Biological Services Program

FWS/OBS-81/37
March 1982

THE ECOLOGY OF BOTTOMLAND HARDWOOD SWAMPS OF THE SOUTHEAST: A Community Profile

Fish and Wildlife Service

U.S. Department of the Interior

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Cover design by Graham Golden

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THE ECOLOGY OF BOTTOMLAND HARDWOOD SWAMPS OF THE SOUTHEAST: A COMMUNITY PROFILE

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This report should be cited as follows:

Wharton, C.H., W.M. Kitchens, E.C. Pendleton, and T.W. Sipe. 1982. The ecology of bottomland hardwood swamps of the Southeast: a community profile. U.S. Fish and Wildlife Service, Biological Services Program, Washington, D.C. FWS/OBS-81/37. 133 pp.

PREFACE

This report is one in a series of community profiles whose objective is to synthesize extant literature for specific wetland habitats into definitive, yet handy ecological references. To the extent possible, the geographic scope of this profile is focused on bottomland hardwood swamps occupying the riverine floodplains of the Southeast whose drainage originates in the Appalachian Mountains/Piedmont or Coastal Plain (see study area Figure 1). References are occasionally made to studies outside this area, primarily for comparative purposes or to highlight important points. The sections detailing the plant associations and soils in the study area are derived from field investigations conducted specifically for this project.

In order to explain the complexities of the ecological relationships that are operating in these bottomland hardwood ecosystems, this report details not only the biology of floodplains but also the geomorphological and hydrological components and processes that are operating on various scales. These factors, in concert with the biota, dictate both the ecological structure and function of the bottomland hardwood ecosystems. We have utilized the ecological zone concept developed by the National Wetlands Technical Council to organize and explain the structural complexity of the flora and fauna.

The information in this profile will be useful to environmental managers and planners, wetland ecologists, students, and interested laymen concerned with the fate and the ecological nature and value of these ecosystems. The format, style, and level of presentation should make this report adaptable to a variety of uses, ranging from preparation of environmental assessment reports to supplementary or topical reading material for college wetland ecology courses. The descriptive materials detailing the floristics of these swamps have been cross-referenced to specific site locations and give the report the utility of a field guide handbook for the interested reader.

The senior author wrote the original manuscript and accepts the responsibility for all statements, theories, and figures not credited otherwise. The co-authors extensively revised, reorganized the format, and contributed parts of the manuscript, especially Chapters 3 and 4.

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ACKNOWLEDGMENTS

The authors reserve their most profuse thanks to those individuals (and their organizations) who devoted time to assist in the field: L.L. Gaddy, H. Boyd, A.E. Radford, J.M. Lynch, L. Peacok, J. Moore, R. Sharitz, M.M. Brinson, R. Sniffen, C. Gresham, J. Pinson, H.M. Leitman, A. Redmond, P. Grover, N. Eichholz, R. Kautz, G. Bass, and N. Young. The special logistical support of the Florida Game and Fresh Water Fish Commission through Grey Bass, Norman Young, and Neal Eichholz is particularly acknowledged.

We deeply appreciate the efforts of those who aided in species identification: S. Gilchrist, W. Heard, R. Guard, T. Wilkins, R. Godfrey, University of Georgia Herbarium. Those who supplied other assistance were R. Jones, C. Coney, J. Cely, D. Shure, H.L. Ragsdale , R. Sharitz, J. Adams, G. Guill, F. Parrish, and A. Benke. We are grateful to the following who critically read all or portions of the manuscript: Jay Benforado, Robert Huffman, Robert Meade, Helen Leitman, J.M. Lynch, Roger T. Saucier, Arville Touchet, and Eugene Turner. We acknowledge the very special help of Mark Brinson, Steven Forsythe, John Coffin, and Parley Winger.

We extend our sincere appreciation to Linda C. Lewis, Gladys V. Russell, and Kathy B. Waggoner of the Institute of Ecology, and to Elizabeth Krebs and Daisy Singleton of the U.S. Fish and Wildlife Service, for their dedication to the many hours of typing provided for the publication of this manuscript. We are also indebted to Kate Benkert and Hal Rienstra, U.S. Fish and Wildlife Service, for their valuable assistance. Finally, profound thanks are expressed to Gaye Farris, U.S. Fish and Wildlife Service, for her extraordinary editorial efforts.

INTRODUCTION

Bottomland hardwoods occupy the broad floodplains that flank many of the major rivers of the Southeastern United States as they flow through the Piedmont and Coastal Plain to the sea. These forests and their fauna comprise remarkably productive riverine communities adapted to a "fluctuating water level ecosystem" (Odum 1969) characterized and maintained by a natural hydrologic regime of alternating annual wet and dry periods.

The bottomland hardwood communities support recognizably distinct assemblages of plants and animals that are associated with particular landforms, soils, and hydrologic regimes. The fluctuating hydrologic regime dictating the ecologic functioning of modern floodplains is relatively recent, perhaps originating around 18,000 years ago in the late Pleistocene period, when changes toward present strong seasonal climates began (Martin 1980). Many floodplain species are traceable to Tertiary times, and others originated as far back as the Mesozoic. Apparently, rivers and their floodplains have served as refugia for numerous relict life forms which found the dynamic conditions there suitable. Plants such as tupelo gums, and animals such as alligators, turtles, gar, bowfin, sturgeon, and amphibians (Siren) survive essentially unchanged on modern floodplains as relicts from the Age of Dinosaurs. Ironically, in the face of massive land use of surrounding uplands, floodplains today remain some of the last refuges not only for floodplain species but also for upland species.

Because the floodplains occupied by bottomland hardwoods are transitional in the aquatic continuum between permanent water and terrestrial uplands, they are elusive to classify. The scheme of Cowardin et al. (1979) used here classifies bottomland hardwoods as forested wetlands in palustrine and estuarine ecosystems. Other terms or categories which have been used to classify this community include "seasonally flooded basins or flats" (Shaw and Fredine 1956); "mixed bottomland hardwoods and tupelo-cypress swamps" (Stubbs 1973); "oak-gum-cypress" and "elm-ash-cottonwood" (Boyce and Cost 1974); and "deep swamps," "narrow stream margins," and "broad stream margins" (Forest Service Resource Bulletins 1970, 1972, 1974, 1978).

The extent and distribution of bottomland hardwoods in the Southeast are indicated in Figure 1 and Table 1. Diverse classification schemes and the inclusion of other categories of forested wetlands make difficult precise calculation of the areal extent of the community; however, acreages appear to be equal in the four States (North Carolina, South Carolina, Georgia, and Florida) focused upon in this profile. The latest U.S. Forest Service Forest Surveys, standardized in 1930, have been used in preparing Table 1, which gives combined acreages of the two forest types occurring in each of the Forest Survey's physiographic classes. Each forest type, oak-gum-cypress or elm-ash-cottonwood, is dominated singly or in combination by these species (Boyce and Cost 1974).

Table 1 also includes the acreage of forested wetlands other than bottomland hardwood floodplains. Cypress and willow strands, where water spreads out and moves downslope through a wide forest of cypress, are not included as bottomland hardwoods; similarly, bays, pocosins, and cypress ponds are excluded from this community profile. Small drains, defined as poorly drained narrow strands lacking a well defined stream, include many tiny headwater branches and drainways. Although not specifically floodplains, they are certainly important in filtering drainage from the uplands into the larger systems. Their acreage is large but they are excluded from our calculation of bottomland floodplain acreage. Large swamps such as the Okefenokee and Dismal Swamp have been excluded as well.

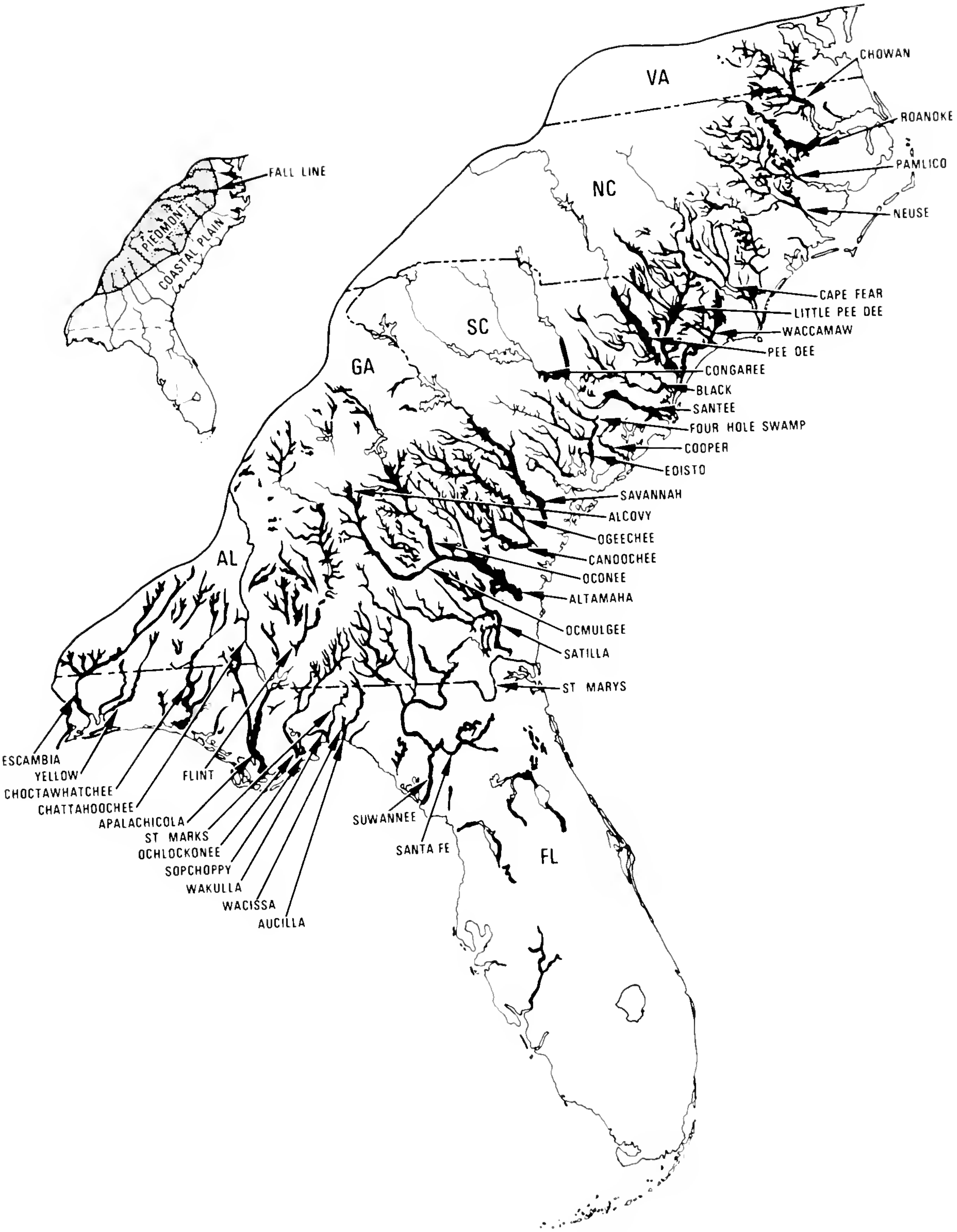

Figure 1. Major river foodplains and their associated bottomland hardwood communities within the Carolinas, Georgia, and Florida. Inset indicates physiographic provinces within the study area.

Table 1. Acreages of bottomland hardwoods (oak-gum-cypress and elm-ash-cottonwood) and other forest wetland classes in the south Atlantic States[a]. (Data courtesy Noel Cost, Southeastern Forest Experiment Station, U.S. Department of Agriculture Forest Service, Asheville, NC.)

Forested wetlands classes	States			
	FL	GA	NC	SC
Total bottomland hardwoods on floodplains	1,149,891	1,435,453	1,618,135	1,110,343
Total other	2,160,906	1,623,052	565,942	717,138
Cypress strands	268,988	9,730	3,037	11,635
Cypress ponds	594,857	200,641	2,581	56,298
Bays & wet pocosins	564,359	186,088	221,307	217,650
Willow heads & strands	39,492	8,405	-	1,098
Marl flats & forested prairies	2,743	-	2,745	-
Small drains	589,291	1,154,151	328,722	398,629
Other hydric	101,176	64,037	7,550	31,828

[a] Inventory dates: Florida, 1980; North Carolina, 1974; South Carolina, 1978; Georgia, primarily 1972 but includes 1981 survey of southwest Georgia.

This community profile has been prepared in part to provide information for management decisions. Like most natural communities, bottomland hardwoods have felt the impact of man. Unfortunately, the absence of uniform treatment of data and the screening of it as indicated above in publications such as Boyce and Cost (1974), Langdon et al. (1981), and Turner et al. (1981) make it difficult to use earlier survey figures to calculate this impact in terms of loss of bottomland hardwoods on southeastern floodplains over time.

Losses of bottomland hardwoods in areas outside the specific study region have been severe, none more so than the floodplains of the Mississippi River drainage. There conversion of forest to agriculture, primarily soybeans, has reduced by 60% the areal extent of the hardwood community; by 1995, only a projected 3.9 million acres will remain intact, down from 11.8 million acres in 1937 (MacDonald et al. 1979). Although losses of floodplains bottomland hardwoods in the Carolinas, Georgia, and northern Florida have been much less extensive, few areas in the Southeast have escaped some direct or potential impact of man.

Besides conversion to agriculture, another impact on bottomland hardwoods has been conversion to tree-farm monoculture. Numerous examples occur along the floodplains of the Ocmulgee and Oconee Rivers, GA, where the higher elevated bottomland hardwood communities are logged, the stumps bulldozed into windrows, and the terrain prepared for pine (or other) monoculture.

Floodplain rivers have also been subject to severe impacts, including construction of impoundments, diversion canals, channelization, dredging, and shortening of channels. These alterations change the hydroperiod and may permanently alter the ecology and functioning of the floodplain.

It has not always been recognized that the entire bottomland over which flooding occurs is a functional part of the wetland system and must be considered as a unit when making resource decisions. Because the bottomland hardwoods in the study area still retain their ecological functions and value, environmental managers have the opportunity to consider and weigh management alternatives. This profile provides information to aid them in this task.

CHAPTER 1

MODERN AND PALEO-GEOMORPHOLOGY OF FLOODPLAINS

INTRODUCTION

The complexities of hydroperiod, climate, soils, and watershed characteristics have produced an often bewildering mosaic of vegetative zones and associations in the bottomland hardwood community. To understand better the complex relationship between hydroperiods and the bottomland hardwood community, one must first consider the geomorphology of the floodplain itself. The biota of the floodplain cannot be wisely interpreted or managed, nor can the impact of man's modifications be correctly evaluated without understanding watershed-dependent floodplain hydrology and geomorphology. The biota alone provide too narrow a viewpoint.

The energy of flowing water and the sediment load of river flows are ultimately responsible for the geomorphic landforms on southeastern floodplains. This chapter discusses processes of water and sediment distribution on floodplains and landforms characteristic of both modern and ancient environments.

ORIGIN AND DYNAMICS OF FLOODPLAINS

The flows and sediments carried by a river are responsible for the origin, character, and maintenance of the floodplains and their forest cover. The gently sloping coastal plains of the Southeastern United States provide an ideal environmental setting for floodplain formation. Erosional and depositional processes culminate in a sinuous river channel within a broad flat plain bounded by valley walls or bluffs--the floodplain (Figure 2).

Striking examples (Figure 2) of floodplain formation occur along rivers in the study area at the fall line, the abrupt transition between the Piedmont and the Coastal Plain. The excess energy of river flows in passage over the bedrocks and red clays of the Piedmont begins to dissipate at the fall line, where the river first encounters the easily erodible sedimentary strata of the Coastal Plain. This dissipation results in deposition of alluvium (sands, silts, and clays) which in turn is reworked by riverine processes into meanders. The residual energy of the flowing water is expended by this lateral meandering which serves to widen the river valley. Rivers adjust their slopes by meandering until they reach a nearly steady-state, with sediment load balanced with water velocity and volume. As the floodplains widen out, more sediments can drop out from overbank deposition. Remarkably broad, flat floodplains are the result of these processes. Mountain and Piedmont rivers, on the other hand, although they form floodplains when topography and soils permit, still retain much potential channel energy.

First order variables that determine the behavior of water and sediments include climate, geology, soils, land-use, and vegetation (Morisawa and LaFlure 1979). Variables that describe the channel are velocity, slope, flow-depth, plan-form (shape from an aerial viewpoint), and width (Gregory 1977). Other variables are meander length and meander belt width (Blench 1972), discharge (volume of water/unit time), and roughness of river bed (bottom presence of trees, cobbles, dunes, etc.) (Leopold and Wolman 1957). These variables are extremely interdependent.

The dominant depositional/erosional processes on floodplains are: (1) point bar deposition, (2) overbank deposition, and (3) sheet or gully erosion (scour) and redeposition on floodplain surfaces in a sequence of floods (Sigafoos 1964).

The point bar is built on convex banks of streams or river meanders by lateral accretion (Figure 3). Since deposi-

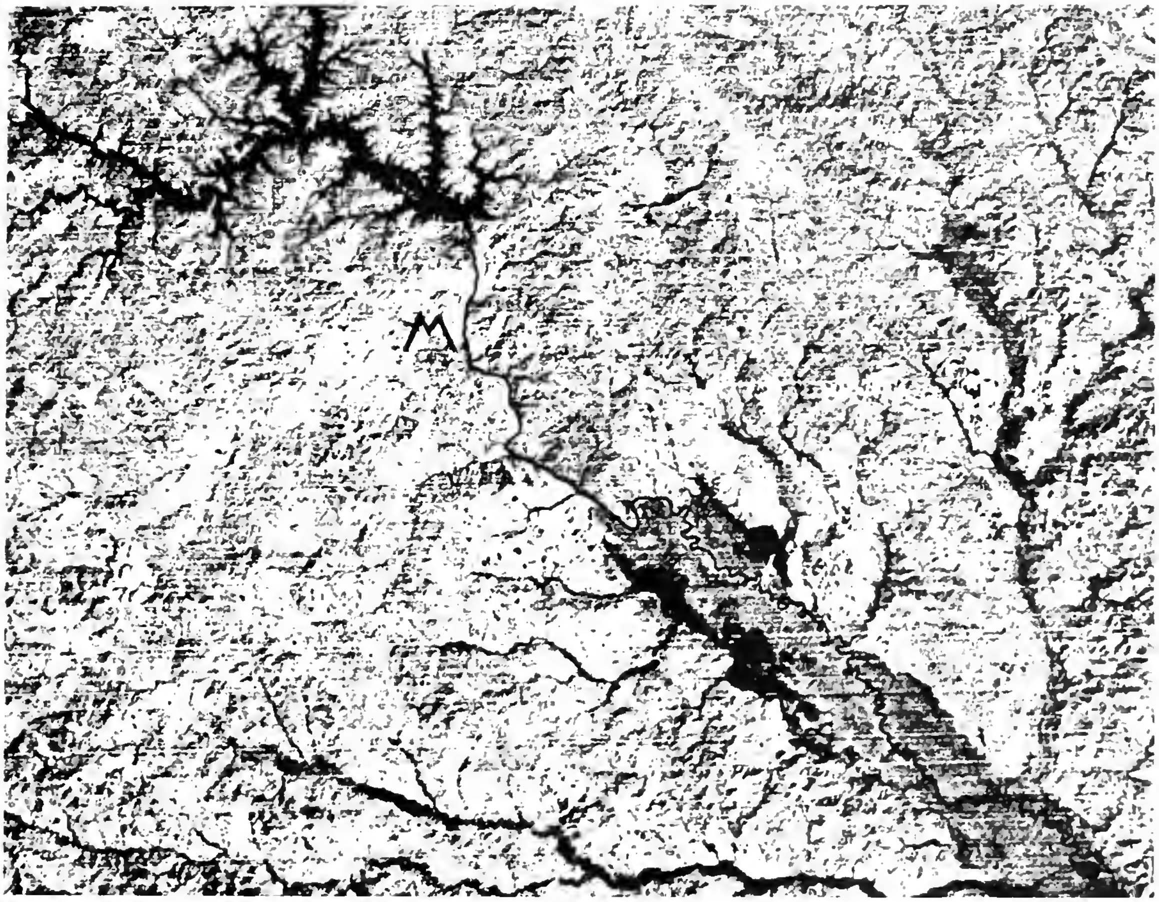

Figure 2. Landsat image of the floodplain of the Oconee River, GA, showing how large alluvial rivers that drain the Piedmont form extensive tracts of bottomland hardwoods below the fall line, which in this photo runs diagonally from lower left to upper right. Milledgeville, GA, is marked M. Photo courtesy Georgia Department of Natural Resources.

tion on the convex bank keeps pace with erosion of the opposite concave bank, the bulk of the sediment remains stored in the floodplain (Leopold and Wolman 1957).

Though much slower than point bar formation, vertical accretion by overbank deposition also builds most southeastern floodplain surfaces. Overbank deposition results from high water losing its velocity and dropping sediments as it traverses the floodplain, usually by sheetflow or overflow channels. The amount of sediment deposited can vary widely. For example, a single flood in the Atchafalaya River Basin, LA, caused sediment accumulations of up to 46 cm (18 inches) over portions of this vast flood plain. Accumulations ranging from 0.3 cm (.125 inches) to 3.8 cm (1.5 inches) have been documented for floods in the Potomac River Basin, VA (Sigafoos 1964). Average deposition, however, ranges between 0.3 m (1 ft) and 0.6 m (2 ft) in 200 to 400 years (Wolman and Leopold 1957). The bed of the channel, as well as the surface of the floodplain, accumulates sediment deposits during floods. Channels are also created and maintained by these overbank flows and accommodate the excess discharge of flood waters.

On forested floodplains, local erosion by overbank flows may produce rapid recycling and overturn of deposited sediments. Surface erosion or scour is followed by deposition of comparable magnitude, and the floodplain becomes a spatial

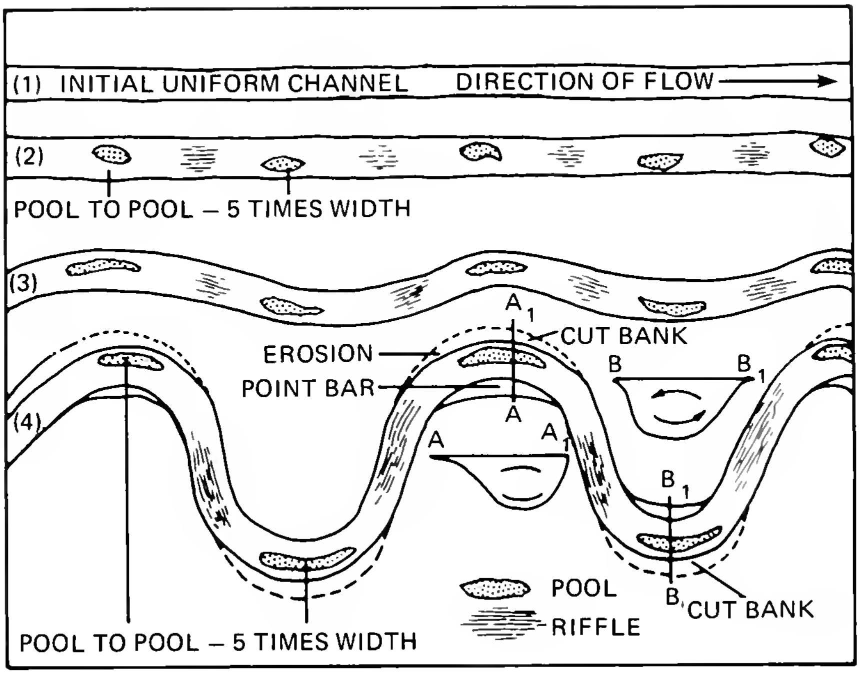

Figure 3. Point bar and meander formation in floodplains. Unstable stream flow in uniform river channels (1) forms pools and riffles (2). A meandering channel (3) develops and eventually exhibits erosion on the concave banks of meanders as well as deposition and point bar formation on the convex banks (4). (After Muller and Oberlander 1978, courtesy of Random House, Inc.)

mosaic of erosional and depositional surfaces superimposed over material deposited earlier by point bar accretion (Sigafoos 1964). The features resulting from these processes are detailed in the following sections.

Sediment

Sediment source is provided by continual erosion of the landscape throughout geological time. In the Piedmont and mountains, this source is igneous and metamorphic rocks (granites, schists, and gneisses) which decay or weather under the influence of rainwater. Released components are sands, silts, and clays, which are transported by sheet-wash or gully-wash into streams. In the Piedmont this decay produces a soil horizon (vertical layer) of saprolite (decomposed rock) up to 9.2 m (30 ft) thick.

The weathered Piedmont saprolite little by little washes downstream. Piedmont sands are transported as bedload rolling along the bottom of stream channels, whereas silts and clays are carried as suspended matter in the water column. Silts and clays, the principal components of surface floodplain soils, settle out or form overbank deposits during floods. A reduction of particle size downstream may result from the weathering of silt and clay particles that remain in place for long periods of time between episodes of downstream transport (Curry 1972).

Land uses in uplands profoundly affect the quantities of sediment entering a stream. Before the 1900's, sediment inputs to southeastern river systems were minimal according to some observers. River pilots recalled that as late as 1912 the Tennessee River was relatively clear even after heavy rains (Ellis 1936). According to one report, the turbid Altamaha River of coastal Georgia was once a relatively clear stream, and as late as the 1840's it was possible to determine on which tributary (Ocmulgee or Oconee) rains were falling since much of the Oconee drainage was in agriculture (Lyell 1849).

Sediment losses from forested uplands are usually modest (2.5 cm or 1 inch/ 16,000 years; Soil Conservation Service 1977). However, the losses after the forest is removed can be quite substantial (Table 2). When forest cover was reduced from 80% to 20% in the Potomac Basin, sediment loading increased eight times (Patrick 1972). The Soil Conservation Service (1977) reported losses from croplands (some of which were once forested floodplain) of 38.4 tons/acre/year of topsoil to the Obion-Forked Deer River (TN).

It is difficult to distinguish whether sediments are derived from natural or culturally accelerated sources (Strahler 1956). Several investigators have attempted to estimate losses from the uplands by measuring the thickness of sediment layers in coastal floodplains. Soils surveys indicate a loss of 15.2 cm (6 inches) of topsoil from the South Carolina Piedmont in 150 years. Between 1910 and 1934, one Georgia Piedmont watershed lost 218 tons/km^2/year, but by 1974 this rate was reduced by 86% (30 tons/km^2/year) (Meade and Trimble 1974). Happ (1945) concluded an average Piedmont upland soil loss of 9.4 cm (3.7 inches) since earliest settlement.

Although agriculture has heavily accelerated the loss of soil from uplands, 90% of the sediment from accelerated Piedmont erosion remains on hill slopes and in stream bottoms (Trimble 1979). In fact, the composition of alluvial sediments and their rate of deposition in some floodplains do not reflect a marked change in rate due to agriculture. In South Carolina, both Coastal Plain rivers (blackwater) and rivers originating in the Piedmont (alluvial) have three terraces (Pleistocene) above the present floodplain that are similar in type of landform, slope, particle size, and composition of sediments to those of the present (Holocene) floodplain (Thom 1967). For example, the quartz sands of the present point bars of the Little Pee Dee River (a blackwater stream) are similar to those of the higher terraces. In the Great Pee Dee River (a Piedmont, or alluvial, stream), the three older terraces also have the same composition of silts and sands as does the present floodplain.

Water and sediment supply are not continuous but result from discrete climatic events (Harvey et al. 1979). The largest portion of the total load of many rivers is carried by high flows on the average of once or twice a year. As flow variability increases and as size of watershed decreases, a larger percentage of sediments is carried by less frequent flows. In many basins 90% of sediment is moved during floods recurring at least once every 5 years (Wolman and Miller 1960). Piedmont streams carry 10 times the sediment of Coastal Plain streams at the same discharge rate during floods (Meade 1976).

Slope and Meandering

River systems are remarkably dynamic. Changes of slope (elevational gradient) which cause rivers to flow can be due to (1) crustal uplifting or downwarping responses of the coast to the removal of the Pleistocene ice mass, (2) scour or erosion which steepens headwaters, or (3)

Table 2. Comparative sediment losses and land-use practices (Happ et al. 1940).

Land use practices	Sediment loss (tons lost/acre/year)
Oak forest	0.05
Bermuda grass	0.19
Cotton (contour plowed)	69.33
Cotton (down slope plowed)	195.10
Barren abandoned field	159.70

deposition which flattens downstream reaches. Deposition by tributaries often increases river slope in the region immediately downstream of their junction with the main river. This increase in slope results from elevation of the river channel bed due to sediment accretion at the juncture of the two streams.

Basic features of swamp rivers and streams are their sinuous meanders (Figure 3). Meandering is one way the river accommodates slope. Meanders lengthen the path of the water, adjusting the energy of the flow to a uniform rate of energy loss per unit of stream length (Leopold and Langbein 1966). In other words, the flow rate is stabilized as the slope of the stream is made more uniform and less steep by increasing the distance that the water traverses in its vertical descent from the Piedmont to the coast. The process can be compared to a skier whose rate of descent is slowed by meandering: the consistency and resistance of the snow determine the meander path which he follows for his particular weight. The path of the water bends as uniformly as possible (conforming to a sine-generated curve), minimizing bank erosion and the expenditure of energy (Leopold and Langbein 1966). After the water rounds the meander curve, it flows straight until centrifugal and inertial forces are diminished to the point where gravity can turn the water back downslope and the process is repeated. The greater the volume, velocity, or density (water containing sediment weighs more than water without sediment), the greater the force and the further the river travels before it is turned back to form the next meander loop. It follows that meander length and radius are closely related to the width of the river. The width of meanders is a function of water volume, velocity, and density. The development of meanders occurs at bankful (flood) stages (Thorne and Lewin 1979). Meanders occur at fairly consistent intervals of 7 to 15 times the width of the channel (Dury 1977).

River slope adjusts naturally to the velocity required to transport the load of water and sediment supplied by the drainage basin. As slope increases, a stream must cut down (degrade) or develop a sinuous course. A meandering reach is stabler than a straight reach (Yang and Song 1979) because it more closely approaches uniformity in the rate of work over the various riverbed irregularities than does the straight channel (Leopold and Langbein 1966). In addition, the meandering river and its floodplain apparently present the most efficient geometry to accommodate the mean and extremes of flow variability that have occurred throughout its history.

The types of sediment through which meanders pass are important. In a river system, meanders will occur where bank material is comparatively uniform. Meanders move slowly if banks are cohesive (silt or clay) and rapidly if banks are easily erodible (sands, silty sands). Depending on the type of sediment load, meander wavelength can vary ten-fold at a given discharge (Schumm 1969; Thorne and Lewin 1979).

FEATURES OF MODERN FLOODPLAINS

Although floodplains appear flat and featureless from the air, in reality they are characterized by diverse topographic features as a result of the continual, dynamic reworking of their sediments by rivers. The low topographic relief of the floodplain landscape is deceptive; a matter of inches in elevation may produce quite distinct ecological zones (see Chapter 4). The following sections detail the origin and the dynamic nature of the major geomorphic features of the floodplain (Figure 4).

Channels

The river channel processes, as discussed earlier, create and maintain the floodplain. As a precursor to developing meanders, basically unstable flows in the stream create a series of pools (scoured areas) and riffles (areas of redeposition) through erosion of the stream bank. Erosive forces continue to act in meanders. Scouring occurs on the concave bank of a meander; conversely, scoured material is deposited on the opposite convex bank (Figure 3). Good basic references on channel geomorphology are Leopold et al. (1964), Allen (1965) and Schumm (1971) as well as overviews by Thorne (1977) and Winger (1981).

The stream channel morphology (width, depth, slope, and meander characteristics)

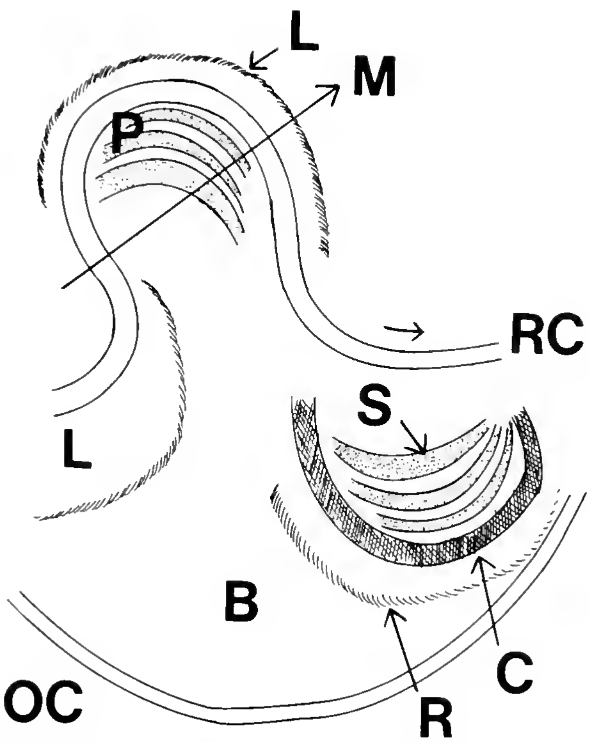

Figure 4. Diagram of an idealized alluvial floodplain with various depositional environments. RC = river channel; M = direction of meander movement; L = natural levee; P = point bar deposits (alternating ridge and swale topography); B = backswamps; C = channel fill deposits (former ox-bow lake); R = ridge (former natural levee around adandoned channel); OC = overflow channel; S = swale deposits.

depends on long-term patterns of flow (Blench 1972). High flow regimes are principally responsible for the formation of channels, while low flows are responsible for only minor adjustments in channel morphology (Keller 1977). The process of channel formation is greatest at bankful stage. Therefore, the annual to biennial flood intervals are more important than periodic catastrophic flooding (Wolman and Miller 1968). When flows exceed the capacity of the river channel, the entire floodplain becomes the channel, and additional physical factors come into play.

Since current velocities are a function of the slope of the water surface, it is not surprising that water velocities over the floodplain during overbank flows are comparable to the mean velocities of natural channels and transport sands and silts (Wolman and Leopold 1957). In fact, during overbank flows when the waters leave the meandering channel, the floodplain surface becomes the high water channel with the current directed straight downslope (valley-axial direction) shortening the path of flow and increasing the slope of the water surface (Carlston 1965). Only the structure of the intact forest impedes the ravaging flows and prevents catastrophic scouring of the floodplain surface and valley walls.

Under certain conditions, specialized channels are formed. Termed braided and anastomosing channels, they are characterized by the main river channel dividing into numerous interconnected channels. Braiding results from a change in grade or slope so abrupt that coarse sediment, usually sand, is precipitously deposited. Braiding, however, can occur at any point in a stream where large deposits of coarse sediments occur. For example, large amounts of sand brought down by a channelized reach of a tributary (Flat Branch) of the Alcovy River (GA) have been deposited on the main stream floodplain, causing the main flow to braid. Braiding may also occur at river confluences (e.g., Little Pee Dee and Lumber River, SC). Braiding is often a temporary phenomenon. When a river divides and rejoins on a vegetated floodplain and the channel configurations are relatively unchanging, it is better termed an anastomosing stream. Both Four Hole Swamp (SC) and parts of the Chipola River (FL) are examples of anastomosing channels.

Natural Levees

During periods of overbank flow, as waters spread out over the floodplain, water currents abruptly slacken, and suspended sands and silt are deposited as a levee immediately adjacent and parallel to the channel.

Natural levees (Figures 4-6) are best developed on concave stream banks. They also may occur along straight reaches, although they are usually higher on one side than on the other. Some large rivers may have mile-wide levees; however, the average river in the Southeast has levees between 30 m (98 ft) and 100 m (328 ft) wide. Natural levees slope gently to flood basins and backswamps. The height

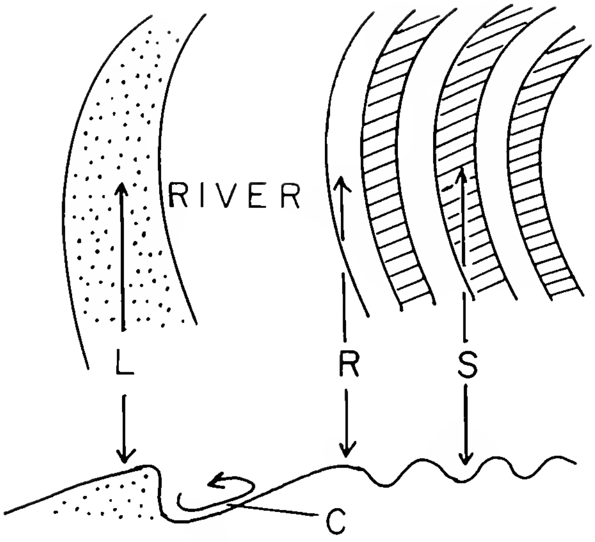

Figure 5. A meander bend and cross section showing levee (L) and ridge (R) and swale(S) topography so common on modern and relict surfaces. Pioneer and successional plant species anchor the newly formed sandy ridges leading to even more deposition at each high water episode. Normal helicoidal currents (C) conduct sediments up the bar slope.

of levees diminishes as rivers approach the coast because the stream's energy to move sand also decreases downstream (Table 3 and Figure 6). Some deeply incised streams with headwaters arising from clay-rich soils (Tallahala River, MS) have barely discernible levees. Many blackwater streams have unimpressive levees, apparently due to lack of sufficient gradient in the outer Coastal Plain. A breach (or crevasse) in the levee may produce an alluvial fan-shaped feature termed a crevasse-splay deposit which spreads out over the floodplain (Allen 1965).

Floodbasins, Flats and Backswamps

The term floodbasin specifically applies to vast underfitted floodplains (floodplains developed under a significantly higher flow regime than at present) where channel meanders may occupy only a portion, or belt, of the floodplain width. Along southeastern rivers that are not markedly underfitted, the floodplain between the natural levees and high valley wall is generally called ambiguously a "backswamp" or more succinctly a "flat" where elevational relief is limited to shallow depression basins and almost imperceptible rises. The term backswamp also may be applied specifically to peat-forming environments occupying relict channels along the outer rim of the floodplain.

Table 3. Changes in levee height in upper, middle, and lower reaches of typical southeastern floodplain rivers.

Rivers	Levee height (ft) Upper	Levee height (ft) Middle	Levee height (ft) Lower
Roanoke (NC)	13.0	6.0	0
Great Pee Dee (SC)	6.0	3.0	<2
Apalachicola (FL)	9.6	4.5	-

Floodbasin, flat, and backswamp sediments are composed of fine silt and clay particles. Acid backswamps are environments where deposition is minimal and are constantly wet, having water tables at or near the surface. Most of the floodplain, however, dries out annually. The fine clays tend to dry and crack in polygonal patterns, allowing oxygen to enter. Deposits in these areas vary with frequency of flooding, proximity to the channel, sediment load, flow velocity, and substrate texture. In many eastern floodplains devoid of significant relief, overbank deposits may be coarse and layered. Coarse layers represent the rise to maximum stage of an individual flood; the alternating fine layers represent recession of flow (Allen 1965).

Point Bars and Ridge and Swale Topography

Most deposition occurs along the main channel of the swamp stream. Materials are eroded from concave sides of channel meanders and redeposited on convex bends to form point bars (Figure 3). Small ridges formed on the point bar by deposition of bed load material during floods form a temporary natural levee on the convex side of meanders. The crests of these ridges may stand higher than natural levees on the concave side. As the river bed moves laterally and downstream (Figure 5), a series of ridges forms with intervening

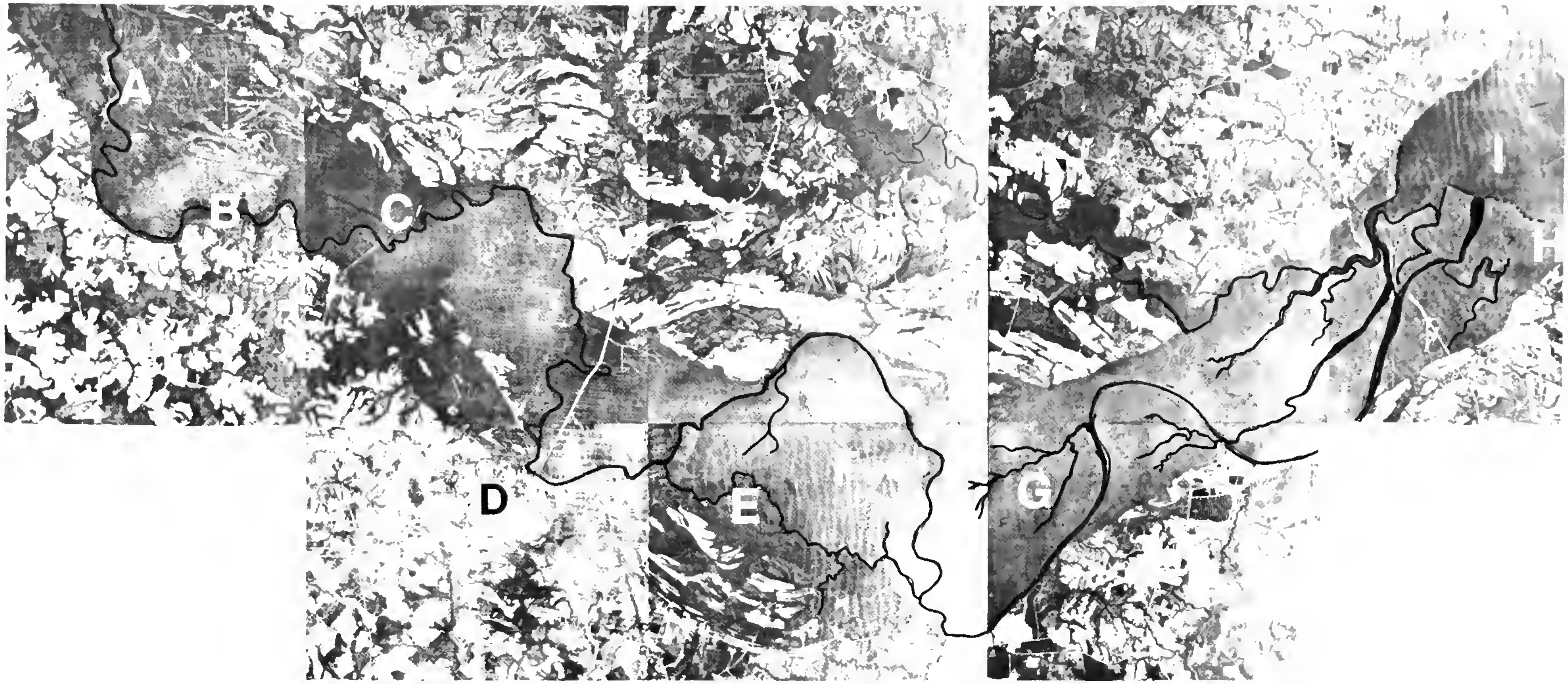

Figure 6. Aerial photomosaic of the lower Roanoke River indicating floodplain features characteristic of rivers approaching the coast. (A) Many oak-dominated ridges occur. (B) Levees are high (4 m or 13 ft) and broad (91-594 m or 300-1950 ft). (C) Large tracts of water tupelo-cypress with logging road networks. (D) Levee heights drop to 2 m (6 ft). (E) Due to mix of late Pleistocene and Holocene influences, floodplain features are very diverse. (F) Levees absent, river at base level; floodplain almost pure gum-cypress (logged by barge). (G) Tributaries now arise de novo from floodplain, indicating tidal influence. (H) Shrub bog with deep peat. (I) Albemarle Sound. (Photoquads: North Carolina Department of Natural Resources and Community Development; data from Lynch and Crawford 1980.)

depressions or swales. Vegetation quickly invades and stabilizes each point bar ridge, encouraging further deposition. Ridges are composed primarily of sands. Silts and clays are deposited mainly in swales, forming a sticky clay subsoil (gley), sometimes called "blue mud." Material eroded from the concave side of one meander loop is deposited on the convex side of the next downstream meander. The floodplain is thus "reworked" to the depth of the deepest part of the channel. Sediments are resuspended by powerful bottom-flowing crosscurrents (Figure 5). Meanders migrate because of the constant erosion (undercutting) and/or slumping of the concave bank laterally and downslope. Meander migration is slow (<3 m or <10 ft/yr) in small southeastern rivers, particularly those with forested banks. On the other hand, meanders in India's huge Kosi River moved 750 m (2,460 ft) in 1 year (Wolman and Leopold 1957).

Dune Deposits

Aeolian dunes form when strong winds blow exposed sand from point bars or other sources onto the floodplain. Dunes 13.7 m (45 ft) high sometimes are formed by the deflation (wind removal) of point bar sands and other bare areas of the floodplain (Allen 1965). Several linear series of large dunes occurring on the east side of the Altamaha River (GA) floodplain are of probable aeolian origin (Bozeman 1964). So extensive are these dunes that the proposed Big Morter-Snuffbox Project (Soil Conservation Service) recommended that they be artifically joined to create a huge levee to block off part of the floodplain and divert water from eventually flowing into certain tidal river distributaries. Aeolian dunes and those associated with the relict braided stream channels (e.g., Little Pee Dee floodplain, SC; Thom 1967) probably were formed by gale-force Pleistocene winds blowing across the unvegetated part of the floodplain from the southwest. Dune chains are more likely to be formed where discharge varies widely and the floodplain is not heavily vegetated (Allen 1965). Discharge is thought to have varied much more during the Pleistocene when strong seasonality developed.

Scour Channels, Hummocks and "Mini-Basins"

Scour channels, hummocks, and minibasins are microtopographic features producing only slight elevational and drainage changes; however, their effect on plant species distribution is often marked.

Scour channels are small waterways within the floodplain generally formed during high water as flows seek shortcuts: for example, cuts or chutes across bends, or tributary connections to the main channel. A high percentage of sand is present in the scour channels (and on the adjacent floodplain as well) because scour channels are areas where sheet flow may carry a substantial bed load of sand across the floodplain flats.

Hummocks are small "islands" left after years of erosion by scour channel currents. Usually the curved channels in hummock terrains are weblike, weaving around the bases of trees which may be "stooled," often bearing ferns and shrubs on swollen bases. The top of hummocks may bear trees characteristically found in areas of higher elevation, although in some cases trees such as tupelo gums and cypress form hummocks themselves.

Minibasins are shallow depressions that sometimes occur between tree bases. Some may be created by swirling water; others are of ambiguous origin. They are frequently filled with rainwater. Any detritus trapped in them is rapidly decomposed by frequent fluctuations between dry and moist conditions. This is in contrast to areas around the drier, raised tree bases where detrital accumulations tend to increase floodplain floor elevations. In addition, much of the aerobic-anaerobic nutrient cycling is accomplished in rain-filled minibasins (Wharton and Brinson 1979b) (see Chapter 3).

PALEO-GEOMORPHOLOGY

It is now recognized that Pleistocene ice age climates and hydrology strongly influenced both terrestrial and aquatic landforms. Glacial and interglacial periods during the Pleistocene produced dramatic changes in climate, precipitation, and sea level. Increased precipitation and more intense. frost action during glacial advances caused considerable downslope movement and subsequent translocation and deposition of surface materials (Whitehead and Barghoorn 1962). The diminished relief and aggraded (filled in) valleys of today's Piedmont are evidence of the tremendous impact of the lateral migration of soils during that era (Eargle 1940). Many common Piedmont soils are underlain by organic deposits as much as 3.7 m (12 ft) thick representing downslope transport and deposition; in one study in South Carolina more than 50% of the surface was underlain by these soils (Eargle 1940). Pollen dating of the soils indicated they were deposited more than 35,000 years ago, possibly during the waning of the first of the two periods of Wisconsin glaciation, the so-called Altonian substage.

Some floodplains in the Southeast apparently were affected by the climatic changes associated with continental glaciation. One striking feature reflecting these past climatic regimes is the dramatic discrepancy between the size of the floodplain and the size of the present-day river. Today many streams are too small (in terms of discharge volume and meander dimensions) to have produced such wide floodplains. Such streams are described as "underfitted" (Dury 1977). This phenomenon is common in alluvial rivers and may occur in coastal blackwater streams (Wharton 1977). A growing body of evidence indicates that the geomorphology of underfitted stream floodplains can be explained by the sequence of different hydrologic regimes resulting from prehistoric climates (Fisk 1947, 1951; Schumm 1971; Dury 1977; Froehlich et al. 1977; Mycielska-Dowgiallo 1977).

Floodplain width is a function of sediment deposition and redistribution by meandering during periods of greatest stream discharge, coupled with periods of relatively high sea level. Increased discharge over that of the present was probably due to increased precipitation. Ancient flow regimes can be determined through studies of ancient paleochannels in present floodplains (Schumm 1971; Dury 1977; and others). Dury calculated, from ratios of former to present channel bedwidths and meander wavelengths, that discharge 12,000 years ago was 18 times greater than that at present. Sediment delivery rates were three times those of today. This increased discharge was at least in part due to a pluvial (rainy) period of much greater rainfall occurring 18,000 to 10,000 years ago (Thom 1967; W.G. McIntire, Louisiana State University Center for Wetland Resources, Baton Rouge; personal communications). Discharge for many streams subsided about 10,000 years ago. Runoff decreased to one-seventh of its magnitude 2,000 years earlier (Dury 1977). Streams and rivers began to assume their underfit characteristics at this time.

Climatic changes, coupled with the more subtle influences of change in gradient brought about by lowered sea levels (Figure 7) or tectonic rebound of the land, formed another characteristic geomorphic feature of southeastern floodplains--the floodplain terrace. Increased flow volume or, in some cases, an increased gradient, changed the hydrologic regime and created a new floodplain surface, often lower than the old one. Decreased flow volume or increased sediment sometimes reversed the sequence, filling the floodplain back up with new sediments. In any event, steplike terraces resulted, many of which are remnants of prehistoric surfaces. This sequence of alternating high (degrading) flows and lower (aggrading) flows is diagrammed in Figures 7 and 8. Because precipitation generally has declined into modern times,

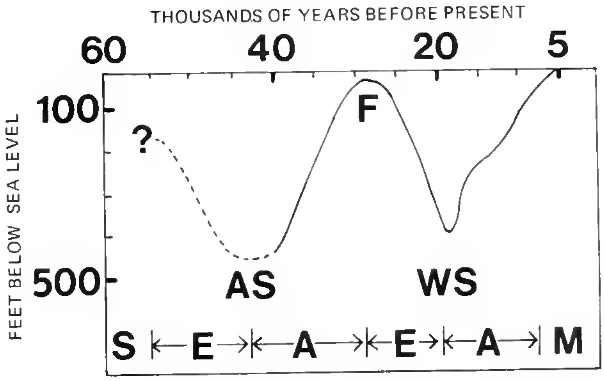

Figure 7. Sea level changes between the Sangamon interglacial period (S) and modern times (M) covering two periods of Wisconsin glaciation, the Altonian (AS) and the Woodfordian substages (WS), and a warmer interglacial period, the Farmdalian (F). Periods of entrenchment (E) occurred during glacial buildup. (A) represents periods of alluviation when alluvial river valleys were filled with sediments. (Modified from Saucier and Fleetwood 1970.)

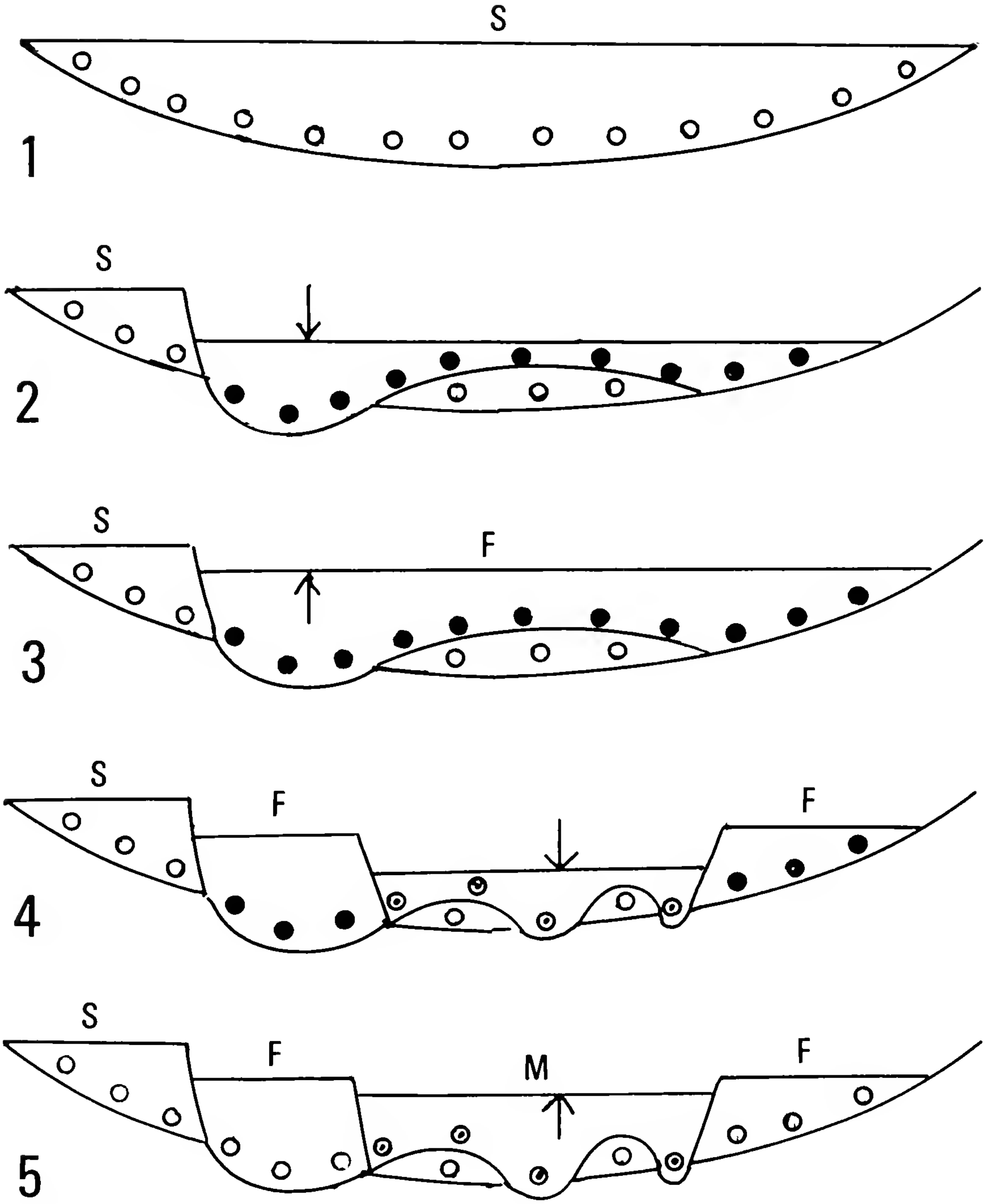

Figure 8. Development of present-day relict and modern floodplain surfaces. (1) Sangamon (S) interglacial stage. (2) Entrenchment (scouring) during waxing Altonian substage. (3) Farmdalian (F) interglacial with substage alluviation filling in the former entrenched valley. (4) Entrenchment during waxing Woodfordian substage. Remaining Farmdalian (F) deposits are also known as Deweyville (or Terrace I). (5) Post-Woodfordian alluviation forming modern day Holocene floodplain surface (M) about 4-5,000 years ago. Drawings highly modified from Saucier and Fleetwood (1970).

and rivers have made drastic changes in their courses, the floodplain has become a succession of relict surfaces, each bounded by terraces older than those closer to the river. Their importance lies in the hydrologic control they still exert over the modern floodplain.

At least three terraces can usually be found in southeastern floodplains. The Holocene terrace is usually the most recent; such terraces are known as "first bottoms." The next lowest terrace is known as the Terrace I, Deweyville, or in South Carolina "second bottom," and is distinguishable on many southern floodplains, including the Altamaha (GA), Pee Dee (SC), Cape Fear (NC), the Pearl and Pascagoula (MS), and the Sabine, Trinity, and Brazos (TX) (Gagliano and Thom 1967). Terrace I sediments were deposited during a fluvial period 17,000 to 36,000 years ago with flows that were five to seven times greater than at present forming giant meander scars or a braided topography of sandy bars and fossil dunes (Pee Dee River, SC) (Thom 1967). In South Carolina, Terrace I lies 1.5 to 3.0 m (5 to 10 ft) higher than the modern floodplain and 1.5 to 6.0 m (5 to 20 ft) below a still higher Pleistocene fluvial or river terrace known as Terrace II (Gagliano and Thom 1967). Another floodplain terrace classification scheme for the Ouachita River of Arkansas and Louisiana combines three terraces into a "Deweyville sequence" lying between the original pre-Wisconsin glacial sediments deposited in the Sangamon interglacial period (the Prairie Terrace) and the modern Holocene floodplain (Saucier and Fleetwood 1970).

Prehistoric floodplain surfaces still function in the modern hydrologic regime. Some are inundated by present high water, and relict channels, ridges, and swales bear vegetation associations indistinguishable from those on their recent analogues. The Pleistocene has left its imprint in many other ways. The mouths of numerous rivers at the coast (Roanoke, Chowan, NC; Escambia, Choctawhatchee, FL) are narrow, drowned floodplains entrenched during the Woodfordian phase of Wisconsin glaciation. The sediments of Terrace I may have provided much of the sands for the barrier islands of the gulf and Atlantic coasts (Thom 1967).

Other ancient floodplains have been variously used by man. Along the Waccamaw (SC) the relict ridges support roads and pine plantations while the swales bear bog vegetation. Along the Roanoke (NC) row-crop agriculture occupies most of the ridges of the higher Pleistocene terraces (3 m or 10 ft above MSL).

CHAPTER 2. HYDROLOGY

Water is the driving force of the bottomland hardwood community. As has been shown, water plays a crucial role in forming and maintaining the floodplain by transporting and redistributing sediments within the system. The rivers and their floodplains are fluctuating water level ecosystems. Their high flows are brought about by winter-spring rains (peak flow is in the summer in Florida). Their low flows correlate with high evapotranspiration during late summer and dry fall months (Wharton and Brinson 1979a). Sources of water to bottomlands include precipitation and runoff from mountains and Piedmont (alluvial rivers), groundwater from local convective and storm-front rainfall (lower Coastal Plain blackwater streams), underground aquifers (spring-fed alkaline streams), continuous seepage from sand aquifers (bog and bog-fed streams), and tidal flow.

Before development, when intact forests with thick, organic soil layers covered the landscape of mountains and Piedmont, almost all water to alluvial streams was derived via subsurface (ground water) flow. Today exposed subsoil horizons in the Piedmont lead to surface runoff which is now the primary source of water to these streams. On the flat Coastal Plain terrain, surface runoff occurs only sporadically except when the soils are saturated (water table at or near the surface); therefore, rainfall in the Coastal Plain reaches blackwater streams via ground water (base flow) in fall and by ground water and surface runoff in winter and spring. Base flows become the primary source to streams during low water or drought conditions.

Surficial aquifers (Hawthorne, Cretaceous) may contribute markedly to base flow. During a fall drought Thompson and Carter (1955) computed base flow discharge from the Tuscaloosa formation to minor Georgia streams ranging from the rainfall equivalent of 28 cm (11 inches) to as much as 102 cm (40 inches) per year from this Cretaceous aquifer. Blackwater rivers become visibly clearer in the fall because their flow is derived largely from groundwater base flow.

It is reasonable to assume that rivers recharge the shallow aquifers at high water in the flat Pleistocene deposits, but it is yet to be proven how much rivers contribute to the deeper aquifers. The net contribution of alluvial rivers to the principal limestone aquifer is thought to be insignificant (Stringfield and LeGrand 1966). Surface streams and swamps may recharge valley aquifers (Wharton 1970; Bedinger 1980).

ALLUVIAL RIVERS

Alluvial rivers in the Southeastern United States originate in the mountains and Piedmont and form huge swamps at the junction of the Piedmont and Coastal Plain. Most of these rivers have periods of sustained high flow resulting from the cumulative effect of many tributaries and distant rainfall (Figure 9A). Generally, the annual high winter-spring runoff water overflows the floodplain features. Patterns of river discharge vary in different sections of the watershed. For example, discharge peaks are higher in the Apalachicola River (FL) in the comparatively narrower upper section with high levees and steeper gradient, as compared with the flatter stage hydrograph approximately 48 km (30 mi) downstream where the water spreads out over a much wider (5 x) and flatter floodplain (Figure 10). Differences in wet (flooded) and dry stages can be dramatic (Figure 11). Discharge volumes may cease to rise and sometimes even fall as the water flows through the floodplain toward its mouth (Figure 12). Evapotranspiration after March leafout and surficial aquifer recharge may help account for some of this flow reduction (Mulholland 1979; Brown et al. 1979).

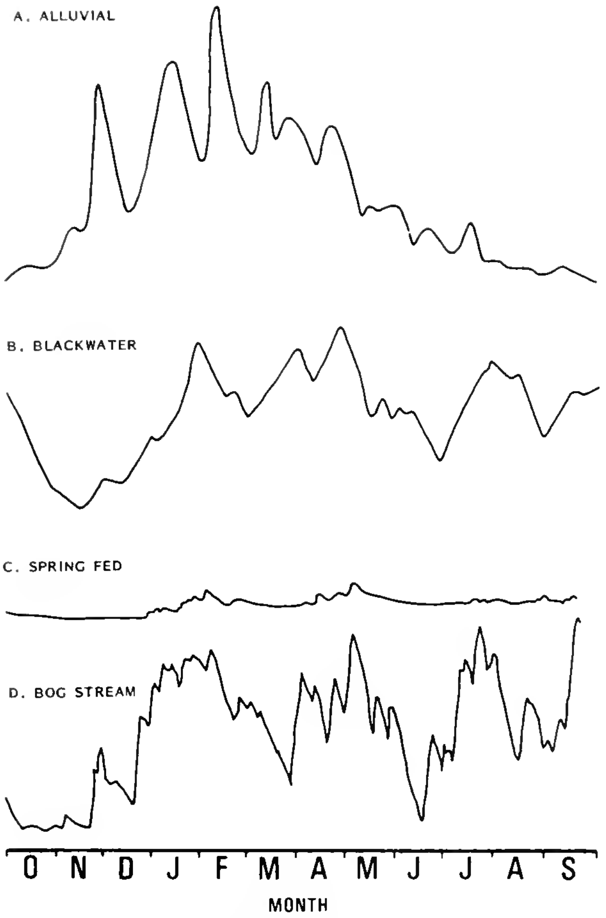

Figure 9. Hydrographs of four types of southeastern floodplain rivers and streams.

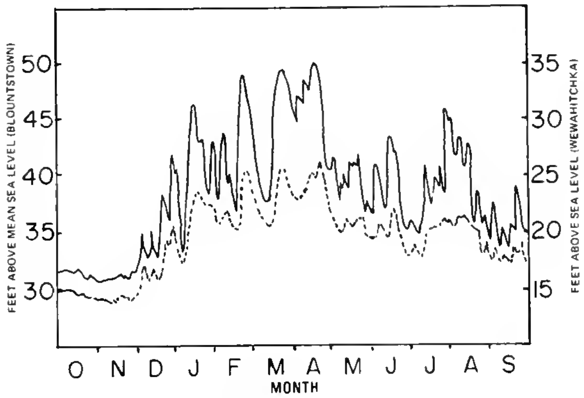

Figure 10. Hydrographs (1974-75) of an alluvial river (lower Apalachicola River, FL) showing the possible effects of an increase in floodplain width on water levels, between upstream (solid line, River Mile 126) and downstream (dashed line, River Mile 68). (After Leitman 1978.)

BLACKWATER RIVERS

Blackwater rivers and tributary streams originate in the Coastal Plain and receive most of their discharge from local precipitation. These streams have narrower, less well-developed floodplains and reduced sediment loads compared to those of alluvial rivers. The waters are relatively clear, but highly colored (coffee-colored) due to the presence of organics (humic substances) derived from swamp drainages. A hydrograph of a blackwater stream (Figure 9B) is characterized by irregular discharge peaks that are due almost wholly to frontal or local weather events. Summer flooding, as well as more typical winter-spring flooding, may result from local storms. Unlike that of larger alluvial streams (Figure 9A), the hydrograph of a smaller blackwater stream may register dry periods during which discharge may dwindle to near zero.

Many blackwater streams are coastal plain tributaries to alluvial rivers. Water levels in some of these streams may be controlled by the discharge levels in the main river creating a "water dam" effect (Wharton and Brinson 1979a).

Ground-water seepage, or base flow, is a particularly important component of the discharge of blackwater streams. A study (Winner and Simmons 1977) of a small North Carolina Coastal Plain blackwater stream (Creeping Swamp, NC) (Figure 13) resulted in a water budget in which overland runoff accounted for 17.75 cm or 6.99 inches (17%) and base flow runoff for 21.69 cm or 8.54 inches (20%) of the total precipitation of 107.29 cm or 42.24 inches. Evapotranspiration accounted for 65.81 cm (25.91 inches) (61%) of the rainfall. A negligible 2% seeped underground and was lost to the watershed.

SPRING-FED STREAMS

Spring-fed streams, characterized by clear, alkaline flow issuing principally from underground aquifers are common in northwest Florida and in other areas underlain by Tertiary limestone aquifers (Figure 14). The discharge hydrograph of a predominantly spring-fed stream (St. Marks River, FL). (Figure 9C) is quite flat compared to those of alluvial and

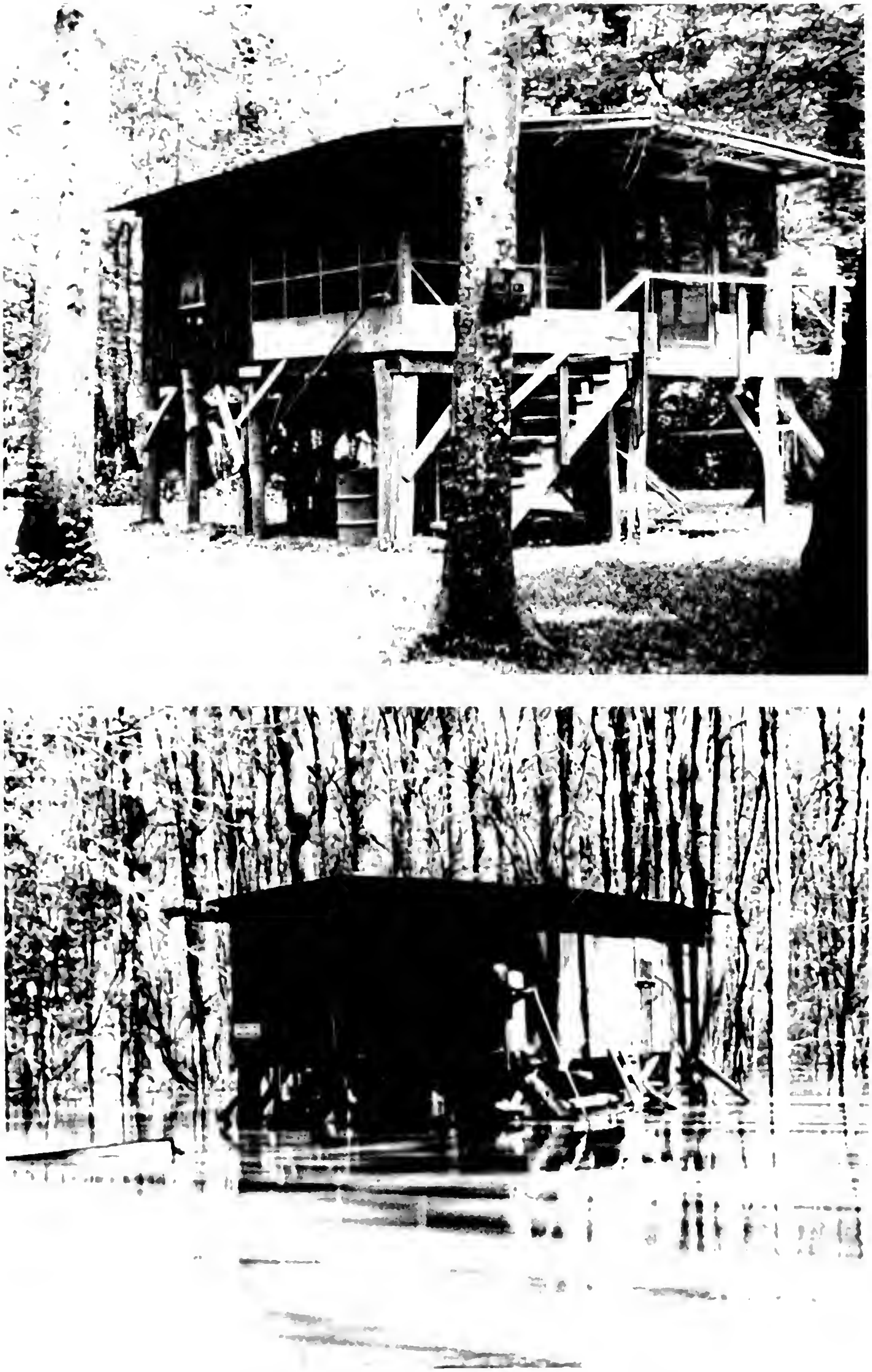

Figure 11. Two photos showing drydown (upper) and inundation (lower) of the floodplain in the Congaree Swamp National Monument (SC). Photo courtesy of U.S. National Park Service.

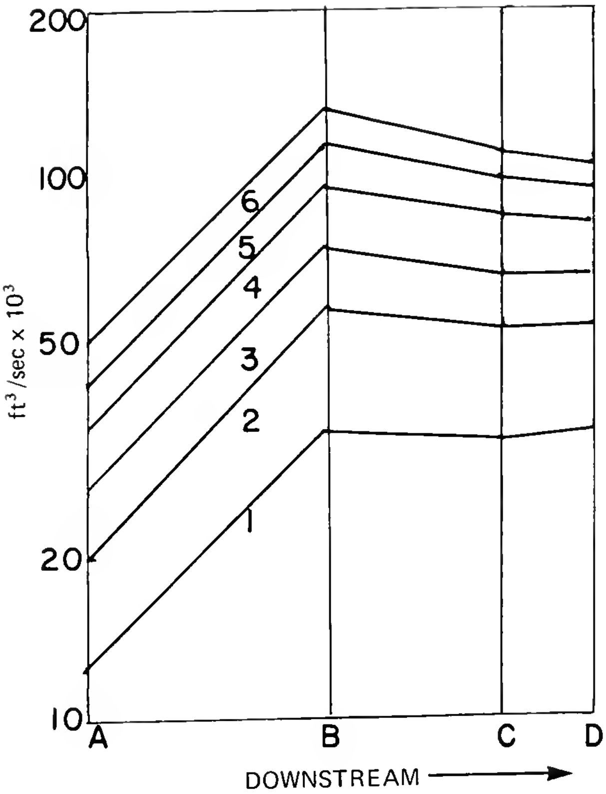

Figure 12. Relation of flood discharge of Oconee River (GA) to distance downstream. (A) = Piedmont station (Greensboro); (B) = fall line station (Milledgeville, drainage area 7770 km^2 or 3000 mi^2) just above the Oconee swamps in the upper Coastal Plain; (C) = downstream station at Dublin; (D) = junction with the Ocmulgee (Mt. Vernon, drainage area, 13,338 km^2 or 5150 mi^2). (1) = 2-year flood, (2) = 5-year flood, (3) = 10-year flood, (4) = 20-year flood, (5) = 50-year flood, (6) = 100-year flood. (Wharton 1980.)

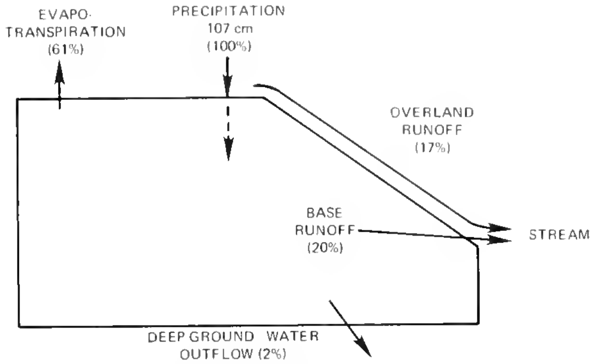

Figure 13. Diagram of the water budget for Creeping Swamp (NC), July 1974-June 1975 (after Winner and Simmons 1977).

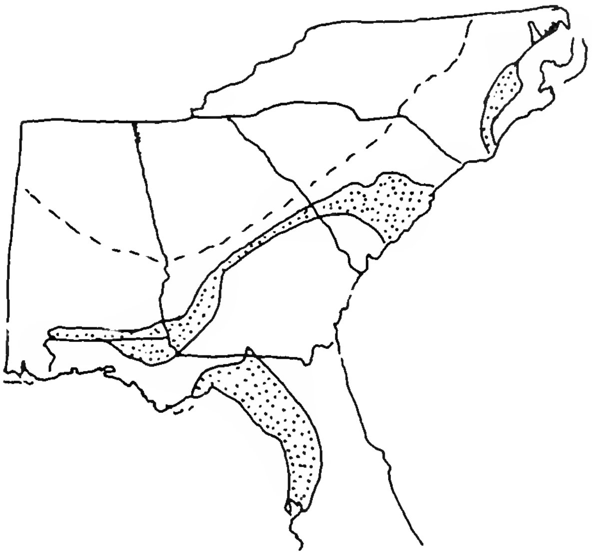

Figure 14. Dotted areas indicate where Tertiary limestones lie at or near the surface, often giving rise to spring-fed streams such as Florida's Chipola, Wakulla, Wacissa, and St. Marks and contributing heavily to the Suwannee-Santa Fe system. The dashed line is the inner margin of the Coastal Plain. (Adapted from Stringfield and LeGrand 1966.)

blackwater streams. In Figure 9C, the highest flows are only about twice the lowest flow. Although most of the base flow of the stream arises from the uniform discharge of the spring, hydrographs may also indicate local rainfall (Rosenau et al. 1977).

Spring-fed streams are influenced by surface and ground-water fluctuations. During flood stages of the Suwannee River (FL), the flow from Falmouth Spring is reversed, and the darker waters of the Suwannee flow into the spring. At the other extreme, these streams may go dry annually, leaving an exposed bed as does, for example, the Alapaha River (FL); or the entire river channel, bed and all, may disappear as the river drops into underground corridors (lower Aucilla River, FL).

BOG AND BOG-FED STREAMS

Two additional swamp stream types occurring on the Coastal Plain of the Southeast are bog and bog-fed streams. Bog streams have limited distribution and generally occupy the linear depressions or swales between adjacent sand ridges and reworked Coastal Plain relict dune deposits. An example is White Water Creek in Georgia, located in Cretaceous residual dune sands. Many bog streams occur within the Florida Panhandle area. Bog streams are characterized by a steady lateral seepage from the surrounding sand ridges. Therefore, substrates of these systems are constantly wet and support fire-resistant, bog-type vegetation. The linear nature of these streams precludes any significant watershed interception of rainfall beyond that falling directly on the stream.

Bog-fed streams, on the other hand, flow intermittently due to discharge from expansive bog-filled depressions. This intermittent discharge occurs only after significant runoff from rainfall exceeds the water storage capacity of the bog. The depressions which feed these streams are areas of internal perched drainage underlain by clay aquicludes (impervious soil layers that retard the downward movement of groundwater). These basins are not incised by streams, water tables generally occur at the surface, and excess flow from precipitation discharges readily into the receiving bog-fed stream. The streams receive little or no sediment load; therefore, few have floodplains and most resemble shallow ravines. Their hydrographs exhibit extreme fluctuations in response to rainstorms, with little or no base flow (Figure 9D). Examples are the New and Sopchoppy Rivers in Florida, which drain giant shrub bogs and bay swamps in the Bradwell Bay Wilderness Area (FL). Typically the streams flood rapidly and drain gradually due to the baffling effect of their dense bay vegetation.

FLOODING DURATION AND FREQUENCY

Flooding on alluvial floodplains depends on the size and slope of the watershed, which, together with soil and slight elevation differences, help explain the variability in forest communities on various floodplains. The duration of flooding also directly relates to watershed drainage area. Bedinger (1980) concluded that drainage areas in the mid-West with less than 776 km^2 (300 mi^2) have fast runoff characteristics, with flooding occurring 5% to 7% of the year. Flooding occurs in drainage areas ranging between 12,950 and 18,130 km^2 (5,000 and 7,000 mi^2). Floodplains for rivers with watersheds exceeding several tens of thousands of square miles are inundated from 18% to 40% of the year. Flood peaks are significantly lower in basins with lake and wetland areas (Carter et al. 1978).

Steep watersheds with dense clay soils have "flash" inundations of comparatively short duration. Rivers with intact floodplain swamp forest slow down the rise and fall of floodwaters (Wharton 1970). Flood heights diminish markedly as soon as alluvial (Wharton 1980) and blackwater (Benke et al. 1979) rivers top bankful stage and begin to utilize their floodplain swamps.

Leitman (1978) showed the importance of local rainfall in maintaining saturated conditions at several locations on the Apalachicola floodplain where residual water is often perched in backswamps 1 to 2 m (3 to 7 ft) higher than river level. Water levels in these floodplain pools and sloughs rise from local rainfall independently of river stage.

CHAPTER 3. PHYSICOCHEMICAL ENVIRONMENT

The physicochemical environment of floodplains (including both aquatic and soil environments) is a function of the interactions or processes occurring in the water column, in soil, and at the soil-water interface. These processes are facilitated by the prolonged periods of flooding (inundation) which saturate the soils and the subsequent periodic intervals of drydown which de-water the soils. This cyclic wet/dry regime imparts a unique chemical environment that has profound effects on nutrient cycling and the character and adaptations of the floodplain biotic communities.

CHEMICAL CHARACTERISTICS OF RIVERS

The chemical composition of floodplain rivers and streams reflects water sources, headwater origin, and the composition of geological formations through which rivers flow to the coast. Of the three major chemical classes of world rivers (rock-dominated, precipitation-dominated, and evaporation-dominated; Gibbs 1970), floodplain rivers fall into two: rock-dominated and precipitation-dominated. Alluvial rivers are rock-dominated rivers whose inorganic chemical load is derived from the products of weathering and leaching of the parent rocks and soil in the mountains and Piedmont. Concentrations of inorganic ions are typically higher than total organic carbon (TOC) concentrations (Table 4). Blackwater rivers arising in the Coastal Plain, on the other hand, are precipitation-dominated. Rainfall, which represents most of the water input to these streams, contains relatively low concentrations of dissolved inorganic solids (specific conductance). A comparison of river data in Georgia (Wharton and Brinson 1979a) indicated that alluvial rivers usually were higher than blackwater rivers in nitrogen, phosphorus, calcium, and magnesium (the latter two constituents increasing water hardness) (Table 4). Blackwater rivers were more acidic (lower pH) and characterized by high concentrations of total organic carbon and low concentrations of dissolved inorganics.

Distinctions among blackwater streams can be explained by their different origins within the Coastal Plain (Wharton and Brinson 1979a) (Table 4). The waters of the Satilla River, arising in the lower coastal plain of Georgia, were soft, acidic and highly organic, while the chemistry of the Ogeechee, Canoochee, and Ochlockonee Rivers reflect the input (increased hardness, pH, and nutrients) from geological formations at their headwaters. In Florida many rivers clear during low flows, and pH approximates that of subsurface aquifers (pH = 7.7). During high flows, however, surface leachates add organic acids and lower the pH to 4.0. The blackwater Santa Fe River typifies a phenomenon especially evident in many Florida rivers. In its swampy headwaters the Santa Fe has a pH of 5.3. In the central section, with swamp drainage during high flow and alkaline ground water drainage during low flow, the pH is 6.4; in the lower river, fed by artesian springs, the pH rises to 7.4.

The distinction between blackwater and alluvial river water chemistry is best reflected in the difference in the ratios of inorganic to organic constituents. The high concentrations of organic matter in blackwater rivers result in a 1:1 ratio of dissolved inorganics to total organics whereas the predominance of inorganic components in alluvial rivers leads typically to a 10:1 ratio (Beck et al. 1974). The magnitude of the organic load affects the concentrations of some of the inorganic load constituents. For example, only those inorganic ions such as iron and aluminum, which form complexes with the dissolved organic matter (DOM), are present in greater concentrations in blackwater streams (Table 5). Additionally, since the bulk of the dissolved organic constituents are organic acids (humic and fulvic), the waters of blackwater streams are considerably more acidic (low pH) and highly colored than alluvial streams.

Table 4. Physicochemical data summarized for Georgia rivers in water year 1977 (Wharton and Brinson 1979a). Figures in parentheses are numbers of streams for which data were averaged.

Rivers	TOC (mg/l)	pH	Hardness (Ca, Mg) (mg/l)	Specific conductance (μmho/cm)	Total nitrite + nitrate-N (mg/l)	Total phosphorus (mg/l)
Mountain river	1.8(2)	6.6(2)	3.5	16(2)	<0.04(2)	<0.02(2)
Alluvial river-Piedmont	2.9(6)	6.9(6)	12-18(4)	48-83(6)	0.14 -0.50(3)	0.06(3)
Alluvial river-Coastal Plain						
Ocmulgee-Oconee	4.1(2)	7.2(2)	18-33	68-122	0.09 -0.38	0.08(2)
Flint (Newton)	5.5	7.5	30-50	84-144	0.34 -0.63	0.06
Altamaha (Everett City)	7.9	6.6	13-33	60-191	0.02 -0.55	0.07
Blackwater river						
Ogeechee (Oliver)	8.1	6.9	12-28	47-104	<0.18	0.04
Canoochee (Claxton)	13.2	5.6	6-11	35-57	<0.08	0.06
Ochlockonee	9.0	7.0	11-56	49-327	<1.70	0.32
Satilla-Suwannee	21.7(2)	4.9(2)	5(2)	40-59	<0.06	0.04(2)

Table 5. Mean inorganic constituents (ppm) in selected Georgia coastal plain rivers and in the "world average river" (modified from Beck et al. 1974).

Rivers	pH	HCO_3	Cl	SO_4	Na	K	Mg	Ca	SiO_2	Al	Fe	Mn
Satilla	4.58	2.6	6.1	0.8	3.70	1.00	0.74	1.32	6.6	0.41	1.05	0.06
Ohoopee	6.25	8.8	5.9	1.0	2.73	0.86	1.00	8.69	11.1	0.04	0.11	0.01
Ogeechee	6.28	30.2	5.4	1.2	3.42	0.74	1.01	6.78	12.3	0.03	0.12	0.03
Altamaha[a]	6.80	29.6	4.0	2.6	3.95	1.29	0.96	6.25	10.3	0.24	0.08	0.01
World average river	-	58.4	7.8	11.2	6.30	2.30	4.10	15.00	13.1	-	0.67	-

[a] Represents conditions in the Georgia coastal plain below the confluence with the Ohoopee River.

In both blackwater and alluvial systems organic matter represents the link between the river and its floodplain. Most of this organic matter is in the dissolved form termed dissolved organic matter (DOM) or dissolved organic carbon (DOC), composed principally of humic substances leached from soil, peat, and leaf litter. For example, up to 95% of the total organic matter in the Altamaha River was DOM (Reuter and Perdue 1977). Total organic matter averages around 15 mg/l (Windom et al. 1975), ranging up to 100 mg/l in waters leaching peat deposits (Malcolm and Durum 1976). These materials are often chemically and biologically inert (i.e., refractory) with concentrations changing principally in response to discharge additions or dilutions. A small proportion of humic substances flocculate in fresh water and can be seen as "silts" on white sand bars, or are rolled as bed load particles (J.H. Reuter, Department of Geophysical Science, Georgia Institute of Technology, Atlanta; personal communication).

PHYSICOCHEMICAL CHARACTERISTICS OF FLOODPLAIN SOILS

The alternation of inundation of floodplains during extended high flow periods of the river with drydown periods during low flow conditions produces a spectrum of soil types across the floodplain. These soil types are associated with elevational gradients which in turn dictate flooding frequency and duration: the hydroperiod. Differences in elevation and hydroperiods are the basis of a system of classifying the environmental and biotic zonation that result from this continuum of fluctuating water levels and soil moisture. A system of six zones, developed by the National Wetlands Technical Council (NWTC) (Larson et al. 1981), provides a convenient framework for portraying the relationship between the bottomland hardwood community and environmental factors necessary for effective management considerations. Throughout the remainder of this report these zones will be referred to as either ecological or bottomland hardwood zones.

Briefly, the classification generally corresponds to the following broad geomorphologic floodplain features:

Zone I: river channels, oxbow lakes, and permanently inundated backsloughs

Zones II-V: the active floodplain including swales (II and III), flats and backswamps (IV), levees, and relict levees and terraces (V)

Zone VI: the floodplain-upland transition to terrestrial ecosystems

Examples of floodplain zonation are depicted in Figure 15. An idealized floodplain proceeds sequentially from the river channel to the surrounding uplands (Zone I-VI) along a gradually increasing elevational gradient (Figure 15A). The presence of natural levees interrupts this sequence (Figure 15B); depending on elevation, the levee may be characteristic of Zones II, III, IV or V. Accordingly, levees are generally excluded from the NWTC zonal concept. Other geomorphic features (Figure 15C) contribute further to the complexity of zonation patterns on most southeastern floodplains (see Chapter 4).

Flooding produces and regulates the chemical properties of floodplain soils by (1) continually depositing and replenishing minerals, including essential nutrients on the floodplain (the mineral subsidy); (2) producing anaerobic conditions in the soils; (3) importing particulate and dissolved organic matter (POM, DOM); and (4) removing or exporting accumulations of organic detritus (principally degraded leaf litter). The degree to which these processes operate in the six zones is determined by the hydroperiod (Table 6).

An example of the relationship of floodplain soil types to bottomland hardwood zones is illustrated in Figure 16 for an alluvial river floodplain, the Congaree River (SC). The bulk of the floodplain floor is Taw Caw silty clay loam, supporting principally Zone IV forest. However, variations in microrelief or subsurface water table height can make differences in surface soils even in small quadrats. Reynolds and Parrott (1980), found specific soil differences on a 1-ha plot coincidental with different patterns of tree distribution and postulated (from 28 wells) that water table differences accounted for the numerous soil differences

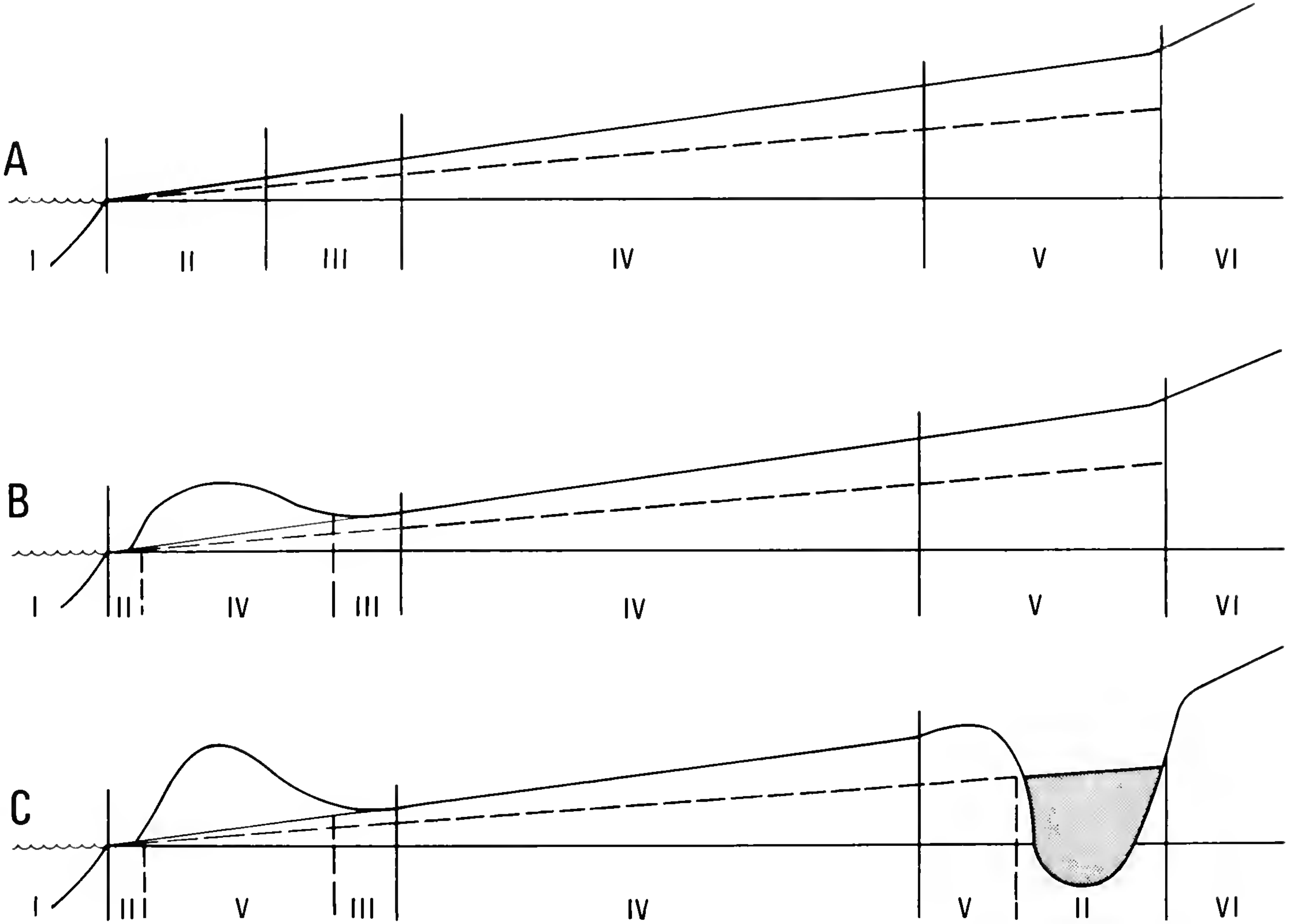

Figure 15. (A) An idealized sequence of NWTC bottomland hardwood zones from a water body to an upland, along a moisture continuum (dotted line represents the depth of the water table). (B) One-half of a floodplain, from mid-alluvial river to bluff, indicates modification of the idealized sequence by the intrusion of a natural levee between Zones II and III. If low enough, the levee may bear Zones II and III; if higher, Zone IV, and higher still, Zone V (C). (C) Further modification of the idealized sequence by inclusion of an abandoned river channel (filled with a clay plug and/or peat).

Table 6. Physicochemical characteristics of floodplain soils by National Wetland Technical Council (NWTC) Zones (partially derived from Clark and Benforado 1981). Zone I (permanent water courses) is excluded from this table.

Characteristic	Zones II	 III	 IV	 V	 VI
Degree of inundation and saturation	Intermittently exposed; nearly permanent inundation and saturation	Semipermanently inundated or saturated	Seasonally inundated or saturated	Temporarily inundated or saturated	Intermittently inundated or saturated
Timing of flooding	Year-round except during extreme droughts	Spring and summer during most of the growing season	Spring for 1-2 months of the growing season	Periodically for up to 1 month of growing season	During exceptionally high floods or extreme wet periods
Probability of annual flooding[a]	100%	51%-100%	51%-100%	10%-50%	1%-20%
Duration of flooding	100% of the growing season	>25% of the growing season	12.5%-25% of the growing season	2%-12.5% of growing season	<2% of the growing season
Soil texture	Dominated by silty clays or sands	Dominated by dense clays	Clays dominate surface; some coarser fractions (sands) increase with depth	Clay and sandy loams dominate; sandy soils frequent	Sands to clays
Sand:silt: clay (% composition)[b]					
Blackwater	69:20:12	-	74:14:12	-	-
Alluvial	29:23:48	34:22:44	34:20:45	71:16:14	-
Organic matter %[b]					
Blackwater	18.0	-	7.9	-	-
Alluvial	4.5	3.4	2.8	3.8	-
Oxygenation	Moving water aerobic; stagnant water anaerobic	Anaerobic for portions of the year	Alternating anaerobic and aerobic conditions	Alternating: mostly aerobic, occasionally anaerobic	Aerobic year-round

(continued)

Table 6. (Concluded).

Characteristic	Zones II	III	IV	V	VI
Soil color	Gray to olive gray with greenish gray, bluish gray, and grayish green mottles	Gray with olive gray mottles	Dominantly gray on blackwater floodplains and reddish on alluvial with brownish gray and grayish brown mottles	Dominantly gray or grayish brown with brown, yellowish brown, and reddish brown mottles	Dominantly red, brown, reddish brown, yellow, yellowish red, and yellowish brown, with a wide range of mottled colors
pH[a]					
Blackwater	5.0	-	5.1	-	-
Alluvial	5.0	5.3	5.5	5.6	-
Phosphorus (ppm)[b]					
Blackwater	11.2	-	9.8	-	-
Alluvial	9.1	6.3	8.1	4.8	-
Calcium (ppm)[b]					
Blackwater	607.0	-	346.0	-	-
Alluvial	1,079.0	752.0	669.0	186.0	-
Magnesium (ppm)[b]					
Blackwater	98.0	-	36.0	-	-
Alluvial	154.0	140.0	145.0	39.0	-
Sodium (ppm)[b]					
Blackwater	46.0	-	31.0	-	-
Alluvial	94.0	31.0	28.0	23.0	-
Potassium (ppm)[b]					
Blackwater	48	-	29	-	-
Alluvial	51	28	32	20	-

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[a] Range includes drought years.

[b] See Appendix.

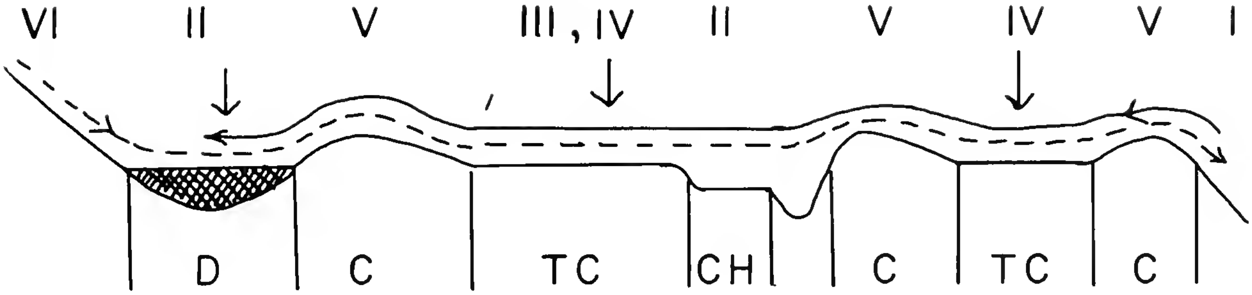


Figure 16. Diagrammatic scheme of the relationship of bottomland hardwood zones to soil types on a large alluvial river floodplain (Congaree Swamp National Monument, SC). Three sources of water are indicated: vertical arrows, rainfall; horizontal solid arrows, normal cyclic flooding from river; and dashed arrows, periodic but irregular side flooding by "hill freshets" from a tributary stream. Orders and suborders of recent soil classification are given in parentheses (Soil Conservation Service 1975): D (Zone II), Dorovan muck (Histosol, typic medisaprist); C (Zone V) Congaree silt loam (Entisol, typic udifluvent); TC (Zone III, IV) Taw Caw silty clay loam (Inceptisol, fluvaquentic dystrochrept); CH (Zone II) along distributary, Chastain loam (Inceptisol, typic haplaquept); VI, upland; I, river.

within the plot. Hay (1977) noted that blackwater floodplain soils only 1 m (3 ft) apart varied in radiocesium levels by as much as 190%.

Mineral Subsidy

Both inorganic sediments and nutrients are deposited on the floodplain during overbank flooding, although average sediment deposits are so thin as to be unnoticeable. The fates of these materials vary. Residence time and biotic utilization remain key questions. Some sediments may reside in the floodplain long enough to be mineralized by weathering. As flood waters subside, leaves in swamp pools become coated with silt and clay which may be trapped by the biotic slime. Other sediments are redistributed by scour during flooding. Mineral nutrients may be transported or trapped adsorbed to sediment particles (Delaune et al. 1976). Nutrients are incorporated into tissues of the biotic community and into sediments in response to vegetative growth and decay cycles (see Chapter 6). The shallow root systems of many floodplain trees (Figure 17) enable them to take advantage of this imported mineral subsidy.

Nutrients, notably nitrogen, also are conserved and recycled on the floodplain (Brinson et al. 1981). Inorganic nitrogen (N), especially ammonium, is immobilized by heterotrophic microorganisms in leaf litter in the fall, held for several months, then mineralized and absorbed by filamentous algal mats in winter and early spring. It is then released by the dying algae and absorbed by trees and shrubs at leaf-out, with little or no net release into the water from autumn leaf fall until tree growth in the spring. This tight nutrient recycling offsets potential loss by flooding or leaching.

Sediment inputs to alluvial streams include a high proportion of fine-grained clays and silt from Piedmont runoff (Table 6). These are deposited during the relatively long residence time of water in Zone IV backswamps and sloughs. Coincident with clay deposition is the deposition of various materials adsorbed to the clay particles, including nutrient ions, metal ions, and pesticides.

Soil Oxygen Conditions

Over the course of a year, floodplain soils may vary from being completely oxygen-depleted to being as saturated with oxygen as upland soils. Because gas exchange is curtailed drastically in waterlogged soils (Ponnamperuma 1972) and biological respiration of the soil microbes rapidly depletes the available oxygen, inundated or wet saturated floodplain soils become anaerobic for extended per-

Figure 17. Many bottomland hardwoods have a dense surface mat of minute rootlets which may extract essential minerals from the water following mineralization of bacteria, hyphomycete fungi, algae, or organic detritus and may exchange nutrients with the surfaces of silts, clays and organic matter.

iods. The high clay content of floodplain sediments contributes to the impermeability of the sediments to water movement and oxygen saturation. Retention of surface water and restriction of oxygenation result in anaerobic conditions usually within 3 days of flooding (Phung and Knipling 1976). This condition is maintained until the soils de-water during drydown periods.

A consequence of floodplain soil anoxia is that it severely limits nutrient uptake by plant roots. Plant species which thrive in zones that are flooded throughout most of the growing season often have adapted to anoxic conditions by developing efficient methods of transporting oxygen to the roots (see Chapter 4). Oxygen diffusion through the roots creates an aerobic microlayer in the surrounding sediments which facilitates nutrient uptake. Penetration of roots into swamp soils is, however, hampered by the impermeability of soils due to waterlogging and settling out of fine-grained silts and clays during flooding. As a result, conditions of nutrient unavailability exist over large portions of the swamp floodplain despite soil nutrient concentrations that are equal to or higher than those in Coastal Plain, Piedmont, or mountain soils (Table 7).

Table 7. Comparison of some floodplain soil nutrients to those of Coastal Plain, Piedmont, and mountain soils. Floodplain values are averages from Zones II-V (blackwater and alluvial). Samples are from top 6 inches below litter layer. Upland soil samples are from the A horizon.

Nutrients	Overall floodplain (ppm)	Coastal Plain (Long et al. 1969) (ppm)	Piedmont (Perkins et al. 1962) (ppm)	Mountains (Perkins et al. 1962) (ppm)
Calcium	606	61.0	70	1.5
Potassium	35	9.3	56	20.0
Magnesium	102	33.0	21	40.0
Sodium	42	31.0		
Phosphorus	8	0.5	8	11.0

pH

Another consequence of prolonged anaerobic conditions is pH change. Under waterlogged conditions, acid soils increase their pH while basic soils decrease in pH. The pH of swamp soils in particular tends to remain acid throughout the period of saturation (Kennedy 1970). Flooding and resultant pH changes increase the "mobilization" (or availability to plants) of the macronutrients phosphorus (P), nitrogen (N), magnesium (Mg), and sulfur (S), and the micro-nutrients iron (Fe), manganese (Mn), boron (Bo), copper (Cu), and zinc (Zn) (Teskey and Hinckley 1977). This may offset nutrient limitation by anoxia.

Further, pH controls the amount of DOM leaching out of leaves, the amount precipitated as particles, and the size of these particles (Kaushik 1975). Acid pH delays precipitation of aggregated particles from DOM leachates.

Organic Matter

Organic matter concentrations of floodplain soils are intermediate between those of bogs and pocosins and those of uplands (Table 8). In situ deposition is the primary fate of organic detritus in peat-forming and internally draining bogs and pocosins. Decomposition and remineralization are the major pathways of litter in the upland forest. The floodplain swamp receives large inputs of organic matter through leaf fall, and some decomposition and incorporation of this matter occur. Organic matter decomposition under anaerobic conditions, however, is slow (2%-5% per year) in contrast to that of oxygenated waters or aerobic soils (>10%).

The highest soil organic matter occurs on floodplains draining vast, acid bogs along rivers such as the Sopchoppy and New (FL), and on floodplains along spring-fed rivers (32%), tidal forests (40%), and on peat systems (up to 44%). Percent organic matter of Zone II soils in spring-fed river floodplains and Zone II backswamps with swamp tupelo is also quite high (about 36%). Alluvial river floodplains have the lowest organic matter, averaging <5%, a good working figure to separate blackwater and alluvial floodplains (Wharton et al. 1977).

Soil Characteristics of NWTC Zones

Overall, macronutrient concentrations on floodplains differ markedly from those of the uplands (Table 7 and Appendix). Except for phosphorus, nutrients (especially calcium and magnesium) are generally higher in floodplain soils than in uplands. Unusually high concentrations occur in spring-fed and tidal systems in particular.

Table 8. Percentage of organic matter in selected wetland and upland soils.

Sites	Organic matter (%)	References
Pocosin	66.8	Woodwell 1958
Swamp	31.3	Woodwell 1958
Floodplain		This study
Zone II (alluvial)	4.5	
Zone II (blackwater)	18.2	
Zone II backswamps with swamp tupelo	35.3	
Zone II springfed rivers	36.0	
Zone III (alluvial)	3.4	
Zone IV (alluvial)	2.8	
Zone IV (blackwater)	7.9	
Zone V (alluvial)	2.8	
Coastal Plain pines	0.4	Long et al. 1969
Piedmont pines & hardwoods	1.4	Perkins et al. 1962
Mountain hardwoods	1.5	Perkins et al. 1962

Some zones (see Appendix) are roughly comparable in calcium concentrations (660 ppm) to a tulip poplar forest (Shugart et al. 1976), which is considered eutrophic (Jordan and Herrera 1981). Some floodplain sites (blackwater .Zone IV, alluvial Zone V) approach oligotrophy (44-75 ppm Ca). In the study area, the lowest nutrient levels occur in Zone V.

There are marked differences in organic matter concentrations among the various zones. Some zones (II and blackwater IV) have low nutrient availability due to "lock up" of nutrients in organic matter. This condition occurs particularly in swales and peat-forming soil types. Periodic drydown is very important to nutrient release from organic matter and litter. When drydown is rare or aperiodic (as in the specific zones above), nutrients tend to be bound in complexes with organic matter. On other sites nutrient concentrations are low as a result of a lack of inorganic inputs (as in remote swales adjacent to the upland). In blackwater rivers, nutrients may be complexed and exported as particulates or refractory humic substances.

Soil micronutrient concentrations tend to be high, especially in acidic sites, although this may depend on the amount of inorganic input, or distance from the channel (Appendix). Cobalt storage by swamp tupelo (Eyde 1966) and the high zinc demand of cultivated pecan trees suggest that some floodplain vegetation may accumulate or need high levels of micronutrients.

The precise relationship between soils and vegetational responses in floodplains is unresolved. It is unknown, for example, why the low-nutrient, low-organic flats of the Oconee support a magnificent willow oak stand, or why the old growth diamondleaf oak on Turkey Creek has the lowest organic matter of any Zone IV floodplain. Equally challenging is why the mineral-rich Taw Caw silty clay loam of the virgin Congaree Swamp National Monument supports extensive Zone IV wet flats with few or no large trees.

CHAPTER 4. FLORA OF BOTTOMLAND HARDWOOD COMMUNITIES

INTRODUCTION

Having established in the preceding chapters the geological and biochemical setting unique to river floodplains, we now turn to the component of the ecosystem that gives it its name--the bottomland hardwoods. The plant species that thrive here are well adapted to the stresses imposed by the hydroperiod; these trees and their adaptations are a fundamental and integral part of the geological and chemical functioning of the ecosystem.

The plant species and communities that inhabit the floodplain can be usefully thought of as buffers that absorb and dissipate the physical energies of the riverine system. Water movement is slowed and erosion is held in check through the anchoring of sediments by root systems, the deposition of sediments that are dropped from the slowed water column, and the reduction of the water column by the spreading out of water (Leopold and Wolman 1957). Without the stabilizing forces of the biota to reduce water velocities and inhibit subsequent meander movement and floodplain scour, these physical alterations would be extremely rapid.

The buffering role of the plant communities is also evident in the biogeochemical cycles of the riverine-palustrine system. Essential mineral nutrients are captured from the water-soil complex and fixed in plant tissues which ultimately support the floodplain's detritus-based trophic network (Wharton and Brinson 1979a). Remineralization by the soil microbiota and rapid uptake by plants during favorable (nonflooded) conditions partially close the nutrient cycles. But the nature of the riverine-palustrine system, in which the variable patterns of flooding and drydown continually interact with the floodplain substrate, requires active nutrient conservation by the biota (Brinson et al. 1980). Floodwaters transport nutrients not immobilized in organisms or bound to soil constituents back to the river, as particulate or dissolved organic matter, material adsorbed to suspended sediments, or solutes in the water column (principally dissolved organics). The relatively high levels of productivity exhibited by floodplain ecosystems (discussed later) are sustained only through the water and nutrient subsidies provided by the watershed and transported by the river (Brown et al. 1979; Brinson et al. 1980). The floodplain flora, in partnership with the macro- and micro-fauna, merely postpones the loss of elements to the sea. The trapping, assimilation, and partial cycling of nutrients in the floodplain, essentially a diversion in the relentless movement of water and sediments to the ocean, yield an extremely productive and unique ecosystem.

THE ANAEROBIC GRADIENT

The distribution of flora in the bottomland hardwood ecosystem revolves around three aspects of anaerobic conditions:

(1) the presence and intense selective power of anaerobic conditions generated by the hydroperiod on the floodplain;

(2) the anaerobic gradient, varying in space and time across the floodplain due to microelevational relief, the soil mosaic, and the hydroperiod; and

(3) the tolerances of plant species to this gradient.

Though factors such as light intensity, soil pH, and nutrient availability affect plant distributions in other forest communities, they are secondary to anaerobiosis in the floodplain community. In fact, these other factors are, except for light intensity, functions of saturated soils and thus anaerobic conditions.

The anaerobic gradient in the floodplain and its effects on plant distributions have been noted, often as "moisture gradient" or "moisture continuum" (Lindsey et al. 1961; Gemborys and Hodgkins 1971; Bedinger 1978; Richardson et al. 1978; Fredrickson 1979; Huffman 1979; Whitlow and Harris 1979; Huffman and Forsythe 1981). These terms may be misleading; it is not the availability of water, but the inavailability of oxygen due to the presence of water. The emphasis on the anaerobic aspect of this gradient generates a clearer picture of the actual effects of flooding and saturated soils on plant survival; hence, its use in this report.

PLANT RESPONSES TO ANOXIA-RELATED STRESSES

Stresses Generated by Anaerobic Conditions

The effects of periodic or permanent flooding are the crucial selective stresses on bottomland hardwood plants and are responsible for the sorting of species into broad community types (Huffman and Forsythe 1981). The plant growing in a saturated substrate must respond to several physical and chemical changes, among them:

(1) depletion of available oxygen in soil water, in a period as short as 3 days (Nuritdinov and Vartapetyan 1976; Phung and Knipling 1976; Teskey and Hinckley 1977);

(2) shifts in soil pH--variable, though in general a convergence toward neutrality, with acidic soils becoming more alkaline and calcareous soils becoming more acidic (Grable 1966; Kennedy 1970; Rahmatullah et al. 1976; Teskey and Hinckley 1977);

(3) accumulation of potentially toxic compounds in the plant, the rhizosphere, and in the larger soil solution; examples are carbon dioxide, ethanol, sulfides, nitrites, aluminum, iron, and manganese (Teskey and Hinckley 1977);

(4) shifts in the redox states of chemical species, including essential nutrients, generally from more oxidized to more reduced; the reduced forms are considered generally less desirable for plant uptake and assimilation (Brady 1974; Teskey and Hinckley 1977); and

(5) shifts in nutrient availabilities, partially due to item (4) (Teskey and Hinckley 1977).

The responses of plants to these and other flood stresses were reviewed by Teskey and Hinckley (1977), who emphasized that the key to plant survival in flooded conditions is the adaptability of the root system.

The cessation of uptake and exchange functions through root dormancy or death during flooding affects plant metabolism in several ways. The immediate losses of these root processes is due to the lack of oxygen. The root system has access to free oxygen, necessary for normal respiration, through only two routes: (1) absorption from the soil-air-water complex by the roots themselves, or (2) transport from aboveground plant tissues through the vascular system or intercellular spaces to the roots. Although all plants probably have a shoot-to-root intercellular space network through which oxygen can diffuse to the root system (Salisbury and Ross 1978), this system is well developed in only a few plants (rice, for example). Thus the depletion of soil oxygen by the roots eventually shuts down respiration in root cells. As respiration ceases, water and ion uptake is inhibited (1) by changing membrane permeabilities in root cells, affecting movement of both water and ions, and (2) by reducing the amount of energy available for membrane transport, affecting primarily ion movement.

The inability of flood-intolerant species to absorb and use water and nutrients leads to foliar water deficits, stomatal closure, and reduced gas exchange. Consequently, transpiration and photosynthetic rates are slowed, cellular synthesis requiring unavailable nutrients is curtailed, and overall plant growth is impeded (Teskey and Hinckley 1977). The plants literally die of dehydration in standing water.

Plant Adaptations to Flood Stresses

Plant adaptations to flood stresses may be categorized as physical or metabolic. The former includes the provision of oxygen to the roots or the restoration of proper root function, or both. Metabolic mechanisms adjust plant biochemistry to decrease the potentially harmful effects of anaerobic respiration. The most successful species in saturated conditions are those that possess both physical and metabolic adaptations (Teskey and Hinckley 1977).

The abilities of plant species to restore and maintain the stressed root system lie on a continuum (Teskey and Hinckley 1977):

(1) very tolerant--primary root maintenance, secondary and adventitious root growth,

(2) moderately tolerant--primary root deterioration, adventitious root growth, and

(3) intolerant--primary root deterioration, no adventitious root growth.

Adventitious and secondary roots produced under flooded conditions are anatomically different from primary roots in ways that enhance root function in saturated soils. They are more porous, facilitating (1) oxygen diffusion from the aerial shoots (Luxmoore et al. 1973), (2) gaseous exchange between root cells and soil solution, and (3) perhaps better movement of water and ions into the root (Jat et al. 1975). They are also more tolerant to elevated carbon dioxide concentrations and exhibit increased anaerobic respiration (Hook and Brown 1973).

Some tree species produce special root structures other than secondary and adventitious roots. The classic example is the pneumatophores of baldcypress and pond cypress (knees) (Figure 18) and water tupelo and swamp tupelo (arched roots). Aerial roots may supply additional oxygen to the root system (Teskey and Hinckley 1977). Buttress formation (Figure 19) and "stooling" not only provide stabler anchoring in the less firm floodplain soils but also may help aerate the root system.

Similar functions are provided by the characteristically wide, shallow, matted root systems (Figure 20) of bottomland trees which (1) provide support, (2) increase oxygen use efficiency in saturated conditions by their proximity to more highly oxygenated surface sediments, (3) reduce losses of nutrients from the system through rapid uptake, and (4) protect the floodplain from erosion.

The primary metabolic mechanism in flood-tolerant species is a shift in the end-products of glycolysis. Normal glucose metabolism and energy (ATP) production in the cell proceeds via three steps: (1) glycolysis (anaerobic), (2) Kreb's citric acid cycle (aerobic), and (3) oxidative phosphorylation (aerobic). In the absence of free oxygen, only glycolysis is completed, and ethanol normally accumulates as an undesirable end product. Flood-tolerant species can generate organic acids instead of ethanol as products of glycolysis (Crawford and Tyler 1969) and thus avoid ethanol toxicity. Furthermore, the organic acids may be transported to the stem and leaves (Chirkova and Gutman 1972; Vester 1972) and used in cellular synthesis (Crawford 1976).

A second metabolic adaptation has been described for some tolerant trees by Hook et al. (1970). The roots of these species oxidize the rhizosphere, preventing root deterioration and enhancing nutrient uptake.

Finally, there is some evidence that flood-tolerant species can substitute nitrate for free oxygen as a terminal electron acceptor in cellular reactions (Crawford 1976). The reduction of nitrate to ammonium (denitrification) then would help maintain cellular energy production and biosynthesis in roots. This benefit could occur only if excess nitrate were available in an environment where denitrification is the prevalent process.

Factors Affecting Plant Response to Flooding

Of the many factors that influence plant survival during flooded conditions, the timing, depth, and duration of floodwaters are the most critical (Teskey and Hinckley 1977; Huffman and Forsythe 1981). These characteristics are themselves functions of regional precipitation and local

Figure 18. A remarkable example of multiple-trunked stooling of Ogeechee tupelo at Sutton's Lake (Apalachicola River, FL). This slough floods to depths of 4.2 m (14 ft); cypress knees may exceed 3.7 m (12 ft) in height.

weather patterns, watershed size and morphology, floodplain size and topographic variation, and drainage rates of floodplain soils. The effects of flooding are most critical during the growing season, particularly during the period of leaf-out. Floods during the dormant season have relatively little effect on the physiology and survival of bottomland species (Hall and Smith 1955), other than possible damage due to mechanical abrasion or breakage.

Flood depth is critical in at least three ways. First, stem lenticels (pores) may be blocked. These structures are important in some species in both root aeration (Armstrong 1968; Chirkova 1968) and the release of volatile end-products of anaerobic respiration, such as ethanol, ethylene, and acetaldehyde (Chirkova and Gutman 1972). Floodwaters deep enough to inundate major portions of the stem lenticels thus cause reduced oxygen supply to the roots and toxic accumulation of the anaerobic respiratory products. The second effect of flood depth is the reduced rate of oxygen diffusion through the water column to the roots with increasing flood depth. Finally, seedlings submerged by the water column may undergo severe mortality through anoxia, mechanical damage, and siltation.

Figure 19. Oak displaying buttressing, common among bottomland hardwoods.

Figure 20. A windthrown diamondleaf oak on a small blackwater creek floodplain (Creeping Swamp, NC) illustrates the large diameter of the root crown of bottomland hardwoods. The thickness ranged from 30 to 46 cm (12 to 18 inches). Such width is probably an adaptation to the high water table, but it also increases contact with the surface water during inundation. Root mats are so wide that few areas of floodplain surface are unprotected from floodplain scour.

The importance of flood duration should be obvious. With the exception of species of tupelo and cypress, stresses associated with saturated soils and standing water cannot be handled by plants after varying amounts of time that depend on the range of tolerance mechanisms of the individual species. Broadfoot and Williston (1973) stated that the majority of the bottomland species will not survive 2 years of continuous flooding.

Factors that increase the dissolved oxygen concentrations in floodwaters are rainfall (Broadfoot 1967), moving water (Hook et al. 1970; Harms 1973), and lower water temperatures (Broadfoot and Williston 1973). In contrast, oxygen concentrations may be reduced through microorganismal respiration, especially in waters with high concentrations of organic matter or nutrients or both.

In addition to the above factors that directly affect plant survival, the activities of soil microbiota are modified by flooded conditions. Decomposition and conversion processes mediated by these organisms, such as mineralization and nitrification, are affected. Wharton and Brinson (1979a) proposed a nitrogen circulation model for forested wetlands that summarizes nitrogen flows and the effects of floods. Extended anaerobic conditions and shutdowns in organic matter decomposition may lead to the immobilization of nitrogen and other nutrients in microorganismal tissues.

PLANT COMMUNITY PATTERNS IN THE FLOODPLAIN

The wide variations in factors that influence southeastern bottomland hardwood ecosystem structure and dynamics make a comprehensive treatment of plant distributions in these ecosystems a difficult task, one more detailed than is appropriate for this community profile. Although the selective power of the hydrologically generated anaerobic gradient is sufficient to separate broad community types based on dominant woody species (Figure 21), associated factors blur the distinctions between categories. These factors include soil characteristics, detrital decomposition rates, soil and water pH, nutrient availability and turnover rates, flood depth and water velocity, light intensity, and disturbance (natural and man-caused). Differences in community structure and composition among otherwise similar sites sometimes occur. The mere presence of a species may not be related to present local topography. For example, apparently dislocated cypress may indicate the existence of an old buried waterway (A.L. Radford, University of North Carolina at Chapel Hill; personal communication).

The reasons for such complexity in floodplain floral distributions are the individual responses of plant species to the highly variable and dynamic floodplain environment. This section on plant community distributions emphasizes the dominant types of forest cover, and notes associated understory, shrub, and herbaceous components where field observations allow.

The National Wetlands Technical Council Zonal Classification

The zonal classification of floodplain forest sites proposed by Huffman and Forsythe (1981) and implemented by the National Wetlands Technical Council (NWTC) was introduced in Chapter 3. Six zones based on soil moisture and hydrology are defined, ranging from aquatic (Zone I) to upland (Zone VI) ecosystems; Zones II through V represent the floodplain.

The mosaic distribution of floodplain microtopography (Figure 22), soil types, and plant communities makes the use of the term zone somewhat misleading. While many examples of southeastern bottomlands exist where the plant dominance types are arranged in discrete bands, many others are arranged in a mosaic pattern.

The zonal classification is a practical system, but like all man-devised classification, it is flawed. Its use in the analysis of floodplain vegetation is complicated by several problems, among which are (1) the recognition of zones in the field, (2) common species whose adaptations permit them to occur in several zones and (3) the system's exclusion of natural levees. In spite of these drawbacks, the zonal system is a useful framework for the understanding of broad floodplain community patterns, and hence is used here.

Woody Species Attributes

A familiarity with the structural and functional characteristics of the woody species of the southeastern floodplains prepares the reader for a better understanding of community distributions. The extant data support the concept of individual species adaptations to the selective forces of the floodplain environment. The distribution of bottomland tree, shrub, vine, and herb species over the floodplain zones is shown in Table 9. Structural and functional attributes of most of the important woody bottomland species may be found in Putnam (1951), Putnam et al. (1960), and Eyre (1980).

The survival of bottomland hardwood species under different hydroperiods provides a validation of the gradient concept

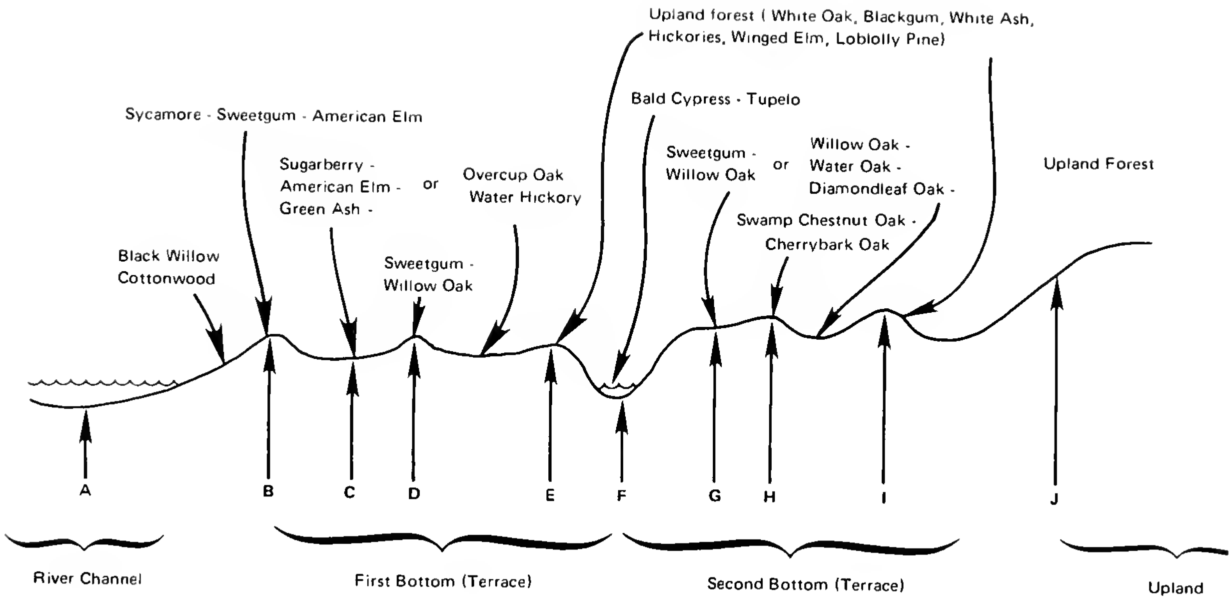


Figure 21. The correspondence between alluvial floodplain microtopography and forest cover types. (A) = river channel; (B) = natural levee (front); (C) = backswamp or first terrace flat; (D) = low first terrace ridge; (E) = high first terrace ridge; (F) = oxbow; (G) = second terrace flats; (H) = low second terrace ridge; (I) = high second terrace ridge; (J) = upland. The vertical scale is exaggerated.

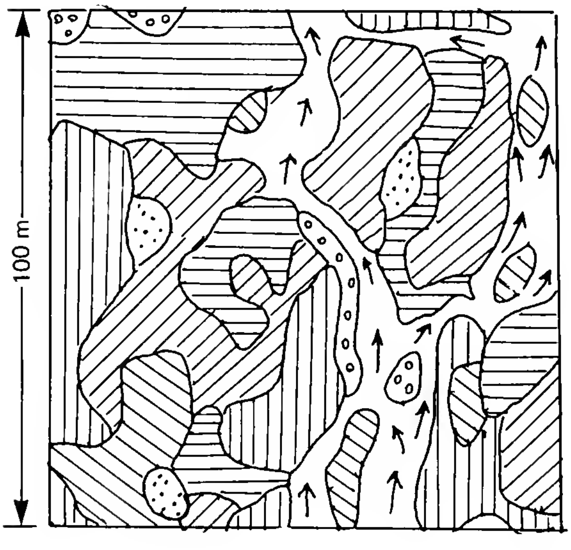


Figure 22. Microtopographic relief on a small blackwater creek floodplain (Lower Three Runs Creek, Barnwell County, SC). Areas of similar elevation are similarly marked. Arrows indicate channels which are always filled with water. Quadrat is 100 m on a side. (After Hay 1977.)

and the zonal classification system (Table 10). Trees in the almost constantly inundated Zone II may survive with roots partially inundated as much as 90% of the time and die only when inundation is permanent. On the other hand, upland (Zone VI) trees not so adapted to maintain themselves during flooding may begin to show signs of stress if constantly inundated as little as 2% of the time (dogwood and black cherry) and die as the flooding interval increases to 12% to 17% of the time.

Dominance Types and Their Distribution

Based upon field observation and studies in the four-state study area, we have classified bottomland hardwoods on floodplains into 75 dominance types organized by zones (Tables 11-14). Although Zones I (open water) and Zone VI (uplands) are relevant, they are not presented other than to introduce the nature of Zone I species.

Each table organizes the dominance types for each zone by topographic setting or uses other features to aid field identification. The reader should review

Table 9. Trees, shrubs, vines (V), and herbs (H) characteristic of southeastern bottomlands and the floodplain zones in which they most frequently occur (A = abundant, C = common, U = uncommon or localized, R = rare). Species (except some herbs and vines) are in approximate order of their position on the moisture gradient from wettest to driest. Species largely restricted to ecotones (E), levees (L), and peat soils (P) are also distinguished. Nomenclature generally follows Kurz and Godfrey (1962) and Little (1979).

Species	Ecological zones			
	II	III	IV	V
Taxodium distichum (baldcypress) A	X			
Taxodium ascendens (pond cypress) C	X			
Proserpinaca sp. (proserpinaca) C	X			
Nyssa aquatica (water tupelo) A	X			
Nyssa biflora (swamp tupelo) A	X			
Nyssa ogeche (Ogeechee tupelo) A	X			
Crinum americanum (strap lily) A	X			
Leitneria floridana (corkwood) U-R	X			
Tillandsia setacea (needleleaf wild pine) (H) C	X			
Planera aquatica (water elm) A	X			
Orontium aquaticum (goldenclub) (H) C	X			
Fraxinus caroliniana (water ash) A	X			
Fraxinus profunda (pumpkin ash) C	X			
Iris virginica (blue flag) (H) C	X			
Chamaecyparis thyoides (Atlantic white cedar) U	X			
Pinus serotina (pond pine) C	X			
Magnolia virginiana (sweet bay) C, P	X			
Persea borbonia (red bay) C, P	X			
Sabal palmetto (cabbage palm) C	X			
Ilex myrtifolia (myrtle-leaf holly) C, P	X			
Ilex cassine (dahoon) C, P	X			
Lyonia lucida (fetterbush) A, P	X			
Viburnum nudum (southern witherod) C, P	X			
Leucothoe racemosa (swamp leucothoe) C, P	X			
Clethra alnifolia (sweet pepperbush) C, P	X			
Lyonia ligustrina (male-berry) C, P	X			
Ilex coriacea (large gallberry) C, P	X			
Cyrilla racemosa (titi) A, P	X			
Alnus serrulata (alder) A	X			
Myrica cerifera (wax myrtle) A	X			
Crataegus aestivalis (may haw) U	X			
Forestiera acuminata (swamp privet) C-U	X	X		
Hymenocallis crassifolia (spiderlily) (H) C	X	X		

(continued)

Table 9. (Continued).

Species	Ecological Zones II	 III	 IV	 V
Hymenocallis occidentalis (spiderlily) (H) C, P		X		
Impatiens capensis (jewelweed) (H) C	X	X		
Triadnum tubulosum (St. Johns wort) (H) U	X	X		
Vernonia gigantea (iron weed) (H) U	X	X		
Senecio glabellus (butterweed) (H) C	X	X		
Woodwardia areolata (small chain fern) (H) A	X	X		
Onoclea sensibilis (bead fern) (H) A	X	X		
Osmunda regalis (royal fern) (H) C	X	X		
Thelypteris palustris (marsh fern) (H) C	X	X		
Smilax laurifolia (laurelleaf greenbrier (V) A	X	X		
Salix nigra (black willow) A		X		
Cephalanthus occidentalis (buttonbush) A		X		
Salix caroliniana (Ward willow) C		X		
Ilex verticillata (winterberry) U		X		
Gleditsia aquatica (water locust) U		X		
Itea virginica (Virginia willow) A		X		
Carya aquatica (water hickory) C		X		
Quercus lyrata (overcup oak) A		X		
Juncus effusus (rush) (H) A		X		
Acer rubrum var. *drummondii* (red maple) A		X		
Saururus cernuus (lizardtail) (H) A		X		
Diospyros virginiana (persimmon) R		X		
Illicium floridanum (star anise) U, E		X		
Styrax americanum (American snowbell) U		X		
Amorpha fruticosa (lead plant) C		X		
Cornus (stricta) foemina (stiff dogwood) C, E		X	X	
Viburnum dentatum (arrowwood) C, E		X		
Fraxinus pennsylvanica (green ash) A			X	
Quercus laurifolia (diamondleaf oak) A			X	
Quercus phellos (willow oak) U			X	
Ulnus americana (American elm) C			X	
Liquidambar styraciflua (sweetgum) A			X	
Leucothoe axillaris (coastal doghobble) C			X	
Betula nigra (river birch) A, L, E			X	
Crataegus viridis (green haw) C			X	
Ilex decidua (possum haw) C			X	
Carpinus caroliniana (ironwood) A			X	
Viburnum obovatum (Walter's viburnum) C			X	
Gleditsia tricanthos (honey locust) R			X	
Sabal minor (swamp palm) A			X	
Populus heterophylla (swamp cottonwood) U, L		X	X	

(continued)

Table 9. (Continued).

Species	Ecological zones			
	II	III	IV	V
Platanus occidentalis (sycamore) U, L		X	X	
Rhapidophyllum hystrix (needle palm) U			X	
Populus deltoides (cottonwood) U, L		X	X	
Crataegus marshallii (parsley haw) C			X	
Celtis laevigata (sugarberry) U			X	
Rhododendron viscosum (swamp azalea) C			X	
Rhododendron canescens (hoary azalea) C			X	
Sebastiana ligustrina (Sebastian bush) C			X	X
Smilax walteri (coral greenbrier) (V) C		X	X	
Smilax smallei (Jackson greenbrier) (V) C			X	
Berchemia scandens (supplejack) (V) A			X	
Wisteria frutescens (wisteria) (V) C			X	
Rhus radicans (poison ivy) (V) A			X	X
Trachelospermum difforme (trachelospermum) (V) U			X	
Brunnichia cirrhosa (ladies eardrops) (V) U			X	
Bignonia capreolata (cross vine) (V) A			X	X
Commelina virginiana (spiderwort) (H) C			X	
Ampelopsis arborea (peppervine) (V) A, L			X	
Tovara virginiana (jumpseed) (H) C			X	
Elephantopus caroliniana (elephants foot) (H) C			X	
Justicia ovata (justicia) (H) C			X	
Carex intumescens (sedge) (H) C			X	
Carex typhina (sedge) (H) C			X	
Carex lurida (sedge) (H) C			X	
Carex louisianica (sedge) (H) C (CP)			X	
Carex greyii (sedge) (H) C			X	
Leersia lenticularis (cutgrass) (H) C			X	
Leersia virginica (cutgrass) (H) C			X	
Oplisemenus setarius (H) C			X	
Erianthus strictus (plume grass) (H) C			X	
Panicum agrostoides (panic grass) (H) C			X	
Panicum rigidulum (panic grass) (H) U			X	
Morus rubra (red mulberry) U			X	X
Acer negundo (boxelder) L		X	X	
Pinus glabra (spruce pine) C				X
Arundinaria gigantea (river cane) (H) A				X
Vaccinium elliottii (Elliott's blueberry) C				X
Quercus michauxii (swamp chestnut oak) C				X
Ilex opaca (American holly) A				X
Quercus nigra (water oak) U-R				X

(continued)

Table 9. (Concluded).

Species	Ecological zones			
	II	III	IV	V
Carya cordiformis (bitternut hickory) U				X
Carya glabra (pignut hickory) U				X
Catalpa bignonioides (catalpa) U, L				X
Quercus pagoda (cherrybark oak) C				X
Asimina triloba (paw paw) C				X
Pinus taeda (loblolly pine) C				X
Quercus shumardii (Shumard's oak) U-R, L				X
Quercus virginiana (live oak) U				X
Serenoa repens (saw palmetto) U				X
Lindera benzoin (spicebush) U				X
Fagus grandifolia (beech) C, E				X
Aristolochia serpentaria (Virginia snakeroot) (H) C				X
Podophyllum peltatum (mayapple) (H) U				X
Chasmanthium laxa (river oats) (H) C				X

floodplain features (Chapter 1) and refer to Figure 40, which illustrates the microtopography of nine selected floodplains. Table 15 is cross-referenced to Figure 40, thereby providing precise locations of many dominance types.

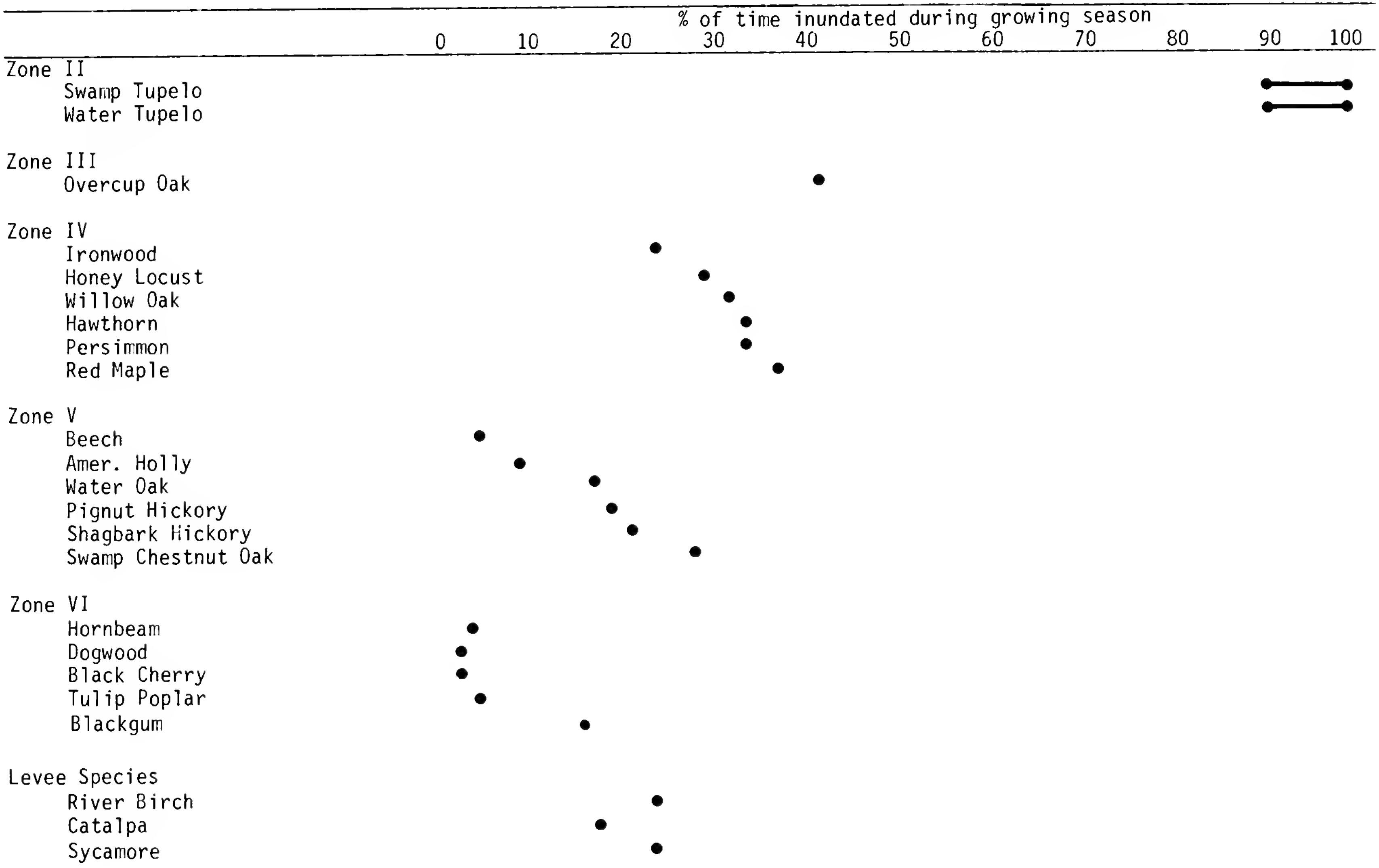
The best examples of each dominance type have been documented by locality and are listed in Tables 11-14. These dominance types are intended to prepare the reader for the incredible variety of bottomland forest communities and associations which, as yet, have been little studied. Occurrence is also indicated in each table as common, ecologically or geographically localized, or rare.

Where possible, reference is made to Society of American Foresters' (SAF) forest cover types (Eyre 1980); though general and not always applicable in this study area, this publication is useful. Huffman and Forsythe (1981) classed a number of SAF types in their zonal descriptions, including Zone VI, and related them to soil moisture regimes for a broad regional spectrum of floodplain types.

Plant Communities in Zone I

Submerged vascular aquatic plants are confined to Zone I: rivers, guts, sloughs, pools, and other permanently inundated areas. The dominant aquatic plant in the Santee River floodplain swamp was an introduced species, alligator weed (*Alternanthera philoxeroides*) (Dennis 1973). Other species noted in this floodplain which are characteristic of the region in general are water weed (*Egeria densa*), hornwort (*Ceratophyllum*), water milfoil (*Myriophyllum*), Brazilian elodea, duckweed (*Lemna perpusilla*), *Spirodela polyrrhiza*, water or mosquito fern (*Azolla caroliniana*), *Proserpinaca*, and frog's-bit (*Limnobium spongia*). The submerged, thin-leafed form of spatterdock (*Nuphar luteum*) is common in many spring-fed rivers. On floodplains with tidal flushing, an intertidal zone vegetated by quillwort (*Isoetes flaccida*), eelgrass (*Sagittaria kurziana*), water milfoil, and *Ludwigia* may occur (Figure 40, St. Marks River).

Table 10. Response of mature bottomland hardwoods, some upland species, and some levee species to varying lengths of time of inundation during growing season. Symbols (●) indicate the limit beyond which species cannot survive inundation of root crown and remain healthy. (Data from Teskey and Hinckley 1977.)



Dominance Types of Zone II

The dominance types of Zone II (Table 11) occur in the wettest parts of the floodplain: very wet flats, swales, sloughs, and backswamps. Soils are saturated throughout the growing season (100% of the time; Leitman et al. 1981) although fall drydown of water occurs in a number of types. Saturation in some types is maintained by seepage or by tidal fluctuation. The liverwort (Porella pinnata) growing on trunks of trees in this and other zones in an indicator of flooding depths and duration (Figure 23).

Gum-cypress dominance types (1-10) (Figures 24-27). Subtle factors determine the relative dominance of baldcypress (Taxodium distichum), water tupelo (Nyssa aquatica), swamp tupelo (N. biflora), and Ogeechee tupelo (N. ogeche) in the tupelo gum-cypress types. Although water tupelo occurs on disjunct Piedmont sites, it is restricted primarily to alluvial floodplains of the Coastal Plains. Swamp tupelo is prominent in floodplains of the Coastal Plain, but it is also common in upland swamps and ponds and in the brackish waters fringing estuaries (Penfound 1952). Water tupelo tolerates deeper and longer flooding than does swamp tupelo and dominates on sites characterized by this hydroperiod. Ogeechee tupelo is limited to the Coastal Plain and occurs in two distinct growth formations (see types 4, 7, 8, 9) on both alluvial and blackwater floodplains. Baldcypress is replaced by the tupelos on many sites because of its erratic reproduction, slower growth rates, and insignificant stump and root sprouting. These factors are intensified by frequent disturbance, such as periodic logging, further favoring tupelo dominance (Putnam et al. 1960; Eyre 1980). Pond cypress (Taxodium ascendens) is the codominant with tupelo gums on some blackwater floodplains.

Tree and shrub subcanopies occur in many gum-cypress types (2, 3, 4, 9, 10, 15, 17-21) and may be extremely dense in some (types 15, 17, 20, 21). Subcanopy vegetation in other types may be limited (type 1) because of low light intensities and extended flooding. The herbaceous layer is insignificant in most types but is surprisingly dense in others (types 4, 12, 16).

Swamp tupelo dominance types (11-16, 18, 19) (Figure 28). These types occur on organic black mucks or peats (the latter if bays are present). The deeper the peat, the denser the shrub understory (see type 15, which may be characteristic of blackwater river floodplains at elevations approaching sea level). These types on alluvial floodplains often occupy the swales and filled-in oxbows that flank the upland. Swamp tupelo types dominate stagnant, non-flowing, oxygen-poor sites and can tolerate saturated soils for long periods.

Bay swamps and shrub bogs dominance types (20, 21). These comparatively rare floodplain environments strongly resemble their upland wetland counterparts. Field observations were made at two sites (Table 11). The shrub bog on deep peat (type 20) had an unclosed pond pine canopy and appeared somewhat raised above the floodplain surface. The bay swamp (type 21) was moist from constant seepage.

Tidal forest dominance types (22-27) (Figures 29-31). Tidal forest types occupy the floodplains of all rivers within the zone of tidal influence, as far as 32 km (20 mi) inland along larger rivers. Soils are peats, tightly bound by interwoven root mats (Figure 29). The water table is continually high because of lunar or "wind" tides. Herbaceous layers are remarkably diverse and little studied. These flat floodplains include higher "islands" or hummocks whose tops are all at the same level (about that of storm tides) and supporting species that occur on alkaline floodplains (type 26). Southern red cedar (Juniperus silicicola) occupies the banks and higher elevations of the tidal forest floodplains along spring-fed (alkaline) rivers (Figure 30). It prefers a basic or high-calcium substrate. Stands of southern red cedar have been severely reduced in Florida by extensive logging by pencil companies (Wharton et al. 1977). The southern red cedar is an important component of the "hydric hammock," a seepage wetland vegetated by live oak (Quercus virginiana) and cabbage palm (Sabal palmetto), along Florida's gulf coast (Wharton et al. 1977).

Atlantic white cedar dominance types (28-30). Atlantic white cedar (Chamaecyparis thyoides) is believed to be a distur-

Table 11. Dominance types of Zone II.

Floodplain setting	Topographic setting	Dominance type	Occurrence	Representative site locations
Flats, sloughs, swales, and backswamps. Organic soil component low. Flooding regime annual, with water usually flowing during inundation. Most flats and some sloughs with annual dry-down. Principal dominants are baldcypress, water tupelo, Ogeechee tupelo, and pumpkin ash (corresponds most closely with SAF type 102).	Flats with single channels	(1) Baldcypress-water tupelo, no characteristic understory	Common, widespread	Roanoke below Williams; NC; Santee at Hwy 411 bridge, SC
		(2) Baldcypress-water tupelo, water elm-water ash understory	Ecologically or geographically localized	Apalachicola Forbes Is., FL; Chocktawhatchee above Hwy 20 bridge, FL
		(3) Tall, straight Ogeechee tupelo-water tupelo-cypress pumpkin ash	Ecologically or geographically localized	Lower Suwannee below Manatee Springs, FL
		(4) Tall, straight Ogeechee tupelo-sweet bay-strap lily	Ecologically or geographically localized	Apalachicola, FL at River Mile 15.6 (Figure 25)
	Flats with anastomosing channels	(5) Baldcypress-water tupelo-Ogeechee tupelo-water elm-water ash	Ecologically or geographically localized	Chipola above Hwy 71 bridge, FL
		(6) Baldcypress-water tupelo	Ecologically or geographically localized	Four Hole Swamp, SC
	Sloughs on alluvial river	(7) Large, stooled Ogeechee tupelo dominant, with scattered cypress canopy	Rare	Apalachicola at Blountstown, FL; Ochlockonee, Porter's Lake, FL
	Sloughs on blackwater river	(8) Baldcypress-tall, straight Ogeechee tupelo-water tupelo	Ecologically or geographically localized	Ogeechee above Hwy 25 bridge, GA

(continued)

Table 11. (Continued).

Floodplain setting	Topographic setting	Dominance type	Occurrence	Representative site locations
		(9) Baldcypress with stooled Ogeechee tupelo, water ash, and water elm	Common	Canoochee, Ft. Stewart, GA
	Linear backwater swamp	(10) Large buttressed cypress with stooled water ash and water elm. Water tupelo stands entirely separate (SAF type 103)	Ecologically or geographically localized	Ebenezer Creek below Hwy 21 bridge, GA (Figures 26, 27); Ogeechee, Dee Lake, GA
Swamp tupelo and swamp tupelo-water tupelo dominated flats, swales, and backswamps. Organic soil component high. Flooding regime annual, with water usually standing and anoxic rather than flowing. Complete drydown usually only in drought years. Also included are rare examples of floodplain shrub bogs and bay swamps.	Alluvial floodplain flats	(11) Swamp tupelo-water tupelo-swamp palm flats	Ecologically or geographically localized	Choctawhatchee above Hwy 20 bridge, FL; Yellow at Hwy 87 bridge, FL
		(12) Wet flats with swamp tupelo-water tupelo-baldcypress with dense emergents (*Sagittaria* *Thalia*, *Justicia*, royal fern)	Ecologically or geographically localized	Apalachicola below Forbes Is., FL
	Blackwater floodplains	(13) Swamp tupelo-pond cypress	Common	Satilla at Hwy 252 bridge, GA
		(14) Swamp tupelo-cypress with surface peats	Ecologically or geographically localized	Little Wambau Natural Area, SC
		(15) Swamp tupelo-pond cypress with dense evergreen shrub understory over deep peat	Common	Chowan near Virginia border, NC

(continued)

Table 11 (Continued).

Floodplain setting	Topographic setting	Dominance type	Occurrence	Representative site locations
	Swales	(16) Swamp tupelo with unique herb zone (*Hypericum tubulosum*, *Hydrocotyl verticillata*, royal fern)	Ecologically or geographically localized	Roanoke, Devil's Gut, NC
		(17) Dwarfed sweet bay-red bay-pond cypress canopy with shrub bog understory over deep peat	Ecologically or geographically localized	Waccamaw, Hwy 9 bridge, SC
	Backswamps adjacent to upland slope	(18) Swamp tupelo canopy with *Cyrilla* and *Itea* as dominant shrubs	Common	Escambia at Hwy 184 bridge (Figure 28)
		(19) Swamp tupelo-sweet bay	Common	Congaree Swamp National Monument, SC; Altamaha near Cox, GA
	Floodplain shrub bog (SAF type 98)	(20) Pond pine canopy with dense evergreen shrub bog over deep peat	Rare	Upper Three Runs, Aiken, SC
	Floodplain bay swamp	(21) Sweet bay canopy with dense evergreen shrub understory, royal fern	Rare	Chipola above Hwy 71 bridge, FL
Tupelo gum-cypress forests with moderately organic soils. Annual flooding regime present but influenced by lunar or wind tides maintaining saturated soil conditions. Some fauna (*Uca* and *Sesarma* crabs, manatee) of coastal marine affinities		(22) Baldcypress-water tupelo-sweetgum	Ecologically or geographically localized	Altamaha, Lewis Is., GA (virgin remnant) (Figure 31)

(continued)

Table 11. (Concluded).

Floodplain setting	Topographic setting	Dominance type	Occurrence	Representative site locations
Tidal forests usually dominated by swamp tupelo and sweet bay (corresponds most closely with SAF type 104). Trees in lower reaches often dwarfed. Organic soil component high, root mats continuous or interwoven at or near the surface. Annual flooding present but regime dominanted by daily tidal fluctuations. An intertidal zone with fauna of marine affinities (fiddler crabs, *Neretina* snails) usually present.		(23) Baldcypress-water tupelo-red bay	Ecologically or geographically localized	Apalachicola at Pinhook, FL (dwarfed alluvial river forest)
		(24) Cypress-swamp tupelo-sweet bay-pumpkin ash	Ecologically or geographically localized	Suwannee at East Pass, FL (dwarfed blackwater river forest) (Figure 29)
		(25) Swamp tupelo-sweet bay with dense titi-ericad understory	Ecologically or geographically localized	Lafayette Creek at Hwy 20 bridge, FL
		(26) Swamp tupelo-sweet bay with cabbage palm and southern red cedar	Ecologically or geographically localized	St. Marks, Wakulla, and Wacissa below Hwy 98 bridges, FL (Figure 30)
		(27) Swamp tupelo-cypress-sweet bay with shrub bog over deep peat	Rare	Roanoke, Albemarle Sound, NC (wind tide dominated)
Tidal forests dominated by white cedar-sweet bay		(28) White cedar-sweet bay and tall shrubs in subcanopy (*Ilex cassine*, *I. myrtifolia*, *Cyrilla*, *Myrica*)	Ecologically or geographically localized	Yellow below Hwy 87 bridge, FL
Nontidal riverine forests, peat-forming with Atlantic white cedar codominant. Saturation maintained along bay streams by seepage from sandhills (Type 29) or in riverine backswamps adjacent to high ground (Type 30).		(29) White cedar-pond pine	Ecologically or geographically localized	Whitewater at Hwy 137 bridge, GA
		(30) White cedar-swamp tupelo	Ecologically or geographically localized	Yellow at Hwy 90 bridge, FL

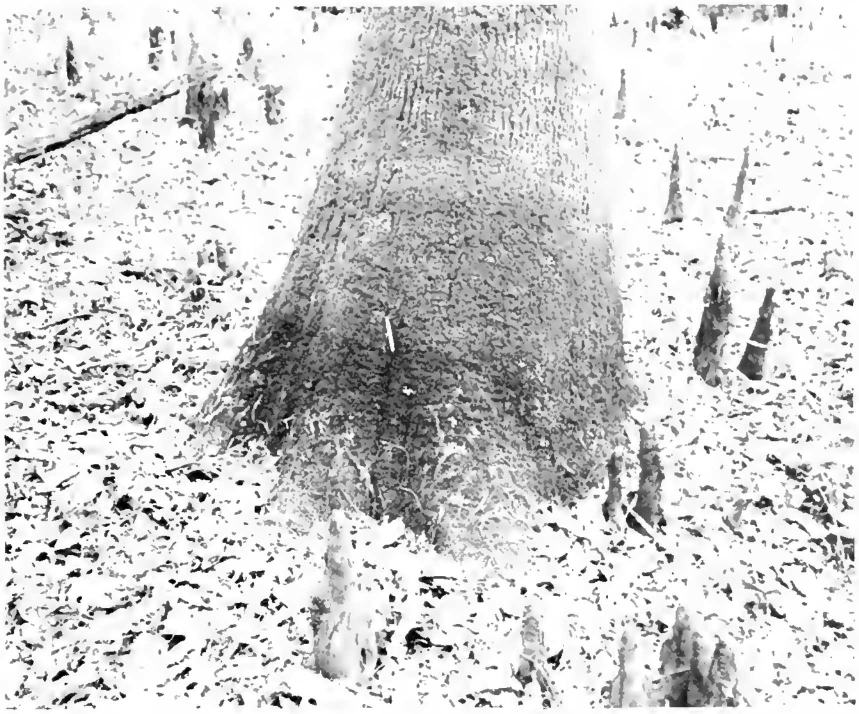


Figure 23. The dark area below the pencil is a liverwort (Porella pinnata) zone, the upper boundary of which indicates that high water has stayed at that level for at least 16% of the year (58 days, not necessarily consecutive). The zone above it is a green moss. The upper boundary of Porella growth is helpful for quickly determining depth and duration of flooding.

Figure 24. The outermost swale (next to the upland) along the lower Roanoke River (NC) supports almost pure stands of either swamp or water tupelo on black, muck soils. Here, in a water tupelo stand, in response to the anaerobic muck, roots form blocky aerial knees which resemble black rocks.

Figure 25. These Ogeechee tupelos on the Apalachicola River floodplain (River Mile 15.6) are tall, straight, and large, measuring 1 m DBH (diameter at breast height) although along many Coastal Plain rivers they form grotesque, many-trunked stools. In the forest pictured, water tupelo is a co-dominant, and strap lily (<u>Crinum americanum</u>) is a characteristic herb.

Figure 26. Scenic Ebenezer Creek (Effingham County, GA) is a unique variant of Zone II, with a deep lake-like channel. Cypress buttresses are abnormally enlarged.

Figure 27. Drydown in water tupelo (Zone II) on Ebenezer Creek (GA). These backwater environments are dominated exclusively by tupelo and cypress. During drydown, nutrients concentrate, and duckweeds form dense surface layers. Note: (1) the precise height of the high water line (approximately 2 m or 7 ft), (2) relation of buttress swell to high water mark, and (3) counter-clockwise "swirl" of buttresses.

Figure 28. The outermost backswamp (Zone II) on many alluvial floodplains is dominated by a swamp tupelo on acid, highly organic muck soils. Here on the Escambia (Hwy. 184 bridge, FL) the shrub zone (Cyrilla, Itea) is sparse but prominent. There is a clay aquiclude several feet below the surface mucks. Seepage moisture from the adjacent upland, as well as rainfall, may be important to some of these associations.

Figure 29. This tidal forest (Zone II) of sweet bay, pumpkin ash, swamp tupelo, and cypress at West Pass (Suwannee River, FL) has a characteristic interwoven mat of large roots close to the surface. This extremely tough layer protects the forest and the shore from the destructive erosion of constant wave action and storm tides. There is no natural levee. High tide comes nearly to the top of the root crowns. Fiddler crabs and olive nerite snails are abundant on the forest floor. Showy herbaceous plants such as iris, butterwort (Senecio glabellus) and aster (Aster vimineus) are surprisingly common.

Figure 30. Three shoreline dominants, sweet bay (B), red cedar (C), and cabbage palm (P), are characteristic of the tidal zone of an alkaline blackwater river (St. Marks, FL). An intertidal zone (T) can be seen between the root zone (H) at the high tide line (partly in shade) and the dark water (W), which has a band of submerged plants (S), here partly exposed.

Figure 31. A small grove of virgin cypress is preserved on Lewis Island (Altamaha River, McIntosh County, GA) where they grow in unique association with both sweetgum and water tupelo. Such giant cypress were characteristic of the upper tidal zone of the great alluvial rivers of the Southeast. Apart from a few shallow sloughs, most of the grove has a moderately dense herb layer including the swamp palm (Sabal minor). Both it and sweetgum are typically found in Zone IV. Cypress here do not have the large swollen base.

bance-adapted successional species. Fire is the most common precursor to white cedar development, though flooding, windthrows, or logging yield the same effects. Atlantic white cedar is usually found in bog stream swamps on peat overlying sandy soils that are characteristically poor in nutrients, in a unique tidal forest type, or in acid backswamps of certain Florida rivers.

Dominance Types of Zone III

Zone III includes the wet flats, bank-edge strips, low levees, and depressions in Zones IV and V. Dominance types (Table 12) in this zone are semi-permanently inundated for a major part of the growing season, as well as in winter and spring. Although the hydroperiod is long (about 6 months), Zone III areas are subject to annual drydown. Soils are saturated 40% of the year (Leitman et al. 1981).

Pioneer dominance type (1). The banks and point bars of the southeastern rivers often are occupied by the black willow (*Salix nigra*) and other species such as silver maple (*Acer saccharinum*), and sometimes cottonwood (*Populus deltoides*). These early seral stages are succeeded by Zone IV types as elevation increases from soil accumulation. The successional sequence is a function of meander movement rates and point bar formation. Rivers with intact forests on fine cohesive sediments migrate so slowly that mature forest establishment keeps pace with the river channel, and pioneer stages never develop. Swift meander movements over unconsolidated sands produce tapered slopes on point bars, and several seral stages may be found.

Shrub, small tree, and herb dominance types (2-4). Semi-permanent pools occur in depressions, old oxbows, and scour channels. They are dominated by several species of willows, shrubs (e.g., may haw (*Crataegus aestivalis*)), and small trees (e.g., water elm (*Planera aquaticum*)).

Overcup oak-water hickory dominance types (5-10). The most poorly drained flats of the floodplain, in which water stands well into the growing season, are characteristically dominated by the overcup oak-water hickory (*Quercus lyrata-Carya aquatica*) type (Figure 32) and its variants. These flats are relatively small (about 2 ha or 5 acres) in the Southeast, and seldom are dominated exclusively by these two species. The wet flats of the Congaree River (SC) are dotted with numerous depressions, so small as to be occupied by a single overcup oak. Overcup oak, undesirable for lumber, often is left by loggers. A near-virgin stand of overcup oak on the Santee River floodplain (SC) contains trees approaching 1.2 m (4 ft) in diameter. Additional sites occupied by this type include small shallow depressions in Zones IV and V, and narrow bands bordering deeper depressions that contain cypress-tupelo or water elm. Both overcup oak and water hickory avoid seedling and sprout mortality from inundation by leafing out late in the spring. Both species reproduce well; overcup oak through consistently good acorn crops, and water hickory through good mast and prolific sprouting (Eyre 1980). Water locust (*Gleditsia aquatica*)-water hickory stands are rare variants of this type. The extended hydroperiod in the sites occupied by overcup oak-water hickory and water locust-water hickory forests inhibits herb growth, and thus the understory is restricted to small trees and shrubs (Eyre 1980).

Dominance Types of Zone IV

Zone IV (Table 13) forms the bulk of the floodplain on Coastal Plain alluvial rivers above tidal influence, chiefly on flats or terraces of low relief. Two irregularities are common: "washboard" terrain caused by parallel scour channels (often sandfloored) and "hummocky" terrain where trees either stand above the general floodplain level on hummocks or have tortuous scour channels around and through them. Zone IV is seasonally inundated or saturated for 1 to 2 months of the growing season, and more or less continuously inundated during winter and early spring. Soils are saturated about 22% of the year (Leitman et al. 1981). Shrub and herb layers are scanty. Stiff clay soils or subsoils act as aquicludes which pond rainwater on alluvial floodplains, while the more porous sands dominating blackwater floodplains preclude this ponding. The diamondleaf oak (*Quercus laurifolia*) appears to dominate both the alluvial and blackwater floodplains. It is remarkably

Table 12. Dominance types of Zone III.

Topographic setting	Dominance type	Occurrence	Representative site locations
Banks and point bars	(1) Black willow-Ward willow-silver maple with occasional cottonwood and swamp privet	Common	Altamaha, Wayne Co., GA; Flint, Dooley Co., GA
Pond and depression pools which dry down (includes some beaver ponds not drying down annually) (Closest to SAF type 95)	(2) Water elm ponds	Ecologically or geographically localized	Choctawhatchee above Hwy 20 bridge, FL
	(3) May haw ponds	Ecologically or geographically localized	Canoochee, Fort Stewart, GA
	(4) Marsh ponds (beaver origin)	Common	Flint at Hwy 278 bridge, GA
Wet flats (SAF type 96)	(5) Overcup oak-water hickory	Ecologically or geographically localized	Apalachicola at Blountstown, FL; Santee at Hwy 41 bridge, SC
Shallow depressions in Zones IV and V	(6) Overcup oak depressions	Common	Congaree Swamp National Monument, SC (Figure 32)
	(7) Depression borders (fringing swamp gum ponds)	Common	Apalachicola, Muscogee Reach, FL
River edge associations	(8) Water hickory-water locust (bank edge strip)	Ecologically or geographically localized	Altamaha, Sansavilla Bluff, GA
	(9) Overcup oak-water hickory (strip inside levee)	Common	Choctawhatchee above Hwy 20 bridge, FL; Suwannee at Fowler's Bluff, FL
Old levee ridge edges	(10) Overcup oak-water hickory	Common	Santee at Hwy 52 bridge, SC; Apalachicola, Chipola Cutoff; FL

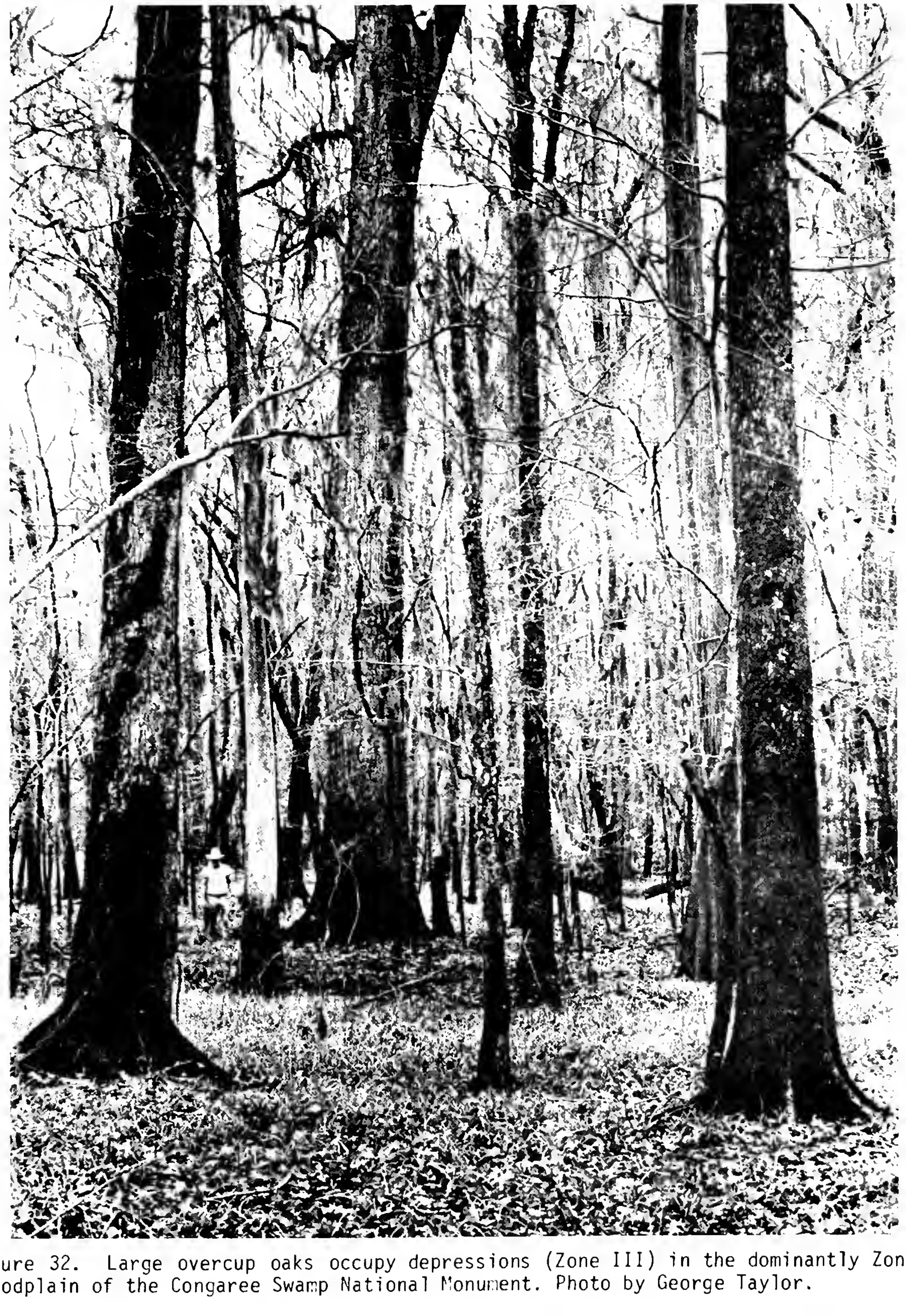


Figure 32. Large overcup oaks occupy depressions (Zone III) in the dominantly Zone IV floodplain of the Congaree Swamp National Monument. Photo by George Taylor.

Table 13. Dominance types of Zone IV.

Topographic setting	Dominance type	Occurrence	Representative site locations
Oak flats-alluvial and blackwater floodplains	(1) Diamondleaf oak (usually with swamp palm understory)	Common	Ogeechee at Hwy 25 bridge, GA; Indiana Field Swamp at Hwy 78 bridge, GA
	(2) Diamondleaf-willow oak	Ecologically or geographically localized	Altamaha at Seaboard Railroad bridge, GA; Ogeechee at Hwy 78 bridge, GA
	(3) Willow oak	Ecologically or geographically localized (Rare)	Oconee at Hwy 280 bridge (nearly virgin forest)
Moderately wet to drier alluvial floodplain flats	(4) Sweetgum diamondleaf oak-green ash	Rare	Savannah, Bear Is., GA (nearly virgin forest)
	(5) American elm-sugarberry (SAF type 93)	Ecologically or geographically localized	Roanoke, Scotland Neck, NC
Wet flats-alluvial floodplains	(6) Diamondleaf oak-green ash	Common	Congaree Swamp National Monument, SC
	(7) Red maple-green ash	Common	Alcovy at Hwy 278 bridge, GA (Piedmont)
Wet flats-blackwater floodplains	(8) Diamondleaf oak-swamp a. with red maple b. with American holly, *Styrax americana*	Ecologically or geograpically localized (Rare)	a. Creeping Swamp, Pitt Co., NC b. Waccamaw, Vaughn Place, SC
Oak-pine flats-alluvial floodplains	(9) Diamondleaf oak-spruce pine	Ecologically or geographically localized	Oconee between Hwy 280 and Hwy 46 bridges, GA; Choctawhatchee above Hwy 20 bridge, FL

(continued)

Table 13. (Concluded).

Topographic setting	Dominance type	Occurrence	Representative site locations
Oak-pine flats-blackwater floodplains	(10) Diamondleaf oak-spruce pine a. with *Vaccinium elliotii*, river cane b. with *Sabal minor* and *Sebastiana*	Ecologically or geographically localized	a. Canoochee, Fort Stewart, GA (Figure 35) b. Ohoope at Hwy 15 bridge, GA
Islands in Zone II anastomosing floodplain	(11) Diamondleaf oak a. with *Ilex decidua* understory b. with *Sebastiana* understory	Common	a. Chipola above Hwy 17 bridge, FL b. Aucilla at Hwy 19/27 bridge, FL
Low natural levees	(12) Diamondleaf oak with large, tall Ogeechee tupelo	Common	Apalachicola at River Mile 12, FL
Scour channel topography	(13) Diamondleaf oak with mix of Zone III, IV, and V species	Common	Apalachicola, Muskogee Reach, and Chipola Cutoff, FL
Low ridges of ridge and swale topography	(14) Diamondleaf oak	Ecologically or geographically localized	Waccamaw at Hwy 9 bridge, SC
Low Pleistocene dune oak-pine ridges (closest to SAF type 89)	(15) Live oak-diamondleaf oak-willow oak-spruce pine	Ecologically or geographically localized	Altamaha, Fulton Ridge, GA
	(16) Live oak-diamondleaf oak-willow oak	Rare	Little Pee Dee, SC
Old levee oak-pine ridge	(17) Live oak-spruce pine	Ecologically or geographically localized	Ochlockonee, Porter's Lake, FL
Successional associations	(18) River birch (closest to SAF type 61) (Piedmont floodplains)	Common	Yellow, Rockdale Co., GA
	(19) Cottonwood (old diked areas)	Rare	Roanoke, Seaboard Railroad bridge, Scotland Neck, NC

wet-tolerant, occasionally found as a co-dominant with swamp tupelo (type 10), and rarely can be found mixed with a few cypress.

Floodplain flats dominance types (1-10). The diamondleaf oak dominates the Zone IV flats of all the major river types. Even so, these forests are more diverse than the wetter overcup oak-water hickory types in Zone III. Frequent associates in this zone are green ash (*Fraxinus pennsylvanica*), American elm (*Ulnus americana*), sweetgum (*Liquidamber styraciflua*) (Figure 33) and, less commonly, sugarberry (*Celtis laevigata*). The swamp palm (*Sabal minor*) (Figure 34) is a good general indicator species for this zone, as is possum haw (*Ilex decidua*), Walter's viburnum (*Viburnum obovatum*) and various hawthorns (*Crataegus* spp.). Occasionally, the spruce pine (*Pinus glabra*) occurs although it is considered to be associated with lowest elevations of Zone V. It has a wide moisture tolerance and may occur with diamondleaf oak on both alluvial (type 9) and blackwater (type 10) floodplains.

Dominance types on other sites (11-17). Zone IV oaks (diamondleaf, willow) occur in a variety of other situations: scour channels (type 13), ridges of ridge and swale topography (type 14), and the lower elevations of relict dune ridges (types 15, 16) where they occasionally mix with wet variants of live oak. Narrow sandy ridges (type 15) may bear shrubs that are not usually considered wetland species: wild olive (*Osmanthus*), yaupon (*Ilex vomitoria*) and saw palmetto (*Serenoa repens*).

The reader should be cautioned that delineating Zones IV and V on some blackwater and Piedmont rivers can be confusing. Due to the sandy soils of some blackwater floodplains, microedaphic and microtopographic mosaics become even more divided. On some floodplains (Zone IV, type 10) an apparent mix of Zone IV and V species may occur (Figure 35). On Piedmont floodplains, owing to the numerous scour channels and fast-draining clay soils, there also may be this apparent mix of Zones IV and V to the casual observer.

Dominance Types of Zone V

Zone V comprises the highest elevation floodplain associations occurring on old natural levees, flats, higher terraces, and Pleistocene ridges and dunes. Inundation averages once yearly (Congaree, SC). See Figure 11 for graphic example. Duration of flooding ranges from 2% (5.3 days) to 12.5% (33 days) of a 265-day growing season. Soils are usually sandier and less fertile than those of lower zones.

Zone V dominance types observed in the study area are listed in Table 14. Zone V associations appear to dominate many Piedmont floodplains; however, in the Coastal Plain these associations may be restricted to 5% to 10% of the floodplain surface. As in Zone IV, the plant associations grow on both Pleistocene and Holocene floodplain surfaces. Understory species are more conspicuous in this zone. In fact, two understory species, the paw paw (*Asimina triloba*), a subcanopy tree, and river cane (*Arundinaria gigantea*) are generally good indicator species. River cane is most luxurious in this zone although dwarfed stands grow in Zone IV. The diversity of both herbs and shrubs is maximal in this zone.

Zone V flats and old levee ridge dominance types (1-11) (Figures 36 and 37). Two hardwood species are characteristic and widely distributed: swamp chestnut or cow oak (*Quercus michauxii*) and cherrybark oak (*Q. pagoda*). Water oak (*Q. nigra*) occasionally occurs as a co-dominant species in these associations. Two pines are present: spruce pine at the wetter end of the spectrum and loblolly (*Pinus taeda*) at the drier end. In the Congaree, record loblolly pines grow on old levee ridges slightly elevated above Zone IV surfaces (Figure 36). Spruce pine seems to require a more continuous water supply and even occurs on upland slopes under seepage conditions. Some species that are widespread on the uplands apparently can adapt to the floodplain conditions of Zone V. Some hickories are common in Zone V over clay-rich subsoil sites (types 6-8) and, rarely, form hickory flats (type 6).

Figure 33. The sweetgum is a long-lived component of virgin alluvial bottomland forests throughout the Southeast. These giants in the Congaree Swamp National Monument (CSNM) occupy the higher portions of Zone IV floodplain. Lower Zone IV areas may lack the larger trees. The CSNM contains a number of national and state record trees.

Figure 34. Many Zone IV bottomland hardwoods on Coastal Plain alluvial river floodplains (Ocumulgee River, GA) have an understory of Sabal minor, a dwarf palm confined to Zone IV floodplains. The similar but rarer needle palm (Rhapidophyllum hystrix) also occurs here.

Figure 35. The floodplain of the blackwater Canoochee (Fort Stewart, GA) is somewhat anomalous in the co-dominance of diamondleaf oak (Zone IV species) with either spruce pine or loblolly pine (Zone V species). The herbaceous ground cover is dominated by river cane and grasses such as Panicum rigidulum and Erianthus strictus. American holly is present. The shallow flooding and permeable soils are probable factors allowing for a mix of Zone IV and V species. Diamondleaf oaks here grow more slowly than those on the alluvial Oconee floodplain.

Table 14. Dominance types of Zone V.

Topographic setting	Dominance type	Occurrence	Representative site locations
Low flats (overlapping with Zone IV)	(1) Swamp chestnut oak-green ash	Common	Alcovy at Hwy 278 bridge, GA (Piedmont); Congaree Swamp National Monument, SC
	(2) Swamp chestnut oak-American elm	Ecologically or geographically localized	Congaree Swamp National Monument, SC
High flats	(3) Swamp chestnut oak-cherrybark oak-spruce pine	Common	Oconee at Hwy 280 bridge, GA; Ocmulgee, Glass Tract, Telfair Co., GA (nearly virgin area)
	(4) Water oak	Rare	Flint, Upson Co., GA (Piedmont)
	(5) Cherrybark oak-water oak-loblolly pine-American holly	Common	Alcovy at Hwy 278 bridge, GA (Piedmont)
	(6) Bitternut hickory-pignut hickory with paw paw and swamp palm	Ecologically or geographically localized	Oconee, Wilkinson Co., GA
	(7) Cherrybark oak-bitternut hickory-pignut hickory	Ecologically or geographically localized	Ogeechee at Hwy 78 bridge, GA (on rises)
	(8) Water oak-loblolly pine	Common	Congree Swamp National Monument, SC (Figure 36); Edisto at Hwy 78 bridge, SC

(continued)

Table 14. (Concluded).

Topographic setting	Dominance type	Occurrence	Representative site locations
Old levee ridges	(9) Water oak-swamp chestnut oak-spruce pine with river cane-swamp palm understory	Common	Yellow at Hwy I-10 bridge, FL; Apalachicola, Chipola Cutoff, FL
	(10) Beech-American holly	Ecologically or geographically localized	Congaree Swamp National Monument, SC (Figure 37); Alcovy at Hwy 278 bridge, GA
	(11) Swamp chestnut oak-southern magnolia-American holly and river cane	Ecologically or geographically localized	Apalachicola, Muscogee Reach, FL
Floodplain "island" with incipient beech-magnolia hammock	(12) Beech-American holly with *Symplocus*	Ecologically or geographically localized	Upper Three Runs, Aiken, SC
	(13) Beech-southern magnolia	Ecologically or geographically localized	Kiokee, Fowler Tract, Dougherty Co., GA
Pleistocene ridge (ridge and swale topography, Terrace I)	(14) Swamp chestnut oak-cherrybark oak-loblolly pine	Ecologically or geographically localized	Roanoke, Devil's Gut, NC (Figure 38)
Pleistocene Terrace I braided dune (border)	(15) Water oak-loblolly pine	Ecologically or geographically localized	Little Pee Dee below Hwy 378 bridge, SC
Scour channels	(16) Water oak (mix of Zones III, IV, and V species)	Common	Apalachicola, Muscogee Reach and Chipola Cutoff, FL

Figure 36. Although normally an upland species, the loblolly pine also grows in Zone V areas of many floodplains. These large examples occur on old levee ridges and low terraces in the Congaree Swamp National Monument (SC) only a foot or so in elevation above the lower Zone IV floodplain. Photo by George Taylor.

Figure 37. An old levee ridge near Cedar Creek (Congaree Swamp National Monument, SC) supporting Zone V vegetation. The large tree to the left of the figure is a cherrybark oak. Paw paw and spicebush are common in the understory. On slightly higher parts of this same ridge, beech occurs. Some upland herbs (may apple, broad beech fern, wild yam, poison oak) may occur. Photo by George Taylor.

Low ridges with certain edaphic conditions sometimes support a few white oak (Quercus alba) in Zone V associations. Although tulip poplar (Liriodendron tulipifera) is extremely rare in the study area, it can occur in Zone V associations.

Dominance types of other sites (12-16). Beech (Fagus grandifolia) or beech-magnolia hammock is frequently the first association encountered at the ecotone of floodplain and upland. A beech "fringe" is characteristic of many Piedmont alluvial floodplains. Since beech-southern magnolia hammock also exists under seepage conditions on the uplands (usually adjacent to the floodplains, Zone VI), the high water tables of Zone V often enable these species (primarily beech) to grow on "islands" (types 12, 13) and old natural levee ridges (types 10,11). Southern magnolia (Magnolia grandiflora), however, is rare on floodplains in the study area.

In areas of ridge and swale topography (type 14) (Figure 38), Zone V associations occupy the higher elevations, succeeding the associations of lower elevations. Scour channels, because they allow rapid drainage, frequently contain Zone V species mixed with those of Zones III and IV (type 16). This is similar to the occurrence of live oak (and saw palmetto) at the "lip" or edge of banks and scour channels.

Figure 38. Narrow, long ridges between swales on the lower Roanoke floodplain (NC) of probable late Pleistocene age have an almost diagrammatic zonation of Zone V hardwoods beginning with diamondleaf oak at the edge of Zone II and progressing up through swamp chestnut oak to cherrybark oak.

Plant Communities on Natural Levees, Floating Logs, and Stumps

The zonal classification scheme does not make specific provision for the plant communities that occur on natural levees and on floating logs and stumps, and thus they will be discussed here.

Natural levees. The height, width, soil texture, and drainage characteristics of natural levees vary considerably, often fostering the highest plant species diversity on the floodplain. Species characteristic of all floodplain zones (II-V) commonly occur on levees, not only because of the differences among levees, but also because of variations on individual levees, which are often a mosaic of microenvironments (Radford et al. 1980).

Recently formed levees on nontidal reaches of alluvial rivers support pioneer tree species, particularly on front sides (cottonwood, black willow, river birch (Betula nigra), silver maple), while mid-seral species (sycamore (Platanus occidentalis), sugarberry, American elm, green ash, and sweetgum) occupy stabilized levee ridges and backslopes (see Figure 21 and the discussion of Zone IV dominance types). Boxelder (Acer negundo) and catalpa (Catalpa bignonioides) are pioneer species that seem to prefer levees to any other floodplain sites. River birch is often the dominant on sandy Piedmont levees as well as on disturbed floodplains.

Baldcypress (Zone II), and overcup oak, water hickory, and water locust (Zone III) are found on low stable levees. Higher, well-drained broad levee ridges, such as those on the Roanoke River in North Carolina, may host Zone V species, including swamp chestnut oak, cherrybark oak, Shumard's oak (Quercus shumardii), paw paw, and spicebush (Lindera benzoin) (J.M. Lynch, Department of Community Development and Natural Resources, North Carolina Heritage Program, Raleigh; personal communication). Live oak frequently occupies the high river front edges because of the "dry lip" effect discussed earlier (Zone V discussion).

Tidally influenced forests, like those found on the St. Marks River (FL), show zonation on the present levee (Table 15). The drier river front is dominated by live oak and saw palmetto (Zone IV); the levee top supports southern red cedar, cabbage palmetto, and sweetbay (Zones II and III); and the backside contains inner swamp species such as swamp tupelo in addition to dahoon (Ilex, cassine) groundsel tree (Baccharis glomeruliflora), cabbage palmetto, southern red cedar, sweet bay (Magnolia virginiana), and wax myrtle.

There are distinct differences between the communities that occupy old levees and the present developing levee, primarily because of the changing hydroperiod. The trend is for older levees to become dominated by species characteristic of drier sites as the floodplain geomorphology changes. Good examples are found in the ridge and swale topography of sections of the Roanoke River (NC). The ridges (old levees) show distinct zonation from Zone IV species (primarily diamond-leaf oak) near the swale edge, through wet-site Zone V species (swamp chestnut oak and cherrybark oak), and finally to dry-site Zone V loblolly pine.

Floating logs and stumps. In addition to the communities of Zones II-V and natural levees, a unique flora sometimes occurs on floating logs (Figure 39) and stump remnants. Dennis (1973) described such communities in the Santee Swamp (SC). Twenty-four species were noted, eleven of which did not occur in the larger survey of the swamp. The community samples were homogeneous, dominated by Boehmeria cylindrica and Hypericum walteria. The selective forces acting on fallen logs and stumps are uniform and severe, efficiently eliminating species that cannot tolerate shifting conditions of inundation, exposure, and possible substrate instability. In addition to Dennis (1973), Conner and Day (1976) noted several plants that grew on rotting logs and stumps, including ferns, strap lily (Crinum americanum), Hymenocallis eulae, spiderlily (H. occidentalis), Hydrocotyle spp., southern wild rice (Zizaniopsis miliacea), and Panicum spp.

Understory Species

A structured understory community exists beneath the floodplain forest canopy that may rival it in species diversity. Of 110 species found on the Santee

Table 15. Forest dominance type distributions across the nine floodplain transects illustrated in Figure 40. The letters in each zone description refer to the site letters in Figure 40. Where applicable, cross-reference is made in parentheses to specific dominance types/variants as they appear in Tables 11-14 in the discussions of each zone. For example, (II-1) refers to Zone II (Table 11), baldcypress-tupelo dominance type 1. Table 12 has Zone III dominance types; Table 13, Zone IV; Table 14, Zone V.

River, river class, and location	Zones				Other sites & remarks
	II	III	IV	V	
Congaree, SC, alluvial	D) Baldcypress-water tupelo (II-1)	E) Depression pools (III-6)	B) Flats (IV-6)	C) Tributary levee with some beech (V-10)	A) Present river levee (Zones III-IV-V)
	G) Swamp tupelo-sweet bay backswamp adjacent to upland (II-19)			F) Old levee ridge with loblolly pine (V-8)	H) Upland slope
Ochlockonee, FL, quasi-alluvial, at Porter's lake	J) Pond, with stooled water ash and water elm (II-7)	D) Overcup oak flat (III-5)	F) Old levee, with live oak, spruce pine, and swamp palm (IV-17)	G) Present natural levee, with water oak, *Vaccinium elliotii* (V-8)	A) River channels
	H) Shoreline cypress with water elm (II-2)	I) Overcup oak-water hickory flat (II-I5)			
	E) Slough with water ash (II-9)				

(continued)

Table 15. (Continued).

River, river class, and location	Zones II	 III	 IV	 V	Other sites & remarks
Ochlockonee, FL (continued)	C) Slough, with Ogeechee tupelo (II-7)				
	B) Acid bog with swamp blackgum-sweet bay-sphagnum dominance				
	B Swamp tupelo-sweet bay-sphagnum backswamp adjacent to upland (II-19)				
Apalachicola, FL, large alluvial, near mouth at Forbe's Island	C) In hummock terrain (II-2)				A) River channel B) Present low levees
	E) Slough, with Ogeechee tupelo (not stooled) (II-2)				Note: Hummocks are 4 ft above mean water level; also support a mix of Zone IV and Zone IV species (Ogeechee tupelo, water tupelo-red maple-green ash-sweet bay)
	D) Wet flats, with baldcypress-water tupelo canopy, water elm-water ash subcanopy (II-2)				

(continued)

Table 15. (Continued).

River, river class and location	Zones				Other sites & remarks
	II	III	IV	V	
Alcovy, GA, Piedmond alluvial (at Hwy 278 bridge)	E) Old oxbow with water tupelo (II-1)		F) Low wet flats, with red maple-green ash (IV-7)	B) Broad levee with swamp chestnut oak (V-2) C) High levee ridge (dotted line), with beech (V-10) D) Scour channel topography, diverse plant composition, often white oak and pignut hickory (V-16) G) High flats, with swamp chestnut oak and green ash (V-1) H) Old flat levee, with cherrybark oak-lobolly pine-American holly (V-5)	A) River channel

(continued)

Table 15. (Continued).

River, river class, and location	Zones: II	III	IV	V	Other site & remarks
Canoochee blackwater at Fort Stewart, GA	B) Slough; baldcypress with stooled Ogeechee tupelo-water ash-water elm (II-9)	C) Pond with mayhaw (III-3)	E) Flats, with diamondleaf oak-spruce pine canopy and American holly, river cane, and *Vaccinium elliotti* (IV-8)	D) Scour channel edge, with live oak or water oak and saw palmetto (VI-16)	A) River channel
Roanoke Northern alluvial river at Devils Gut, NC	C) Wet flat, with water tupelo-baldcypress; formerly dominated by baldcypress (II-1) D) Swales, with water tupelo-baldcypress (II-1) F) Terminal swale, with swamp tupelo on deep muck (II-6)			E) Middle and upper position of ridges: transition from swamp chestnut oak to cherrybark oak to loblolly pine pine (V-14)	A) River channel B) Natural levee G) Second terrace, now mostly cultivated Note: Zonation from Zone IV to Zone V on ridges (E) in ridge and swale topography; ecotone between Zone II swales and ridges with diamondleaf oak (IV-2)

(continued)

Table 15. (Continued).

River, river class, and location	Zones				Other sites & remarks
	II	III	IV	V	
Chipola, spring-fed, alkaline, anastomosing at Hwy 71 bridge, FL	C) Wet flats; baldcypress-water tupelo canopy, and water elm-water ash subcanopy (II-5)		D) Island, with diamondleaf oak, swamp dogwood, and possum haw (IV-11)		A) Anastomosing river B) Shallower channel on slough H) Upland
	E) Peat depression adjacent to upland; bay swamp on peat with ericad subcanopy (II-21)				
Suwannee tidal forest on alkaline blackwater river at Suwannee, FL	C) Floodplain surface (approximately high tide level), with pumpkin ash-swamp tupelo-sweet bay-dwarfed baldcypress (II-24)		D) Flat "islands," with cabbage palmetto-southern red cedar-swamp palm-wax myrtle		A) River channel B) Exposed root mat of riverbank trees Note: The islands in (D) bear levee and hydric hammock species. Until further study, they are placed in Zone IV.

(continued)

Table 15. (Concluded).

River, river class, and location	Zones				Other sites & remarks
	II	III	IV	V	
St. Marks, tidal forest of spring-fed alkaline river at St. Marks, FL	H) Inner swamp; blackgum-sweet bay-cabbage palm-southern red cedar-wax myrtle (II-26)				A) River level at low tide; dense submerged bed (*Sagittaria kurziana*) B) River level at high tide C) Intertidal zone, with (D) quillwort (*Isoetes flaccida*) mats and (E) *Ludwigia repens* F) Exposed root mat of tree G) Natural levee 1. Front side: live oak-saw palmetto 2. Top: southern red cedar-cabbage palmetto-sweet bay 3. Backside: groundsel tree and dahoon, in addition to Zone II inner swamp species

Figure 39. An example of understory species taking advantage of the dry environment of a floating log in order to exist in Zone II. Photo by Gordon Fritz.

River, SC floodplain, for instance, 25 were canopy trees, while 28 species were shrubs or subcanopy trees, 15 woody vines, 2 woody grasses, and 40 herbaceous species (Dennis 1973). The importance of the herbaceous ground cover on a floodplain is a function of light and areal extent of zones of higher elevation (Zones IV and V) where these species are most often found (Knight 1973). In Zone IV floodplains, "sedge glades" are sometimes found. In the Congaree Swamp (SC), dominant sedges are *Carex lurida* and *C. grayi*, while *C. intumescens*, *C. atlantica*, and *Leersia virginica* are common. Other common ground cover plants are crossvine (*Aniso stichus capreolata*), southern vein orchid (*Habaneria flava*), violet (*Viola affinis*), poison oak (*Rhus toxicodendron*) and swamp milkweed (*Asdepias incarnata*). The major composite is the butterwort (*Senecio glabellus*). Common shrubs and vines on North Carolina floodplains are spicebush (*Lindera benzoin*), buckeye (*Aesculus sylvatica*), *Viburnum* spp., Japanese honeysuckle (*Lonicera japonica*), greenbrier (*Smilax rotundifolia*), poison ivy (*Rhus radicans*), grapes (*Vitis* spp.), and blackberry (*Rubus* spp.) (Knight 1973). Herbaceous ground cover is less extensive in more frequently inundated parts of the floodplain. A characteristic and widespread herb in Zone II of many floodplains (in the Coastal Plains) is goldenclub (*Orontium aquaticum*). Useful species lists for floodplain understory and ground cover plants are found in Oosting (1942), Houck (1956), Beard (1958), and Wells (1970).

Floodplain Transects of Selected Southeastern Rivers

To provide a sharper focus on the complexity of floodplain ecosystems, Figure 40 portrays nine southeastern alluvial, blackwater, spring-fed, and tidally influenced floodplains via horizontal transects. The spatial relationships between ecological zones and forest dominance types are diagrammed and accompanied by Table 15, which depicts these relationships. The rivers profiled here are the same referenced in Tables 11 through 14, where specific site locations were given for dominance types and variants observed in the field.

The diversity of the bottomland hardwood canopy increases with the complexity of floodplain topography. Figure 40 and Table 15 describe examples of the variations encountered on floodplain transects. Alluvial rivers, such as the Congaree, Ochlockonee, and Alcovy (Figure 40) often exhibit the greatest topographic and plant community diversity. In contrast, the floodplains of many Coastal Plain blackwater and spring-fed rivers (Figure 40) generally are more uniform topographically, and the plant community diversity is lower.

Regular tidal flooding caused by lunar or wind energy imparts a distinct character to plant communities under its influence. These forests are the least studied of all river swamps (Beaven and Oosting 1939). They occupy the lower 16 to 32 km (10 to 20 mi) of many unaltered floodplains, primarily in Florida and Georgia (Figure 40). High tides raise the water levels in the floodplain (or "tideplain") to the most elevated portions of the relief with fair regularity. Tidal swamp forests usually extend upstream until levees appear. The floodplains of these forests are dominated by Zone II species, except for higher islands containing Zone IV species such as diamondleaf oak, swamp palm, southern red cedar, and cabbage palm. These floodplains are distinctive in harboring animal species characteristic of more brackish downstream waters, such as fiddler crabs (*Uca*) and square-backed crabs (*Sesarma*). Another interesting aspect of the tidal forest is the presence of an intertidal zone, either mud or sand, which is often vegetated by extensive mats or beds of submerged or aquatic vegetation (such as *Isoetes*, *Ludwigia repens*, *Cabomba cardiniana*, *Elodea* spp., or *Nuphar luteum*).

DISTURBANCE AND SUCCESSION IN BOTTOMLAND HARDWOOD PLANT COMMUNITIES

Several examples of distrubance and successional trends have been referenced in the preceding sections of this chapter. They will be summarized here along with others that have not yet been mentioned.

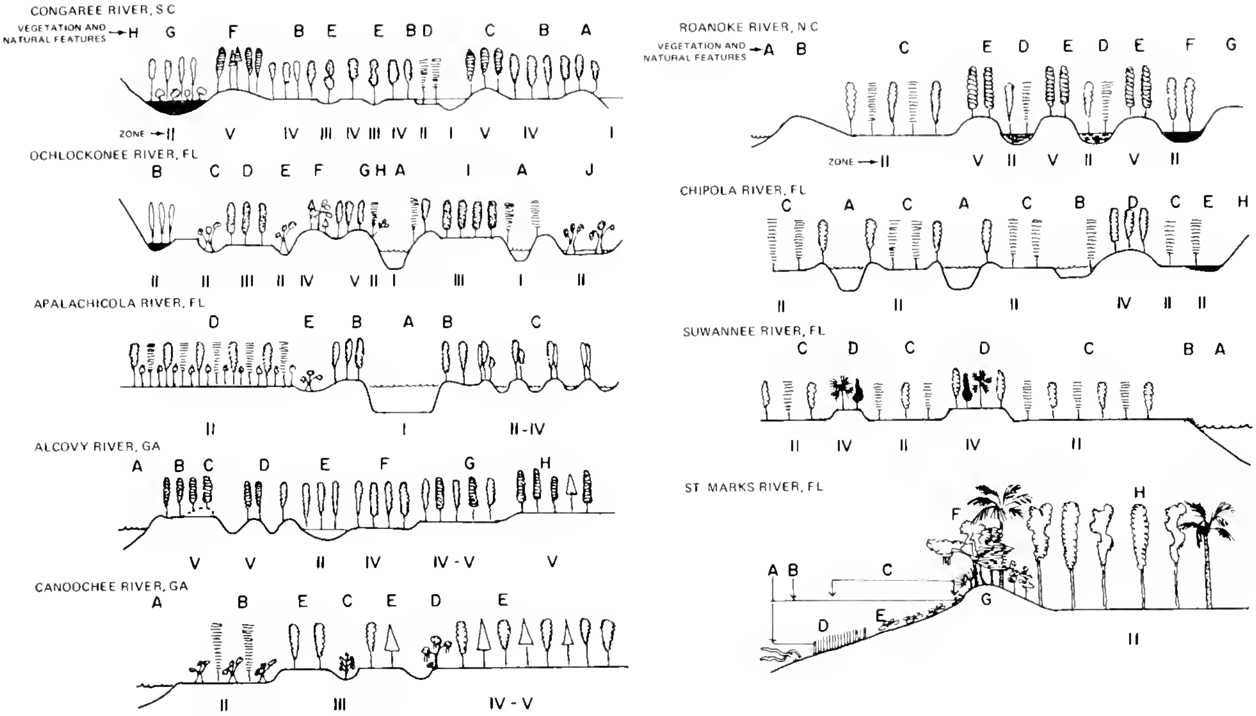


Figure 40. Cross-sectional transects (aspect is looking downstream) of nine southeastern rivers and floodplains, indicating zones (I-V) and major vegetational and natural features (A-J). This figure is cross-referenced to Table 15, which provides an explanation for each vegetational or natural feature category (A-J) of each floodplain. See Table 15 also for cross references to dominance types (Tables 11-14) found on these transects.

Flooding

The most common natural disturbances in bottomland ecosystems are associated with floods. The biota are to a variable degree adapted to flood forces. Annual inundations adapt the bottomland hardwoods for the larger and more catastrophic flood events that occur with low frequencies (100- to 1000-year floods). The wide, shallow root crowns and trunk buttresses, which are adaptations to the moist, anaerobic conditions, serve to counter excessive scour and toppling by flood or wind. Deleterious effects may occur, however, depending on flood timing, frequency, depth, and velocity. The categories of flood disturbances include (1) anaerobic conditions, (2) mechanical abrasion and breakage of plant tissues, (3) siltation, (4) propagule and seedling washout, and (5) erosion.

Flooding may retard or speed successional trends. Severe erosive flooding inhibits point bar succession (see Chapter 1), slows natural levee development and community establishment on levees, and can forestall the filling in of scour channels, swales, and depressions between hummocks. Moderate flooding enhances mature community development through less damaging effects on plant survival and growth and through reduced erosion and net deposition of floodwater sediments.

Fire

Fire is not important as a natural disturbance in bottomlands because of the prevalence of water and the lack of a substantial litter layer. This is especially true of the wetter portions of alluvial floodplains. However, Putnam (1951) states that a serious fire season occurs on an average of about every 5 to 8 years in bottomland hardwood forests (in the Mississippi Valley). It is conjectured that the Indians maintained canebrakes in Zone V understory by deliberate fall burning, perpetuating and increasing large cane stands, which are now relict. Though crown fires are rare, ground and surface fires may occur. These fires move rapidly across the floodplain floor, damaging or destroying all trees less than 10 years old, as well as shrubs and herbaceous growth. In addition, ground fires open wounds in larger trees, increasing susceptibility to disease and insect attack.

Fire is a major determinant of community composition in selected vegetation types. Infrequent but regular fires favor Atlantic white cedar while inhibiting southern red cedar (Eyre 1980).

H.S. Larsen, writing in Eyre (1980) indicates that fire may sweep into the dense shrub zone of sweet bay-swamp tupelo-red bay sites along the narrow bottom of perennial streams during drought years. It is possible that the narrow peaty swamps along small streams with Atlantic white cedar or pond pine canopies (type 29) may burn in drought years. The only recent instance of a widespread fire on a floodplain in the study area occurred prior to 1976 on the Oklawaha River (FL).

Gaddy et al. (1975) described the successional sequence in the Congaree Swamp (SC) that begins with either fire or clearcutting, and proceeds from even-aged sweetgum-intolerant hardwood stands to more mature communities dominated by diamondleaf oak and more tolerant hardwoods.

Windthrow

Windthrow is the primary disturbance to plant succession on floodplains in the study area. Gaps in the canopy resulting from fallen canopy trees (Figure 41) are common in the floodplain. Topplings due to old age, disease, soft sediments and insecurely anchored root systems, root scour, lightning strike, or fire cause openings in the canopy that temporarily stimulate understory woody and herbaceous growth. The factors that influence successional response to such gaps include gap size, existing composition of seedlings and saplings and their relative shade tolerances, possible inhibition due to shading by extensive understory tree (paw paw, holly (Ilex opaca), ironwood (Carpinus caroliniana)) or canebrake development, site characteristics, and probability of propagule recruitment. Understory shading may limit the development of diverse, well-stocked seedling and sapling layers, retarding succession (Gaddy et al. 1975).

Biotic Disturbances

At least three categories of biotic disturbances exist in the floodplain: (1) propagule predation and seedling and sapling herbivory by browsing animals, (2) disease, and (3) insect outbreaks. The quantitative effects of these variables on plant community structure and composition have received little attention. Cattle and deer browsing can kill seedlings, particularly if floodwaters concentrate browsing on higher ground in the floodplain. Baldcypress seedlings are even eaten, and water tupelo will survive only one cropping by deer (F. Vande Linde, forester, Brunswick Pulp Land Company, Brunswick, GA; personal communication).

Conner and Day (1976) discussed the effects of grazing by the forest tent caterpillar on both baldcypress-water tupelo and bottomland hardwood forests in Louisiana. Water tupelo is most severely affected, suffering extensive defoliation. These authors suggested that the increasing frequency of outbreaks over wide areas is due to a corresponding increase in the areal extent of tupelo-dominated sites. These sites, in turn, occur as a result of the selective logging of baldcypress (see below). Conner and Day (1976) also speculate that the susceptibility of water tupelo to defoliation may be one factor that formerly favored the maintenance of nearly pure stands of baldcypress.

Lumbering

Selective cutting and clearcutting generate some of the most noticeable changes in floodplain forests. The heavy exploitation of baldcypress is the classic example. Such logging has shifted the forest composition on countless sites. Cypress stumps endure for many years, and their presence may indicate what the original forest on a given site was like and something of the hydrology. Many areas which now support water tupelo (e.g., the Altamaha River, GA), green ash (e.g., the Great Pee Dee River, SC), or water tupelo-green ash (e.g., the Oklawaha River, FL)

Figure 41. This windthrown bitternut hickory on the floodplain of the Murder Creek Special Management Area (Oconee National Forest, GA) illustrates the large opening created by this natural event. In mature forests such openings are common enough to provide vegetation in all states of succession. The virgin forest thus has its own system of uneven-aged management.

formerly bore forests of very large cypress. Klawitter (1962) discussed the three periods of baldcypress logging on the Santee River (SC).

Clearcutting of hardwoods other than baldcypress may also lead to entirely new forest overstories. Sweetgum and shade-intolerant hardwoods pioneer after clearcutting in the Congaree Swamp (Gaddy et al. 1975), and mid-seral sugarberry-American elm-green ash stands follow extensive logging of Zone IV (Nuttall oak-willow oak) forests in the Mississippi Valley.

Agriculture

The growing of rice has completely altered many floodplains. Rice culture was introduced around 1700 in Zone II swamps on smaller streams that emptied into large navigable rivers (e.g., Wambau Creek and Santee River, SC). Reserve dams were constructed across small feeder creeks, providing a reservoir to supply water to the rice fields, even on coastal islands (e.g., Hobcaw Barony, SC). This system persisted until 1885 (Klawitter 1962). When the tidal flooding method was developed in South Carolina in 1750, large-scale rice plantations became feasible, and entire floodplain forests of cypress were burned or buried by slave labor (e.g., Santee River, SC). The fields with their remnant levees from these plantations are used today as waterfowl refuges (Figure 42).

Unsuccessful attempts at cotton and other agriculture have taken place on many southern floodplains, especially in the great fall line swamps of the Flint and Oconee Rivers in Georgia (Wharton 1977). These abandoned areas support a variety of forest cover. One area on the Roanoke River (NC) bears an almost pure stand of large cottonwoods. Boxelder flats can be found in such disturbed areas along the Chattahoochee and Alcovy Rivers (GA).

Figure 42. Aerial view of relict rice fields on former bottomland hardwood forests that are presently managed for waterfowl. Photo courtesy of the Georgia Department of Natural Resources.

PRIMARY PRODUCTIVITY OF FLOODPLAIN FORESTS

High productivities of the floodplain forest (Conner and Day 1976) are made possible by several subsidies offered to the floodplain by the watershed and river, including particulate and dissolved organic matter, water, soil (especially clay and silt), and nutrients (inorganic, sediment-adsorbed, and organically complexed). These inputs support what is essentially an increased rate of ecosystem community metabolism, reflected in (1) annual litterfall and nutrient turnover rates as high or higher than most temperate deciduous forests; (2) relatively high detrital decomposition rates, except in systems with permanently ponded water; (3) periodic "flushing" of accumulated refractory organic detritus and metabolic byproducts; and (4) the operation of several microbial conversion processes characteristic of widely varying conditions, such as nitrification, denitrification, ammonification, methanogenesis, sulfate reduction, and general nutrient mineralization (Wharton and Brinson 1979a).

In addition to these physical and chemical subsidies, the river contributes macro- and microfauna during flood periods that both speed detrital decomposition and participate in the floodplain's food chains, nutrient cycles, and import-export pathways.

The major factor contributing to the high productivity of the floodplain forest is the pulsing of the wet-dry cycle. Conner and Day (1976) made an analogy between these floodplain forests and the tidal marshes in terms of the positive effects of fluctuating water levels:

> "This periodic flooding acts somewhat in the same manner as tidal flooding in saline marshes, in that fluctuating water levels are energy subsidies which control variations in hydric conditions, temperature, nutrient levels, and available oxygen (Hester 1973; Butler 1975)."

Bottomland hardwood communities that either are permanently flooded with slow-moving to stagnant water, or are regularly damaged by unusually high and irregular destructive floods are not as productive as communities that undergo periodic moderate floods. This has been illustrated clearly (Figure 43) by Odum (1978), who graphically compared the productivity of stagnant, seasonally flooded, and abrasively flooded systems with a regional average of all wetland and upland forest types.

Communities in permanently ponded conditions, or on sites where poor drainage leads to continuously high water tables and the accumulation of acidic peat soils, have lower productivities primarily because of low nutrient turnover, due to anoxia, nitrogen limitation, and low pH. Brown et al. (1979) and Conner and Day (1976) presented data that demonstrate the reduced productivities of still water systems.

Productivity values gleaned from the literature for 19 upland and bottomland forest types are presented in Table 16 and generally support the concept of a flood subsidy depicted in Figure 43. A second verification of this concept is shown in Figure 44, where productivity data from sites in several zones are plotted (from Gosselink et al. 1981). Gosselink et al. (1981) stated:

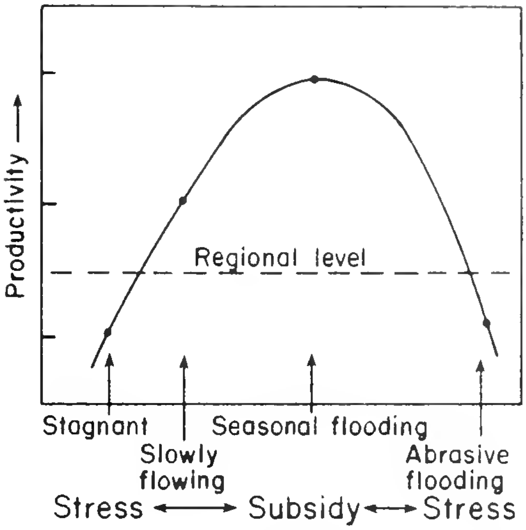


Figure 43. The effect of a gradient of flooding on productivity as compared with a regional level that might be expected in the absence of standing or flooding water. The graphic model takes the form of a stress-subsidy curve. For southern swamps Conner and Day (1976) estimated annual net production for stagnant, slowly flowing and seasonal flooding conditions as of the order of 0.2, 0.7, and 1.2 kg dry matter per square meter, respectively (Odum 1978).

> "Forest production appears to peak at the once-per-year flood frequency if flooding is during the winter because this regime furnishes the optimum environment for plant growth in terms of nutrient input by flood waters, summer soil moisture, and possibly aerobic conditions during the summer leading to inorganic nutrient release from organic debris."

Primary productivity data in the literature are much more common for the tree canopy and woody subcanopy (small trees and shrubs) components of floodplain communities than for the herbaceous, aquatic vascular, and nonvascular components. Aquatic plant productivity in river channels and drainage tributaries, permanent ponds, and temporary sloughs and swales has received the least attention. Brinson and Wharton (1979a) suggested that the productivity of alluvial stream communi-

Table 16. Net primary productivity (g dry wt/m^2/yr) for bottomland hardwood communities (primarily Zone II), compared with other wetland and upland environments.

Community type	New primary productivity (g dry wt/m^2/yr)	References
Dwarfed cypress strand (FL)	367	Carter et al. 1973
Okefenokee cypress forest (GA)	595	Schlesinger 1978
Oak-hickory upland (MO)	600	Rochow 1974
Cypress-water tupelo (IL)	678	Mitsch et al. 1977
Drained cypress strand (FL)	681	Burns 1978
Cypress-tupelo (Green Swamp, FL)	760	Mitsch and Ewel 1979
Oak-pine uplands (NY)	796	Whittaker and Marks 1975
Slash pine flatwoods (FL)	830	Golkin 1981
Northern hardwood upland (NH)	898	Whittaker and Marks 1975
Cypress-hardwood (Green Swamp, FL)	950	Mitsch and Ewel 1979
Mature cypress dome (FL)	956	Brown 1981
Elm-ash-sweetgum (Zone IV) (IL)	967	S. Brown (pers. comm.)[a]
Spruce-fir upland (Great Smokies)	980	Whittaker and Marks 1975
Upland cove forest (TN)	1050	Whittaker and Marks 1975
Cypress strand (FL)	1111	Burns 1978
Riverine cypress-water tupelo (LA)	1140	Conner and Day 1976
Mixed bottomland hardwoods[b] (LA)	1174	Conner and Day 1976
Cypress-water ash creek forest[c] (FL)	1607	Brown 1981
Tulip poplar upland forest (TN)	2400	Whittaker and Marks 1975

[a] Sandra Brown, Department of Forestry, University of Illinois, Urbana.

[b] Red maple-water tupelo-box elder-cottonwood-cypress-swamp dogwood-willow (mix of Zones II and IV with pioneer species).

[c] Also contains diamondleaf, oak, sweetgum, red maple (mix of Zones II and IV). Flow partially regulated by low dam.

ties is probably low because of heavy silt loads. Productivity of the Satilla River and Okefenokee Swamp does not seem to be limited by low nutrient availability and acidic conditions. Brinson observed extensive production of filamentous algae in floodplain ponds during the winter dormant season and suggested that this component may provide a temporary sink for inorganic nutrients during winter and early spring.

Aquatic vascular productivity can be high in localized areas, depending on light intensity and water velocities. Species that may contribute heavily to community productivity are *Alternanthera philoxeroides*, *Myriophyllum* spp., *Lemna* spp., *Spirodela* spp., *Egeria densa*, *Ceratophyllum* spp., *Limnobium* spp., and *Azolla* spp. (Dennis 1973).

The prominence of the herbaceous ground cover varies dramatically among the forest cover types, as discussed in the previous section on dominance types. In general, the highest herb densities and productivities are found on the driest floodplain sites (heavy growths of various composites follow drydown in Zone IV). This is a function of hydroperiod and light intensities. One species that can produce tremendous amounts of biomass in

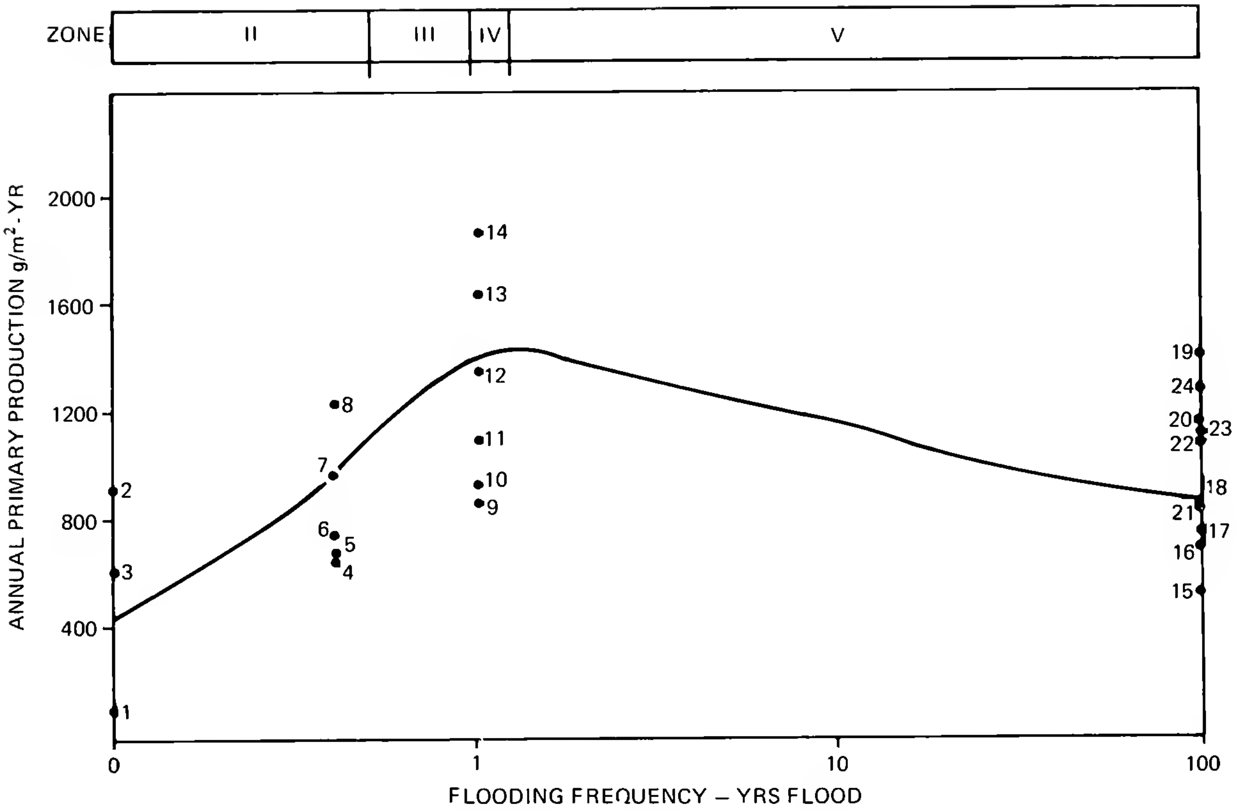


Figure 44. Organic matter production in ecological zones (adapted from Gosselink et al. 1981). Numbers represent specific floodplain sites.

short periods is river cane. Wharton (1977) reported that this plant may produce 4506 kg of edible leaves per hectare (4000 lb per acre) per year, and 11 to 16 tonnes of organic material per hectare (5 to 7 tons per acre) within the first 3 years of growth.

A striking feature of many floodplain plant communities is the prominence of woody vines. Dennis (1973) recorded 15 species in study plots in the Santee Swamp (SC), including Smilax spp., Vitis spp., cross vine (Anisostichus capreolata), supplejack (Berchemia scandens), poison ivy (Rhus radicans), climbing hydranger (Decumeria barbara), Virginia creeper (Parthenocissus quinquefolia), and trumpet vine (Campsis radicans). The contribution of this component to community productivities may be large locally, particularly in canopy gaps created by windthrow and along river banks.

CHAPTER 5. FAUNA OF BOTTOMLAND HARDWOOD ZONES

Bottomland hardwood forests support a diverse fauna that matches the floristic and hydrologic complexity which is so characteristic of these communities. The moisture gradient and hydroperiods of floodplains provide a habitat continuum for a wide range of aquatic to terrestrial to aerial species. The fauna is here also treated within the zonal concept. Because of the large numbers of taxa, only abundant or dominant animals or groups can be mentioned. (For further information, see Wharton et al. 1981.) Some overlap among zones occurs, especially between Zones IV and V, which share many species. The mobility of many species and their overlapping distribution in response to varying environmental regimes make combining discussions of faunal assemblages in Zones II and III useful. It should be recognized that placing an animal in one or even two zones does not necessarily restrict it to these areas. Floodplain inhabitants are opportunists, and many move freely into irregularly flooded or dry areas over the year.

FAUNA OF ZONES II AND III

Invertebrates

Given the diversity of vegetational dominance types in Zone II, it is not surprising to find that faunal components also vary. In terms of fauna, the environment of a tupelo gum-cypress forest with hydroperiods approaching a year is markedly different from a similar forest in a tidal area with daily water level fluctuation or a forested site with permanently saturated soils. An example of this phenomenon is illustrated in Figure 45 for a coastal section of the blackwater Suwannee River (FL). The tree associations within Zone II of the Suwannee change with distance from the coast in response to lessening tidal influences (i.e., to the extent of daily inundation and salinities). The vegetative changes are changes in species morphology as well as species replacements. The coastal forest comprises dwarfed swamp tupelo, pumpkin ash, sweet bay, cabbage palm, and cypress which transform upstream to an association of taller Ogeechee tupelo, water tupelo, pumpkin ash, and cypress. The faunal associations change abruptly from a brackish water snail-fiddler crab community (Neretina-Uca) to a freshwater snail-crayfish community (Vivipara-Cambarus) at the point upstream where natural levees first occur.

Macroinvertebrates dominate Zone II and the wetter depressions and pools of Zone III. Parsons and Wharton (1978) documented a cyclic sequence of dominant macroinvertebrates in isolated pools (Figure 46) (Zone III) in Piedmont floodplains: initially stoneflies dominated, followed sequentially by the isopod Asellus sp. and amphipod Hyalella azteca, small oligochaete worms and midge fly larvae, and finally an association of sphaeriid clams (Sphaerium and Musculium). Sklar and Conner (1979) found an almost equal distribution of amphipods, oligochaetes, gastropods, and turbellarians (densities of 10,700/m^2) on vegetation in a tupelo gum-cypress association. Beck (1977) found that detrital substrates, such as Zone II soils, were extremely productive, averaging 2885 organisms/m^2 in a large alluvial system (Atchafalaya Basin, LA). The dominant macroinvertebrates were a tubificid annelid (Peloscolex multisetosus), an isopod (Lirceus lineatus), an amphipod (Gammarus tigrinus), a mayfly (Caenis), a phantom midge larva (Chaoborus punctipennis), a chironomid (Chironomus), a pulmonate snail (Physa), and a fingernail clam (Pisidium). Ziser (1978) found an average density of 1296 organisms per 100 g of duckweed and water hyacinths in a Louisiana swamp. The dominants were the naidid worm (Dero), three snails (Physa, Ferrissia and Promenetus), an oribatid mite (Hydrozetes), two damsel flies (Enallagma, Ischnura), a back swimmer (Neoplea striola), and midge and biting midge larvae.

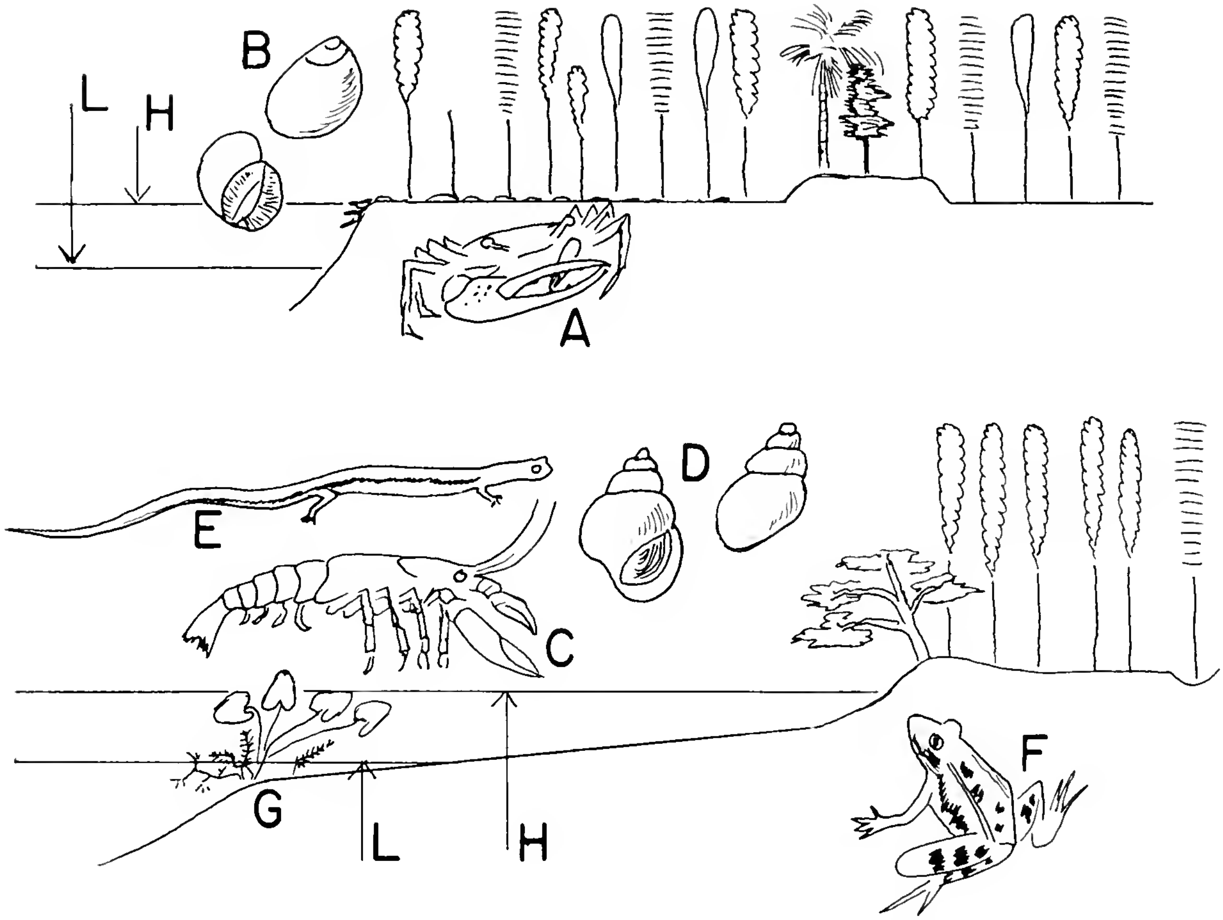


Figure 45. Comparison of the bottomland hardwoods and characteristic fauna at different reaches of a blackwater river near the coast (Suwannee, FL). (H) is high tide; (L) low tide. Upper figure: River Mile 4, intertidal zone, largely exposed roots; tidal forest of dwarfed swamp tupelo, pumpkin ash, sweet bay and cypress with: (A) fiddler crab (*Uca minax*) and (B) olive nerite snail (*Neretina reclivata*). Lower figure: River Mile 15, intertidal zone wide, with: (G) spatterdock (*Nuphar luteum*), fanwort (*Cabomba carolina*) and *Elodea* sp.; forest is tall Ogeechee tupelo-water tupelo-pumpkin ash-cypress with: (C) crayfish (*Procambarus seminolae*), (D) snail (*Vivipara georgianus*), (E) dwarf salamander (*Eurycea quadridigitata*), (F) southern leopard frog (*Rana utricularia*).

Figure 46. Floodplain pools (Zone III) on this Piedmont alluvial floodplain (Alcovy River, GA) are concentration centers for detrital decomposition and teem with invertebrate life. Mayfly nymphs reach densities of $1000/m^2$, crustacea average $1750/m^2$, stoneflies average $828/m^2$, and fingernail clams reach a maxima of $1500/m^2$. High productivity in small pools is due to silt enrichment, abundant detritus (biomass $1.24\ kg/m^2$ dry wt), and absence of predators (Parsons and Wharton 1978).

Arthropods, crustaceans, and mollusks dominate the macroinvertebrates of the Congaree, Swamp (SC). Three dragonflies (Epiaeschna heros, Tetragoneuria cynasura, Gomphus exilis) are abundant and assumed associated with Zone II. Crayfish such as the red Procambarus clarkii (west of the Mobile system) and P. troglodytes (east of Altamaha system) are (along with crayfish from Zones IV) an important food for a host of vertebrates such as the eel, catfish, warmouth, amphiuma, glossy water snake, ibis, otter, and raccoon. Densities ranging from 21 to $46/m^2$ have been reported (Konikoff 1977; V. Lambou, Environmental Protection Agency, Las Vegas, NV; personal communication). Crayfish, in fact, form one-third of the faunal biomass of the Suwannee River floodplain (Wharton 1977). Large fishing spiders (Dolomedes spp.) and Pirata maculatus, which are found under the liverwort Porella platyphylloidea, are characteristic of Zone II. Several snails (Vivipara, Campeloma, Pomacea, and Lioplax) live in and around Zones II and III (Figure 47). Fingernail clams of the genera Sphaerium, Eupera, Musculium, and Pisidium often dominate the benthic biomass of Zones II and III. These tiny (<10mm) clams are present in enormous numbers. Some clams (Anodonta, Ligumia, Corbicula) occur in Zone II sloughs, but the clam fauna is in general poorly known. The Altamaha River (GA) is unique in possessing six endemic clam species, all in the family Unionidae (Figure 48). These clams require particular species of fish as hosts for their larvae; a diverse fish fauna may be essential to clam diversity and survival.

Vertebrates

The most characteristic fish fauna of inundated Zone II sloughs are top minnows (Fundulus spp., Gambusia affinis), killifishes (Heterandria formosa, Lucania parva), swamp darter (Etheostoma fusiforme), pirate perch (Aphredoderus sayanus), lake chubsucker (Erimyzon sucetta), yellow bullhead (Ictalurus natalis), flier (Centrarchus macropterus), warmouth (Lepomis gulosus), and three top predators: the bowfin (Amia calva), redfin pickerel (Esox americanus), and chain pickerel (Esox niger).

Dominant amphibia are the lesser siren (Siren intermedia) and amphiuma (Amphiuma means), which seek refuge in root holes and crayfish holes during drydown. The amphibious salamanders include the southern dusky (Desmognathus fuscus auriculatus), the many-lined (Sterochilus marginatus), and the dwarf (Eurycia quadridigitata). The mud salamander (Pseudotriton montanus) and the two-lined salamander (E. bislineata) occur around the edge of Zones II and III.

Frogs are less specific to Zone II but include the cricket frog, river frog (Rana heckscheri), and southern leopard frog, and at breeding times several other species such as the bird-voiced tree frog (Hyla avivoca). Some depression pools (Zone III) may support annual breeding aggregations of spotted and marbled salamanders, as well as temporary water-breeding frogs and toads from Zones IV and V.

Only a few reptiles are locally abundant in Zone II areas. The dominants appear to be the eastern mud turtle (Kinosternon subrubrum), glossy water snake (Natrix rigida), perhaps the mud snake (Farancia abacura), and certainly the red-bellied water snake (Natrix erythrogaster) and cottonmouth (Agkistrodon piscivorus). In a tupelo gum-cypress association of an anastomosing blackwater creek (Zone II, Four Hole Swamp, SC) the yellow-bellied turtle (Chrysemys scripta), brown water snake (Natrix taxispilota), "greenish" rat snake (Elaphe obsoleta), and anole (Anolis spp.) were abundant (Hall 1976).

Passerine (perching) birds characteristic of Zone II are limited largely to the prothonotary warbler, tufted titmouse, parula warbler, and common grackle. The wood duck nests near water if possible and often in Zone II. The yellow-crowned night heron and green heron are common breeding residents, and rookeries of great blue heron, great egret, and white ibis also occur in Zone II.

The red-shouldered hawk is a characteristic raptor of Zone II. Swallow-tailed kites feed and nest in this zone on Wambau Creek (SC) and perhaps on the Altamaha River (GA). The snail-eating limpkin is found chiefly here (and along sloughs in Zones IV and V) above tidal range where Vivipara georgiana and other snails abound. Many wintering birds such as robins make heavy use of tupelo fruits;

Figure 47. Snails of the genera *Vivipara* (shown) and *Campeloma* are often abundant in shallow aquatic zones (Zone II) above tidal influence.

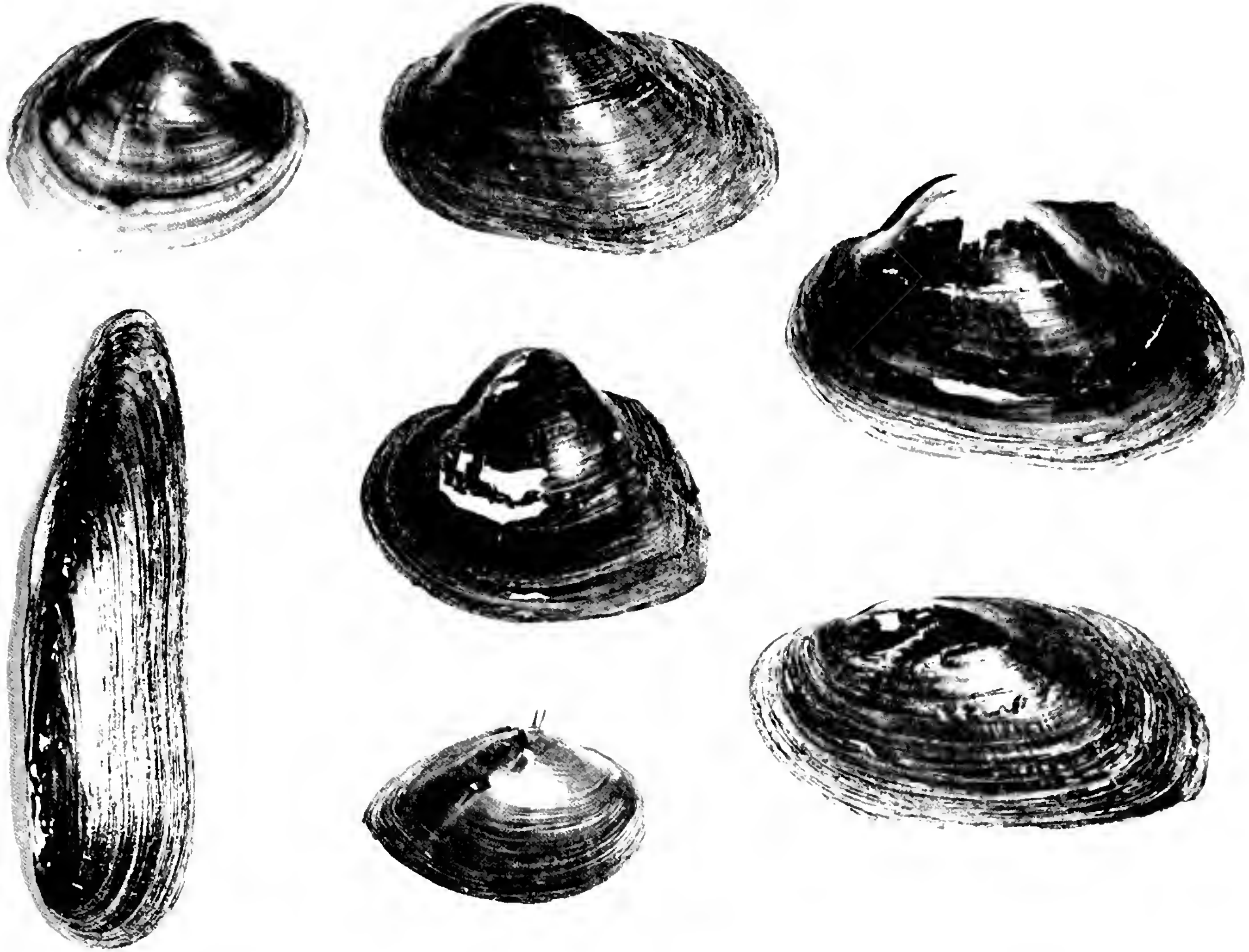


Figure 48. The six endemic species (and *Lampsilis splendida*) of unionid clams recorded (Johnson 1970) for the Altamaha River, GA. First column: *Lampsilis dolabraeformis*, *Elliptio shepardiana*; second column: *Lampsilis splendida*, *Alasmidonta arcula*, *Elliptio spinosus* (the unique spiny clam, a relict species); third column: *Anodonta gibbosa*, *Elliptio hopetonensis*. Specimens and assistance courtesy Georgia Power Company Environmental Laboratory, Atlanta.

the seeds are eaten by squirrels.

Although the rice rat occasionally appears in Zone II, small mammals are usually absent in most of it. Mink, raccoon, beaver and otter may use tupelo gum-cypress forests (Zones II and III) in particular.

FAUNA OF ZONE IV

Invertebrates

The invertebrate fauna of Zone IV can be subdivided according to their dominant use of this floodplain zone:

(1) inundation fauna -- invertebrates occupying the substrate and water column during periods of flooding

(2) litter fauna -- invertebrates occupying the leaf litter layer during dry periods

(3) persistent fauna -- invertebrates occupying the floodplain habitats in various life history stages throughout most of the year.

Sniffen (1980) characterized the inundation fauna of the Creeping Swamp (NC) floodplain (Zone IV) as a large and diverse component of this small blackwater floodplain. The most conspicuous invertebrates were six species of "red" lumbriculid worms and four species of "white" enchytraeid worms, three tubellarian flatworm species, and several roundworm species. Oligochaete worms and copepods were numerically the most abundant invertebrates (16,470/m^2). Isopods, although fewer in number than the worms, were the dominant biomass component (1114 mg dry wt/m^2). Ostracods were numerous (829/m^2), as were nematodes (4348/m^2). Midge fly larvae, amphipods, water mites and collembola were also abundant.

There are relatively few definitive studies of the litter fauna of floodplain communities in Zone IV. Grey (1973) conducted the most thorough faunal survey of this particular habitat. His study of the Santee River (SC) floodplain determined that mites (Acari) and springtails (Collembola) were by far the dominant litter organisms, accounting for about 92% to 95% of the organisms during any season. The mites comprised 48.1% and 77.4% of the total population count in the summer and fall, respectively; the springtails, 47.6% and 13.1%. Both groups are detrital "shredders" important to the decomposition processes in the upper litter and humus layers.

Earthworms, important food sources for salamanders and shrews, are also an abundant and important component of the litter fauna. Parsons and Wharton (1978) found three genera of earthworms (*Eisenia*, *Allolobophora*, and *Sparganophilus*) in the floodplain of the Alchovy River (GA). Harper (1938) noted that earthworms (principally the genera *Diplocardia* and *Helodrilus*) preferred dense, packed floodplain soils with water tables below 23 cm (9 inches).

Other invertebrate fauna using Zone IV throughout the year and throughout their entire life cycles are principally crayfish and insects. Some 23 chimney-building floodplain crayfish species occur east of the Mississippi River and 19 east of the Escambia River (FL) (Wharton et al. 1981). Several, such as *Procambarus pubischelae* and *P. seminolae*, seem to favor blackwater floodplains; others on almost all floodplains are *Cambarus diogenes* and *Procambarus acutus*. Many insect species whose larvae inhabited sloughs and pools within Zones II and III may be found in Zone IV as flying adults during drydown. Mobile species, such as dragonflies and butterflies, span many zones. Some, like the abundant snout butterfly (*Libytheana bachmanii*) and the hackberry butterfly (*Asterocampa celtis*), can be categorized by their larval preference for sugarberry, a Zone IV tree.

Vertebrates

Amphibians, especially salamanders, are abundant in Zone IV. The marbled salamander (*Ambystoma opacum*) is generally restricted to this zone; others such as the mud salamander (*Pseudotriton montanus*) seldom occur elsewhere. The dominant plethodontid salamanders include the two- and three-lined salamanders (*Eurycia*). The four-toed salamander (*Hemidactylum*) occurs here and in Zone II. The green and leopard frogs (*Rana*) and cricket frogs (*Acris*) are dominant anurans; the upland chorus frog (*Pseudacris nigrita*) and grey tree frog (*Hyla versicolor*) are common locally. The bird-voiced tree frog (*Hyla avivoca*) occurs here and in other zones, especially at breeding time.

Reptiles in Zone IV are represented by the abundant box turtle (*Terrepene carolina*); the giant gulf coast form (*T. c. major*) also occurs on floodplains. There are few snakes in Zone IV other than the rat snake (*Elaphae obsoleta*) and subspecies. Boyd (1976) encountered copperheads and rattlesnakes in Zone IV study areas, but these snakes (more characteristic of Zone V) may have come from a nearby hillside. Tinkle (1959) reported the black racer (*Coluber constrictor*), kingsnake (*Lampropeltis getulus*), and ribbon snake (*Thamnophis sauritus*) on a narrow levee ridge, assumed to be Zone IV from the site description (or in succession to Zone V), although these snakes are not frequently encountered in Zone IV.

Many bird species are found in Zone IV. In a study in the Congaree Swamp, numbers of species were similar among floodplain Zones II, IV and V; however, population densities were almost always highest in Zone IV (Hamel 1979; Hamel and Brunswig 1980). Characteristic birds in the Congaree Swamp are the barred owl, downy and red-bellied woodpeckers, and cardinal (Hamel 1979). The wild turkey is known to nest and feed in Zone IV (Kennedy 1977). In fact, bottomland hardwoods support the highest population densities (1 per 10 acres vs 1 per 25 acres of upland) of eastern wild turkey (Florida Game and Fresh Water Fish Commission 1978).

Dominant Zone IV floodplain mammals are the deer mouse in the Piedmont, the cotton mouse in the Coastal Plain, and the golden mouse in creek swamps and areas of dense shrub and vine growth. Short-tailed and southeastern shrews are abundant in this zone but may retreat to higher zones during innundation. Most of the larger mammals in Zone IV are also common to Zone V. The woodrat (*Neotoma floridana*), which nests in the ecotone adjacent to the uplands, forages in Zones IV and V. It nests in Zone IV along spring-fed rivers.

Two of the few vertebrates that are confined almost exclusively to Zones IV (and V) are the semiaquatic swamp and marsh rabbits (*Syvilagus aquaticus* and *S. palustris*). Swamp rabbits are found more often in Piedmont floodplains while marsh rabbits are confined mainly within the Coastal Plain. The swamp rabbit is adapted with large feet and slightly splayed, strong-nailed toes for swimming and traversing unconsolidated terrain (Lowe 1958). Herbivorous swamp rabbits reached a density of 5.6 individuals per 100 acres in the Lowe study on the Oconee River, GA.

FAUNA OF ZONE V

Invertebrates

Many invertebrate species are common both to Zones IV and V as well as to levees (Wharton et al. 1981). The detritivore community of the predominantly Zone V Alcovy River (GA) floodplain is characterized by abundant millipedes (*Cherokia georgiana*, *Narceus americana*) and camel crickets (*Ceuthophilus gracilipes*). Also abundant are a scarab (*Onthophagus*) and three carabid beetle genera (*Carabus*, *Abacidus*, and *Chlaenius*). The grazer community includes two katydids (*Pterophylla camellifolia*, *Scudderia rhombifolium*). Other grazers common to Zones IV and V and abundant in the Congaree Swamp are the zebra swallowtail (*Graphium marcellus*) (whose larvae feed on the paw paw), the Carolina satyr (*Euptychia hermes sosybia*), the red spotted purple (*Limenitis archippus astanax*) and the pearl crescent (*Physoides tharos*) butterflies.

Of the spiders shared by Zones IV and V, the most abundant ground dwellers on a Piedmont floodplain are the wolf spiders (*Schizocosa ocreata*, *Lycosa helluo*), and in the Congaree, *Schizocosa crassipes*. In the Congaree the dominant aerial spiders are the orb weaver (*Neoscona arabesca*), the spinyback (*Micrathena gracilis*), and *Frontinela* spp.

Most of the 11 species of snails recorded from Congaree probably inhabit Zone V. The dominant ones are the great zonite (*Mesomphix vulgatus*), the white-lipped forest snail (*Mesodon thyroidus*) and the cannibal snail (Haplotrema concavum).

Vertebrates

Zone V shares vertebrate species common to uplands as well as Zone IV. The large, spotted salamander (Ambystoma maculatum) and mole salamander (A. talpoideum) seem confined to Zone V. The red salamander (Pseudotriton ruber) is shared with Zone IV. Two common upland species are the ubiquitous slimy salamander (Plethodon glutinosus) and the red-backed salamander (Plethodon cinereus). Two toads, the narrowmouth (Gastrophryne carolinensis) and spadefoot (Scaphiopus holbrooki), inhabit sandier portions of Zone V. In Zone V are skinks of upland mesic slope forests, such as the ground skink (Leiolopisma) and Eumeces inexpectatus, in addition to E. fasciatus. Among the snakes recorded are the copperhead, canebrake rattlesnake (Cratalus horridus atricaudatus), northern brown (Storeria dekayi), garter (Thamnophis sirtalis), rough green (Opheodrys aestivus), and ribbon snakes. Occasionally, even upland species such as the black racer and coachwhip (Masticophis flagellum), are found. We do not know how many species migrate annually from upland areas into Zone V when high water recedes, or conversely, from Zone V to the uplands during short periods of high water.

In the Congaree Swamp the common yellowthroat, pine warbler, wood thrush, and eastern wood peewee seem to prefer Zone V habitats. Zone V is perhaps the preferred nesting and feeding ground of the wild turkey (Figure 49). North Carolina's only breeding colonies of cerulean warblers (outside the Blue Ridge Mountains) and Mississippi kites occur in a 60-km (37-mi) section of old growth timber along the levees of the Roanoke River, two-thirds of which (a 200-m or 656-ft wide strip) is dominantly Zone V vegetation. A number of birds that are commoner in Zones IV and V than in other zones include the white-breasted nuthatch, Swainson's warbler, Carolina wren, and yellow-throated vireo. Breeding bird densities are generally higher in the floodplain than in adjacent upland forests (Dickson 1978). Kennedy (1977) noted that more birds preferred Zone IV and V hardwoods than other dominance types (e.g., cottonwood-willow-sycamore or cypress-tupelo).

Zones IV and V are the principal environments of the rare and endangered ivory-billed woodpecker, Bachman's warbler and probably the cougar (Wharton et al. 1981). Black bears (on Bear Island) congregate on the higher, unlogged, acorn-rich Zone IV and V bottomlands. Upland forest forms sometimes occurring in Zone V are the least shrew (Cryptotis), pine vole (Pitimys), and, rarely, the common mole. Other mammals are the same as reported for Zone IV.

Although Zone V environments may comprise a relatively small part of the total floodplain acreage (for example, only 5% in Congaree Swamp), these old levee ridges are extremely important in the life histories of many floodplain species. They provide food, winter hibernacula, and for the more terrestrial forms, high water refuge and migration and dispersal routes. In a number of southern swamps lacking a Zone V, mounds of earth ("cattle mounts") often were constructed by early human residents to provide refuge for livestock during high water. Tinkle (1959) found narrow, long levees indispensible for the egg-laying activities of many amphibious snakes and turtles; he also discovered that the swamp palm (Sabal minor) growing there provided a major hibernaculum for small vertebrates.

THE USE OF BOTTOMLAND HARDWOOD ZONES BY FISH

Many fish species use Zones II through V during inundation. At least 20 families and up to 53 species of fish spawn and/or feed on the floodplain (Lambou 1963; Holder et al. 1970, 1971; Bryan et al. 1975, 1976; Huish and Pardue 1978; Walker 1980; Wharton et al. 1981; and others). The catfish, sunfish, gar, perch, and sucker families are particularly well represented.

Fish depend on an annual water level fluctuation to limit intra- and interspecific competition for food, space, and spawning grounds (Lambou 1959). Fish distribution and abundance are thus keyed to this cyclic phenomenon (Lambou 1959, 1962; Bryan and Sabins 1979; Hern et al. 1980). As most swamp-wise fishermen know, the time and extent of overflow control the size of the year classes of black bass and sunfish (Lambou 1962). On the Danube

Figure 49. The crop contents of a wild turkey killed in April in the Arkansas River bottomlands. Food items include snails, scarabeid beetles, pecans, jack-in-the-pulpit leaves, and fruits of hackberry, supplejack, and poison ivy. In Florida, crayfish have been found in turkey crops. Photo by Brooke Meanley.

floodplain (Germany) fish yield was 14.6 kg/ha (13 lb/acre) with a 20-day inundation, increasing to 49.2 kg/ha (44 lb/acre) with a 198-day inundation, with the delayed effects recognizable a year later (Stankovic and Jankovic 1971).

The use of the floodplain by fishes in a blackwater creek (Creeping Swamp, Pitt County, NC) was studied by Walker (1980) by use of two-way weir traps in shallow drainways on the floodplain (Zone II) (Figure 50). With the exception of the redfin pickerel, fish moved on the floodplain only at night. Most fish were caught in January through March, the time of maximum inundation, although large fluctuations occurred at other times in these small streams (watershed approximately 80 km^2 or 31 mi^2). Common species (in order of abundance on the floodplain) were pirate perch, redfin pickerel, flier, mud sunfish, eastern mud minnow, American eel, banded sunfish, creek chubsucker, blue-spotted sunfish, redear sunfish (shellcracker), bowfin, shiner, brown bullhead, pumpkinseed, bluegill, golden shiner, warmouth, redbreast sunfish, swamp darter, and green sunfish. Included in the catch of the floodplain weirs were 928 adult crayfish (Procambarus acutus and Fallicambarus uhleri), both floodplain varieties.

Fish trapped on the Creeping Swamp floodplain feed on floodplain invertebrates, principally copepods, ostracods, amphipods, isopods and midge fly larvae (Chironomidae) (Robert Sniffen, Institute of Marine and Coastal Research, East Carolina University, Greenville, NC; personal communication). Delicate forms such as oligochaete worms and flatworms (Planaria) disintegrate rapidly and leave few or no identifiable fragments; hence their contribution to fish diet may be underestimated. Both Woodall et al. (1975) and Arner et al. (1976) on the Luxapalila River (MS, AL) found a preponderance of "terrestrial" invertebrates in stomachs of fish collected on the floodplain.

Holder et al. (1970) compared the fish populations of inundated floodplains (Zone II) and sloughs of the Suwannee River. While the standing crop over the floodplain averaged much less (11-17 kg/ha or 10-15 lb/acre during the 3- to 10-month inundation period) compared to that of the sloughs (262 kg/ha or 234 lb/acre),

Figure 50. Two-way traps with wire mesh wings, set in this small Coastal Plain blackwater creek (Creeping Swamp, NC) and in shallow drainways on the floodplain, revealed that 21 fish species used the floodplain extensively. With the exception of four species, more individuals were taken on the floodplain than in the channel. Although most fish utilized the floodplain from January through March, flooding occurred frequently at other times in this small watershed (80 km^2 or 31 mi^2) (Walker 1980).

the surface area of the floodplain was much larger. Sloughs were sampled after the water had ceased flowing off the floodplain, and fish were concentrated by falling water levels. Holder et al. (1970) stated that "high water over the floodplain provided space, food, and increased habitat for the reproduction and growth of fish."

Movement of fish on floodplains often is keyed to temperature. Holder et al. (1970) found ripe males and females of several species trying to cross the sill between the Okefenokee Swamp and the Suwannee River coincident with high water at the following time and water temperatures: fliers, bowfin (February, March, 11°-13°C or 52°-56°F); yellow and brown bullheads (March, 11°C or 52°F); warmouth (March-April, 16°-19°C or 60°-67°F); chain pickerel (March-April); lake chubsucker (April, 21°-24°C or 70°-76°F).

Floodplains are important spawning areas for several species of herring (Clupeidae). Hickory shad (Alosa mediocris) spawn in oxbow lakes, sloughs, and tributary streams of the Altamaha River (GA) (between River Mile 20 and 137). Blueback herring (Alosa aestivalis) spawn in the same areas of the bottomland hardwoods; they have remarkably adhesive eggs which adhere to twigs and objects on the floodplain floor and resist being swept away by sheet flow. Ripe bluebacks were taken in an over 161-km (100-mi) long section of the Altamaha in backwater lakes and flooded low areas "that are accessible to these fish only during spring flood stages" (Adams and Street 1969).

Studies of larval fish on the floodplain or in sloughs and waterways deep within the floodplain suggest that the immature stages of roughly one half of the fishes of the lower Mississippi River used the floodplain as a nursery (Gallagher 1979). Analysis of the temporal, spatial, and size distribution of larval fishes supported this contention; spawning of 7 out of 10 of the most common taxa took place in backwater habitats (Atchafalaya Basin, LA) (Hall 1979). Temporal and spatial delineation of niches of larval fish on the floodplain have been summarized further by Larson et al. (1981) and Wharton et al. (1981).

TROPHIC RELATIONSHIPS

Energy flow in riverine systems involves both detritus and grazing pathways. Although rivers appear to shift from autotrophy (predominantly grazing pathway) in mid-sections to heterotrophy (predominantly detritus pathway) in lower sections (Vannote et al. 1980), many lower river "detrital" food chains may still involve zooplankton "grazing" on phytoplankton. For example, Wallace et al. (1977) found over 300,000 diatoms/liter in the lower Altamaha River (GA). The grazing pathway is important even in Coastal Plain blackwater streams; Patrick (1972) characterized these streams as being dominated by the diatom genera Eunotia and Actinella. For clarity, trophic pathways on the floodplain have been divided into two systems (dry system pathways and wet system pathways). These two "systems" are not always clear cut. For example, mallards prefer to feed on acorns when they float during inundation. The dry system (Figure 51) is functional during drydown when the floodplain is not inundated. While the system is largely detrital, the grazing pathway of the terrestrial faunal assemblage is also pronounced, with appreciable consumption of the products (nuts, berries, leaves, bark) of the bottomland hardwoods and other primary producers.

Trophic pathways in the litter layer of the dry system are similar to those in the uplands. Gist and Crossley (1975) in trophic studies of upland forest found that millipedes consume up to 120 g/m^2/yr of deciduous litter detritus. Fungal hyphae were the principal food of snails and collembolans. The predatory mites consumed primarily collembolans.

The second trophic system, (Figure 52) is a wet system functioning in pools and during inundation. Primarily detrital, it involves the bulk export of detritus into sloughs, oxbows and rivers, thus feeding a largely aquatic fauna. Aerial swarms of midge flies, mosquitoes, and mayflies emerge periodically, however, to regale legions of swifts, tree frogs, bats, and dragonflies.

Since much of the energy of the wet system is exported, the process needs to be summarized in more detail. Detritus

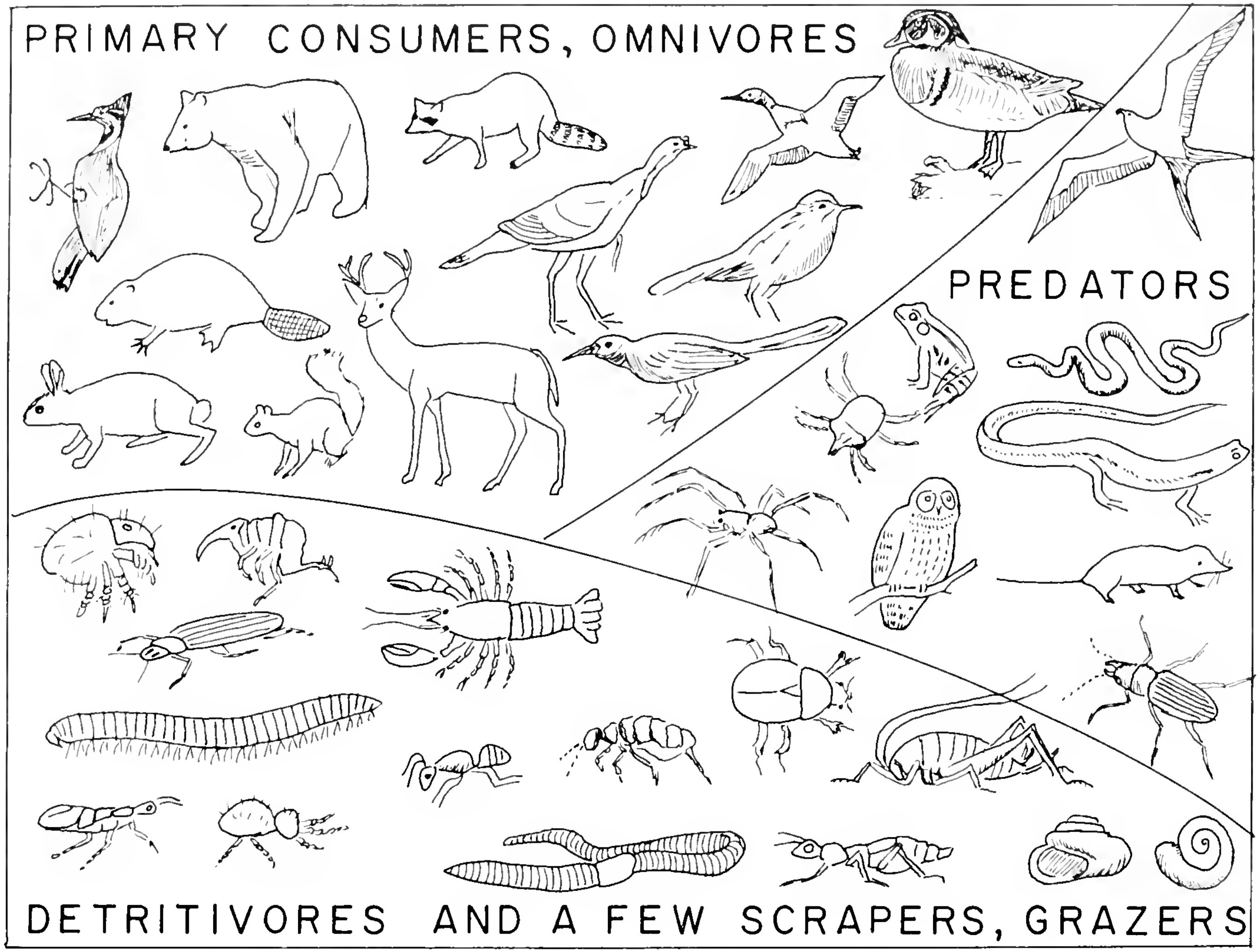


Figure 51. Largely terrestrial food chains involving detritus, granivory, frugivory, and herbivory. The detrital chains begin with the most abundant invertebrates, probably oribatid mites and three groups of collembolans, followed by earthworms, rove beetles, camel crickets, millipedes and crayfish. Their predators include mesostigmatid mites, wolf spiders, carabid beetles, salamanders, and various frogs and shrews. Top predators include the barred owl (which also takes crayfish), rat snake, and swallow-tailed kite. Other important food chains are based on grazing of the plant products. Acorns are eaten by bluejays, grackles, woodpeckers, ducks, wild turkey, raccoons, various mice, squirrels, deer, and bear. Other nuts (hickory, pecan, beech, etc.) also are important. Rodents and box turtles graze fungi. Beaver and swamp and marsh rabbits are direct grazers on herbs and barks. Berries (haw, holly, possumhaw, grapes, supplejack, sugarberry and water, swamp and Ogeechee tupelos) feed wintering birds like robins, as well as omnivores such as raccoons and bears.

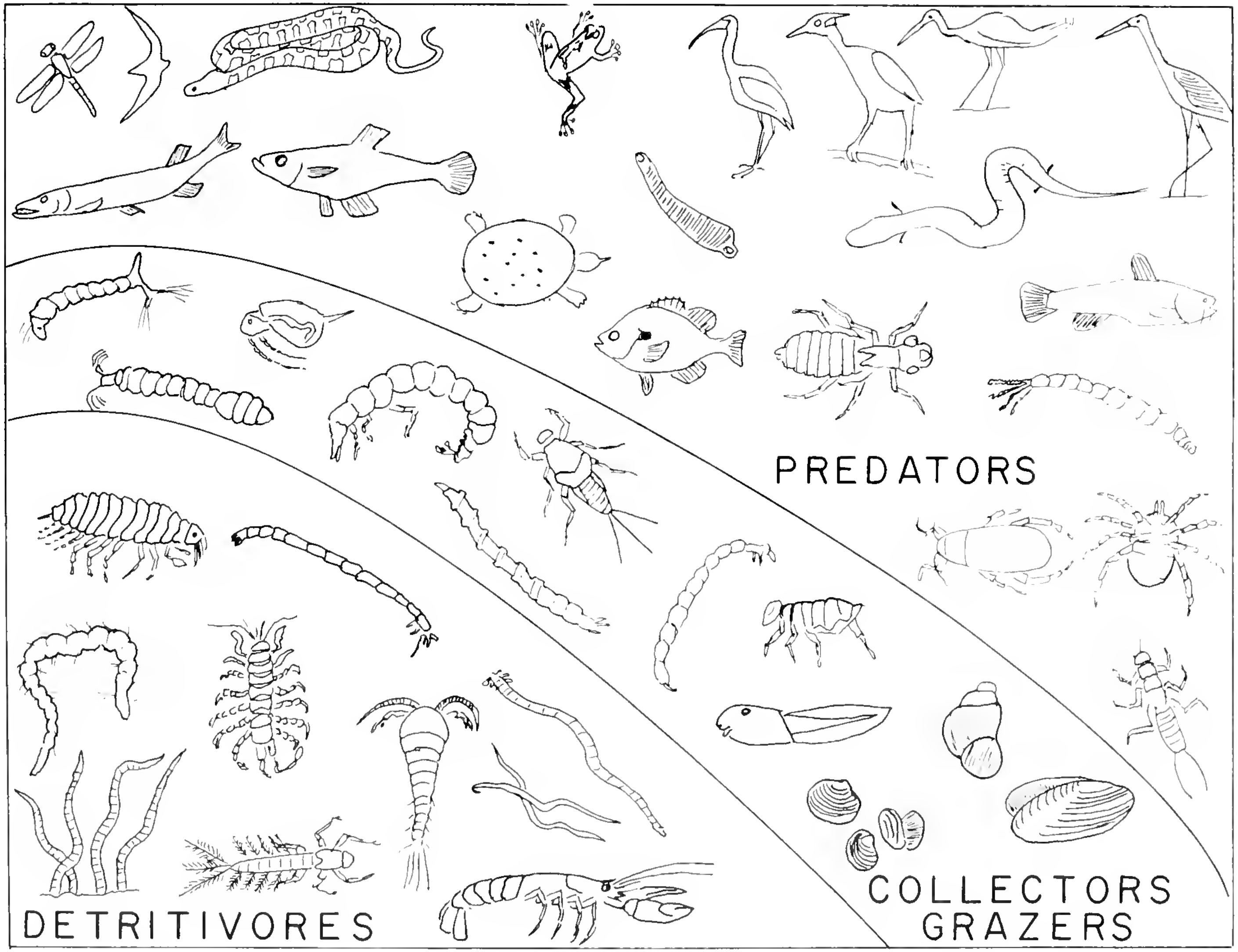


Figure 52. Largely aquatic food chains based upon detritus processed by enormous numbers of detritivores: various annelids (*Tubifex*, *Nais*), collembolans, crustaceans (isopod *Asellus*, amphipod *Hyalella*, copepods, crayfish); nematode worms and larval insects (midge and biting midge, mayfly). Coarse and fine particulate organic matter is filtered from the water by a host of organisms, including cladocerans, larval insects (caddisfly, blackfly) and clams. Other animals, such as mosquito larvae, tadpoles and snails are scrapers and grazers. Aerial swarms of midge flies and mosquitoes are preyed upon by dragonflies, chimney swifts, bats, and tree frogs. Aquatic predators include water mites, diving beetles, larvae of stoneflies and dragonflies. some cranefly larvae and many fish, leeches, turtles and amphiumid salamanders. Top predators include softshell turtle, pickerel, water snake, alligator, otter and the wading birds (limpkin, egret, yellow-crowned night heron, white ibis).

(leaves, twigs) is in the form of coarse particulate organic matter (CPOM, particle size >1 mm), fine particulate organic matter (FPOM, particle size <1 mm), or dissolved organic matter (DOM, particles <0.5 microns) (Cummins and Spengler 1978). Following autumn leaf fall, leaves are first enriched by bacteria and aquatic hyphomycete fungi which partially digest leaf tissue and build their own cellular protein. Both the quality of POM and the rate of its formation depend on the tree species involved. Elm, ash, and maple leaves disappear faster than oak and beech (Kaushik 1975). Floodplain tree diversity thus insures food over a longer time span. Insect larvae called shredders (some Trichoptera, Plecoptera, and Diptera) as well as crayfish and amphipods (Thomas 1975) then reduce the leaves to FPOM. In the meantime some scrapers such as snails may "graze" on the attached periphyton (diatoms) on the CPOM particles. The feces of both groups become FPOM.

Quantitative estimates of POM are limited. Wallace et al. (1977) found 7.8 x 10 particles per liter in the Altamaha River (GA) in April. Other data suggest that 11,000 kg/day move down the Altamaha (Wharton 1980). Though particulate organic matter is probably the most important source of carbon to the floodplain trophic system, DOM is a far more abundant source (about 257,000 kg/day transport estimated for the Altamaha River; Wharton and Brinson 1979a). Labile DOM fractions can be removed by some organisms (Lush and Hynes 1973, 1978; Lock and Hynes 1976; Sepers 1977); much of the DOM, however, may not be usable by the biotic community because of their refractory nature. Most of the DOM (up to 30%-40% of their dry weight) leaches out of leaves within a few days after falling into the water. Depending on the pH and the presence of divalent cations such as calcium, some DOM can flocculate and form clumps of FPOM. These abiotic aggregates can then be colonized by bacteria and fungi in quiet backwaters (Kaushik 1975) and consumed by filter feeders.

Whatever the source, FPOM is used by detrital processors which obtain it from the sediments (some Ephemeroptera and Diptera) or filter it from suspension (some Ephemeroptera, Trichoptera, and Diptera) (Cummins 1973). While some caddisflies and other organisms are algal grazers, and blackfly larvae (*Simulium*) can even trap bacteria, it is the FPOM which fuels the river channel ecosystem. In the permanent waterways (Zone I) an innumerable host of larval blackflies, caddisflies, stoneflies, mayflies, midge flies, and adult clams screen these tiny fragments from the water as their energy source. Incredible densities of organisms are supported on snags (20,000/m^2), and in sands (40,000/m^2) of the Satilla River (Benke et al. 1979). Figure 53 indicates the dominant species which live on snags in a blackwater river and in bottom sands and also portrays the dominant organisms which wash down (drift fauna) in both blackwater and alluvial rivers.

The high productivity of blackwater streams has been documented (Beck 1965; Holder et al. 1970, 1971; Benke et al. 1979). The blackwater Okefenokee Swamp has predominantly peat substrates and a summer pH as low as 3.8 (normal pH 4.0), yet has an abundant fauna of amphipods, freshwater shrimp, insect larvae, ancylid snails (F.C. Parrish, Department of Biology, Georgia State University, Atlanta; personal communication), and fish (Wharton 1977). Furthermore, the swamp is filled with carnivorous plants such as *Utricularia*, indicative of low nitrogen levels. Some biologists are surprised that such apparently nutrient-poor waters can have such a large and varied fauna. Evidently, since blackwater systems recycle nutrients poorly by conventional means (decomposition and mineralization of plant debris) and have minimal inputs of inorganic nutrients from the watershed, a conservation strategy has evolved. Animals in the food web consuming detritus and/or aggregated particles of DOM thus incorporate the large amounts of organic nitrogen present. Organic nitrogen is obtained from animals directly (insectivorous plants) or indirectly (animal excretory products); thus this limited nutrient is recycled and conserved. Other food chains involving grazing of both algae and higher plants may be present, but their importance is undocumented.

Apart from their toxicity, radionuclides (^{90}Sr, ^{137}Cs, ^{60}Co, ^{131}I, ^{140}Ba, ^{3}H) are of interest in tracing the fate of minerals in the floodplain ecosystem (Garten et al. 1975; Pinder and Smith

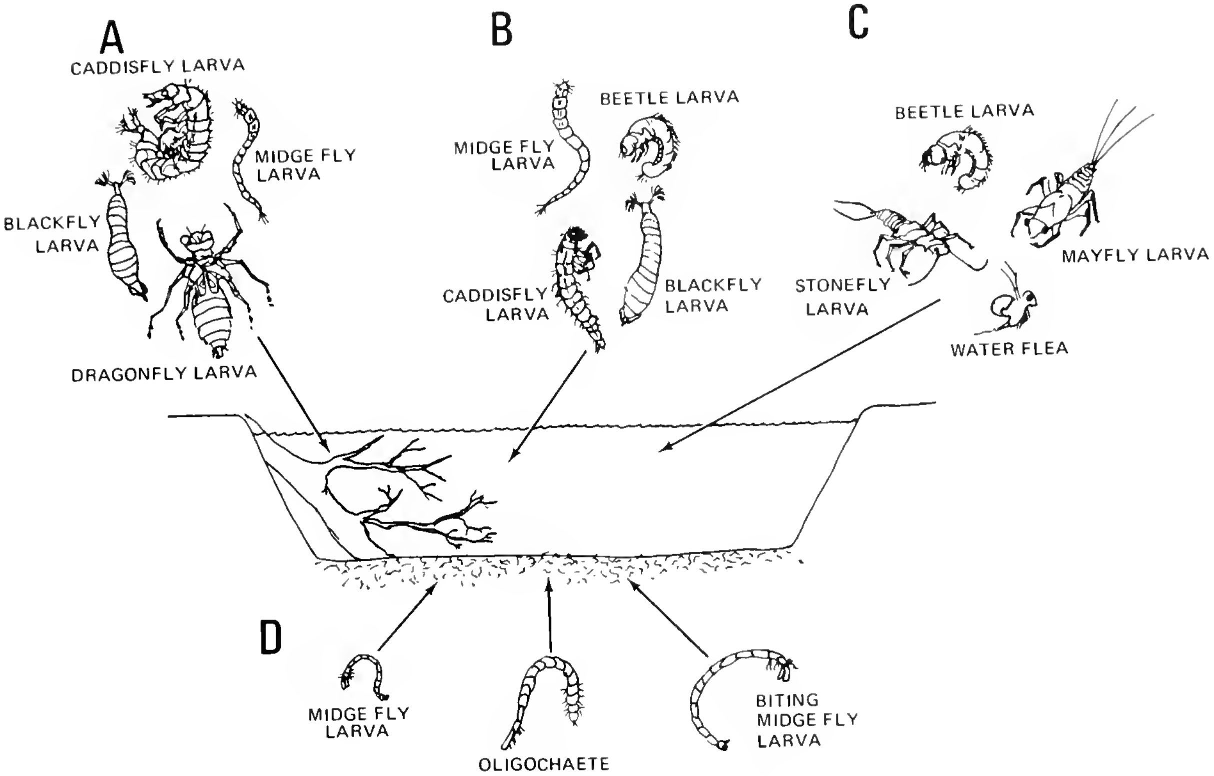


Figure 53. Common invertebrates of southeastern rivers: (A) snag fauna of a Coastal Plain blackwater river, (B) blackwater river drift fauna, (C) Coastal Plain alluvial river drift fauna, (D) bottom sand fauna of a Coastal Plain blackwater river. Blackwater river data from Satilla River, GA (Benke et al. 1979); alluvial river data from Altamaha River, GA (Gardner et al. 1975). (Modified from Wharton et al. 1981.)

1975), especially where some follow normal metabolic mineral pathways in organisms (^{90}Sr as Ca, ^{137}Cs as K). Radioactive elements adsorb on algae and particulate matter, but their assimilation by aquatic fauna is strongly reduced (from 90% to 10%) by adsorption to inorganic clays ingested with the food.

Unlike the bioaccumulation of pesticides, studies suggest that highest concentrations of radionuclides typically occur at lower trophic levels; algae may concentrate ^{137}Cs 25,000 times while fish may do so only 1000 times (Nelson et al. 1972). On the other hand, large hatches of emerging insects such as chironomids carry only small quantities of radionuclides from the system (Nelson et al. 1972) while deer, who graze herbs, shrubs, and mushrooms, may acquire considerable amounts of radionuclides.

Stomach analyses of various vertebrates (Figure 49) have yielded data on food preferences. The use of the huge acorn crop and other foods has been reviewed (Wharton et al. 1981). Tight coupling of dietary needs and floodplain hydrology is suggested by Fredrickson (1979) and Drobney (1977). They found that a high protein intake essential to wood duck egg production is gained from aquatic and terrestrial macroinvertebrates at the edge of high water as it advances or recedes through Zones III, IV, and V.

Unsupported opinions about the value of an animal species in food webs can be highly misleading in floodplains. For example, the largely cryptozoic and fossorial salamanders appear to be an insignificant component of possible food webs, yet they are very efficient converters of energy into biomass and are probably the floodplain's most abundant vertebrate in either numbers or biomass. In a northern hardwood forest just one species of salamander (Plethodon cinereus) made five times more new tissue than the entire bird community, and the biomass of all salamander species was larger than the biomass of breeding birds (Burton and Likens 1975). Net annual production of new tissue by the salamander population was about equal to that of mice and shrews (Potter 1974).

SUMMARY OF FAUNAL UTILIZATION

Faunal resources and diversity among the floodplain zones are summarized in Table 17. The near upland areas of Zone V, although the least extensive of the floodplain zones, support the greatest faunal diversity (Wharton et al. 1981). With Zone IV, Zone V provides larger amounts of forage foods than more inundated zones which lack either nut-bearing hardwoods or a subcanopy and ground cover bearing fruits, berries, and seeds. Zones II and III, important for detrital production and transport, are the primary sites of aquatic secondary production on the floodplain. Coupling between zones notwithstanding (see Chapter 6), it appears in summary that the faunal regimes of the floodplain can be divided into (1) a detritus-dominated aquatic regime centered in Zone II (and to a lesser extent in Zones III-V) and (2) a grazing-foraging food web in Zones IV and V that is more terrestrial than aquatic.

Table 17. Some environmental factors affecting the fauna of the bottomland hardwoods (and the ecosystem in general), and their relative importance in each bottomland hardwood zone. (Zone IIa is tupelo gum-cypress; Zone IIb is swamp black gum-cypress backswamp). Importance: 0 negligible or none, 1 low, 2 moderate, 3 high. (Wharton et al. 1981.)

Factors	Zone				
	IIa	IIb	III	IV	V
Retardation of "side flooding" from tributary streams (damming effect)	1	2	1	2	3
Organic matter production	1	2	2	3	2
Detritus source for feeding downstream life by annual inundation (includes coastal estuary)	3	3	3	2	1
Detritus source for feeding downstream life on 5-7 year pulse cycle (includes coastal estuary)	1	2	2	2	3
Diversity of oak species (acorns for food) (excluding Quercus palustris, bicolor, macrocarpa, imbricaria)	0	0	1	3	3
A mix of white oaks (bear each year) and red oaks (bear every second year)	0	0	-	2	2
Availability of non-coniferous nut-bearing trees other than oaks (hickories, pecan, beech)	0	0	1	2	3
Diversity of berries and soft fruits in high canopy (sugarberry, tupelo, black gum, persimmon, etc.)	1	1	0	2	3
Availability of berries and soft fruits in subcanopy and shrub zone (deciduous holly, haws (Crataegus), mulberry, paw paw, Elliott's blueberry, American holly, swamp palm, tall gallberry, etc.)	1	2	1	3	3
Availability of berries and soft fruits of vines (grapes, poison ivy, supplejack [Berchemia], etc.)	1	1	1	3	3
Availability of herbs as browse for birds and mammals (cane, greenbrier, jewelweed, sedges, etc.)	1	1	1	2	3
Availability of small terrestrial fauna (insects, snails, earthworms, etc.)	0	0	0	2	3

(continued)

Table 17. (Concluded).

Factors	Zone IIa	IIb	III	IV	V
Availability of aquatic macroinvertebrates	3	3	3	3	0
Availability of chimney-building floodplain crayfish	2	2	2	3	1
Forage for adult fish (when flooded)	3	3	3	3	2
Refuge for young fish (when flooded)	2	3	2	3	3
Diversity of forest strata (for bird guilds, etc.)	1	3	1	2	3
Availability of ground-level hibernation sites (stump-holes, logs, leaf base of swamp palm, crayfish burrows)	0	0	0	3	3
Availability of aboreal hibernacula (tree cavity sites in old growth forest)	3	3	3	3	3
Presence of rare and endangered species (e.g., Swainson's and Bachman's warblers, ivorybilled and red-cockaded woodpecker)	0	0	0	2	2
Diversity of fish species	3	2	1	0	0
Diversity of amphibians and reptiles	1	1	1	2	3
Diversity of small mammals	0	1	1	2	3
Breeding bird diversity and density of individuals	1	1	2	3	3
Refuge for "terrestrial" fauna from high water	0	0	0	0	3
Refuge for fish during low water	3	3	2	0	0
Forage and cover for species on adjacent uplands (skink, toad, pine vole, mole, least shrew, fox, etc.)	0	0	1	2	3
Totals:	32	39	35	59	64

CHAPTER 6. COUPLING WITH OTHER SYSTEMS

NATURAL COUPLINGS WITH HEADWATER TRIBUTARIES AND ESTUARIES

Bottomland hardwoods are coupled to other upstream and downstream systems principally by river flows. Tributaries and terrestrial inputs via valley walls serve as linkages to upland ecosystems that flank the floodplains laterally, but upstream-downstream linkages are functionally more important. For example, Apalachicola River flows are coupled both to the mountains of northern Georgia and to coastal estuaries by significant meterological and biological phenomena. The Apalachicola River is a driving force and regulating mechanism mediating the chemistry and biology of Apalachicola Bay. The salinity regime of the bay is largely a function of river flow fluctuations and patterns of local rainfall. River flow in turn is controlled by plant cover and floodplain and upland watershed drainage (Livingston et al. 1976).

Livingston et al. (1975, 1976) showed that the cyclic productivity of Apalachicola Bay not only depends on annual pulses of organic detritus and silt from bottomland hardwoods, but also on the large-scale import of detritus during a major 5- to 7-year pulse originating in the mountains of north Georgia. These longer pulses are linked with peaks in commercial fish catches (Livingston et al. 1976; Meeter et al. 1979) through the trophic dynamics of the detrital food web. Secondary production may be keyed to these linkages to the point that each kind of tree leaf may have its own special estuarine food web (Sheridan and Livingston 1979; White et al. 1979). An important point is that this 5- to 7-year pulse very strongly involves the bottomland hardwood Zone V from which accumulated organic matter is exported. The importance of periodic flooding thus extends well beyond the 1- to 2-year flood cycle.

Apalachicola Bay is not the only example of an estuary dependent on water pulses and intact forests. Day et al. (1977) found that a Louisiana river swamp (Bayou des Allemands) fed pulses of carbon, nitrogen, and phosphorus to Barataria Bay (which produces 45% of the State's commercial fish catch) precisely when migrant species were entering the estuary for feeding and spawning. Similar phenomena have been noted in Chesapeake Bay (Copeland 1966). In fact, estuaries in the Southeast generally are more productive in areas near the mouths of rivers (Copeland 1966).

The importance of freshwater delivery from the Piedmont and Coastal Plain via floodplain rivers cannot be overestimated. Deliveries to estuaries include large amounts of organic matter and vitamins such as B_{12} from blackwater rivers (Burkholder and Burkholder 1956). Both microorganisms and plankton are capable of rapidly and efficiently absorbing leached DOC in coastal environments (Crow and MacDonald 1978) and may be able to use riverine DOC. Thomas (1966) speculated that the Altamaha flushed the rich phosphates of the estuaries seaward as far as 24 km (15 mi). Windom et al. (1975) showed that the nutrient load in riverine discharge in the South Atlantic Bight is equivalent to 100% of the annual inorganic phosphorus requirement and 20% of the nitrogen requirement of salt marshes in the region. Annual freshwater discharge onto shelf areas is equal to 39% of the total water volume out to the 20-m contour, perhaps contributing significant amounts of trace minerals, silicates, organic nutrients, and humic acids (Haines 1975). Under the influence of wind and high water, the Suwannee River (FL) periodically turns the Continental Shelf waters black and pushes water hyacinth rafts as far as the Cedar Keys area, 11 nautical miles from its mouth.

The delivery of upland sediments by the rivers is especially important to estuarine systems. Rivers directly or indirectly provide sands for the construction of coastal features. The Piedmont is one of the major sources of sediments that are deposited in estuaries or picked up by longshore currents and carried southward. The Santee River (SC) is (or was) the possible source of hornblende-rich sands of Georgia's continental shelf (Carver 1971). During extreme floods, silts from upstream may be deposited on downstream salt marshes. Lunz (1938) described the effects of a Santee River flood which deposited a layer of silt 25 mm (1 inch) thick in marshes in the Cape Romain area.

COUPLING WITH RIVER DELTAS

How alluvial rivers are coupled to their deltas was exemplified by the downstream effect of the diversion of 88% of the Santee River's flow into the tidally dominated Cooper River to gain 1.5% of South Carolina's electric generating power (Kjerfve 1976). The Cooper River subsequently eroded so severely that the U.S. Army Corps of Engineers annually dredged 7600 x 10^3 m^3 of sediments from the Charleston estuary. Saltwater intrusion drastically changed the vegetation in the delta of the Santee from fresh to brackish. Santee rice plantation managers had to convert wetlands (former rice fields) which were being managed as freshwater impoundments for waterfowl habitat to brackish water management units. A hard clam (Mercenaria mercenaria) industry evolved within the expanded estuarine zones of the mouth of the river. Upstream the growth rate of water tupelo was apparently reduced following diversion (R.A. Klawitter, retired forester, Northern Forest Fire Laboratory, Missoula, MT; personal communication).

As a result of the nature of the integral coupling, any manipulation in the upstream reaches of a river can have pronounced effects at all levels on the system below. Dredging and especially shortening the river by cutting across meander loops have increased bank erosion by increasing water velocity. Conversely, downstream alterations may affect systems upstream. Dredging the Savannah's channel in the estuarine sector has allowed salt water intrusion much farther upstream (Joseph Birch, University of Georgia, Institute of Ecology, Athens; personal communication). Dredging in the Savannah severely reduced larval mayflies, stoneflies, true flies, and beetles, important aquatic foods for fish (Patrick et al. 1967).

In addition to couplings with headwaters and lower estuaries, floodplains are coupled laterally with the uplands on either side via tributaries as well as sheet flow and colluvial soil deposition directly from the adjoining bluffs. Intact tributaries are extremely important to periodic movements of fish and other fauna (Hall 1971; Gasaway 1973). In North Carolina, tributaries functioned as corridors for mass movements of large fish moving upstream and large movements of smaller fish moving downstream, as well as for significant movements of frogs, crayfish, and turtles in both directions (Hall 1971). These movements are seasonal, a fact making it imperative not to judge the importance of tributaries from limited temporal sampling of the fauna.

CHEMICAL COUPLING WITH THE UPLANDS

Although tributaries and non-point source runoff add pesticides, nutrients, toxic metals, coliform bacteria, and other substances to river systems, water quality may improve significantly as water flows through the floodplain. The floodplain with its vast backswamp functions as an important filter and sink for agricultural excesses of nutrients and biocides. One of the first studies of filtering capacity (Kitchens et al. 1975) indicated that the Santee River floodplain significantly reduced bacterial counts and nutrient concentrations from the polluted Wateree tributary. Nutrient reduction, particularly phosphorus, was attributed to assimilation by aquatic vegetation, mat algae, and trees as water passed through the swamp. Yarbro (1979) found agricultural inputs dominated the phosphorus budget of a small North Carolina blackwater creek swamp, totalling 300 mg $P/m^2/yr$ as compared to 70 mg $P/m^2/yr$ from rainfall and

28 mg P/m^2/yr from additional surface runoff. The swamp effectively removed 30% to 57% of these additions.

The floodplain's capacity for improving water quality operates on two scales. The first is the small, unleveed creek swamps along tributary branches of the major rivers. For example, Lowrance (1981) found comparable swamps along the Little River of Georgia reduced nitrate, sulfate, calcium, and magnesium concentrations in passage to the river. Reductions were dramatic: runoff from a hogpen within 50 m (164 ft) of the creek was not detectable downstream. Lowrance (1981) concluded that conversion of even a small part of the floodplain riparian ecosystem to fields would increase stream loadings of most nutrients except phosphorus, with the largest effect on nitrate movements. Nitrogen and carbon compounds, taken up by anaerobic bacteria, are converted to gaseous forms by processes such as denitrification and respiration during their passage through the riparian zone (Henderickson 1981). On a second and larger scale, a complex network of distributaries in some floodplains slowly partitions the flow out over large areas of the floodplain, accomplishing nutrient reduction of the same magnitude as tributaries (Kitchens et al. 1975).

The magnitude of the problem of point source pollution is in many cases severe. Industrial releases of lignins and wood sugars affect the color and odor of the Altamaha River for at least 40 km (25 mi) downriver, contributing to the growth of the white filamentous bacterium *Sphaerotilus*, which clogs fishermen's nets in the tidal zone. Concentrations of PCB's exceeding FDA maximum levels (5 ppm) have been found in many fish species in southeastern rivers (Veith et al. 1979).

The filtering capacity of the swamp could be useful in treating manmade effluents. Tributaries from the Savannah River Plant (SC) have trapped and held radioactive ^{137}Ce, preventing major contamination of commercial and sport fish species in the Savannah River (Wharton 1977). A cypress swamp above a peat substrate has effectively treated the sewage of Wildwood, FL, for 20 years. Bacterial levels measured in the effluent were actually lower than those in the lake into which they eventually emptied (Brown et al. 1974). For further reviews of swamp filtering action, see Wharton (1970, 1977, 1980), Wharton and Brinson (1979a), and Kibby (1979).

The movement and immobilization of pesticides and metals by humic substances (humic and fulvic acids) is a particularly important aspect of the swamp's filtering process. Humic substances react with metals by exchange, adsorption and chelation. This is particularly important in blackwater rivers (DOM> 10 mg/l) since significant quantities are complexed (Reuter and Perdue 1977). Excess humic acids tend to immobilize mercury (Miller et al. 1975) and other heavy metals (Giesy and Briese 1978). The fate of these substances after complexation is important. Humic acids, being insoluble, tend to be immobilized as bottom sediments. Soluble lighter fulvic acids, constituting the bulk of DOC in southeastern rivers, sometimes complex with water contaminant metals; largely unavailable as microbial foods, they do not enter the downstream food chain (Reuter and Perdue 1977). Some of these flocculate with electrolytes at the interface of fresh- and saltwater.

Another important consideration is the residence time required for processes involved in water quality improvements. Residence time is the time that water remains over the floodplain floor and in the sloughs and depressions. Examples of processes are conversion of DOM to POM by microbes (Slater 1954; Brinson et al. 1980) or by freezing (Giesy and Briese 1978), the complexing of metals with organic matter, the adsorption of ions by clay particles, and the establishment of reducing conditions essential to operate the metabolic pathways of sulfate reduction, denitrification and methanogenesis. Obviously, any human activities which decrease residence time, such as channelization, interfere with or eliminate these vital floodplain functions.

MODIFICATIONS OF RIVER AND FLOODPLAIN

Construction or other modifications on floodplains may cause profound changes in their ecology. Man's direct or indirect manipulation of the hydrologic regime may result in a complete transformation of river and floodplain morphology (Schumm 1969). Clearly, anything that man does to the natural, orderly river channel will induce changes as the river attempts to regain its original efficient configuration. Sediment inputs resulting from clearcutting, or sediment starvation from reservoir construction, dredging, shortening and even snagging and dragging are among potential impacts.

The construction of reservoirs can have both direct and indirect effects, the result of coupling the natural energy of moving water with man's complex of activities on the uplands. While the dissolved solute chemistry of the water is not markedly changed, the sediment load settles and is reduced as a result of the stilling effect of the reservoir. Release of water from the reservoir results in scour and resuspension of sediments that move steadily downstream as the upper segment of the river lowers its bed (Schumm 1971). In the Red River below Denison Reservoir (OK), scour widened the channel from 1.5 to 3.0 m (5 to 10 ft) per year but the river did not regain its pre-reservoir sediment load for 322 km (200 mi) (Einstein 1972). The large dams above Augusta, GA, virtually have stopped sediment movement from the Piedmont (Meade 1976). Reservoirs on the Santee and Savannah trap from 85% to over 90% of incoming sediment. Since as much sediment still is carried in the lower reaches as in pre-dam days, Meade concluded that the immediate source must be the river bed, banks, and floodplain. Other factors may include extensive shortening and dredging of the Savannah by the Corps of Engineers with corresponding gradient increase and much abnormal bank destruction. Meade stated that since 1910 reservoirs on the Savannah River have reduced the sediment load delivered to the ocean by 50%, thus depriving the Continental Shelf of its former river influx of inorganic nutrients.

Flood peaks higher than the 1- to 2-year inundations are also impaired by damming. Much riverborne sediment deposits in estuaries are in the "sediment-trap" at the freshwater-saltwater interface. In pre-dam days the locus of these deposits moved back and forth seasonally in the estuary, and floods flushed out accumulated sediments with a periodicity of 3 to 5 years (Meade 1976). This flushing action no longer occurs, and sediments accumulate in the estuary and must be removed by costly dredging.

Another example of direct downstream effects is flow regulation by huge reservoirs on the Roanoke River (NC). The Roanoke River (NC) has a "dead zone" 6-12 m (20-40 ft) wide from near the levee top down to the river devoid of all bottomland hardwoods except a few willows at the upper edge. This zone, with numerous fallen dead trees, resulted from water levels held artificially high by upstream discharges, well into leafout time. In swales along the Roanoke the lack of former flushing action may have caused several feet of silt to accumulate (Pat White, Williams Lumber Company, Mackeys, NC; personal communication).

Indirectly, flow regulation is having an even more pronounced effect on bottomland hardwood communities. Damming may severely modify or eliminate the seasonal hydroperiod, allowing upland row-crop agriculture and forestry on the floodplain. On the Savannah River (GA) floodplain, below a series of large reservoirs in the Piedmont, hundreds of acres of Zone IV bottomland hardwoods are being sheared off, and the floodplain is being planted in soybeans. Even without flow regulation, the floodplains of many southern rivers are being cleared of bottomland hardwoods and prepared for conversion to pine plantations, although, ironically, hardwoods often outgrow pines on these sites. Planted loblolly stands on the Altamaha, Oconee, and Ocmulgee Rivers in Georgia have developed a thick understory of wax myrtle and sweetgum, typical Zone IV species, which may indicate the land is still most suitable to the natural community. Such system-wide changes threaten or eliminate the life support functions of floodplain zones.

The most serious impacts of reservoirs on bottomland hardwoods downstream arise from regulating the normal annual rise and fall of the river to which the whole system is keyed. The effects of reservoirs can be summarized: (1) reduction of silt and associated nutrient inputs for some distances below dams, (2) excessive bed and bank scour below dams with accompanying modification or extermination of benthic and epibenthic fauna, (3) loss of bank-stabilizing vegetation by frequent flow changes, (4) disruption of normal fish breeding and feeding on the floodplain, (5) elimination of sufficient high water for the annual flushing of detritus from the floodplain, and (6) encouragement of clearcutting, site conversion to tree plantations and row crop agriculture on formerly saturated floodplains.

CHEMICAL COUPLING WITH THE WATER TABLE AND ATMOSPHERE

It is seldom acknowledged that Piedmont alluvial rivers crossing the Coastal Plain may have numerous blackwater tributaries, the DOM of which is subsequently camouflaged by suspended inorganics. The lower sections of alluvial rivers are, in effect, chemically mixed rivers, in proportion to the respective discharges that each type stream contributes. Likewise, there is lateral coupling with the underground aquifer in limesink zones. At times of high water, acid blackwater may enter and corrode underground corridors; conversely, aquifer flow at times raises the pH and the nitrate level of the river (Kaufman and Dysart 1978).

Wetlands, including bottomland hardwoods, modify temperature and moisture content of the lower atmosphere. They ameliorate freeze conditions and provide a more equithermal refuge for many animals which could not otherwise exist at that latitude. Wetlands modify lake and sea breezes, the urban boundary layer, and even the behavior of tropical cyclones. In Florida, relatively minor changes in land-water coverage and soil moisture result in surprisingly large changes in sea breezes, cumulus cloud formations, and precipitation (Gannon et al. 1978).

COUPLING VIA FAUNAL MOVEMENTS

Rivers and their floodplains are also coupled with marine systems through anadromous, catadromous and other marine species. Blue crabs occur to RM (river mile) 50 in the Altamaha. The southern flounder (Paralichthys lethostigma) and striped mullet (Mugil cephalus) migrate and feed as far as 193 km (120 mi) up the Altamaha, while two common coastal fishes, the hogchoker (Trinectes maculatus) and the needlefish (Strongylura marina), actually spawn in the mid-reaches of the river (John Adams, Georgia Power Co., Environmental Laboratory, Atlanta; personal communication). Various shad species partition the river into spawning and nursery sections (Adams and Street 1969; Adams 1970). American shad (Alosa sapidissima) spawn in the Altamaha itself between RM 60 and 120, with primary nursery centers at RM 21-30 and RM 100-110. Hickory shad (A. mediocris) spawn in floodplain oxbows, sloughs, and tributaries between RM 20 and 137. Blueback herring (A. aestivalis) spawn on the floodplain floor between RM 5 and 137, with primary nurseries between RM 10 and 30. Examples of catadromous species are American eel and mountain mullet (Agonostomus monticola), the latter in gulf coast rivers.

Striped bass formerly traveled up the Savannah as far as Tallulah Gorge and still ascend many Coastal Plain streams. Two species of sturgeon (Atlantic and shortnosed) ascend rivers entering the Atlantic slope. Other animals such as manatees use the Altamaha at least to the limit of tidal range and go up the Suwannee to Manatee Springs. The glochidian larvae of many clams can travel up- and downstream attached to fishes, often providing a mechanism for repopulating depleted areas.

Terrestrial fauna may be coupled to the uplands, as when deer who base their home range on floodplains graze in uplands. Conversely, upland forms such as the black racer and pine vole may use the floodplain at drydown. The narrow greenbelts of bottomland hardwoods also provide routes for migration and restocking.

SUMMARY

In summary, bottomland hardwood swamps are integrally coupled to the surrounding uplands, downstream estuarine systems, and the atmosphere. By virtue of these couplings, the swamps provide invaluable services and resources to the environment. These "ecological values" are a function of the interaction of the bottomland hardwood ecosystem and its primary driving force, the fluctuating water levels of the riverine systems. In spite of an apparent resilience to specific disturbance, the ecological values of the bottomland hardwoods can be impaired by development or alterations which do not take into account the openness of these ecosystems to the riverine and upland ecosystems to which they are hydrologically coupled.

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APPENDIX

SOILS OF SOUTHEASTERN FLOODPLAINS

Tables A-1 through A-8 describe soil characteristics in sampled dominance types and river floodplain classes within the study area.

Soil samples were collected nonrandomly from a depth of 8 to 30 cm (3 to 12 inches) below surface litter zones, in the center of the most mature group of trees. No samples were taken from atypical microtopographic relief features at the site, nor were samples taken where there was evidence of logging, vehicle passage, scour channels, or upland erosion sources.

Mechanical analysis of percent clay, silt, and sand was by the Bouyoucos method. Samples with very high organic matter were subjected to hydrogen peroxide or ashed at 500°C for 4 hours prior to analysis.

Organic matter was determined by the Walkley-Black method. Depending on the amounts of silt and clay present, organic matter may be overestimated. The error of overestimation due to water driven off from clay and silt was computed on the basis of 8% error with 5% clay-silt and 30% error with 85% clay-silt (Broadbent 1953; Klawitter 1962); corrected percent organic matter appears in parentheses in Tables A-1 through A-8.

Macronutrient concentrations were determined by plasma emission spectrometry, following extraction by the double-acid method.

Table A-1. Soil analysis for floodplain dominance types, Zone II, alluvial rivers. C=clay, SI=silt, S=sand, O.M.=organic matter.

River floodplain description	pH	% O.M.	Soil components (%)			Macronutrients (ppm)				
			C	SI	S	Ca	K	Mg	Na	P
Escambia: swamp tupelo-cypress	4.8	48[a]				1804	160	484	174	14.0
Roanoke: swamp tupelo swale	5.3	50(39.5)[b]	20	24	50	2728	49	268	47	9.2
Choctawhatchee: water tupelo-cypress	5.4	32[a]				1412	105	448	244	14.0
Escambia: swamp tupelo backswamp	4.7	31[a]				299	94	119	66	11.0
Tar: water tupelo-cypress	5.0	27[a]								
Roanoke: water tupelo swale	5.1	34[a]				1981	105	400	155	12.4
Great Pee Dee: water tupelo-cypress	5.2	4.6	53	22	24	708	71	248	56	9.2
Apalachicola: mixed gum-cypress	5.5	6.0	38	40	22	1920	64	119	39	6.8
Santee: water tupelo-cypress slough	4.9	5.1	71	12	17	884	58	233	40	12.8
Apalachicola: water tupelo-cypress	5.0	5.3	48	27	25					
Apalachicola: gum-cypress wet flat	5.4	5.9	61	23	16	1108	40	113	51	9.6
Escambia: water tupelo backswamp	5.3	4.2	28	27	35					
Choctawhatchee: cypress wet flat	5.2	5.2	43	22	35	960	30	102	24	9.2
Ogeechee: mixed gum-cypress slough	7.3	3.9	49	17	34	1140	44	145	38	7.6
Ogeechee: mixed gum-cypress flats	5.6	5.2	39	19	42	831	52	115	31	6.7

[a] Data uncorrected.
[b] Values in parentheses are corrected for error of overestimation. See Appendix introduction.

Table A-2. Soil analysis for floodplain dominance types, Zone II, blackwater rivers. C=clay, SI=silt, S=sand, O.M.=organic matter.

River floodplain description	pH	% O.M.	Soil components (%)			Macronutrients (ppm)				
			C	SI	S	Ca	K	Mg	Na	P
Little Wambau: swamp tupelo on peat	4.7	51(43.9)[b]	11	9	80	682	59	108	62	10.0
Little Pee Dee: swamp tupelo-cypress	5.3	29(26.1)[b]	3	7	90					
Yellow: swamp tupelo-water tupelo-bay	5.3	21(16.8)[b]	17	37	46	684	60	150	44	9.6
Waccamaw: swamp tupelo swale (Terrace I)	5.0	11(8.7)[b]	17	28	59	456	26	35	32	14.0
Waccamaw: swamp tupelo-laurel oak	5.2	9(7.6)[b]	11	14	75					
Waccamaw: swamp tupelo-cypress flat	4.9	5.9	13	24	63					
Big Wambau: mixed tupelo gum-cypress slough[a]	6.2	6.0	42	21	37					
Big Wambau: mixed Zone II-IV[a]	5.8	5.9	25	31	44	2404	40	187	38	8.4
Suwannee: swamp tupelo-cypress-pumpkin ash	6.2	27(21.9)[b]	23	18	60	6648	86	454	91	42
Suwannee: mixed tupelo gum-cypress-pumkpin ash	6.5	36(27.8)[b]	27	27	46	5176	109	455	78	142

[a] Old rice cultivation areas.

[b] Values in parentheses are corrected for error of overestimation. See Appendix introduction.

Table A-3. Soil analysis for floodplain dominance types, Zone II, tide-influenced sections (tidal forests) of spring-fed blackwater and alluvial rivers. C=clay, SI=silt, S=sand, O.M.=organic matter.

River floodplain description	pH	% O.M.	Soil components (%)			Macronutrients (ppm)				
			C	SI	S	Ca	K	Mg	Na	P
Yellow: sweet bay-white cedar	5.2	53[a]				1404	144	588	196	14.4
Sopchoppy: sweetbay-swamp tupelo-wax myrtle	5.7	77[a]				1324	36	628	183	29.0
St. Marks: swamp tupelo-sweet bay-wax myrtle	6.2	54(45.4)[b]	6	21	73	2462	97	556	145	41.2
Aucilla: (Zones II-III-IV mix)	6.3	23(19.3)[b]	14	13	73	2852	35	400	80	12.0
Suwannee: swamp tupelo-cypress-pumpkin ash	6.0	49(39.7)[b]	17	23	60	5784	323	870	1011	55
Suwannee: swamp tupelo-cypress-pumpkin ash	6.4	52(40.6)[b]	20	30	50	5488	78	499	65	46
Apalachicola: mixed tupelo gum-cypress-*Thalia*	5.3	22(15.4)[b]	46	36	18	1676	92	180	53	8.0
Escambia: sweet bay-cypress-white cedar	5.4	19(15.1)[b]	28	17	55	776	116	456	224	15.2
Choctawhatchee: swamp tupelo-bay	5.5	36[a]				1213	164	616	664	18.0

[a] Data uncorrected.

[b] Values in parentheses are corrected for error of overestimation. See Appendix introduction.

Table A-4. Soil analysis for floodplain dominance types, Zone III, alluvial rivers. C=clay, SI=silt, S=sand, O.M.=organic matter.

River floodplain description	pH	% O.M.	Soil components (%)			Macronutrients (ppm)				
			C	SI	S	Ca	K	Mg	Na	P
Ochlockonee: overcup oak-water hickory	4.7	4.6	2	25	73	188	26	40	19	16.0
Santee: overcup oak-water hickory flat	5.2	3.1	70	13	17	568	28	205	30	8.0
Apalachicola: near levee	5.4	2.2	56	23	21	980	19	106	28	56
Apalachicola: behind levee	5.3	4.8	44	24	32					
Apalachicola: overcup oak-water hickory	5.5	2.1	60	24	16					
Ogeechee: overcup oak-ash-elm flat	6.0	3.3	31	21	43	708	37	82	34	5.3

Table A-5. Soil analysis for floodplain dominance types, Zone IV, alluvial rivers. C=clay, SI=silt, S=sand, O.M.=organic matter.

			Soil components (%)			Macronutrients (ppm)				
River floodplain description	pH	% O.M.	C	SI	S	Ca	K	Mg	Na	P
Santee: mixed Zone IV-V	5.2	3.8	47	20	33	472	37	168	33	8.0
Santee: old growth laurel oak	5.1	3.6	49	14	37	436	46	133	20	7.6
Apalachicola: laurel oak	6.0	3.2	60	11	29	1196	26	128	28	6.4
Great Pee Dee: green ash stand	6.7	2.6	38	31	31	794	34	220	38	12.7
Oconee: willow oak flats	5.2	2.1	25	22	47	448	19	74	20	6.0
Oconee: subsoil of wet flats	5.3	2.0	49	22	29					
Ogeechee: laurel oak	8.2	2.3	24	14	62	1408	15	9	32	2.8
Ogeechee: laurel oak-swamp palm	6.7	2.5	22	11	67	460	32	36	29	3.6
Ogeechee: laurel oak near river	5.4	4.9	44	21	35	932	39	156	42	5.9
Ogeechee: sandy surface soil	5.9	1.3	14	6	80	220	18	34	23	3.4
Ogeechee: clay subsoil	8.3	0.8	33	10	57	778	14	91	64	2.9
Ogeechee: laurel oak away from river	7.4	2.7	33	25	42	484	28	68	33	3.8
Apalachicola: scour channels	5.7	0.9	12	10	78	378	15	37	17	4.0

Table A-6. Soil analysis for floodplain dominance types, Zone IV, blackwater rivers. C=clay, SI=silt, S=sand, O.M.=organic matter.

River floodplain description	pH	% O.M.	Soil components (%)			Macronutrients (ppm)				
			C	SI	S	Ca	K	Mg	Na	P
Waccamaw: laurel oak-willow oak swale	4.3	18(14.6)[a]	15	23	62	84	27	32	34	8.4
Black: laurel oak-willow oak	4.7	11(9.4)[a]	9	12	79	102	30	16	39	11.0
Indian Field: laurel oak flat	5.1	11(9.1)[a]	15	17	68	1144	40	66	33	13.0
Little Pee Dee: laurel oak-red maple	5.4	10(8.5)[a]	12	12	76					
Little Pee Dee: laurel oak	5.7	5.7	13	12	75	160	24	35	31	10.0
Canoochee: laurel oak-spruce pine	5.5	5.5	11	14	75	88	34	47	23	11.6
Turkey Creek: old growth laurel oak	5.2	2.4	10	9	82	496	19	22	23	5.2

[a] Values in parentheses are corrected for error of overestimation. See Appendix introduction.

Table A-7. Soil analysis for floodplain dominance types, spring-fed rivers (Zones II and IV). C=clay, SI=silt, S=sand, O.M.=organic matter.

River floodplain description	pH	% O.M.	Soil components (%)			Macronutrients (ppm)				
			C	SI	S	Ca	K	Mg	Na	P
Wacissa braids: pumpkin ash-red maple	6.3	52(40.1)[a]	19	34	48					
Wacissa: laurel oak-sweet bay-cabbage palm	6.5	17(15.3)[a]	5	5	90	3056	18	234	26	9.2
Wacissa: subsoil at site above	6.6	1.1	18	18	65					
Chipola: laurel oak-American holly-sabal palm	5.8	1.8	8	5	87	320	13	25	20	6.4

[a] Values in parentheses are corrected for error of overestimation. See Appendix introduction.

Table A-8. Soil analysis for floodplain dominance types, Zone V, alluvial rivers. C=clay, SI=silt, S=sand, O.M.=organic matter.

River floodplain description	pH	% O.M.	Soil components (%)			Macronutrients (ppm)				
			C	SI	S	Ca	K	Mg	Na	P
Ochlockonee: water oak-spruce pine	6.4	6.6	8	12	80					
Apalachicola: water oak-swamp chestnut oak-spruce pine	5.5	3.6	24	22	54	540	30	46	24	5.6
Yellow: swamp chestnut oak-spruce pine	5.1	1.4	9	13	78	136	13	16	17	4.0
Ogeechee: cherrybark oak-hickory	7.1	2.7	25	16	57	226	27	56	25	4.0
Ogeechee: cherrybark oak	6.7	0.8	25	21	54	146	12	22	21	2.8

50272-101

REPORT DOCUMENTATION PAGE

1. REPORT NO.
FWS/OBS-81/37

2.

3. Recipient's Accession No

4. Title and Subtitle
The Ecology of Bottomland Hardwood Swamps of the Southeast:
A Community Profile

5. Report Date
March 1982

6.

7. Author(s) Charles H. Wharton (U. of Georgia), Wiley M. Kitchens (USFWS), Edward C. Pendleton (USFWS), Timothy W. Sipe (Wabash College)

8. Performing Organization Rept. No.

9. Performing Organization Name and Address
Institute of Ecology
University of Georgia
Athens, Georgia 30602

10. Project/Task/Work Unit No.

11. Contract(C) or Grant(G) No.
(C)
(G)

12. Sponsoring Organization Name and Address
U.S. Fish and Wildlife Service
Biological Services Program
Department of the Interior
Washington, DC 20240

13. Type of Report & Period Covered

14.

15. Supplementary Notes

16. Abstract (Limit: 200 words)

This report synthesizes extant literature detailing the ecology of bottomland hardwood swamps in the Southeast. The geographic scope focuses the report to the hardwoods occupying the floodplains of the rivers whose drainages originate in the Appalachian Mountains/Piedmont and Coastal Plain (NC, SC, GA, and FL).

The origin and dynamics of the floodplains are described and related to hydrology and physiographic provinces. Further, the biogeochemistry and interactions between the riverine and floodplain environments are discussed in conjunction with floodplain biology.

Plant and animal community structure and ecological processes (productivity) are detailed and organized by ecological zones.

The final chapter discusses the ecological value of the floodplain ecosystems and the nature of their relationships to adjacent uplands, downstream coastal estuaries and the atmosphere.

17. Document Analysis a. Descriptors
swamps, floodplains, soils, vegetation, water quality

b. Identifiers/Open-Ended Terms
bottomland hardwoods, alluvial rivers, blackwater rivers, coastal plain streams, fauna, ecological zones, couplings, anaerobic gradient, nutrient cycles, flood stress

c. COSATI Field/Group

18. Availability Statement
Unlimited

19. Security Class (This Report)
Unclassified

20. Security Class (This Page)
Unclassified

21. No of Pages
133 + xii

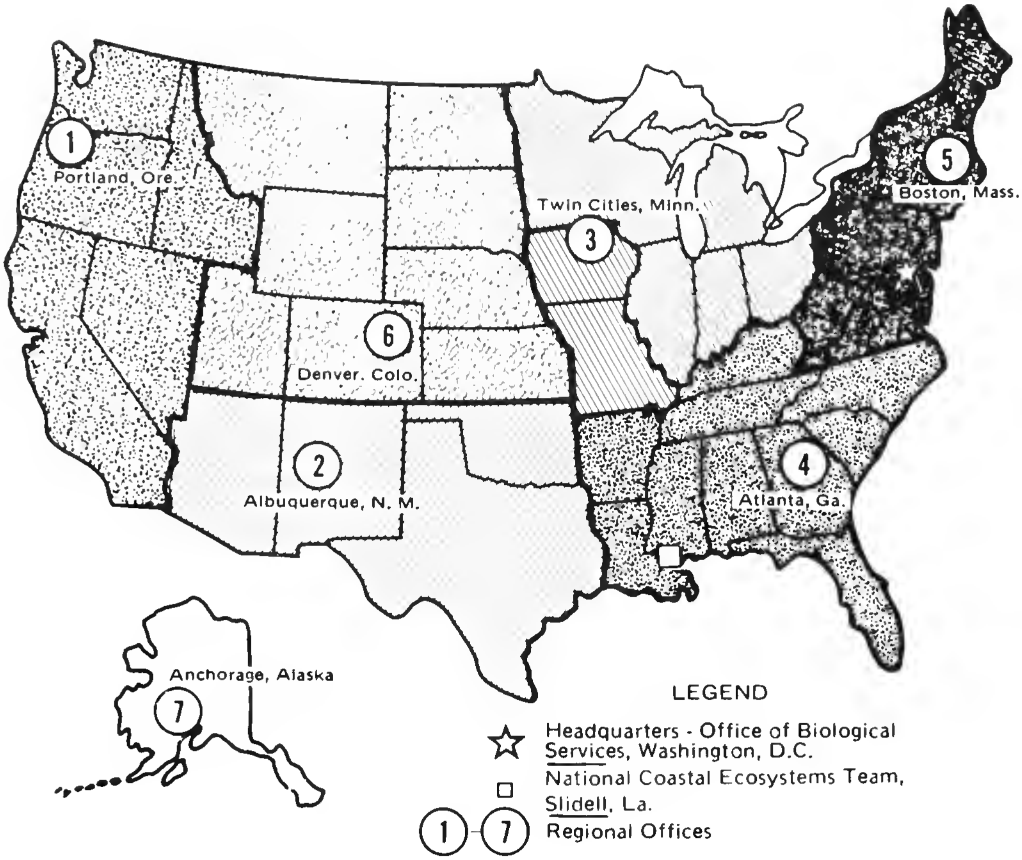
22. Price

(See ANSI-Z39.18)

See Instructions on Reverse

OPTIONAL FORM 272 (4-77)
(Formerly NTIS-35)
Department of Commerce

U.S. GOVERNMENT PRINTING OFFICE: 1982—570-800



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