzyme activities would be expected to be low. The traditional measure of substrate quality and the organic C:N ratio indicated enhanced enzymatic action upon nutrient-poor substrates across the floodplain, though the correlation generally was not observed within treatment (community) combinations.

Table 3.4—Nutrient ratio values[a] of the soils from the Coosawhatchie River floodplain during the first year of data collection

		Autumn 1996		Winter 1997		Spring 1997			Summer 1997		
Hydrology and community type	Depth	$C:N_{org}$	$C:PO_4$	$C:N_{org}$	$C:PO_4$	$C:N_{org}$	$C:NH_3$	$C:PO_4$	$C:N_{org}$	$C:NH_3$	$C:PO_4$
Hydric											
Sweetgum/ tupelo	Organic	38	9.5	35	2.6	25	2.1	3.9	26	2	3
	0 to 10 cm	14	8.2	13	4.5	13	1.8	4.4	14	1.6	5.8
	20 to 30 cm	14	4.8	ND	ND	13	2.8	6.4	13	3	6.5
Mesic											
Laurel oak	Organic	42	9.2	41	2.6	34	4.5	3.6	33	6.1	3.5
	0 to 10 cm	19	6.2	18	2.8	18	2.3	4.9	20	2.4	7.3
	20 to 30 cm	18	3.2	20	.8	17	1.9	2.7	20	1.5	2.2

ND = Not determined. Samples could not be obtained due to flooding.

[a] The $C:PO_4$ and $C:NH_3$ ratios were divided by 1,000 to obtain single-digit ratios.

Table 3.5—Significance level and signs of correlation between enzyme activities and nutrient ratios for the entire data set and for subdivisions of data by hydrology and depth

Hydrology and community type	Depth	Urease with			Phosphatase with			β-D glucosidase with		
		$C:N_{org}$	$C:NH_3$	$C:PO_4$	$C:N_{org}$	$C:NH_3$	$C:PO_4$	$C:N_{org}$	$C:NH_3$	$C:PO_4$
Hydric										
Sweetgum	Organic	NS	NS	NS	NS	NS	—	NS	NS	—
	0 to 10 cm	NS	NS	+++	NS	-	+++	+	NS	+++
	20 to 30 cm	NS	NS	NS	NS	NS	NS	NS	NS	NS
Mesic										
Laurel oak	Organic	NS	NS	++	-	NS	—	NS	NS	NS
	0 to 10 cm	NS	NS	+++	NS	NS	++	NS	NS	+
	20 to 30 cm	NS	+	+++	—	+	+++	NS	+	+++
Overall		+++	+	+++	+++	++	+	+++	NS	NS

+/-, ++/—, +++/— for positive and negative correlations at $p < 0.05$, $p < 0.01$, and $p < 0.001$, respectively.
NS = Not significant.

Nutrient Dynamics—Soil and Vegetation

Marianne K. Burke[1]

The Coosawhatchie River is a typical blackwater river in that it originates in the lower Coastal Plain and tends to be less fertile and carry a smaller sediment load than brownwater rivers, which have drainages originating in the mountains or Piedmont (Hupp and Schening 2000). Blackwater rivers in turn can be more nutrient rich than low order streams in the Coastal Plain, as the latter derive nutrient loads almost exclusively from precipitation. On the lower Coastal Plain of South Carolina, floodplains of blackwater rivers and low order streams support bottomland hardwood forests that differ in structure and function, probably due in large part to differences in nutrient dynamics.

On the Coosawhatchie study site, a relatively large watershed supplies the river with mineral and organic materials that are deposited on the site during floods (Maluk and others 2000, Hupp and Schening 2000). Several studies indicated that nutrients are abundantly available at this site: soil macronutrients, soil organic matter, and cation exchange capacity were relatively high (Burke and others 2000a); there was an underlying stratum of marine deposits (Murray and others 2000) probably contributing to the relatively high macronutrient economy of the streamwater (Maluk and others 2000); and studies of soil microbes indicated that N was abundantly available for microbial use (Stoeckle and Miller-Goodman 2000). This quite fertile site contrasts dramatically with a relatively nutrient poor bottomland hardwood forest in a small watershed off the Chehaw River of the Ashepoo, Combahee, and Edisto River (ACE) Basin of South Carolina. The latter site, described in detail in Burke and others (1999), contains four well-defined vegetation zones along a freshwater flooding gradient created through impoundment in the 18th century. Companion studies were used to explore interrelationships between nutrient dynamics and NPP on these respectively nutrient-rich and nutrient-poor bottomland hardwood forests.

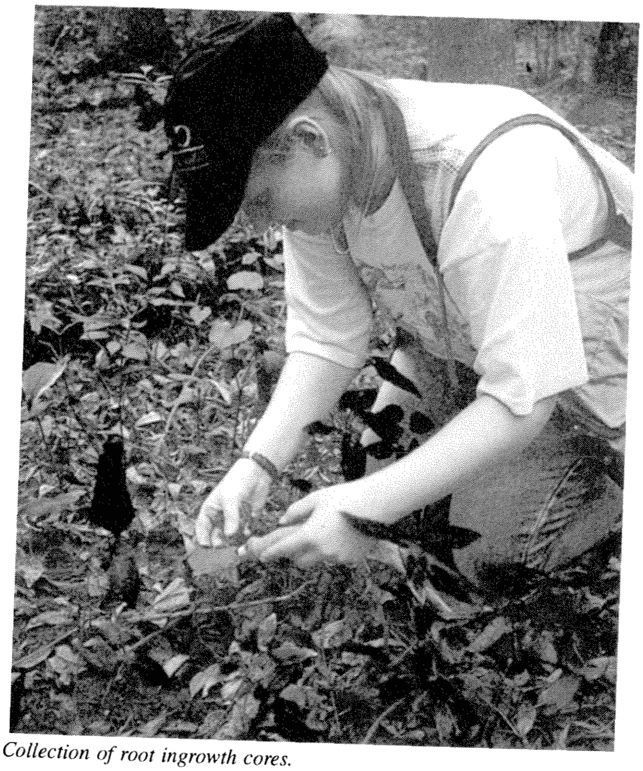

Photo by Marianne Burke

Collection of root ingrowth cores.

In situ soil incubations were employed to estimate soil N availability in the four main communities on both the Coosawhatchie and ACE Basin sites. The four Coosawhatchie River communities had similar estimates for total KCl extractable N, N-mineralization, and nitrification (increase in extractable NO_3^- during incubation) between June and October 1997 (fig. 3.13). In contrast, these estimators of N availability varied dramatically among communities at the ACE Basin site during the same time period: N availability was greatest on the extremely wet and dry ends of the hydrologic gradient, but was relatively low in the transitional (to upland) zones (Burke and others 1999).

Although exchangeable Ca, K, or Mg on the Coosawhatchie site (Burke and others 2000a) was equal to or less than that on the ACE Basin site, variability in these parameters among Coosawhatchie communities was low, and variability among ACE Basin communities was high (Burke and others 1999). It should be noted that the exchangeable cation values were expressed on a soil mass basis. Because soil horizons and rooting volume are generally deeper on the Coosawhatchie site, nutrient capital was substantially lower on the ACE Basin site, and this contributed to the higher variability in soil nutrient availability across the site. Also, the Coosawhatchie site's substantially higher soil CEC capacity and P availability (Burke and others 2000a) contribute to an overall greater and more balanced nutrient capital than on the ACE Basin site. The latter site has previously been

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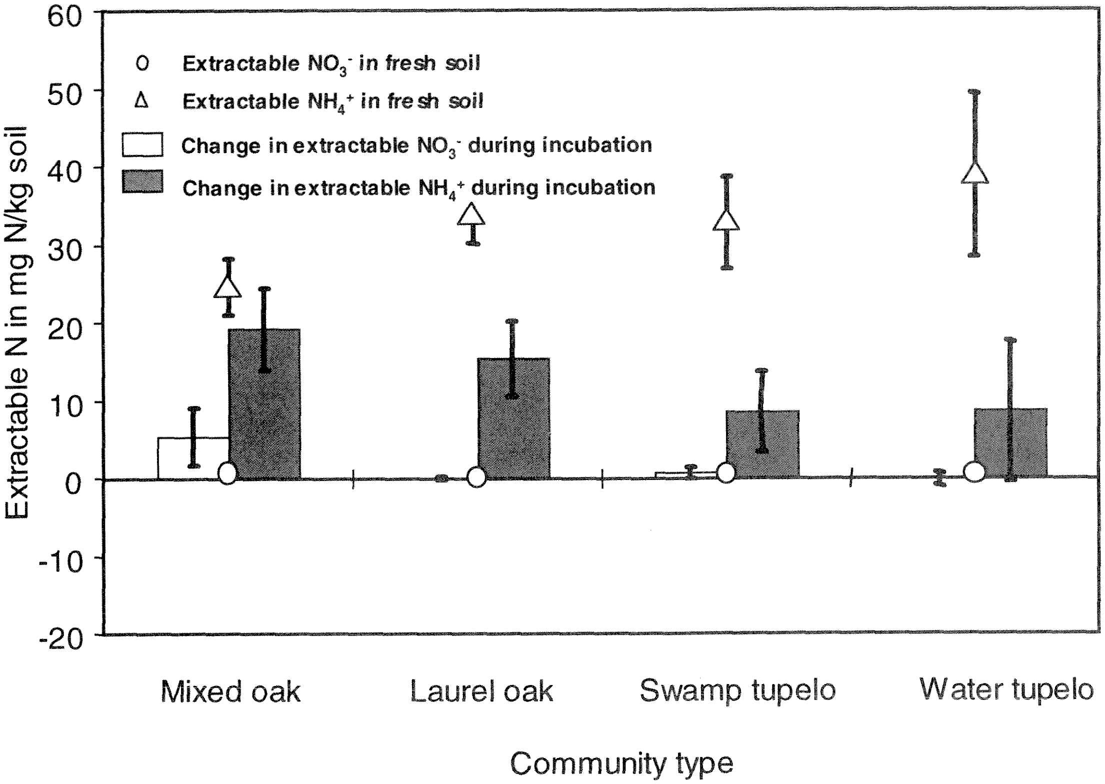

Figure 3.13—Mean total (+/-) of extractable NO_3^- and NH_4^+ in fresh soil and the mean total change in extractable NO_3^- and NH_4^+ for monthly *in situ* incubations on the Coosawhatchie site. (The I indicates standard error.)

identified as being both nutrient-poor and imbalanced, resulting in internal (within trees) nutrient cycling being an important process on that site (Burke and others 1999).

Given the greater nutrient availability and relatively high NPP on the Coosawhatchie site, we hypothesized that foliar nutrient values would be more balanced on the Coosawhatchie site than on the ACE Basin site. Between April 1995 and March 1996, foliage was collected on a regular basis from litterfall traps in each of the sixteen productivity plots on the Coosawhatchie site, as described in Burke and others (2000b). Foliage from the water tupelo (*Nyssa aquatica* L.) community had higher foliar concentrations of N, K and Mg (p = 0.05) than in the laurel oak (*Quercus laurifolia* Michx.) community, but concentrations of these nutrients in foliage from the swamp tulpelo (*N. sylvatica* var. *biflora* [Walt.] Sarg.) community did not differ significantly from those of any other community (table 3.6). Foliar macronutrient concentrations were greater in the most flooded communities, possibly because generally more sediment was deposited there (Hupp and Schening 2000). Also, there may be less competition with microbes for nutrients in flooded areas (Burke and others 1999). On the Coosawhatchie site no significant differences were observed in litterfall nutrient contents among the communities (table 3.7). In general, foliar macronutrient concentrations on the Coosawhatchie site were greater than those measured at the ACE Basin site. More importantly, nutrient levels were balanced on the Coosawhatchie site, suggesting that the trees were more vigorous than at the ACE Basin site: compared with an optimum N/P ratio of 12 (Lockaby and Walbridge 1998), ratios at the ACE Basin site ranged from 6–8 and those on the Coosawhatchie site ranged from 10-13.

Based on the Lockaby and Walbridge (1998) model, N should limit NPP on the ACE Basin site but not on the Coosawhatchie site. The model was supported by a correlation between soil N availability and aboveground NPP on the ACE Basin site (Burke and others 1999) but not on the Coosawhatchie site. In addition, Stoeckle and Miller-

Table 3.6—Mean (standard error[a]) litterfall nutrient concentrations for four communities for 1 year (1995–96)[b]

Nutrient	Water tupelo	Swamp tupelo	Laurel oak	Mixed oak
	Percent of dry mass			
N[c]	1.280(0.065)A[d]	1.048(0.041)AB	0.976(0.019)B	1.090(0.011)AB
P[c]	.100 (.002)AB	.094 (.002)A	.097 (.001)	.116 (.009)B
K	.196 (.020)a	.150 (.0154)ab	.135 (.007)b	.196 (.015)a
Ca[c]	1.040 (.007)	1.131 (.028)	1.145 (.050)	1.133 (.049)
Mg	.300 (.016)A	.265 (.015)AB	.221 (.008)B	.230 (.016)B
S	.143 (.007)a	.123 (.006)ab	.116 (.005)b	.130 (.008)ab
Fe	.094 (.001)B	.121 (.016)AB	.153 (.015)A	.071 (.006)B
Zn	.054 (.003)	.042 (.002)	.036 (.003)	.044 (.003)
Mn	.919 (.225)	.674 (.138)	1.002 (.182)	.645 (.078)
B	.050 (.002)A	.044 (.002)AB	.038 (.002)BC	.036 (.001)C
Cu	.005 (.000)AB	.005 (.000)AB	.005 (.000)B	.006 (.000)A

N = Nitrogen, P = phosphorus, K = potassium, Ca = calcium, Mg = magnesium, S = sulphur, Fe = iron, Zn = zinc, Mn = manganese, B = boron, Cu = copper.

[a] Standard error of the mean is in parentheses.

[b] Concentrations were determined at each litter collection date (Burke and others 2000a), and annual concentrations were weighted by foliage mass at each date.

[c] Concentrations were subjected to Kruscal Wallis (nonparametric) test because variances remained heteroskedastic after transformation.

[d] Different uppercase letters indicate differences at α = 0.05 and different lowercase letters indicate differences at α = 0.10. Lack of uppercase or lowercase letters indicate no significant difference.

Table 3.7—Mean (standard error[a]) foliage nutrient contents in litterfall for four communities for 1 year (1995–96)[b]

Nutrient	Water tupelo	Swamp tupelo	Laurel oak	Mixed oak
	Grams per square meter			
N	6.728(0.347)	6.206(0.324)	5.189(0.474)	5.493(0.526)
P	.520 (.019)	.554 (.017)	.515 (.036)	.596 (.088)
K	1.036 (.128)	.890 (.100)	.717 (.007)	.982 (.114)
Ca	5.492 (.177)	6.712 (.046)	6.081 (.571)	5.736 (.068)
Mg	1.585 (.090)	1.585 (.090)	1.162 (.054)	1.171 (.170)
S	.753 (.041)	.727 (.036)	.614 (.035)	.662 (.094)
Fe	.049 (.003)AB[c]	.071 (.009)A	.082 (.012)A	.036 (.005)B
Zn	.028 (.001)A	.025 (.001)AB	.019 (.003)B	.022 (.001)AB
Mn	.487 (.122)	.400 (.083)	.549 (.121)	.333 (.064)
B	.026 (.000)A	.026 (.001)A	.020 (.001)AB	.018 (.002)B
Cu	.003 (.000)	.003 (.000)	.003 (.000)	.003 (.000)

N = Nitrogen, P = phosphorus, K = potassium, Ca = calcium, Mg = magnesium, S = sulphur, Fe = iron, Zn = zinc, Mn = manganese, B = boron, Cu = copper.

[a] Standard error of the mean is in parentheses.

[b] Concentrations were determined at each litter collection date (Burke and others 2000a) and content was summed for each plot for the year.

[c] Different uppercase letters indicate differences at α = 0.05.

Goodman (2000) concluded that N on the Coosawhatchie site did not limit soil microbes.

To test whether N or other nutrients may limit NPP at either study site, an assay developed by Raich and others (1994) for terrestrial forests was employed. In zones of similar hydroperiod (swamp tupelo on the Coosawhatchie site and wet transition zone on the ACE Basin site), root ingrowth cores impregnated with NH4Cl, Na2HPO4, KCl, CaC12 or distilled water (control) were implanted in May and collected in September of 1997. Root biomass into the N-impregnated microsites at the Coosawhatchie site was greater ($p < 0.05$) than in cores impregnated with other nutrients or water. Also, root biomass in the N-impregnated cores at the Coosawhatchie was greater than in the N-impregnated cores at the ACE Basin site (Figure 3.14). Using the interpretation of Raich and others (1994), the results indicate that NPP on the Coosawhatchie site was more limited by N than by other nutrients, and N limitation on the Coosawhatchie site was more important than on the ACE Basin site. In addition, roots on the Coosawhatchie site were generally more responsive to the root free matrix than were the roots on the ACE Basin site.

These results suggest that (1) nitrogen limits NPP more than other nutrients on the Coosawhatchie site, (2) forests at the Coosawhatchie site are more vigorous and thus better able to respond to nutrient-rich microsites than those on the ACE Basin site, (3) N assimilation and NPP at the ACE Basin site may not be limited by N availability, and (4) external (to the trees) nutrient cycling is more important at the Coosawhatchie site than at the ACE Basin site, suggesting turnover of both nutrients and biomass is greater and more rapid on the Coosawhatchie site.

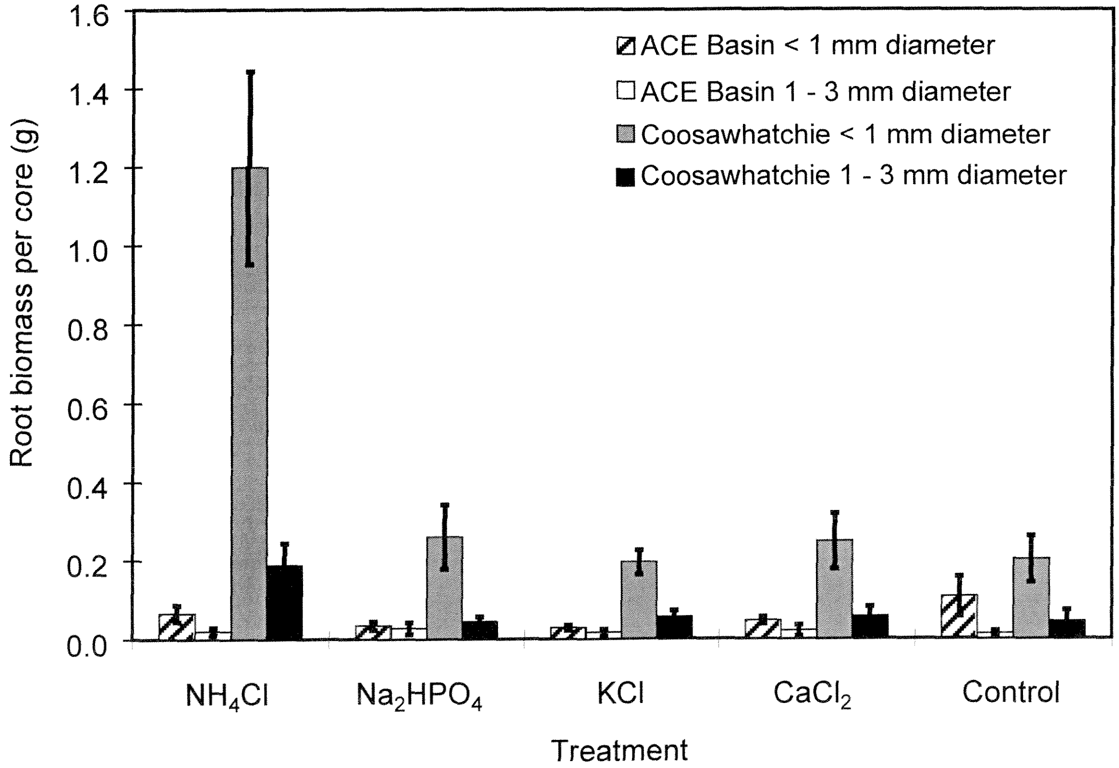

Figure 3.14—Mean (standard error) root biomass in nutrient-impregnated root ingrowth cores after 4 months (June through September) in the swamp tupelo community at the Coosawhatchie site and a similar wet transition community at the ACE Basin site.

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Appendix: List of plant species documented on the Coosawhatchie Bottomland Ecosystem Study Site[1]

Scientific Name	Common Name
Acer rubrum L.	Red maple
Arisaema triphyllum (L.) Schott	Jack-in-the-pulpit
Arundinaria gigantea (Walter) Muhl.	Cane
Asclepias perennis Walter	Milkweed
Asplenium platyneuron (L.)	Spleenwort
Athyrium asplenoides (Michaux) A. Eaton	Southern lady fern
Berchemia scandens (Hill) K. Koch	Supplejack
Bignonia capreolata (L.) Bureau	Cross vine
Boehmeria cylindrica (L.) Swartz	False nettle
Botrychium biternatum (Sav.) Underwood	Southern grapefern
Campsis radicans (L.) Seemann	Trumpet vine
Carex cherokeensis Schweinitz	Sedge
Carex intumescens Rudge	Sedge
Carex joorii Bailey	Sedge
Carex oxylepis Torrey and Hooker	Sedge
Carex sp. L.	Sedge
Carpinus caroliniana Walter	Ironwood
Carya aquatica (Michaux f.) Nuttall	Water hickory
Carya illinoensis (Wang.) K. Koch	Pecan
Carya sp. Nuttall	Hickory
Celtis laevigata Willd.	Hackberry
Chasmanthium laxum (L.) Yates[2]	Chasmanthium
Clethra alnifolia L.	Sweet pepperbush
Commelina virginica L.	Dayflower
Cornus florida L.	Flowering dogwood
Fraxinus caroliniana Miller	Water ash
Fraxinus pennsylvanica Marshall	Red ash
Fraxinus sp. L.	Ash (unknown)
Galium obtusum Bigelow	Bedstraw
Gelsemium sempervirens (L.) Aiton f.	Yellow jessamine
Gleditsia aquatica Marshall	Water locust
Hamamelis virginiana L.	Witch-hazel
Hypericum sp. L.	St. John's-wort
Hypoxis hirsuta (L.) Coville	Yellow star-grass
Hydrocotyle verticillata Thunberg	Hydrocotyle
Isoetes engelmannii A. Braun	Quillwort
Ilex opaca Aiton	American holly
Itea virginica L.	Virginia willow
Juncus sp. L.	Juncus
Leersia lenticularis Michaux	Cut grass
Leersia sp. Swartz	Cut grass
Leucothoe axillaris (Lam.) D. Don	Leucothoe
Liquidambar styraciflua L.	Sweet-gum
Liriodendron tulifera L.	Tulip tree
Lonicera sempervirens L.	Honeysuckle
Lyonia lucida (Lam.) K. Koch	Fetter-bush
Magnolia grandiflora L.	Bull bay
Magnolia virginiana L.	Sweet bay
Mitchella repens L.	Partridge berry
Myrica cerifera L.	Wax myrtle
Nyssa aquatica L.	Water gum

continued

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[1] Scientific and common names according to Radford and others (1968).

[2] Formerly *Uniola laxa* (L.) BSO. According to Godfrey and Wooten (1979).

Scientific Name	Common Name
Nyssa sylvatica var. biflora (Walter) Sargent	Swamp black gum
Nyssa sylvatica var. sylvatica Marshall	Black gum
Panicum dichotomum L.	Panicum
Panicum sp. L.	Panicum
Panicum spretum Schultes.	Panicum
Parthenocissis quinquefolia (L.) Planchon	Virginia creeper
Persea borbonia (L.) Sprengel	Red bay
Pinus echinata Miller	Short-leaf pine
Pinus glabra Walter	Spruce pine
Pinus taeda L.	Loblolly pine
Planara aquatica Walter ex J. F. Gmelin.	Water-elm
Pluchea sp. Cassini	Marsh-fleabane
Polygonum setaceum Baldwin ex Ell.	Persicaria
Proserpinaca palustris L.	Proserpinaca
Quercus alba L.	White oak
Quercus falcata var. pagodaefolia Ell.	Cherrybark oak
Quercus laurifolia Michaux.	Laurel oak
Quercus lyrata Walter	Overcup oak
Quercus michauxii Nuttall	Swamp chestnut oak
Quercus nigra L.	Water oak
Quercus phellos L.	Willow oak
Quercus shumardii Buckley	Swamp red oak
Quercus virginiana Miller	Live oak
Rhododendron canescens (Michaux) Sweet	Wild azalea
Rhus radicans L.	Poison ivy
Rhynchospora odorata C. Wright ex Grisebach	Beak rush
Rubus sp. L.	Blackberry
Rumex obtusifolius L.	Rumex
Rumex sp. L.	Rumex
Sabal minor (Jacquin) Persoon	Palmetto
Sabal palmetto Lodd. Ex Schultes	Cabbage palmetto
Salix nigra Marshall	Black willow
Saururus cernuus L.	Lizard's tail
*Sclaria sp.*Bergius	Nut rush
Sclaria verticillata Muhl.ex Willd.	Nut rush
Smilax bona-nox L.	Greenbriar
Smilax glauca Walter	Greenbriar
Smilax laurifolia L.	Bamboo greenbriar
Smilax rotundifolia L.	Greenbriar
Smilax smallii Morong	Greenbriar
Smilax sp. L.	Greenbriar
Spigelia marilandica L.	Indian pink
Symplocos tinctoria (L.) L'Her.	Sweet leaf
Taxodium distichum (L.) Richard	Bald cypress
Ulmus americana L.	American elm
Vaccinium corymbosum L.	Highbush blueberry
Vaccinium elliottii Chapman	Blueberry
Vaccinium sp. L.	Blueberry
Viola sp. L.	Violet
Vitis aestavalis Michaux	Summer grape
Vitis rotundifolia Michaux	Muscadine
Vitis sp. L.	Grape
Vitis vulpina L.	Frost grape
Woodwardia areolata (L.) Moore	Netted chain-fern
Woodwardia virginica (L.) Smith	Virginia chain-fern
	Grass 1 (unknown)
	Grass 2 (unknown)
	Grass 3 (unknown)
	Sedge 1 (unknown)
	Sedge 2 (unknown)
	Vine 1 (unknown)

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Only 23 percent of the presettlement acreage of bottomland hardwood forests remains today, and the remaining forests have lost many of their original functions. To successfully manage these forests we must be able to compare their functional capacities with reference or model wetlands. This report contains the results of the Coosawhatchie Bottomland Ecosystem Study during Phase I, 1994 through 1999—the baseline calibration period for development of the reference wetland. Information about the physical and community characteristics and the ecosystem processes is presented in 15 individual reports. Where possible, results from this site are compared with results from other sites, both within the Southern Forested Wetlands Initiative and from other bottomland hardwood research sites. Those who use this information should consider these results preliminary and are invited to contact the authors of each chapter for more detailed information about the methods, results, interpretations, and plans for participation in Phase II.

Keywords: Bottomland hardwood, Coosawhatchie River, ecological processes, ecosystem study, neotropical migratory birds, reference wetland, wetland hydrology.