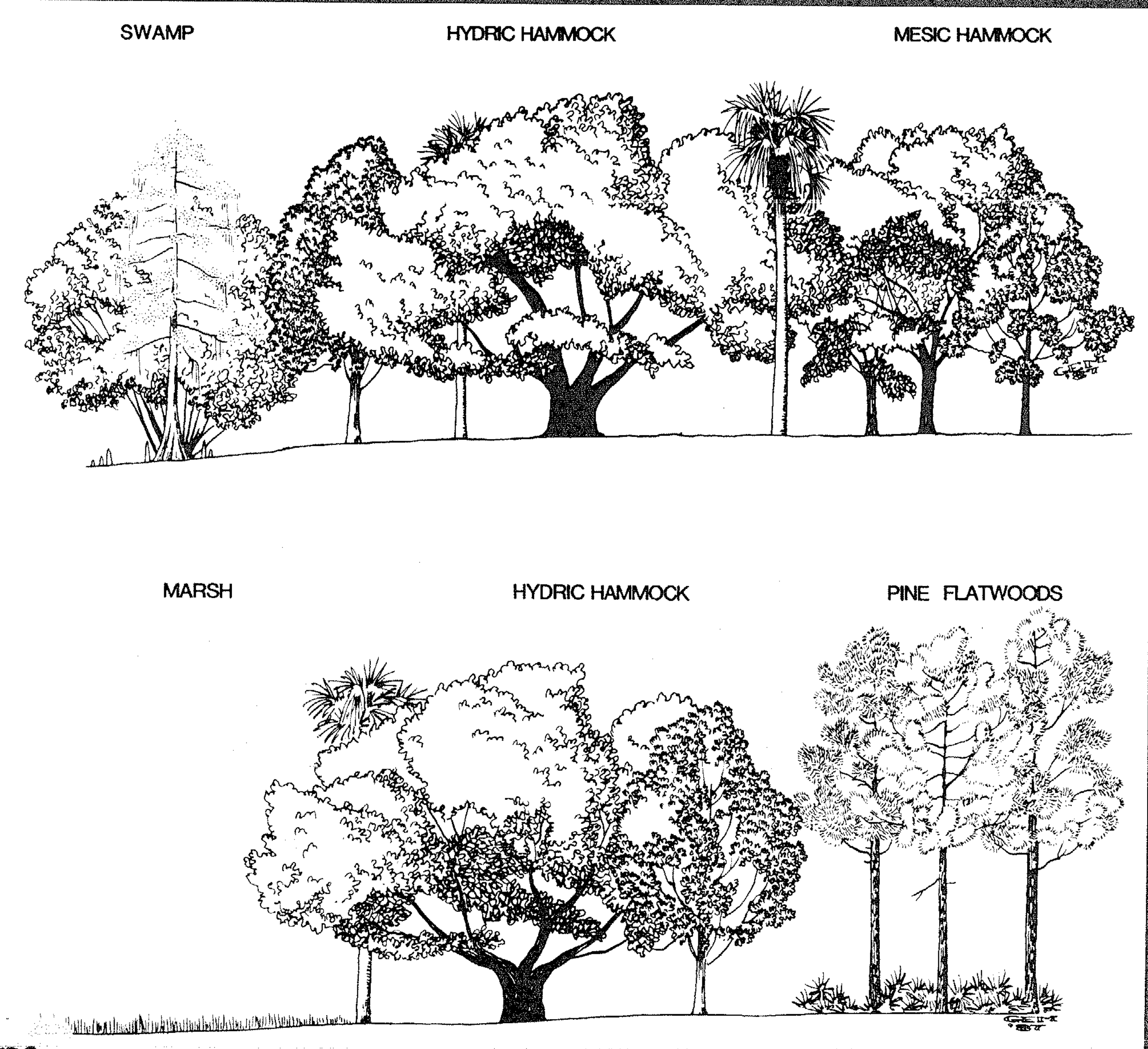
Biological Report 85(7.26)
September 1989

THE ECOLOGY OF HYDRIC HAMMOCKS: A Community Profile



and Wildlife Service
Department of the Interior

Copies of this publication may be obtained from the Publications Unit, U.S. Fish and Wildlife Service, 18th and C Streets, N.W., Mail Stop 1111, Arlington Square Building, Washington, DC 20240, or may be purchased from the National Technical Information Service (NTIS), 5285 Port Royal Road, Springfield, VA 22161.

Biological Report 85(7.26)
September 1989

THE ECOLOGY OF HYDRIC HAMMOCKS: A COMMUNITY PROFILE

by

Susan W. Vince
Stephen R. Humphrey
Robert W. Simons
Florida Museum of Natural History
University of Florida
Gainesville, FL 32611

Project Officer

James A. Allen
National Wetlands Research Center
U.S. Fish and Wildlife Service
1010 Gause Boulevard
Slidell, LA 70458

Performed for
U.S. Department of the Interior
Fish and Wildlife Service
Research and Development
Washington, DC 20240

DISCLAIMER

The opinions and recommendations expressed in this report are those of the authors and do not necessarily reflect the views of the U.S. Fish and Wildlife Service, nor does the mention of trade names constitute endorsement or recommendation for use by the Federal Government.

Library of Congress Cataloging-in-Publication Data

Vince, Susan W.

The ecology of hydric hammocks : a community profile / by Susan W. Vince, Stephen R. Humphrey, Robert W. Simons; project officer, James Allen ; performed for U.S. Department of the Interior, Fish and Wildlife Service, Research and Development.

p. cm. -- (Biological report ; 85 (7.26) (Sept. 1989))

Includes bibliographical references.

Supt. of Docs. no.: I 49.89/2:85(7.26)

1. Wetland ecology--Florida. 2. Forest ecology--Florida. I. Humphrey, Stephen R. II. Simons, Robert W. III. Allen, James A. IV. Title. V. Title: Hydric hammocks. VI. Series: Biological report (Washington, D.C.) ; 85-7.26.

QH105.F6V56 1989 574.5'26325'09759--dc20 89-600215

Suggested citation:

Vince, S.W., S.R. Humphrey, and R.W. Simons. 1989. The ecology of hydric hammocks: a community profile. U.S. Fish Wildl. Serv. Biol. Rep. 85(7.26). 81 pp.

PREFACE

This community profile is one in a series of Fish and Wildlife Service publications compiled to provide a state-of-knowledge synthesis of scientific information and literature on various coastal habitats. The subject of this profile is the hydric hammock, a distinctive type of forested wetland occurring at low elevations along the gulf coast of Florida from Aripeka to St. Marks and at various inland sites in Florida.

Relatively little research has been conducted in hydric hammocks, and no thorough effort has been made previously to define this community. Consequently, no consensus has existed about the extent and nature of this community; some published works and active researchers have differed in their judgments about it; and the entity sometimes is ignored and often is lumped with other types of mixed hardwood forests. The purpose of this profile is to establish or clarify an identification and understanding of the hydric-hammock community. Information for the profile was gathered from published and unpublished literature, from personal communication with many technical experts, and from our own field experience. The profile includes some new data gathered in the field for the purpose of defining this community.

It is hoped that the content and format of the profile will be useful to a broad spectrum of users, including other scientists, students, resource managers and planners, teachers, and interested citizens. The profile includes structural and functional aspects of the community: its physical setting, plant and animal composition and dynamics, interactions of its flora and fauna, and its relationships with other communities.

CONVERSION TABLE

Metric to U.S. Customary

Multiply	By	To Obtain
millimeters (mm)	0.03937	inches
centimeters (cm)	0.3937	inches
meters (m)	3.281	feet
meters (m)	0.5468	fathoms
kilometers (km)	0.6214	statute miles
kilometers (km)	0.5396	nautical miles
square meters (m^2)	10.76	square feet
square kilometers (km^2)	0.3861	square miles
hectares (ha)	2.471	acres
liters (l)	0.2642	gallons
cubic meters (m^3)	35.31	cubic feet
cubic meters ($m^{3)}$	0.0008110	acre-feet
milligrams (mg)	0.00003527	ounces
grams (g)	0.03527	ounces
kilograms (kg)	2.205	pounds
metric tons (t)	2205.0	pounds
metric tons (t)	1.102	short tons
kilocalories (kcal)	3.968	British thermal units
Celsius degrees (°C)	1.8(°C)+32	Fahrenheit degrees

U.S. Customary to Metric

Multiply	By	To Obtain
inches	25.40	millimeters
inches	2.54	centimeters
feet (ft)	0.3048	meters
fathoms	1.829	meters
statute miles (mi)	1.609	kilometers
nautical miles (nmi)	1.852	kilometers
square feet (ft^2)	0.0929	square meters
square miles (mi^2)	2.590	square kilometers
acres	0.4047	hectares
gallons (gal)	3.785	liters
cubic feet (ft^3)	0.02831	cubic meters
acre-feet	1233.0	cubic meters
ounces (oz)	28350.0	milligrams
ounces (oz)	28.35	grams
pounds (lb)	0.4536	kilograms
pounds (lb)	0.00045	metreic tons
short tons (ton)	0.9072	metric tons
British thermal units (Btu)	0.2520	kilocalories
Fahrenheit degrees (°F)	0.5556 (°F-32)	Celsius degrees

CONTENTS

FIGURES

TABLES

ACKNOWLEDGMENTS

We are grateful to G. Ronnie Best, Andre Clewell, Robert Dye, Steve Gatewood, J.D. Slabaugh, Robert Tighe, and Charles Wharton for offering information based on their studies and experience. We thank Karla Brandt, William Buckner, Nancy Szot, Andrew Vince, and Gordon Ward for their assistance in the field and G. Kenneth Scudder for showing us numerous field sites and providing photographs. We appreciate the advice of David L. Auth, Katherine C. Ewel, John A. Fluno, and Paul E. Moler on ways to improve the manuscript.

CHAPTER 1. INTRODUCTION

"Hammock, hommock, or hummock?" queried R. M. Harper in 1905; his answer was one of many attempts by botanists to reduce confusion over the classification of southeastern plant communities. Harper (1905) concluded that a hummock is a geographic feature, a rounded knoll, whereas "hammock" and "hommock" are synonyms for dense, hardwood forests that occur in limited areas amid the wet prairies, marshes, and pine forests of the coastal plain. The etymology of "hammock" and "hommock" is obscure (Oxford English Dictionary 1933). Columbus' sailors learned to use net "hammocks," hanging beds, from Caribbean Indians; perhaps they misapplied the Arawak term, hamacas, intended for the woods in which the sleeping nets were hung. Bartram (1791) and other early expositors of Florida's natural history employed the "hommock" spelling, perhaps in keeping with native pronunciation, but "hammock" became the prevalent form in the writings of the twentieth century.

Hammocks are a small but distinct part of the natural landscape of the Florida peninsula north of Lake Okeechobee. In this region, the uplands are dominated by three fire-adapted communities: (1) a savanna of wiregrass (*Aristida stricta*) and other herbs with an overstory of longleaf pine (*Pinus palustris*) and scattered deciduous oaks on well-drained deep sands; (2) a scrub community consisting of a sand pine (*Pinus clausa*) overstory and dense evergreen understory on deep sands; and (3) pine forests (pine flatwoods) with an understory of saw palmetto (*Serenoa repens*), gallberry (*Ilex glabra*), and other shrubs and herbs on flat, poorly drained sites. Forests of bay trees and evergreen shrubs, called bay swamps or bayheads, occupy depressions on the sides or at the bottom of slopes where soils are kept moist or wet by seepage. Along drainages, in depressions in the uplands, and in other low areas are swamps and marshes. Of lesser extent, and often protected from fire by nearby bodies of water, are the scattered patches of mixed hardwood forest called hammocks (or "southern mixed hardwood forest," Monk 1965).

Some hammocks reside on poorly drained soils or on soils with high water tables, and occasional flooding saturates the soils for a time sufficient to modify plant species composition. These are hydric hammocks. Other names for this wetland forest include "low hammock" (Harper 1915), "wetland hardwood hammock" (Soil Conservation Service 1981), and "lowland oak hammock" (Dunn 1982). Hydric hammocks often have a broad-leaved evergreen appearance and typically contain live and swamp laurel oaks (*Quercus virginiana* and *Quercus laurifolia*), cabbage palm (*Sabal palmetto*), southern red-cedar (*Juniperus silicicola*), sweetgum (*Liquidambar styraciflua*), and hornbeam (*Carpinus caroliniana*). Hydric hammocks are distinguished from the drier mesic hammocks by the absence or scarcity of a number of tree species including pignut hickory (*Carya glabra*), hop hornbeam (*Ostrya virginiana*), winged elm (*Ulmus alata*), and southern magnolia (*Magnolia grandiflora*). While some hydrophytic tree species common to mixed hardwood swamps, such as red maple (*Acer rubrum*) and swamp tupelo (*Nyssa sylvatica* var. *biflora*), are shared by hydric hammocks, others, notably ashes

(*Fraxinus* spp.) and bald cypress (*Taxodium distichum*). are rare. Hydric hammocks frequently are situated on gentle slopes between mesic hammock or pine flatwoods and river swamp, wet prairie, or marsh. The precise boundaries between the communities are elusive, yet a distinct combination of plants, animals, and physical conditions characterize hydric hammocks and make them recognizable in a great variety of settings.

Hydric hammocks are wetlands because they often are saturated with freshwater and are characterized by vegetation that is tolerant of wet soils. The scheme developed by Cowardin *et al.* (1979), and used in the National Wetland Inventory, classifies this community as a palustrine forested wetland with a seasonally flooded water regime. Hydric hammock is one of many types of forested wetlands in Florida (Table 1). The differences in the lengths of the lists and the categories of wetlands identified attest to the variation within and among wetland communities, as well as to the subjectivity inherent in human attempts to impose distinctions upon natural gradients of vegetation. Nevertheless, the three classifications agree that hydric hammocks differ from most other wetlands in their vegetation and hydrology. Swamps of mixed hardwoods or cypress tend to be flooded more frequently and regularly, for a longer period, and to a greater depth than hydric hammocks. Bayheads (also called bay swamps or baygalls) are distinguished by their constant seepage, peat substrate, and abundance of bay trees. River flow influences floodplain and bottomland forests,

Table 1. Classifications of freshwater, forested wetlands in Florida. Communities on the same line are approximately equivalent. In some cases, a class in one list is subdivided into several classes in another list.

Soil Conservation Service (1981)	Florida Natural Areas Inventory (1984)	Wharton *et al.* (1977)
Bottomland hardwoods	Floodplain forest; Floodplain swamp	Alluvial river swamp
Swamp hardwoods		Blackwater river swamp
		Backswamp
		Springrun swamp
	Freshwater tidal swamp	Tidewater swamp
Cypress swamp	Strand swamp	Cypress strand
	Dome	Cypress pond (dome)
	Basin swamp	Gum pond and swamp
		Lake border swamp
Scrub cypress		Dwarf cypress
Shrub bog-bay swamp	Baygall; Bog	Bay swamp; Shrub bog
	Seepage slope	
Pitcher plant bog		Herb bog
		Bog swamp
		Seepage swamp
		South Florida hammock
Wetland hardwood hammock	Hydric hammock	Hydric hammock
Cabbage palm hammock		
	Wet flatwoods	
	Bottomland forest	

whereas hydric hammock is a still-water wetland (Wharton *et al.* 1977). Typically on alluvial floodplains, bottomland hardwood forests contain a number of species that are absent from hydric hammocks, notably overcup oak (*Quercus lyrata*), water hickory (*Carya aquatica*), cottonwood (*Populus heterophylla*), and sycamore (*Platanus occidentalis*).

The most extensive stands of hydric hammock are found in Florida along the Gulf of Mexico from Aripeka in the south to St. Marks in the panhandle (Figure 1). Almost a continuous belt, the hammock forest lies just landward of salt marsh. Another large stand inhabits part of the west bank of the upper St. Johns River and, inland of coastal dunes, a narrower strip of hydric hammock parallels the Atlantic shore of northeastern Florida. Many smaller stands are scattered about, primarily in the northern and central regions of peninsular Florida. Hydric hammocks are scarce in the panhandle west of St. Marks, and their southern limit is subject to debate. Hydric hammocks of cabbage palm, live oak, swamp laurel oak, and red maple to the west and north of Lake Okeechobee were described by R. Harper (1927); probably this is the southern extent of their range (Figure 1). Farther to the west, hydric hammock dominated by

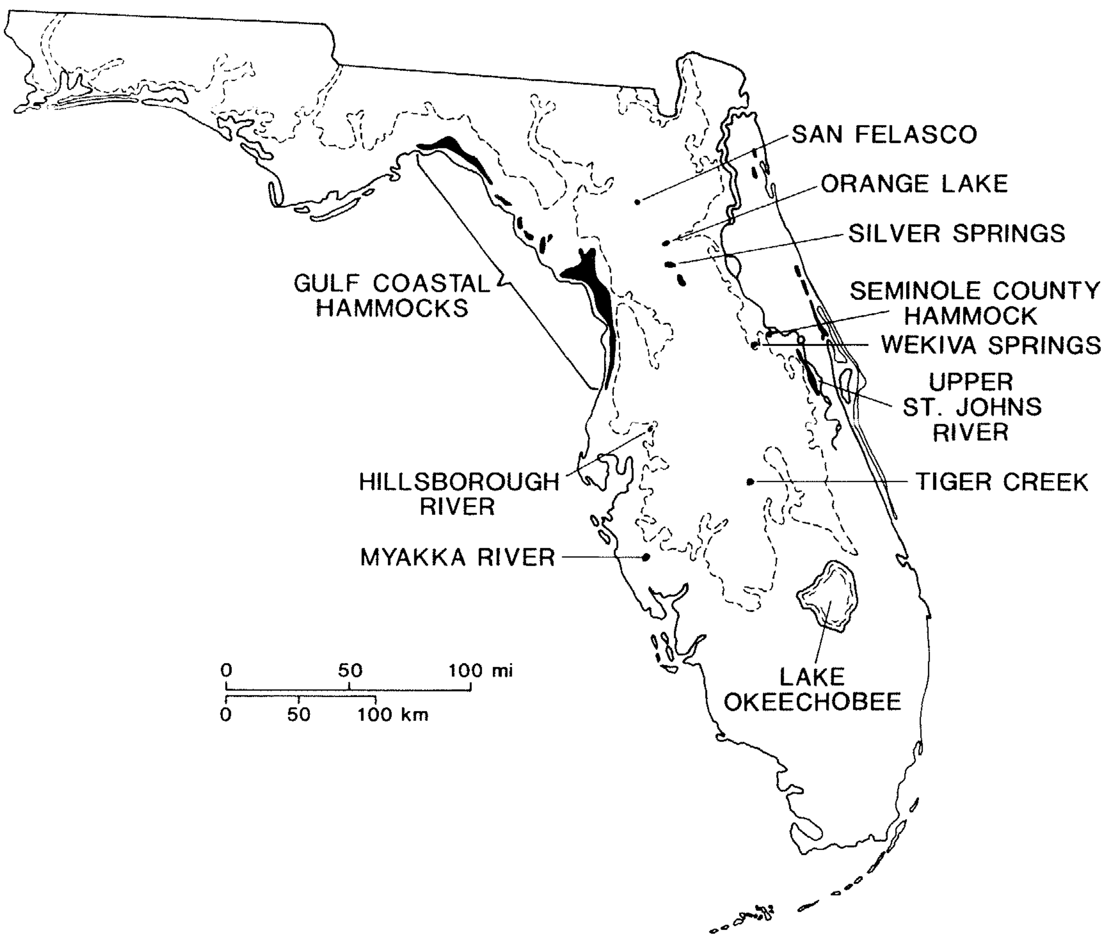


Figure 1. Distribution of hydric hammocks in Florida. Locations of the largest stands and those sampled in the present study are shown. Numerous stands too small to delineate at this scale occur throughout the northern and central sections of the peninsula. Dashed line is the contour of 15-m elevation.

cabbage palm and live oak adjoins the marshes of the Myakka River. We follow the examples of R. Harper (1927) and Davis (1943) in differentiating the temperate-subtropical hydric hammocks from the tropical hammocks or tree islands common to southern Florida. The tropical hammocks feature a diverse assemblage of West Indian, flood-intolerant plants (Olmsted and Loope 1984). They also may inhabit slight mounds within marsh, prairie, and mangrove vegetation, physiographic settings different from those of most hydric hammocks. The Fakahatchee strand in southwestern Florida is difficult to classify because it contains stands of cabbage palm and swamp laurel oak that resemble hydric hammock. However, these forests most likely are transient stages resulting from the harvesting of cypress.

Hydric hammocks seem to be rare outside of Florida. Wharton (1977) noted only small patches of comparable forest in Georgia, mainly in the coastal lowlands near Savannah. Reviews of the vegetation of South Carolina (Barry 1980) and the lowland forests of its northern coastal plain (Jones 1981) included no descriptions of forests similar in vegetation and hydrology to hydric hammocks. Although Harper (1905) reported that hammocks ranged from North Carolina to Florida and Mississippi, the vegetation surveys of Georgia and South Carolina suggest that, beyond Florida, the hammocks are mainly of the drier mesic and xeric types.

All wetlands--forested and nonforested, saltwater and freshwater--covered more than 8.3 million acres of Florida, about 22% of its land area, in 1972-74 (Hampson 1984). Forested wetlands accounted for about 2.1 million ha; of that amount, hydric hammock probably comprised 120,000 to 140,000 ha. Hydric hammock is estimated to cover 80,000 to 100,000 ha at present (Simons *et al*. 1988). A precise determination is not available because the boundaries of hydric hammocks are difficult to delineate on aerial photographs. Neither can data on its extent be extracted from the periodic inventories of southeastern forests (e.g., Bechtold and Knight 1982), because hydric hammock does not correspond to a U.S. Forest Service forest type or physiographic class. However, it is evident that the area of hydric hammock has significantly declined in modern times, due primarily to clearing for agriculture, real estate development, and, especially in the past 20 years, for pine plantations. The management guide that accompanies this profile details the various uses of hydric hammocks, both deliberate and inadvertent alterations of this community, and the impacts on forest structure, wildlife habitat, and hydrology (Simons *et al*. 1988). This community profile summarizes what is known of the ecology of hydric hammocks and includes new data on the variation of plant composition among stands. Since hydric hammocks have been little studied, many inferences are made from similar communities. The scarce scientific attention afforded hydric hammocks in no way reflects their value. The beauty of hydric-hammock forests and their provision of wildlife habitat, timber, and flood control argue for their preservation and sound management.

CHAPTER 2. PHYSICAL SETTING

2.1 CLIMATE

Florida boasts a subtropical climate, but that is technically correct only for the southernmost and coastal portions of the state (Dohrenwend and Harris 1975). Winter temperatures in northern Florida are much lower than in the southern part of the State: mean minimum values are 5 and 16 °C, respectively (Jordan 1984), and extremes in the north range well below freezing. Low-temperature extremes in winter require many plants and animals to overwinter in typical temperate-zone manner. Summer temperatures, influenced by warm, moist air from the Gulf of Mexico and the Atlantic Ocean, are relatively uniform throughout the state. In July the mean daily maximum is about 31 to 33 °C and the mean daily minimum ranges from 22 to 24 °C. The average growing season is 270 days in the north and more than 320 days in the south (Tanner and Smith 1981).

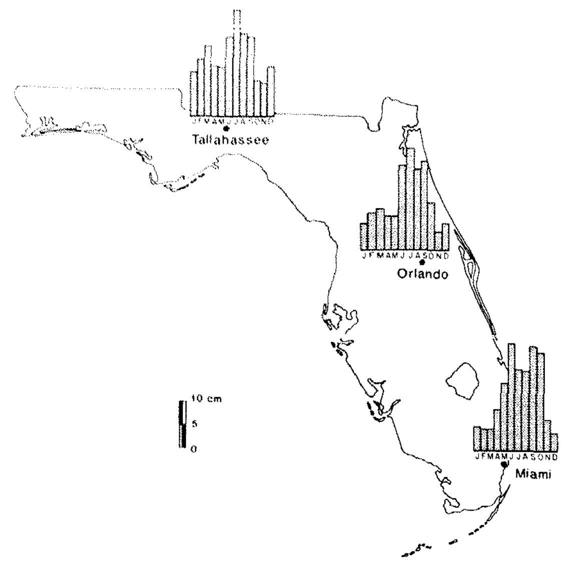


Figure 2. Seasonal distribution of rainfall at three locations in Florida, 1941-70 average (from Jordan 1984).

Rainfall is plentiful everywhere in Florida, averaging between 122 and 152 cm annually (Jordan 1984), but its distribution is highly uneven over the year (Figure 2). Rainfall is at a maximum in summer and a minimum in spring (April-May) and fall (October-November), when conditions become droughty in some years. Southern Florida receives most of its rain in the period from June through September, and its hydric hammocks may flood then. Northern Florida receives an additional pulse of rain in late winter. Because of lower evapotranspiration rates, winter precipitation probably contributes as much or more than summer rain to surface- and groundwater supplies. Hydric hammocks in northern Florida often are flooded at the beginning of the growing season due to the late winter rains. Especially along the gulf coast, hydric hammocks also may flood from hurricanes in late summer and early fall.

Thunderstorms prevail on 70 or more days each year in Florida (Jordan 1984) and bring lightning as well as rain. Bolts of lightning can strike and kill individual trees and ignite fires. Fires are relatively uncommon in hydric hammocks, but their frequent occurrence in some adjacent communities affects the extent and composition of hydric hammocks. Before humans actively suppressed fires and built roads and other barriers to their spread, fires must have burned far more frequently and extensively across the Florida landscape.

2.2 PHYSIOGRAPHY AND GEOLOGY

Florida appears flat and featureless compared with the dramatic landforms of the western United States. All sites are close to the sea horizontally and vertically: no place is more than 120 km from the Atlantic Ocean or the Gulf of Mexico, and Florida's highest point is only 105 m above sea level. Much of the state is elevated 15 m or less (Figure 1). Minor changes in topography--differences on the order of centimeters rather than meters--greatly affect the nature, extent, and distribution of Florida's plant communities.

Florida lies within the Gulf and Atlantic coastal-plain province and contains five major physiographic regions (Figure 3). Finer geomorphic divisions are described by Puri and Vernon (1964) and White (1970). Maximum local relief occurs within the western highlands of the panhandle, where rolling uplands are cut by narrow, steep-walled stream valleys, and is next greatest in the central highlands that run north and south through much of the peninsula. Fringing the entire peninsula and extending to the extreme west of the panhandle, the coastal lowlands have little relief and generally rise slowly via step-like terraces to the central ridges. The land surfaces of the Okeechobee plain of southern Florida and the Big Bend area (northeastern corner of the Gulf of Mexico) are virtually flat.

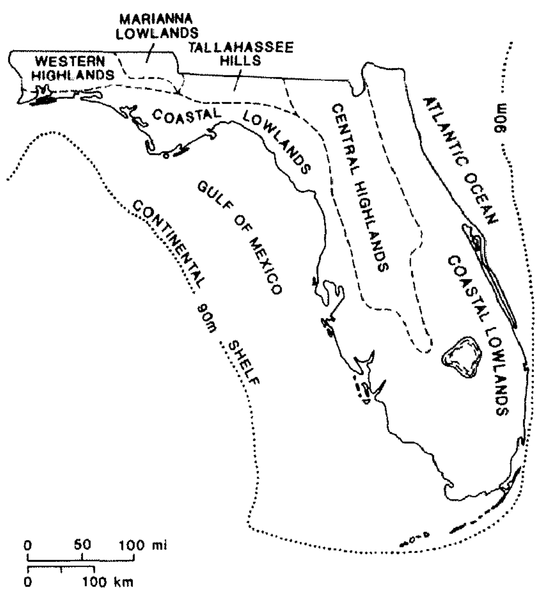


Figure 3. Physiographic regions of Florida. The Floridan Plateau includes Florida and its submerged continental shelves. The edge of the plateau is indicated by the 90 m depth contour (from Cooke 1939).

Florida's topography and physiographic divisions have resulted from the interplay of sediment deposition (mainly marine), erosion, and solution. Since at least the early Cretaceous period, the Florida peninsula has existed as part of the much broader Floridan Plateau, a stable carbonate platform (Puri and Vernon 1964). The relative amounts of land and water on the plateau have varied with fluctuating sea level; at present, the emergent peninsula and the submerged continental shelf that rings the state are roughly equal in area (Figure 3). The Floridan Plateau was formed in warm shallow seas by the deposition of thousands of feet of Cretaceous and Tertiary limestone and dolomite (Figure 4). Some evaporites (e.g., anhydrite) also were deposited, but only small amounts of clastic (sand, silts, clay) sediments accumulated. The deposits amassed atop the coastal-plain foundation of sedimentary and igneous rocks and their thickness and slope were influenced by the Peninsular Arch (Figure 4). Extending down the peninsula from southern Georgia to the southeast, the Arch is Florida's dominant subsurface structure. This deformation probably resulted from crustal stresses that warped the coastal-plain floor during the late Paleocene or early Mesozoic (Applin 1951). In comparison, the overlying carbonate deposits have experienced little deformation. Outcroppings of Eocene and Oligocene limestones indicate the Ocala Uplift in west-central Florida (Figures 4 and

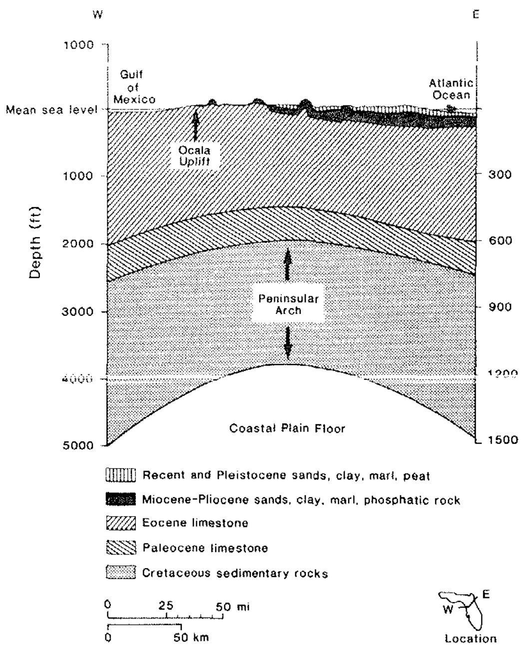


Figure 4. Geologic cross section of peninsular northern Florida. Vertical scale is exaggerated about 160 times (adapted from Faulkner 1973).

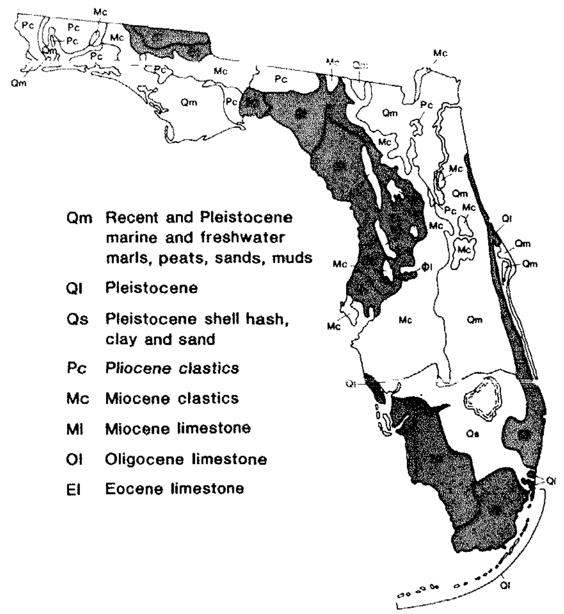


Figure 5. Geologic map of Florida showing dominant rocks at or near the surface. Areas with surface limestone are shaded (adapted from Vernon and Puri 1964; Tanner and Smith 1981).

5), the State's major surficial structure (Vernon 1951).

The beginning of the Miocene period in Florida was marked by a dramatic change in depositional patterns (Puri and Vernon 1964; Winker and Howard 1977; Riggs 1984). A flood of terrigenous sediments began to enter the peninsula from the north; the sands and clays were transported mainly to the east and southeast. Deposition of carbonate sediments, predominantly in southern and eastern Florida, continued intermittently. Phosphorites formed on shallow marine platforms, especially around the Ocala Uplift (Riggs 1984). By the end of the Miocene, a blanket of sand, relatively impermeable clay, and marl covered most of the carbonate plateau. The crest of the Ocala Uplift probably remained above sea level during much of the Miocene and all of the Pliocene, and received no sediment deposits (Vernon 1951). Sand deposition reached its maximum extent during the Pliocene, forming a large beach-ridge plain in the panhandle and parallel shoreline ridges that flanked the sides of the north-south axis of the peninsula (Winker and Howard 1977). Thus, Florida's highlands were born; even today their surface rocks show the dominance of Mio-Pliocene deposits of clastic sediments (Figure 5). The longshore transport of sand in Miocene and more recent times was far greater along the Atlantic coast of the peninsula than on the gulf shore, shown by the significantly thicker strata of Miocene and post-Miocene sediments beneath the eastern half of the peninsula (Figure 4). The surface of the Atlantic coastal lowlands is covered mainly by Pleistocene and Recent sand deposits (Figure 5). In contrast, the coastal lowlands along the Gulf of Mexico, from Pasco County in the south to just past St. Marks in the eastern panhandle, retain Tertiary limestone at or near the surface. Solution of the carbonates has resulted in the development of a karst plain because both the water table and the limestone are at or near the land surface. This is precisely the region where hydric hammocks are most extensive (Figure 1).

Sea-level fluctuations have also greatly influenced Florida's topography. The Mio-Pliocene shoreline ridges are the oldest and highest of a series formed by the regressing ocean. Overall, sea level has dropped during the past 10 to 15 million years, but the process has not been continuous. Reversals of the long-term decline, most evident during the Pleistocene period, occurred when sea level was alternately lowered and raised by the development and subsequent melting of glacial ice in high latitudes. At the height of the Wisconsin glaciation about 17,000 years ago, sea level may have dropped to 130 m below the present mean (Milliman and Emery 1968); during the preceding interglacial period, the ocean rose to a level 8-11 m above the present value. When the sea was stationary for a long period, waves and wind cut seaward-facing escarpments and built dunes and shoreline ridges. Adjacent, shallow ocean floors were eroded, forming nearly level marine terraces that persisted when sea level fell again (Figure 6). The Pamlico marine plain, constructed during the Pleistocene, includes Florida's land surface lying between 3 and 8 m in elevation. Much of its area in the gulf coastal counties of Dixie, Levy, and Citrus is occupied by hydric hammock (Vernon 1951; Puri *et al.* 1967). On the Atlantic side of the peninsula, strips of hydric hammock are found, instead, on the more recent Silver Bluff terrace (U.S. Soil Conservation Service 1980).

The advances and retreats of the sea left their imprints on other features of Florida's environment as well. When the sea was low, especially during Pliocene and Pleistocene times, surface drainage rapidly developed, eroding soft sediments that covered the limestone bedrock (Stringfield and Le Grand 1966; Faulkner 1973). In many places, the limestone became exposed, infiltrated with water, and riddled with solution cavities. Circulation of water in the Tertiary

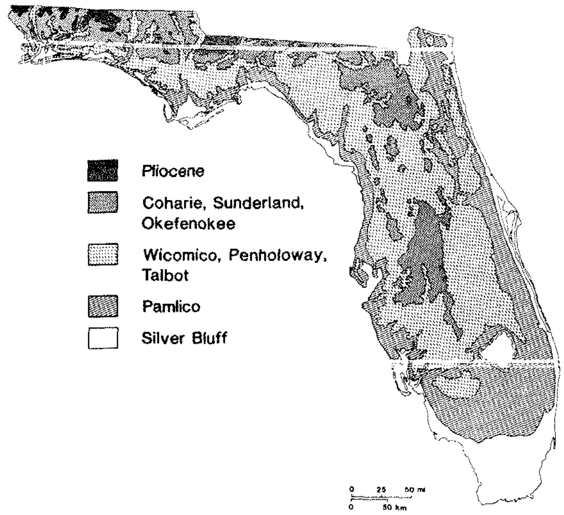


Figure 6. Marine terraces of Florida. The elevations of the terraces are Silver Bluff, <1-3 m; Pamlico, 2-8 m; Wicomico, 8-31 m; Coharie etc., 31-66 m; Pliocene, 66-98 m (adapted from Healy 1975).

limestone accelerated, replacing aboveground flows, promoting even more solution, and becoming the Floridan aquifer, one of the most elaborate ground-water storage and drainage systems in the world (Stringfield and Le Grand 1966).

Low stages of sea level in the Pleistocene were accompanied by declines in the ground-water table (Watts 1971). Because solution of limestone proceeds mainly at and just below the water table (Stringfield and Le Grand 1966), lowered water tables aided growth of the subsurface drainage system. Depressed water tables also meant drier surface terrain. Remains of the mammal assemblage living in the early post-glacial period of the Holocene (about 8,000 BP) suggest that xeric, open woodland and grassland were prevalent (Martin and Webb 1974). Pollen in sediments of Florida and Georgia lakes corroborate the predominance of oak and prairie vegetation at that time of lowered sea level. As the sea, and presumably the water table, rose through the Holocene, pines replaced oaks and modern vegetation associations formed--pine flatwoods, hammocks, cypress swamps, and bayheads (Watts 1980; Watts and Stuiver 1980).

2.3 SOILS

Hydric-hammock soils formed mainly in sandy and loamy marine sediments over soft and hard limestone. A thin veneer of recent and residual weathered sands covers much of the Tertiary limestone in the gulf coastal hammocks. Thompson (1980) measured the depth of the limestone bedrock in six hydric-hammock stands at the northern end of the region; the extent of shallow limestone (less than 90 cm beneath the surface) ranged from 8% to 66% of the area. Outcrops of limestone are common in the gulf coastal hammocks (Figure 7). In contrast, extensive hydric hammocks grow on deep sand along the upper St. Johns River (U.S. Soil Conservation Service 1960). There alkaline materials, such as marl, lie at least 107 cm below the surface. However, the flow of this stretch of the St. Johns River is greatly influenced by the discharge of highly mineralized and saline water (residual sea water trapped in a deep aquifer) from upstream artesian springs (Lichtler *et al.* 1968). High concentrations of calcium and other salts derived from the solution of limestone may become available to the hydric hammocks during high-water periods. Other hydric-hammock soils (e.g., the Tuscawilla and Parkwood series in the Atlantic coastal lowlands) contain shell and limestone fragments rather than solid limestone substratum (U.S. Soil Conservation Service 1974; 1980).

The soils associated with hydric-hammock vegetation are nearly level and somewhat poorly to poorly drained (U.S. Soil Conservation Service 1981).

Figure 7. Limestone outcrop in a gulf coastal hammock.

Sandy surface layers and sandy loam subsoils are common (Table 2). The weakly cemented Bh horizon (hardpan) typical of pine flatwoods is absent. Clayey soils support hydric-hammock vegetation in some areas. Near the Silver Springs run in north-central Florida, hydric hammocks grow on phosphatic clayey soils (loamy fine sands) that contain limestone nodules and shells. Known locally as "gumbo," the soils belong to the Eureka and Paisley series and are poorly drained (U.S. Soil Conservation Service 1979). Shallow limestone bedrock in the gulf coastal hammocks of Levy County, central Florida, is capped by several inches to several feet of sandy loam or sandy clay loam (J. D. Slabaugh, U.S. Department of Agriculture Soil Conservation Service, Bronson, Fla.; pers. comm.). In Waccasassa fine sandy loam (Table 2), permeability is moderately slow to slow. The loamy cap is, in turn, covered by a mantle of sand that gradually thickens with increasing distance from the tidal marshes. Due to the irregular configuration of the bedrock, the sandy mantle also varies in thickness over short distances. Slash pine, *Pinus elliottii*, grows on soils with the sandy mantle; conversely, hydric-hammock vegetation with very few or no slash pines occupies the soils lacking the mantle.

In contrast to the highly acid soils of pine flatwoods and bayheads, hydric-hammock soils generally are slightly acid to mildly alkaline (Tables 2 and 3). Five hydric hammock stands at the northern reach of the gulf coastal hammocks had soil pH values between 5.7 and 6.3, and a sixth had a value of 5.1 (Thompson 1980). The clayey soils that support hydric hammocks near Silver Springs are moderately acid (U.S. Soil Conservation Service 1979). Organic matter content of hydric-hammock soils is variable but often low (Table 2), particularly in relation to the amounts in bayhead soils. More aptly termed "peat," bayhead soil in northwestern and central Florida contains 15%-98% organic matter (Wharton *et al*. 1977; Clewell *et al*. 1982). Thompson (1980) reported organic matter concentrations of 18%-54% in surficial samples of hydric-hammock soils, but the results probably were biased by the inclusion of

Table 2. Characteristics of some soil series associated with hydric-hammock vegetation (from U.S. Soil Conservation Service 1974; 1977; 1980; data for the Waccasassa series are from J. D. Slabaugh, pers. comm.).

Soil series	Depth (cm)	Texture			pH	Organic matter (%)	Cations (Meq./100 g)			
		% sand	% silt	% clay			Ca	Mg	K	Na
Aripeka	0-8	91	7	2	6.2	1.6	3.1	1.6	0.1	0.0
	33-38	70	6	24	7.7	1.0	7.7	1.5	0.2	0.8
Parkwood fine sand	0-18	87	7	6	7.6	5.0	15.8	2.0	0.4	0.7
	28-43	69	7	24	8.3	1.3				
Tuscawilla	0-8	88	11	1	6.0	3.1	9.2	1.0	0.2	0.5
	25-33	82	2	14	6.9	0.9	12.2	0.6	0.1	0.2
Waccasassa	0-5	69	9	22	6.0	5.6	22.5	1.0	0.3	0.1
	5-30	70	8	22	6.4	1.5	9.9	0.5	0.1	0.1

Table 3. Comparison of surface soil characteristics among three hardwood wetland types in Florida (data for mixed hardwood swamps and bayheads from Monk 1966; data for hydric hammocks from this study, Table 2, and Thompson 1980).

Plant community	pH	Cations (Meq./100 g)
Mixed hardwood swamp	3.8-6.8	1.6-134.9
Bayhead	3.6-4.3	0.5-12.7
Hydric hammock	5.1-7.6	6.4-18.9

the surface litter layer. The Aucilla hydric hammock occurs on 15 cm of organic-rich sand (Wharton *et al*. 1977). This wetland adjoins a spring run and shares some features with bayheads: near constant soil saturation and the presence of trees such as sweetbays, *Magnolia virginiana*, that thrive on organic soils. Such hydric hammocks, more constantly wetted than alternately flooded and dried, probably have the highest content of soil organic matter. Nutrient (cation) concentrations are moderate in hydric-hammock soils (Table 2), falling at the low end of the range reported for soils in mixed hardwood swamps (Table 3). Bayhead soils tend to have still lower concentrations, especially of calcium and magnesium (Monk 1966).

2.4 HYDROLOGY

Water is the driving force in wetlands, governing their unique characteristics and functions. Unfortunately, the hydrology of hydric hammocks is poorly known. Insufficient information is available on the nature and rates of hydrological inputs and outputs, and the frequency and duration of flooding, to construct a water budget for a hydric hammock. The following discussion is largely conjectural, based on limited data and personal observations.

Sources of water to hydric hammocks are rainfall, river inundation, overland flow and seepage from adjacent uplands, and discharge from deep aquifers. The relative contributions of these inputs vary among individual hammocks and with season. Wharton *et al*. (1977) distinguished hydric hammocks from floodplain forests (also called bottomland hardwood forests and river swamps) by the source of water: the former are inundated by local water, while the latter are flooded by rivers. However, the demarcation is not as clear-cut as the definitions imply. For example, the major hydrological inputs to the hydric hammocks in the upper St. Johns River basin probably are seepage from upland areas and rainfall. Yet these forests also are flooded occasionally by the river during periods of high water. In the lower basin, narrow strips of hydric hammock lie between river swamp and scrubby pine flatwoods communities (Figure 8). Though Laessle (1942) asserted that the hammock soils were kept saturated by seepage from upslope sandy areas and were not subject to flooding, this description probably is more applicable to nearby bayheads (Figure 8); the hydric hammocks are covered periodically by the St. Johns River. Hydric hammocks also are found on slightly elevated areas adjacent to many spring runs, such as the Homosassa, Wekiva, and Aucilla Rivers, in northern and central Florida. Springs feed the rivers and maintain a relatively constant, high water table through a steady discharge of water from the Floridan aquifer (Figure 9).

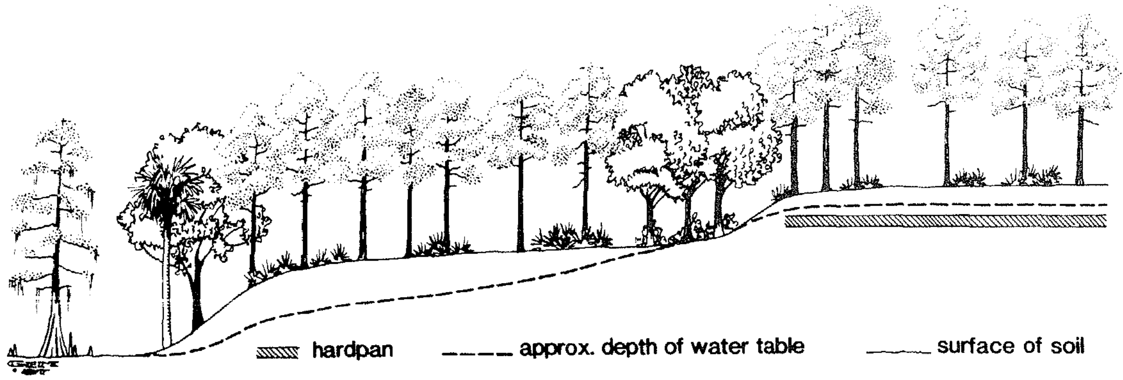


Figure 8. Sequence of plant communities from the lower St. Johns River to upland scrubby flatwoods. In the higher flatwoods, water percolates to the hardpan and moves laterally until it emerges in the bayhead at the base of the slope. Ground water also seeps into the hydric hammock (from Laessle 1942).

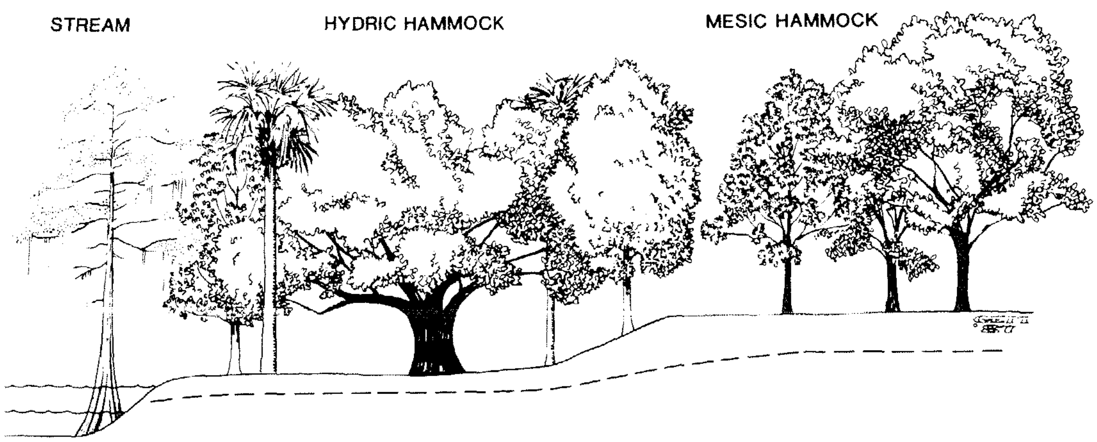


Figure 9. Generalized profile of a spring-fed stream and adjoining hydric hammock. The wavy lines indicate the annual fluctuation in river level. A high water table beneath the hydric hammock is maintained by the spring run (adapted from Wharton *et al.* 1977).

Along the spring runs, hammock vegetation occurs where the water table usually is below the surface and where spring seepage is supplemented by rainfall and runoff from the uplands. These examples suggest that, while considerable variation exists among hydric hammocks, they differ from both bottomland hardwood forests and bayheads in their mixture of water sources. Bottomland hardwood forests receive most of their water from river flow, and bayheads are characterized by ground-water seepage.

Within a hydric hammock, hydrological inputs vary with season. Rainfall is distributed very unevenly throughout the year in Florida, and ground-water level in hydric hammocks fluctuates accordingly. In the Tiger Creek hammock in central Florida, the water table dropped, probably below the root zone, during the period of low rainfall in spring 1986 (Figure 10). Ground-water level reacted quickly to increased rainfall in summer, rising towards the land surface. Evapotranspiration must have removed much of the added water, yet the upward displacement of the water table (46 cm in June) was far greater than the local input of rain (22 cm). The hydric-hammock soils collected runoff and seepage from the uplands, and perhaps river overflow, during the rainy season. In droughty periods, upland seepage probably was the main source of water to the hammock.

A bayhead situated in the Tiger Creek watershed experienced far less change in water-table depth with season than the hydric hammock (Figure 11). Presumably its major source of water, seepage, was more constant than rainfall. Also, the peat soils typical of bayheads hold more water than

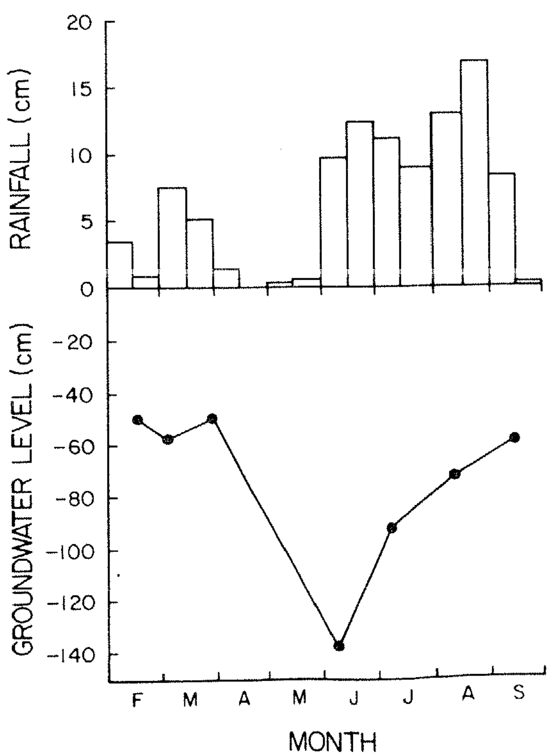


Figure 10. Rainfall and ground-water level in 1986 at Tiger Creek hydric hammock, central Florida. (Ground-water data are from Robert Tighe, Center for Wetlands, University of Florida, Gainesville.)

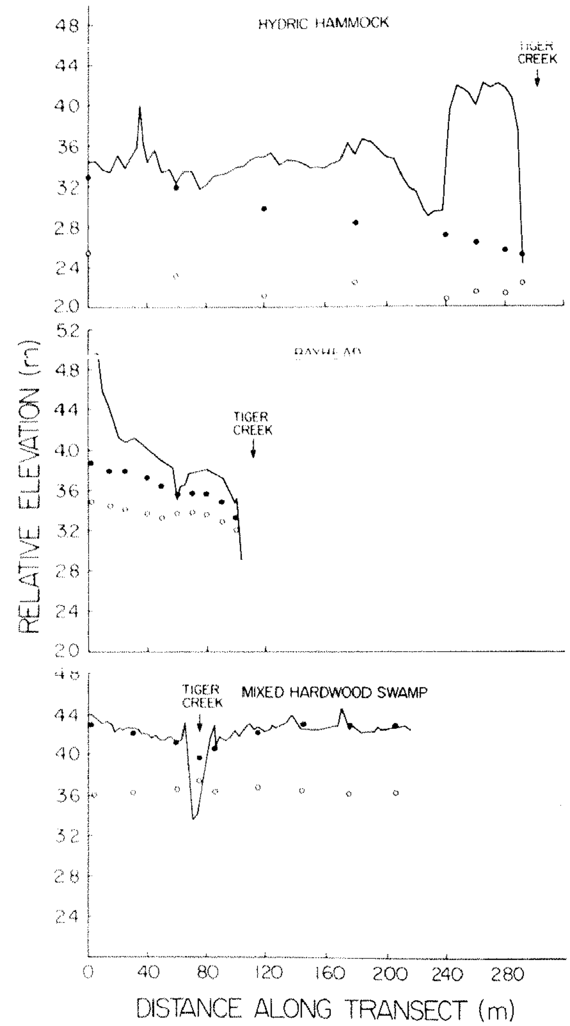


Figure 11. Water-table profiles across three plant communities adjacent to Tiger Creek, showing ground-surface elevation (solid line) and maximum (closed circles) and minimum (open circles) heights of the water table during the period June 1985 to September 1986 (February 1986 to September 1986 for hydric hammock). (Data are from Robert Tighe, Center for Wetlands, University of Florida, Gainesville.)

soils with less organic matter, and they maintain higher water levels due to capillary action.

Water-table depths in a mixed hardwood swamp adjacent to Tiger Creek fluctuated slightly less than in the nearby hammock (Figure 11). The water table sat at or above the surface of most of the swamp at the time of highest ground-water level. In the hydric hammock, the water table remained belowground over the course of study. Although data are lacking, it is generally acknowledged that hydric hammocks flood less frequently, to a shallower depth, and for a shorter period than mixed hardwood swamps (e.g., Brown and Starnes 1983).

Most or all hydric hammocks flood on occasion (Figure 12), but depth, frequency, and duration vary from one hammock to another. Some oaks on the fringe of the Myakka River hammock bear water lines about 1 m above the ground. Extrapolation of high-water lines into hydric hammock in the St. Johns River basin indicates that part of the forest floods annually to a depth of 20-30 cm (G. R. Best and P. Wallace, Center for Wetlands, University of Florida, Gainesville; pers. comm.).

Figure 12. Flooding of hydric hammock along the Myakka River, Sarasota County, Florida. This flood arrived as backwater from the river, three days after rain.

All hydric hammocks feature a high water table seasonally or year-round. For two to six months during most years, the water table is very near (within 30 cm) or above the soil surface of the gulf coastal hammocks in Levy County (J. D. Slabaugh, pers. comm.). Subsurface clay layers probably hold the water table close to the surface of the Aucilla hammock (C. H. Wharton, Institute of Ecology, University of Georgia; pers. comm.). As described previously (Figure 9), spring runs maintain a high water table year-round beneath adjacent hydric hammock. Because the water table is high and the land is flat, hydric-hammock soils quickly become saturated during heavy rains, and excess water collects on the surface. The frequency of inundation may vary from once per decade, especially where hurricanes induce flooding, to once or twice per year.

The rate of water loss from hydric hammock, and so the hydroperiod (duration of flooding), is variable. The gulf coastal hammocks occasionally are flooded by hurricanes and probably drain within several weeks via small creeks. Due to their poorly drained clayey soils, hydric hammocks along the Silver Springs run may remain inundated for two or three months following rains in summer and winter. Sanchez Prairie, a small hydric hammock in north-central Florida, was covered with up to a meter of water for several months in winter and spring 1986 (Figure 13); it also had flooded the previous summer, but for a shorter time. The longer hydroperiod in winter was due both to prolonged rains and to slow losses of water by

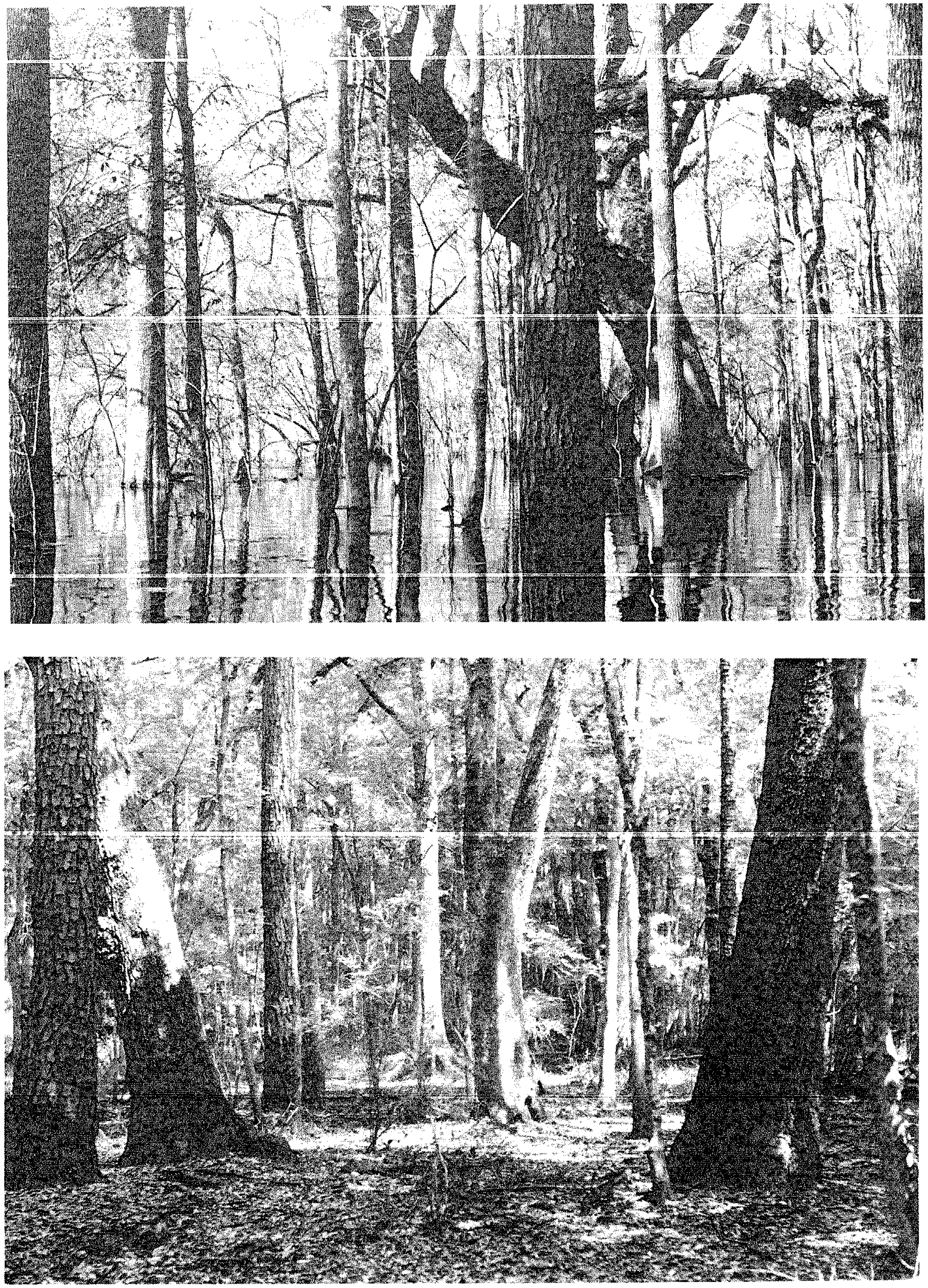


Figure 13. Flooding and drydown of Sanchez Prairie, a small hydric hammock in San Felasco Hammock State Preserve, Alachua County, Florida. Common trees include live and swamp laurel oaks, sweetgum, red maple, and loblolly pine.

evapotranspiration and sink-hole drainage.

Probably the major outputs of water from hydric hammocks are evapotranspiration and surface runoff. Ground-water recharge is unlikely to be significant in most hydric hammocks; recharge is minimal or nonexistent where Tertiary limestone and, therefore, the Floridan aquifer, lie close to or at the surface (Conover *et al.* 1984). Surface water detained in hydric hammocks exits by sheet flow and small streams. Shallow-lying permeable limestone tends to restrict the development of surface drainage, limiting rivers in limestone terrain, such as the Suwannee of northern Florida, to few tributaries (Stringfield and Le Grand 1966). The gulf coastal hammocks are transected by small, poorly-defined streams and drainageways. Discharge of hammock drainage to receiving areas (e.g., the estuaries of the gulf coast) is probably spread over time as well as area. The dense vegetation and flat topography of hydric hammocks probably slows the movement of water and attenuates peak storm flows.

2.5 PHYSICAL CONTROL OF DISTRIBUTION OF HYDRIC HAMMOCKS

A unique combination of physical conditions is required for the existence of hydric hammocks. It includes flat terrain, the influence of limestone, sandy or sandy clay soil, a high water table, and occasional-to-seasonal inundation by a mixture of rainfall, seepage, and, sometimes, river overflow. Southeastern states besides Florida lack the configuration of physical features needed for the development of hydric hammocks. The flat topography of much of peninsular Florida is replaced northward by more varied and hilly terrain. Except in parts of South Carolina's coastal plain, limestone bedrock is buried far beneath the surface (Stringfield and Le Grand 1966). Alluvial rivers originate in the mountains and Piedmont and carry high loads of sediment to the coastal plain. The sediments are deposited in extensive floodplains, providing substrate for bottomland hardwood forests, the predominant type of forested wetland (Wharton *et al.* 1982).

Hydric hammocks are scarce in Florida's panhandle west of St. Marks for the same reasons that they are rare outside of the State. Most of Florida's large river systems and floodplains, and all of the alluvial rivers, are concentrated in that region (Wharton *et al.* 1977). Tributary creeks often occupy deep, narrow ravines that dissect the hilly landscape of the highlands (Clewell 1981). In the flatter coastal lowlands, limestone dips below the surface just west of St. Marks (Figure 5).

The extent and distribution of hydric hammocks within peninsular Florida are greatly influenced by topography and physiography. The largest stands, the gulf coastal hammocks, inhabit ocean-smoothed terraces with limestone and the water table close to the surface. Narrower bands of hydric hammock commonly occur between mixed hardwood swamp and upland forest in northern and central Florida (Figure 14a). Where the slope between lowland and upland increases, hydric hammock thins or disappears (Figure 14b). On the west bank of the upper St. Johns River, a swath of hydric hammock about 50 km long and averaging 1-2 km wide abuts freshwater marsh (Figures 15, 16). In contrast, on the east side of the river, hydric hammock occurs only in small patches among marsh and pine flatwoods communities. The soil types are similar, if not the same (U.S. Soil Conservation Service 1960, 1974), and the elevations of the hammocks with respect to the St. Johns River suggest that the frequency of river flooding is alike. One difference that may account for the more extensive hydric-hammock forest on the west bank of the river is the large number of tributary streams on that side (Figures 15, 16). We speculate that the streams, and their river swamps, promote the establishment of hydric hammocks via their effects on local hydrology and the containment of

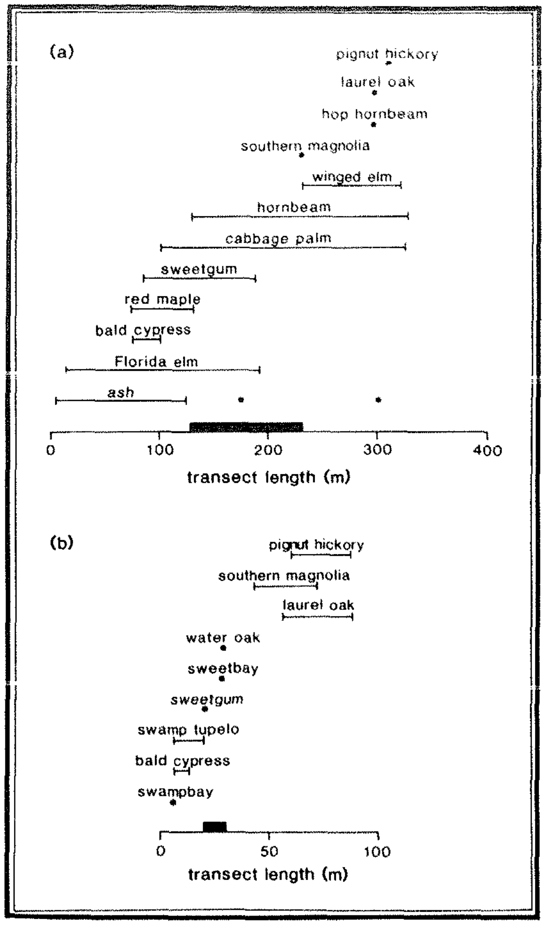


Figure 14. Two vegetation transects from river swamp to upland forest in the Oklawaha River basin, central Florida. Solid bars indicate the approximate width of hydric hammock on a gentle rise (a) and a steeper slope (b). The distributions of various tree species are shown as bracketed lines; asterisks represent single individuals (for scientific names, refer to Table 4; adapted from Florida Game and Fresh Water Fish Commission 1976).

fire. Close study of the local distribution of hydric hammocks would contribute greatly to our understanding of the relationship between physical factors and the development of this community.

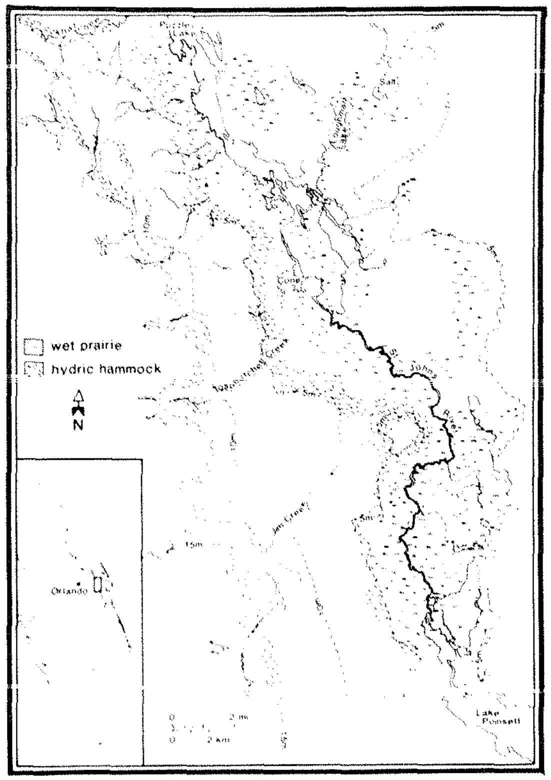


Figure 15. Topographic map of the upper St. Johns River floodplain between Puzzle Lake and Lake Poinsett. The distribution of hydric hammock on the west side of the river is shown. Scattered hydric hammock stands are situated at about 5-m elevation on the east side of the river, but they are too small to delineate on this map.

2.6 SUMMARY

Abiotic characteristics differ from one hammock to another, and some are shared by other plant communities, but their configuration distinguishes hydric hammocks. All hydric hammocks reside on flat terrain, the most extensive stands inhabiting recently exposed, ocean-smoothed terraces. Hydric-hammock soils generally are sandy, low to moderate in organic matter content, and slightly alkaline to mildly acidic; they lack the alluvial sediment on which bottomland hardwoods occur. The influence of limestone is a ubiquitous feature. Limestone

Figure 16. Aerial photograph of hydric hammock on the west bank of the St. Johns River. View is from Puzzle Lake to the west, towards the mouth of the Econlockhatchee River (photo by G. Kenneth Scudder).

bedrock lies close to or at the surface of many hammocks; in others, calcium is provided by flooding or seeping water or by shells and limestone fragments in the soil.

Another characteristic of hydric hammocks, the high water table, is produced in a variety of ways. Exposures of Tertiary limestone in the gulf coastal hammocks bring the Floridan aquifer close to the surface. Hydric hammocks adjacent to spring runs have high water tables due to discharges from deep aquifers. In some hammocks, subsurface clay layers confine seepage and percolating rainfall to shallower strata.

Hydric hammocks receive water from rainfall, river overflow, and seepage and runoff from uplands. The mixture of water sources varies among hammocks, but none is dominated by seepage or riverine floodwater--characteristics of bayheads and bottomland hardwood forests, respectively. At one end of the spectrum, some hydric hammocks are strongly influenced by seepage. The soils are often saturated and relatively high in organic matter. However, ground-water levels in these hammocks are not as constant as in bayheads, and may drop below the root zone for brief periods. In contrast, some hydric hammocks probably experience extremes of flooding and drydown, the former occasioned by periodic river overflow. Most hydric hammocks fall between these two types. Rainfall is the main source of water, but seepage and riverine floodwater also contribute.

Rainfall (acting directly or via overland or river flows) occasionally raises the water table above the surface of hydric hammocks. Flooding frequency may be once per year in southern Florida, timed with the rainy period in summer. Hydric hammocks in northern Florida may flood twice per year, in summer and in winter. Some hydric hammocks are inundated less often, perhaps as infrequently as once per decade, when hurricanes induce flooding. Hydroperiod also varies among hammocks, depending on the rate of evapotranspiration, the extent of drainageways, and soil type. However, both hydroperiod and flooding frequency in hydric hammocks are less than in mixed hardwood swamps.

CHAPTER 3. VEGETATION OF HYDRIC HAMMOCKS

3.1 INTRODUCTION

Set amid the marshes, prairies, and pine flatwoods of Florida, hammocks are conspicuous in their height and density of vegetation. A closed canopy and, often, the dominance of broad-leaved evergreen species (Harper 1915; Laessle 1942; Monk 1965; Greller 1980) create heavy shade within a stand. The lush, jungle-like appearance of some hydric hammocks (Figure 17) belies the largely temperate flora. Many species, including sweetgum, live and swamp laurel oaks, red maple, and sugarberry (*Celtis laevigata*), range far to the north as well as throughout Florida.

Virtually all of the plant species common to hydric hammocks (Table 4) are included in other communities. Only pink-root (*Spigelia loganioides*), an herb, is known to be endemic

Figure 17. A large sweetgum in dense hydric hammock along Tiger Creek, Florida. Rows of holes on the trunk are from repeated feeding by overwintering yellow-bellied sapsuckers.

Table 4. Plants occurring in hydric hammocks[a]. Abundance classes are abundant (A), common (C), occasional (O), and rare (R).

Scientific name	Common name	Abundance
	Woody Plants:	
Acer barbatum	Florida maple	O
Acer negundo	box-elder	R
Acer rubrum	red maple	C
Aesculus pavia	red buckeye	O
Ampelopsis arborea	pepper vine	C
Baccharis halimifolia	groundsel	C
Berchemia scandens	rattan vine	O
Bignonia capreolata	cross vine	O
Bumelia reclinata	buckthorn	O
Callicarpa americana	beautyberry	C
Campsis radicans	trumpet creeper	A
Carpinus caroliniana	hornbeam	A
Carya aquatica	water hickory	R
Carya glabra	pignut hickory	R
Celtis laevigata	sugarberry	O
Cercis canadensis	redbud	R
Cornus foemina	swamp dogwood	C
Crataegus viridis	green haw	O
Crataegus marshallii	parsley haw	O
Decumaria barbara	climbing hydrangea	C
Diospyros virginiana	persimmon	C
Eugenia axillaris	white stopper	O
Forestiera ligustrina	privet	O
Fraxinus caroliniana	pop ash	O
Fraxinus pauciflora	swamp ash	O
Fraxinus pennsylvanica	green ash	C
Gelsemium sempervirens	yellow jessamine	A
Gleditsia aquatica	water-locust	R
Gordonia lasianthus	loblolly-bay	R
Hypericum hypericoides	St. Andrew's-cross	O
Ilex cassine	dahoon	O
Ilex coriacea	big gallberry	O
Ilex decidua	possum-haw	O
Ilex glabra	gallberry	O
Ilex opaca	American holly	O
Ilex vomitoria	yaupon	O
Illicium parviflorum	yellow anise	R
Itea virginica	Virginia-willow	O
Juniperus silicicola	southern red-cedar	A
Liquidambar styraciflua	sweetgum	A
Liriodendron tulipifera	tulip tree	R
Lyonia lucida	fetterbush	O
Magnolia virginiana	sweetbay	C
Morus rubra	red mulberry	O
Myrica cerifera	wax-myrtle	A
Nyssa sylvatica var. *biflora*	swamp tupelo	C
Parthenocissus quinquefolia	Virginia creeper	O
Persea palustris	swampbay	C

(Continued)

Table 4. (Continued).

Scientific name	Common name	Abundance
Pinus elliottii	slash pine	O
Pinus serotina	pond pine	R
Pinus taeda	loblolly pine	A
Quercus laurifolia[b]	swamp laurel oak	A
Quercus michauxii	swamp chestnut oak	O
Quercus nigra	water oak	A
Quercus shumardii	shumard oak	R
Quercus virginiana	live oak	A
Rhaphidophyllum hystrix	needle palm	O
Rubus argutus	highbush blackberry	O
Sabal palmetto	cabbage palm	A
Sabal minor	bluestem palmetto	C
Sageretia minutiflora	climbing buckthorn	R
Sambucus canadensis	elderberry	O
Sebastiana fruticosa	sebastian-bush	O
Serenoa repens	saw palmetto	O
Smilax spp.	greenbriar	A
Tilia caroliniana	basswood	O
Toxicodendron radicans	poison ivy	C
Ulmus alata	winged elm	R
Ulmus americana var. *floridana*	Florida elm	C
Ulmus crassifolia	cedar elm	R
Vaccinium elliottii	mayberry	O
Vaccinium fuscatum	swamp blueberry	O
Viburnum dentatum var. *scabrellum*	southern arrow-wood	O
Viburnum obovatum	walter viburnum	C
Vitis aestivalis	summer grape	A
Vitis rotundifolia	bullace grape	C
	Herbaceous Plants:	
Arisaema triphyllum	jack-in-the-pulpit	O
Arnoglossum diversifolium	indian-plantain	O
Arundinaria gigantea[c]	switch cane	O
Aster spp.	aster	O
Azolla caroliniana	mosquito fern	O
Boehmeria cylindrica	bog hemp	O
Botrychium spp.	grape fern	O
Cacalia suaveolens	indian-plantain	R
Carex spp.	sedges	A
Chasmanthium spp.	spikegrasses	A
Cirsium spp.	thistles	O
Cladium jamaicense	sawgrass	O
Clematis crispa	leather-flower	O
Conyza canadensis	horseweed	O
Cyperus sp.	flat sedge	C
Desmodium spp.	beggarweed	O
Dicondra caroliniensis	pony-foot	O
Dryopteris ludoviciana	Florida shield fern	O
Elephantopus nudatus	purple elephant's-foot	C

(Continued)

Table 4. (Continued).

Scientific name	Common name	Abundance
Elytraria carolinensis	scale-stem	C
Epidendrum conopseum	green-fly orchid	C
Erechtites hieracifolia	fireweed	O
Eupatorium capillifolium	dog-fennel	O
Eupatorium jacundum	ageratina	O
Galactia spp.	milk pea	O
Galium spp.	bedstraw	O
Hydrocotyle spp.	penny-wort	O
Hypoxis leptocarpa	swamp (yellow) star-grass	O
Hyptis alata	musky mint	O
Imperata sp.	cogon grass	R
Juncus spp.	rush	O
Leersia hexandra	southern cut grass	O
Lemna spp.	duckweed	O
Lorinseria areolata	chain fern	O
Melothria pendula	creeping-cucumber	O
Mikania scandens	climbing hempweed	O
Mitchella repens	partridge berry	O
Muhlenbergia schreberi	nimbleweed	O
Oplismenus setarius	woods grass	C
Osmunda cinnamomea	cinnamon fern	O
Panicum commutatum	variable panicum	C
Panicum rigidulum	red-top panicum	O
Panicum spp.	panic grass	C
Paspalum floridanum	Florida paspalum	O
Paspalum spp.	paspalum	O
Phlebodium aureum	goldfoot fern	C
Phyllanthus liebmannianus	pine-wood dainties	R
Polygonum hydropiperoides	mild water-pepper	C
Polypodium polypodioides	resurrection fern	A
Ponthieva racemosa	shadow-witch	O
Psychotria undata	wild coffee	R
Rhynchospora spp.	beak rush	O
Ruellia caroliniensis	wild petunia	O
Salvia lyrata	lyre-leaf sage	O
Salvinia rotundifolia	water spangles	O
Sanicula canadensis	snakeroot	O
Scleria triglomerata	tall nut-grass	O
Senecio glabellus	butterweed	O
Spigelia loganioides	pink-root	R
Spiranthes longilabris	long-lip ladies'-tresses	O
Spirodela spp.	duckweed	O
Stenotaphrum secundatum	St. Augustine grass	O
Sisyrinchium atlanticum	blue-eyed-grass	O
Thelypteris spp.	wood fern	C
Tillandsia bartramii	needle-leaf airplant	C
Tillandsia recurvata	ball moss	A
Tillandsia setacea	needle-leaf airplant	C
Tillandsia usneoides	Spanish moss	C
Trichostema dichotomum	blue curls	O

(Continued)

Table 4. (Concluded).

Scientific name	Common name	Abundance
Urena lobata	caesar weed	O
Verbesina virginica	frostweed	O
Vernonia spp.	ironweed	O
Viola affinis	Florida violet	C
Vittaria lineata	shoestring fern	O
Woodwardia virginica	chain fern	O

[a] The species list was derived by R.W. Simons from numerous field trips and consultations with D.W. Hall (Herbarium, University of Florida), D.B. Ward (Department of Botany, University of Florida), W.S. Judd (Department of Botany, University of Florida), R.K. Godfrey (Department of Biological Sciences, Florida State University), D.K. Younker (Florida Department of Natural Resources), and others; from a review of site surveys done for the Florida Natural Areas Inventory; and from literature (Nash 1895; Harper 1914, 1915; Laessle 1942; Florida Game and Fresh Water Commission 1976; Simons and Hintermister 1984; Simons *et al*. 1984).

[b] Historically, most authors treated laurel oaks as a single species but differed on the appropriate scientific name; the current consensus is to treat the wetland form as swamp laurel (or diamond-leaf) oak, *Q. laurifolia*, and the upland form as laurel oak, *Q. hemisphaerica*. Woolfenden (1967) identified this oak as *Quercus hemisphaerica*, laurel oak. Little (1979) considered laurel oak and swamp laurel oak to be the same species, *Quercus laurifolia*.

[c] Includes *Arundinaria tecta*, sometimes called river cane or bamboo.

(Godfrey 1979). About one-half of the woody plant species listed in Table 4 also are characteristic of southeastern bottomland hardwood forests (Wharton *et al*. 1982). Harper (1915) surveyed the vegetation of a part of central Florida and observed 19 abundant tree species in low (hydric) hammocks; of these, seven also were common in high (mesic) hammock, six occurred frequently in swamps, two were abundant in both high hammock and swamp, and the rest had uncertain identifications. The species lists of hydric hammock, mesic hammock, and mixed hardwood swamp communities greatly overlap, but the relative abundances of the species differ (Florida Game and Fresh Water Fish Commission 1976). Some plant species (e.g., Florida elm) are considerably more common in hydric hammocks than elsewhere. While the plant species of hydric hammocks are not distinctive, their assemblage is.

The canopy of hydric hammocks is about 17-21 m high and is dominated by one or more oak species, cabbage palm, or a combination of these. Also common are sweetgum, loblolly pine, Florida elm, and red maple. Canopy closure is 75%-90%. The trees may be laced with vines--typically trumpet creeper, pepper vine, poison ivy, and wild grape--and epiphytes may be abundant on the tree trunks and limbs. Young canopy trees, especially cabbage palm and sweetgum, may be frequent in the understory, but in some hydric hammocks, hornbeam dominates. Bluestem palmetto, *Smilax* species, or a mixture of shrubs and saplings may occupy the shrub layer. However, cover of the subcanopy and shrub layers is extremely variable; this vegetation often is so sparse that visibility is good at eye level. Likewise, the ground layer may be absent or consist of a dense growth of ferns, sedges, grasses, and *Smilax* species.

Vertical structure and species composition of the vegetation vary considerably from one hydric hammock to another. The objectives of this chapter are to document some of the differences among hydric hammock stands and to suggest factors responsible for this variation. Because hydric hammock vegetation has been little studied, only hypotheses, based upon our observations and relevant data from other communities, are presented. We hope these conjectures will spur further research. Many plant species of hydric hammocks are significant to animals as well as to humans (Simons *et al.* 1988). To preserve and manage these resources, it is necessary to understand the factors responsible for stand composition.

3.2 VEGETATION PATTERNS

Very few quantitative descriptions of hydric-hammock vegetation have been published; these are supplemented by our surveys (Table 5) of stands located throughout the range of hydric hammock in Florida (Figure 1). The

Table 5. Composition of hydric hammock stands (importance values[a] of trees ≥ 10 cm dbh).

	Sites[b]											
Species	ESJ	TOS	MYR	TC	SEM	WEK	NGH	OPH	HR[c]	SS	SFH	IGH
Cabbage palm	80	75	72	56	52	50	43	27	20	26		
Live oak	7	13	23				6	33	13	7	30	3
Swamp laurel oak		2	2	7	6	14	10	8	11	1	22	22
Sweetgum		3		18	11	<1	7	4	10	17	23	17
Florida elm		<1		6	12	5	2	6	2		1	5
Loblolly pine					2		8	1		38	5	4
Red maple				6		14	4				10	5
Hornbeam		2			4		<1	4	29			16
Water oak		<1		<1			2		7	7	2	1
Sweetbay				<1		10	5		1			10
Southern red-cedar	10	4					2			1		
Sugarberry					4			2	4			3
Swamp tupelo				4			2				7	<1
Green ash						1		6			<1	6
Winged elm								6		1		1
Swampbay				<1		2	2					<1
Basswood						2						3
Shumard oak							<1			1		3
Wax-myrtle	3	1					<1					
Persimmon								1			<1	1
Pignut hickory		<1		1				2				
Water-locust			2		<1				2			
Red mulberry		<1		<1			2					
Bald cypress					6		<1					
Water hickory					3							
Swamp ash							2					

(Continued)

Table 5. (Concluded).

Species	Sites[b]											
	ESJ	TOS	MYR	TC	SEM	WEK	NGH	OPH	HR[c]	SS	SFH	IGH
Loblolly-bay						2						
Dahoon				1			<1					
White ash								<1		1		
Southern magnolia							1					
Prunus sp.					1							
Devil wood							1					
Pop ash			1									
Slash pine							<1					
Spruce pine											<1	
Green haw											<1	
Number of species	4	11	5	12	11	10	22	13	16	10	12	17
Trees/ha	1,315	1,051	747	780	565	690	828	411	1,417	496	563	700
Basal area (m^2/ha)	54	71	67	57	29	61	46	42	97	42	49	43
Trees in sample	263	473	224	234	113	69	1,979	113	425	273	197	140

[a] The importance value of a species is one-half the sum of the relative density (percentage of total tree density in the sample) and the relative basal area (percentage total basal area in the sample). Sites were sampled during the present study except where otherwise noted. Ten-meter-wide belt transects were used to sample the trees. The number and length of transects varied with the size and heterogeneity of the hydric hammock.

[b] Site locations are shown on Figure 1. Code for hydric hammocks:
ESJ = east side of upper St. Johns River (Seminole Ranch Recreation Area);
TOS = Tosohatchee State Reserve, west side of upper St. Johns River;
MYR = Myakka River State Park (Shep's Island);
TC = Tiger Creek Nature Preserve;
SEM = Seminole County, northwest corner adjacent to the St. Johns River (data from G. R. Best and P. Wallace, Center For Wetlands, University of Florida, Gainesville);
WEK = Wekiva Springs run, Wekiwa Springs State Park (the spelling of the park differs from that of the spring and river);
NGH = northern gulf coastal hammocks, St. Marks National Wildlife Refuge (Thompson 1980);
OPH = Orange Lake palm hammock, northeastern shore of Orange Lake, Alachua County;
HR = Hillsborough River State Park (Woolfenden 1967);
SS = Silver Springs run (north side), Marion County;
SFH = San Felasco Hammock State Preserve (Sanchez Prairie);
IGH = inland reach of Gulf Hammock (near Otter Creek, Levy County).

[c] All trees, no matter what diameter, were recorded along a 1-m wide, 300-m-long transect. Besides the species for which data on density and diameter were recorded, six additional tree species were noted in the plot (Woolfenden 1967).

sites were not chosen randomly; rather, they were selected to encompass the hydrological and soil conditions associated with this community and to demonstrate the degree of variation in plant composition.

Hydric hammocks range from nearly monospecific stands of cabbage palm (Figure 18) to diverse hardwood forests lacking this species (Figure 19; Table 5). Tree species (woody plants ≥10 cm in diameter at breast height) numbered from 5 to 22 per stand in the present study. Differences in sample size may have accounted for some, but not all, of the variation in species richness among the forests. Hydric hammocks lying between the pine flatwoods and freshwater marshes of the St. Johns (Figure 20) and Myakka (Figure 18) River basins were the least diverse. Not only were few species present--mainly cabbage palm, live oak, and southern red-cedar--but they were very unevenly represented. Hydric hammocks of the Gulf Hammock region (Figure 19), excepting stands immediately adjacent to salt marsh, contained many more species, and the trees were apportioned more evenly among species. Monk and McGinnis (1966) compared diversity of tree species of ten forest community types in north central Florida, including five categories of southern mixed hardwood forest (hammock) delineated by content of soil moisture and soil calcium. The "wet calcareous climax southern mixed hardwoods" type was judged to be the most diverse. Locations of the stands used in the analysis were not given; however, the wet calcareous hardwood stands probably were hydric hammocks similar to the diverse forests we sampled in the inland Gulf Hammock region and in San Felasco Hammock State Preserve (Table 5).

Figure 18. Cabbage palm predominates in hydric hammock along Upper Myakka Lake, Myakka River State Park.

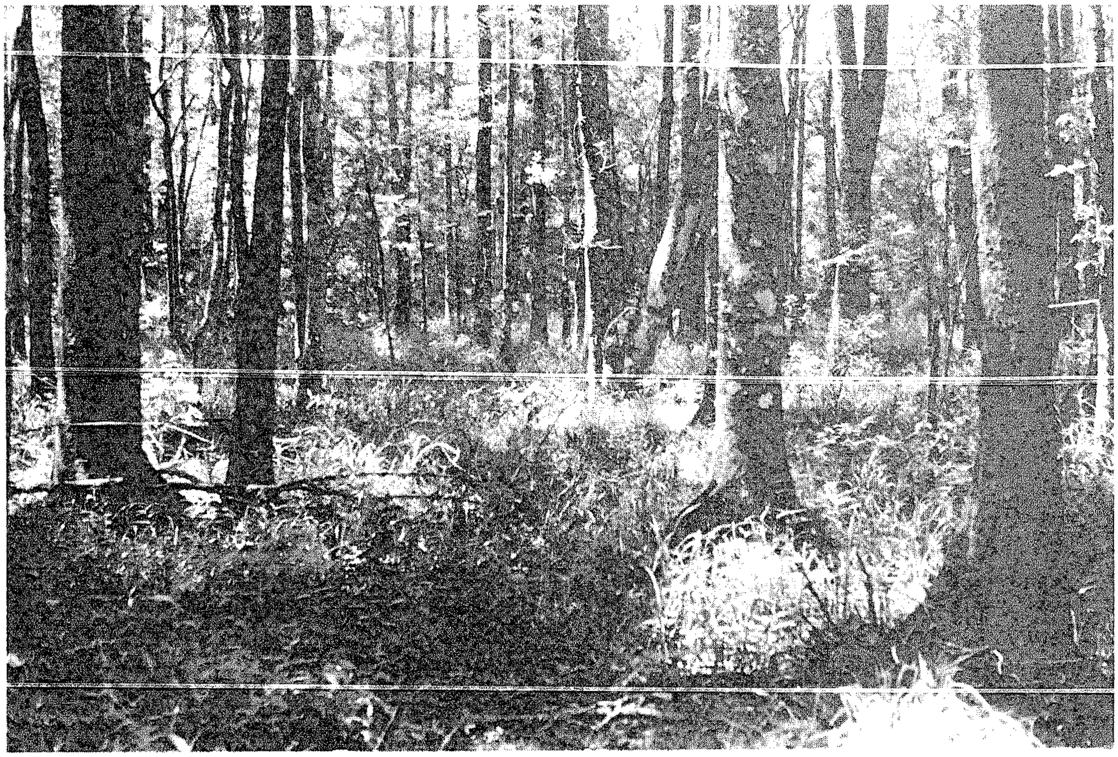


Figure 19. Hydric hammocks at the inland edge of Gulf Hammock feature a diverse mixture of swamp laurel oak, sweetgum, Florida elm, hornbeam, loblolly pine, sweetbay, and red maple. Cabbage palm is absent.

Figure 20. Hydric hammock forest of cabbage palm, live oak, and southern red-cedar adjoins freshwater prairie along the upper St. Johns River.

When present in a hydric hammock, cabbage palm was nearly always the predominant tree (Table 5). *Quercus* species, especially live oak and swamp laurel oak, were always important, and sweetgum and Florida elm often were abundant. Tree species that frequently appeared in moderate numbers included red maple, water oak, sweetbay, sugarberry, swamp tupelo, green ash, and swampbay. Some species were locally abundant, but absent or scarce elsewhere. For example, southern redcedar shared the canopy with cabbage palm and live oak in hydric hammocks along the upper St. Johns River and in the coastal reaches of the gulf coastal hammocks (Figure 21); most other hydric hammocks lacked this species (Table 5). Loblolly pine was far more common in some hydric hammocks than in others and was the dominant species in hydric forest near Silver Springs run (Table 5; Figure 22). There, mature pines averaged 25-35 m in height and towered over a subcanopy of typical hydric-hammock species: cabbage palm, live oak, sweetgum, and water oak (Figure 23). This association of tree species was distinguished from hydric hammock and termed "short-leaf pine and cabbage palmetto bottoms" by Harper (1915) and "loblolly pine hammock" by the Florida Game and Fresh Water Fish Commission (1976). Instead, we consider the Silver Springs forest to be a variant of hydric hammock that contains an unusually high abundance of loblolly pine. Loblolly pine-dominated hammock is very extensive in the Silver Springs region, and it also occurs in small patches within many large hydric hammocks.

Some tree species are characteristic, although infrequent, members of

Figure 21. Coastal hydric hammock where it adjoins salt marsh, Gulf Hammock, Levy County. The canopy consists entirely of cabbage palm, southern red-cedar, and live oak.

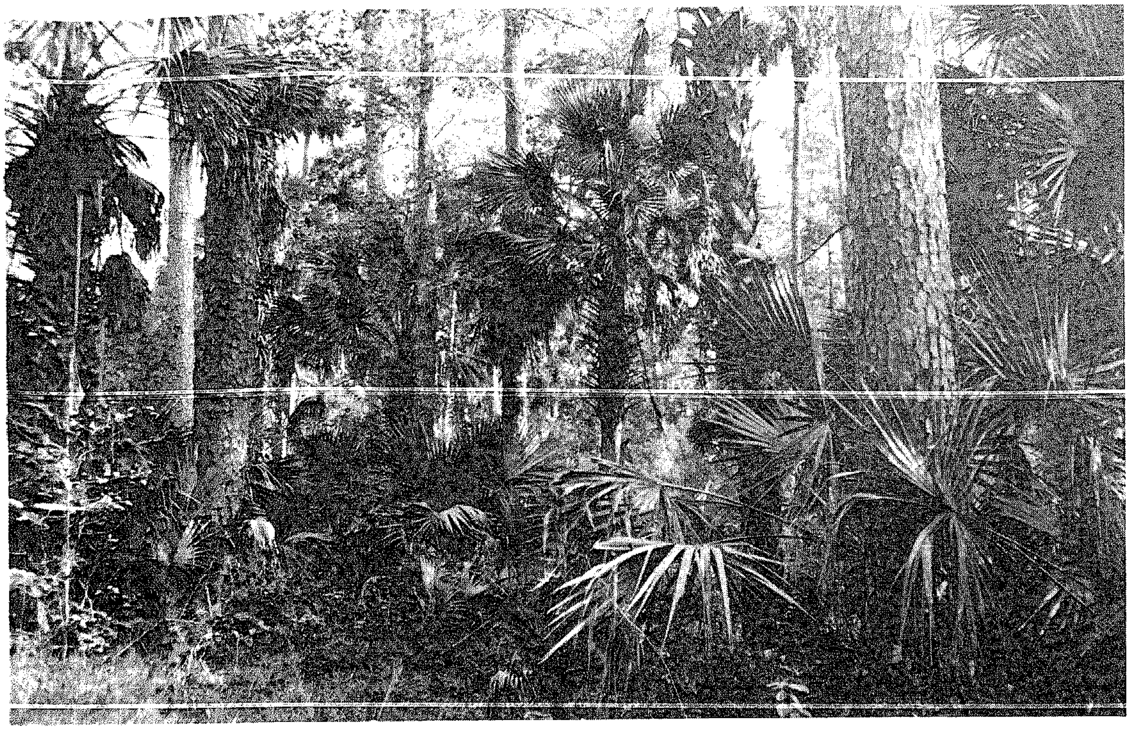


Figure 22. Loblolly pine hydric hammock, Silver Springs, Marion County.

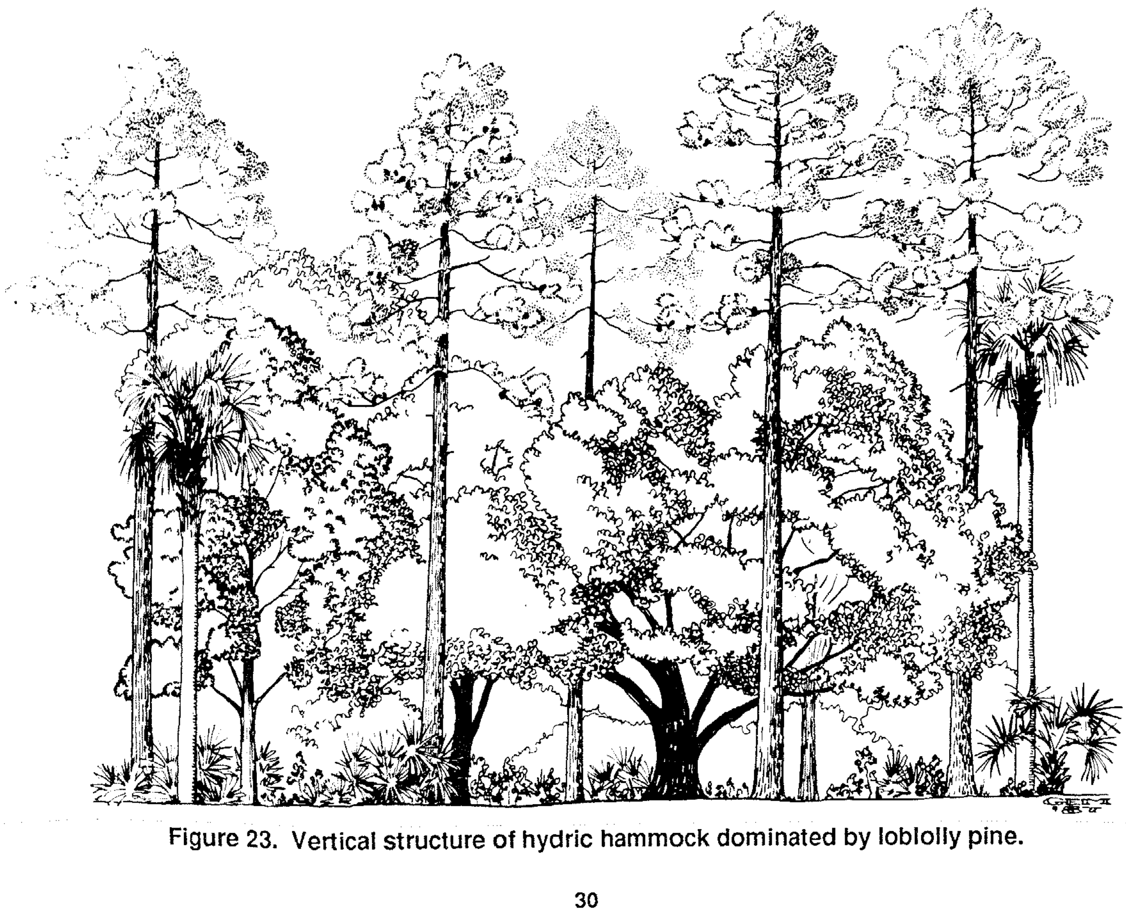


Figure 23. Vertical structure of hydric hammock dominated by loblolly pine.

hydric hammock forests. These species include persimmon and red mulberry, and their apparent absence from some stands in this study probably was due to insufficient sample size (Table 5). Two species not included in the samples, but observed in a few hydric hammocks, were cedar elm and swamp chestnut oak.

A number of species are rare in hydric hammocks; they are virtually restricted to other communities. Bald cypress and loblolly-bay, characteristic of mixed hardwood swamps and bayheads respectively, are examples. The hydric hammock along Wekiva Spring run (Figure 24) contained a scattering of loblolly-bay; it also differed from the remaining stands in its high proportions of red maple and sweetbay and in the absence of live oak (Table 5). This wetland forest was intermediate in composition between "typical" hydric hammock (dominated by cabbage palm, oaks, sweetgum, and Florida elm) and bayhead. The latter forest chiefly consists of loblolly-bay, sweetbay, and swampbay, with smaller amounts of red maple and swamp tupelo (Monk 1966).

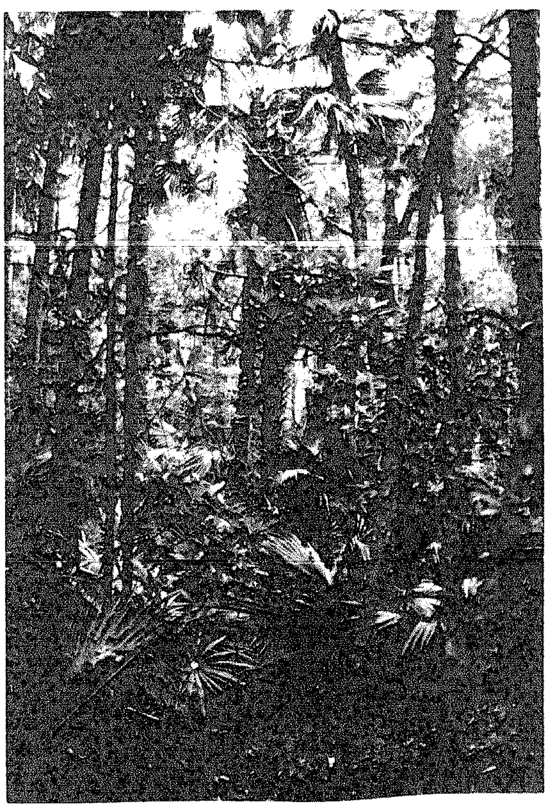


Figure 24. A hydric hammock strongly affected by seepage, Wekiva Springs, Seminole County.

The understory and ground vegetation in hydric hammocks are more variable in composition and abundance than are the trees. Woody plants of two size classes, 2.5-10 cm dbh and ≥10 cm dbh, were sampled in two hydric hammocks, one in Seminole County and the other on the northern gulf coast (Figure 25). These hammocks resembled each other far more in the types and relative abundances of their trees than in the mixtures of their shrubs and saplings. Cabbage palm dominated, and swamp laurel oak, sweetgum, Florida elm, and loblolly pine were common trees in both forests. Sweetgum was an important sapling in both hydric hammocks, but swampbay and swamp ash saplings codominated in the northern gulf hammock, whereas swamp laurel oak, red maple, and hornbeam saplings were abundant in the Seminole County hammock.

Within each of the sampled hammocks, the smaller-size class nearly equaled the larger in the density of stems (about 760 per ha), but species composition differed greatly. Most striking was the near absence of cabbage palm in the smaller size-class. Although stems 2.5-10 cm dbh are usually classified as understory and those greater than 10 cm dbh are considered to be in the canopy, this is not correct for cabbage palms. Their trunks are produced full size in the apical bud (generally 10 cm or more in diameter) and increase in height only. Therefore, essentially all cabbage palms were recorded in the tree category, even though they may have ranged from 1.4 m to canopy height. In some of the hydric hammocks we visited, such as Myakka River (Figure 18), Silver Springs (Figure 22), and Wekiva Springs (Figure 24), cabbage palms formed a dense understory as well as a significant part of the canopy.

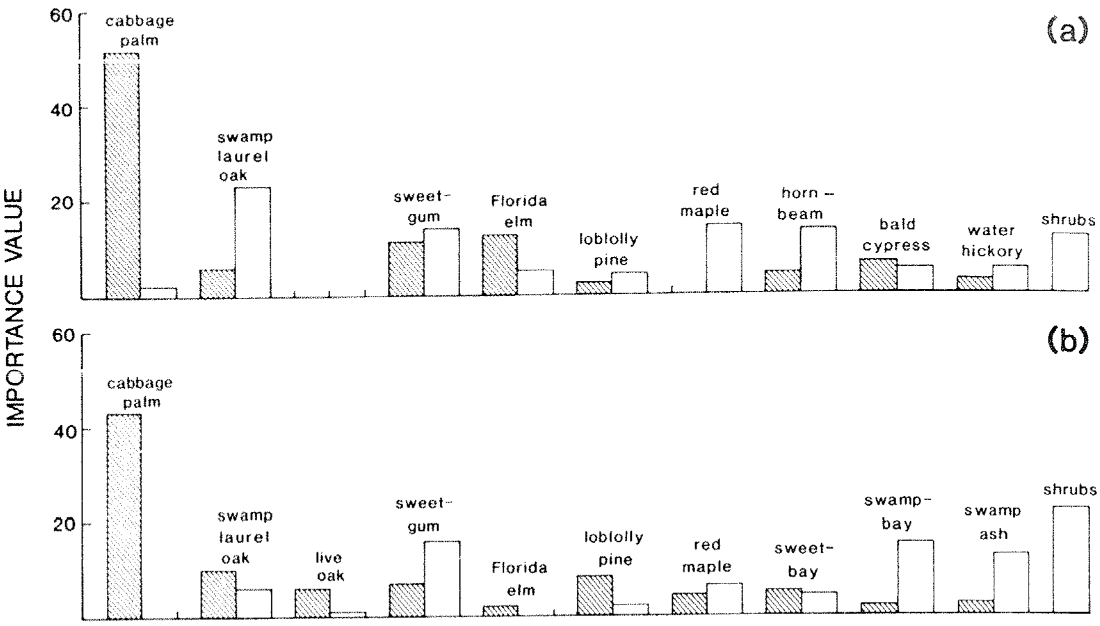


Figure 25. Species composition of common trees (>10 cm dbh; hatched bars) and shrubs and saplings (2.5-10 dbh; open bars) in two hydric hammocks: (a) Seminole County (data from G. R. Best and P. Wallace, Center for Wetlands, University of Florida); (b) northern gulf coastal hammock (Thompson 1980). Importance values (defined in Table 5) were calculated for each size-class within a hammock. Species with importance values of 5 or less in both tree and sapling classes were omitted.

Tree saplings dominated the 2.5-10 cm dbh size class in hydric hammocks of Seminole County and the northern gulf coast (Figure 25); shrubs accounted for less than 20% of the basal area. With the exception of cabbage palm, all tree species were represented in the smaller-sized category. The converse was not true: red maple saplings were abundant in the Seminole County hammock, but mature trees of that species were absent. In the same forest, swamp laurel oak, sweetgum, and loblolly pine had higher importance values as saplings than as trees. Apparently the canopy contained gaps that promoted colonization of these shade-intolerant species (Putnam *et al*. 1960).

Hornbeam and swampbay were more important as "saplings" than as "trees," because they attain maturity at a small size (Figure 25). Hornbeam was an abundant member of the subcanopy of the Seminole County hammock, the Orange Lake palm hammock, and the inland reach of Gulf Hammock, and it must have dominated this stratum in the Hillsborough River hydric hammock (Table 5). However, this species was scarce in the northern gulf coastal hammock (Thompson 1980) and non-existent in many of the hydric hammocks that we visited, including Silver Springs, Wekiva Springs, Myakka River, and Sanchez Prairie (in San Felasco Hammock State Preserve). Hornbeam's absence from the last forest is puzzling, since the species is common in surrounding mesic hammock.

Yaupon, wax-myrtle, and dahoon were the most common shrubs on the northern gulf coast (Thompson 1980), whereas swamp dogwood and wax-myrtle were the only shrubs sampled in the Seminole County hydric hammock (G. R. Best and P. Wallace, pers. comm.). Wax-myrtle was the most frequent shrub in the hydric hammocks that we surveyed. Few shrub species occurred regularly, and several were restricted to one or a few hammocks. Blue-stem palmetto appeared in several stands within the Silver Springs hydric hammock. Needle palm was present only at Wekiva Springs and Tiger Creek. The drier parts of the Sanchez Prairie hydric hammock featured blueberry bushes (*Vaccinium* spp.), but the wetter areas had no shrubs. Among the hydric hammocks we visited, shrub vegetation was densest at Wekiva Springs.

Hydric hammocks with a high abundance of cabbage palm, such as Tosohatchee and Myakka River (Table 5), generally had few plants in the shrub layer, except for very young palms, and no ground vegetation (Figure 18). The extent of the ground layer was extremely variable both among and within the remaining forests. In the Silver Springs hydric hammock, dense patches of spikegrasses (*Chasmanthium* spp.) inhabited clearings. Vegetation, mainly grasses and ferns, covered from 74% to 96% of the ground in six stands at the northern end of the Gulf Hammock region (Thompson 1980). The plants were present in slightly open areas and absent from low, wet places, suggesting that they were limited by low light and extended flooding. Herbaceous vegetation was most lush and diverse in the Tiger Creek, Silver Springs, and inland Gulf Hammock forests. In those hydric hammocks, a profusion of ferns, grasses, sedges, and herbs covered the ground (Figure 19).

The largest contiguous stand of hydric hammock, known locally as Gulf Hammock, comprises the section of gulf coastal hammock between the Suwannee and Withlacoochee Rivers. Originally covering more than 40,000 ha, Gulf Hammock has been reduced by clearing for pine plantations and agriculture (Simons *et al.* 1988). Gulf Hammock is highly diverse, encompassing most of the variation in structure and composition found among hydric hammocks. Few hammocks have such a complete set of the more common plant species, nor of the rare ones, such as cedar elm, American plum, pink-root, pine-wood dainties, and the two indian plantains *Cacalia suaveolens* and *Arnoglossum diversifolium*.

The interface of salt marsh and Gulf Hammock forest (Figure 26) is very irregular. Many islands of hammock are found in the marsh, and the marsh extends into the forest along tidal creeks, sometimes for considerable distances. In most places along the boundary, the forest begins abruptly with a dense, 12- 15-meter-tall stand of cabbage palm, live oak, southern red-cedar, and occasionally water locust. Loblolly pine sometimes occurs at the forest edge, and in a few areas of coastal Gulf Hammock, it dominates the forest, often in association with a dense ground cover of St. Augustine

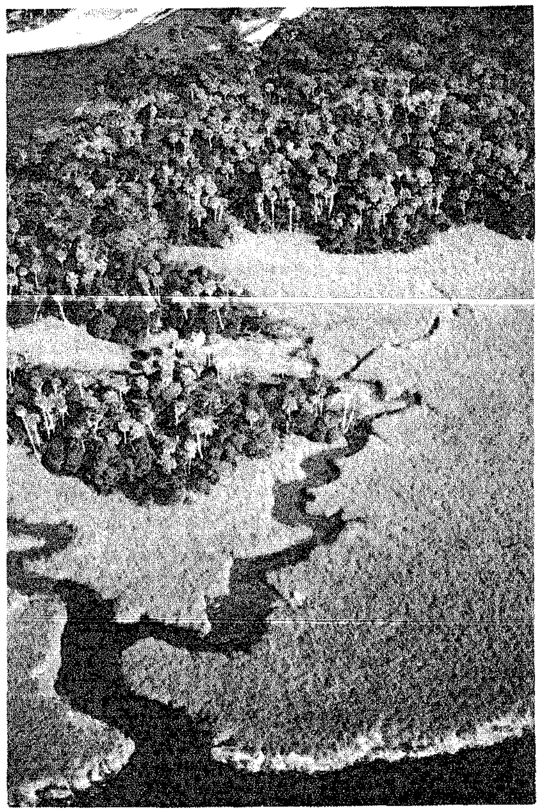


Figure 26. Edge of hydric hammock and salt marsh in Gulf Hammock, along the Gulf of Mexico near the Withlacoochee River, Citrus County, Florida.

grass. Salt-tolerant shrubs such as *Iva frutescens* (marsh elder), *Lycium carolinianum* (Christmasberry), and *Baccharis angustifolia*, *B. glomerulifolia*, and *B. halimifolia* (saltbushes) are abundant at the forest edge in some locations. Vines are rare at the edge, and both vines and shrubs are scarce in the forest interior until at least 1 km inland. The ground cover is very sparse. This coastal part of Gulf Hammock is quite similar to the hydric hammocks bordering the marshes along the St. Johns and Myakka Rivers.

With increasing distance from the salt marsh, cabbage palm, live oak, and southern red-cedar decline and hardwoods increase in dominance. Beginning at about 2 km inland, Gulf Hammock is divisible into three main vegetation types. Swamps of bald cypress, red maple, swamp tupelo, and green ash occur in low areas and along the poorly defined creek drainages. Forests that might be considered either mesic or hydric hammock occupy slightly elevated ridges. The overstory contains swamp chestnut, Shumard, live, laurel, and water oaks, plus sweetgum, southern magnolia, sugarberry, winged elm, Florida elm, Florida maple, loblolly pine, southern red-cedar, pignut hickory, persimmon, red mulberry, and basswood. The understory and ground cover also are diverse. The third type of vegetation, the majority of Gulf Hammock, is between these two "extremes" in species composition and is clearly hydric hammock.

This major hydric hammock (Figure 19) consists mainly of swamp laurel oak and sweetgum in combination with live oak, water oak, loblolly pine, Florida elm, basswood, persimmon, red maple, sweetbay, sugarberry, and cabbage palm. The average height of the dominant canopy trees is about 30 m, with scattered loblolly pines emerging 3-6 m above the canopy. The scattered live oaks are by far the largest trees, averaging about twice the trunk diameter and crown spread of the other canopy tree species. The ground at the bases of these big live oaks often is raised by the root system to form a mound. This microtopography is particularly well suited for the establishment of magnolias, and, in conjunction with the spreading crown of the live oak, for the growth of several species of vines (bullace and summer grape, pepper vine, rattan vine, and climbing buckthorn). A subcanopy dominated by hornbeam, wax-myrtle, swamp dogwood, and various tree saplings often is well developed. The ground layer commonly is a dense mixture of grasses, sedges, and ferns, but in wet areas the cover is mostly leaf litter with only a scattering of herbaceous plants.

Patches of hydric hammock dominated by loblolly pine are found within Gulf Hammock. Some of these are natural and others are the result of human activity. Some of the higher ridges were cleared for farming long ago, apparently by German immigrants, and then abandoned. Now stands of large loblolly pines, locally known as "German Islands", cover the old fields. A modern activity with similar results is the clearcutting of extensive areas of Gulf Hammock followed by the planting of loblolly pine.

Gulf Hammock and its surroundings are very flat, with one exception. Old sand dunes covered with sand pine scrub vegetation are found on the north side, just inland from Cedar Key. A mixture of swamp and hydric hammock occurs adjacent to the dunes, but both of these types are somewhat different in composition than elsewhere in Gulf Hammock, presumably due to the continuous supply of water seeping out of the dunes and to the thicker layer of organic muck. Swamp tupelo, the dominant tree or codominant with green ash, is much more abundant than in other swamps of the region. The hydric hammock also is different in its abundance of needle palm, which is quite scarce elsewhere in Gulf Hammock. This part of Gulf Hammock is most similar to the hydric hammocks at Wekiva Springs, Mormon Branch Botanical Area in the Ocala National Forest, and Tiger Creek.

Gulf Hammock is replaced abruptly at its inland edge by pine flatwoods. However, strips of hydric hammock extend inland along streams such as Rocky Creek, Otter Creek (inland Gulf Hammock site, Table 5), and the Waccasassa River, and these forests gradually become less diverse. Cedar elm and American plum do not occur within these inland strips. Other trees that disappear, roughly in order of disappearance, are red buckeye, water locust, Florida maple, Shumard oak, swamp chestnut oak, cabbage palm, winged elm, sugarberry, basswood, and, finally, loblolly pine. The hydric hammocks farthest inland along the streams consist mainly of swamp laurel oak, sweetgum, red maple, sweetbay, and Florida elm; occasional species include live oak, persimmon, swampbay, dahoon, and slash pine. Wax-myrtle is an abundant shrub. This forest is most similar to other hydric hammocks found adjacent to flatwoods and to sandhill streams such as Tiger Creek.

3.3 SOURCES OF VARIATION

Complex interacting factors probably influence the species composition of hydric hammock and distinguish it from other communities. We propose that the geographical location of a stand, the hydrological regime, edaphic conditions, and fire frequency and intensity are the major determinants of the structure of hydric hammock. Disturbances other than fire and flooding, both natural and human, also may greatly alter the forest's diversity and biomass.

3.3.1 Geography

Plant species whose geographical distributions completely include that of hydric hammock may be characteristic components of this community throughout its range. Live oak, swamp laurel oak, red maple, and many other species that occur in hydric hammocks (Table 4) range throughout Florida (Little 1978); the absence of any of these species from a particular stand is due to factors such as hydrological conditions, soil type, and fire. However, a number of species have restricted geographic distributions that preclude their presence in some hydric hammocks. Absence of such characteristic but not ubiquitous species may cause doubt about the classification of a stand of forest unless a complex model is kept in mind.

Temperate species dominate the flora of hydric hammocks but have various southward limits to their distributions (Figure 27). The ranges of two abundant species, sweetgum and loblolly pine, do not extend south of central Florida. A number of less common trees, including green ash, Shumard oak, swamp chestnut oak, cedar elm, and winged elm, are restricted to northern Florida. So too are some occasional shrubs and herbs: buckthorn, green haw, red buckeye, and switch cane. The depauperate flora of hydric hammock in Myakka River State Park (Table 5) may result, at least partly, from its location south of the ranges of many species common to hydric hammocks.

A few species are found only in a small number of hydric hammocks be-

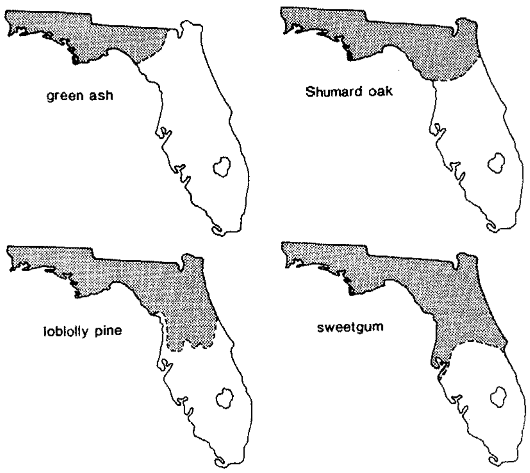


Figure 27. Natural ranges in Florida of four species of trees common to hydric hammock (from Little 1978). The range of green ash actually extends southeastward at least to Wekiva Springs, Orange County.

cause they are tropical plants confined mostly to south Florida. None occur in abundance and only one, white stopper, is a tree. Isolated populations of this species occur north of Lake Okeechobee (Little 1978); one is present in hydric hammock in Tosohatchee State Reserve. The geographical distributions of several herbaceous plants common to hydric hammocks, including goldfoot fern and wild coffee, extend north from the Caribbean to central Florida.

A striking example of the influence of a species' range on the composition of hydric hammock is cabbage palm, the predominant tree species in many hydric hammocks. From North Carolina to northern Florida and west across the panhandle, this species is essentially restricted to the coast (Figure 28). South of a line from about Cedar Key on the gulf coast to St. Augustine on the Atlantic, cabbage palm ranges across Florida's peninsula. North of this line, a few interior populations are scattered along rivers. Hydric hammocks in the northern region, for example in San Felasco Hammock State Preserve (Table 5), lack cabbage palm. The inland Gulf Hammock site that we sampled (Table 5) is situated at the edge of cabbage palm's coastal range. Cabbage palm was absent from much of the forest, but it was common, especially in the understory, in some parts.

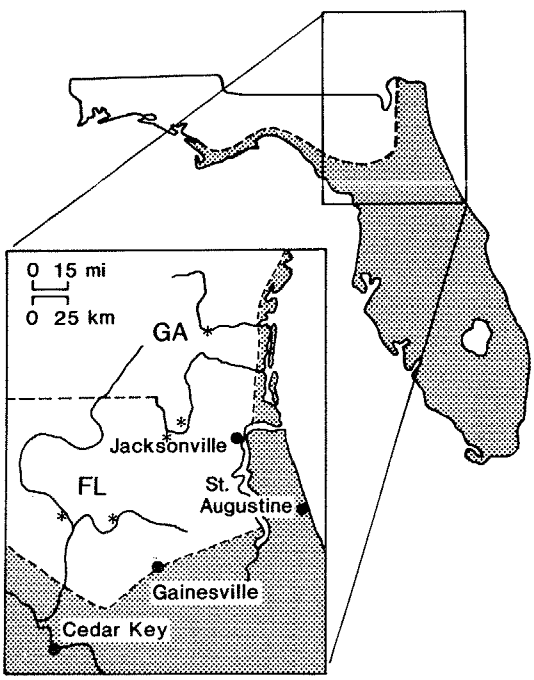


Figure 28. Distribution of cabbage palm in Florida (from Little 1978). Asterisks on the inset map indicate isolated populations of cabbage palm outside of its continuous range (from Brown 1973).

3.3.2 Hydrology

Numerous studies have demonstrated or inferred that patterns of vegetation in southern forested wetlands are strongly influenced by flooding (Bedinger 1978; Huffman and Forsythe 1981; Wharton *et al.* 1982; Leitman *et al.* 1983). Frequency, duration, depth, and timing of flooding are factors that affect the species composition of a forested wetland. The effects of flooding on these communities are mediated by physical and chemical changes in the soils and varying responses to the alterations by plant species.

The nature and extent of the physical and chemical processes that follow soil inundation largely depend on the duration of submergence and on soil properties (Ponnamperuma 1984). When a soil is flooded or saturated, gas exchange between the soil and air is greatly restricted. The slowing of gas diffusion is particularly great in soils with high clay content. Oxygen supply to the soil is drastically cut, and roots and microorganisms deplete the oxygen in the soil water very rapidly. Gases produced by soil metabolism (e.g., carbon dioxide) accumulate. Anaerobic conditions induce a number of chemical changes in the soil, many of which are detrimental to plant growth. Nitrate is replaced by ammonium, often less preferred for uptake and assimilation by plant species. Oxidized forms of iron, manganese, and sulfur are reduced to potentially toxic forms, including sulfides. Ethanol, another potential toxin, is a by-product of anaerobic respiration in most plant roots.

A sequence of changes in plant metabolism and physiological processes follow the onset of anaerobiosis in waterlogged soils (Kozlowski 1984*a*, *b*). Decreased water adsorption and closure of the stomata result in a slowed rate of photosynthesis. Root permeability is reduced, affecting the movement of ions including nutrients. Leaf chlorosis and abscission, and retarded plant growth (especially height-growth) follow. Morphological changes, such as the formation of aerenchyma tissue and the growth of adventitious roots, may take place. If flooding is prolonged, the plant dies. Flood-tolerant plants, characteristic of wetlands, possess a variety of morphological and physiological adaptations (reviewed in Hook and Crawford 1978) that avoid or mitigate flooding stresses. These adaptations commonly facilite oxygen flux to the roots and enhance the ability of plant roots to respire anaerobically without harmful effects.

Plant responses to flooding are strongly influenced by the duration, timing, and depth of inundation, but the condition of the floodwater also is significant. Flowing water is better tolerated than standing water, presumably because of the higher concentrations of dissolved oxygen in the former. The effects of flood duration are clear from the preceding paragraph; changes in plant physiology become progressively more severe with increased period of anaerobiosis. The adverse effects of flooding are exacerbated during the growing season when oxygen demands are greatest. On the other hand, flooding during the dormant season has relatively little impact on the physiology and survival of most tree species (Gill 1970). Depth of inundation is critical to plant survival because oxygen diffusion to the roots is greatly slowed by passage through water. Water depth with respect to plant height also affects plant response to flooding. Most Shumard oak and sweetgum seedlings survived 60 days when flooded only to the root collar (Hosner and Boyce 1962), but all died after 20 days of complete submersion (Hosner 1960). Water deep enough to cover most of the plant decreases light intensity and interferes with stomatal function.

The ability to withstand flooding varies among plant species, sometimes among populations, and with plant age and plant size (Whitlow and Harris 1979). Most assessments of the relative tolerance of woody plants to flooding are based on the results of experimental inundation of seedlings and reservoir flooding of established forests. Results of studies examining the responses of wetland hardwood trees were summarized by Gill (1970), Teskey and Hinckley (1977), Whitlow and Harris (1979), and McKnight *et al.* (1981). Some tree species common to hydric hammocks were included. Care must be taken in applying the results of these tests to interpretations of natural communities. Reservoir flooding is considerably less erratic than natural flooding and, in nature, numerous factors interact with inundation to influence vegetation patterns. Nevertheless, some conclusions from studies of flood tolerance help in explaining plant distributions within and among hydric hammocks.

McKnight *et al.* (1981) assigned southern bottomland trees to four tolerance classes that varied in two regards: length of time during the growing season that the species can withstand flooded or saturated soils, and the extent of anatomical and physiological adaptations. Only one common hydric-hammock species, swamp tupelo, was considered to be tolerant. This species can survive long periods of inundation, and its seeds remain viable when submerged in water for months. Most hydric-hammock species (red maple, sweetgum, Florida elm, loblolly pine, sweetbay, persimmon, green ash, swamp laurel oak) are moderately tolerant of flooding; some morphological or physiological adaptations to flooding may develop (Figure 29), but they do not enable the tree to survive flooding for an entire growing season. Mature trees of six hydric-hammock species remained healthy when flooded for 17%-37% of the growing season; red maple withstood the longest flooding period, and

Figure 29. Buttressed roots of trees in hydric hammock, including Florida elm (in front) and swamp laurel oak (behind), provide stability in wet soils and perhaps help to aerate the root system.

water oak and loblolly pine the shortest (Teskey and Hinckley 1977). Weakly tolerant species include hornbeam, red mulberry, and several oaks--water, live, Shumard, and swamp chestnut. According to McKnight *et al.* (1981), these species are able to survive only short hydroperiods (a few days to a few weeks), and they possess no apparent adaptations to inundation. Seedlings of hydric hammock trees generally are more sensitive to flooding than mature trees, although, as noted above, mortality rates depend on the degree of submersion. In short-term experiments, death usually occurred within 20-30 days when the seedlings were completely submersed and within 0.5-3 months when they were partially flooded; no seedlings died when soils were saturated (Teskey and Hinckley 1977).

The damming of the Oklawaha River in north-central Florida provided additional evidence of the differences in flood tolerance among hydric-hammock species (Harms *et al.* 1980). Probably most of the flooded forest was river swamp dominated by deciduous hardwoods, but part was hydric hammock (Florida Game and Fresh Water Fish Commission 1976). Three years after dam construction, tree mortality was strongly correlated with water depth, with essentially 100% mortality at average depths of 1.2 m or more, decreasing as prevailing water level declined. However, mortality rates significantly varied among tree species. Bald cypress, swamp tupelo, and cabbage palm were the most tolerant of flooding. Cabbage palms were scattered throughout the forest and few died, irrespective of water depth. They accounted for most of the survivors in the most deeply flooded section of the forest. Two species of oaks, water and swamp laurel, were least tolerant of flooding, surviving only at the shallowest depths (about the same and 20 cm deeper than control sites outside of the reservoir). No doubt water levels in the reservoir fluctuated less than in the undisturbed floodplain and long periods of continuous flooding occurred. However, data on the water elevation of the lake indicate that prolonged drydowns also took place (Harms *et al.* 1980).

The placement of tree species within hydric hammocks probably reflects in large part their relative tolerances to flooding. Species abundances along a presumed flooding gradient in Sanchez Prairie, San Felasco Hammock State Preserve, are shown in Figure 30. At the time of sampling, shallow water stood at the beginning of the transect, in a stand dominated by bald cypress and red maple. The transect climbed a very gentle slope into hydric hammock, ending where live and water oaks dominated and the ground was quite dry. Bald cypress was restricted to the wetter (swamp) end of

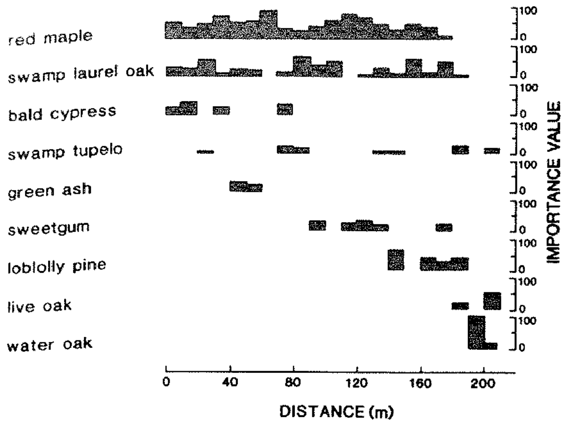


Figure 30. Distribution of tree species along a presumed flooding gradient in Sanchez Prairie, San Felasco Hammock State Preserve. The transect begins in swamp conditions (left) and ends in drier hydric hammock (right).

the gradient, and live oak, water oak, and loblolly pine to the drier (hammock) part. Red maple and swamp laurel oak ranged almost throughout the swamp/hammock transect. Swamp laurel oak was replaced by live and water oaks at the dry end of the gradient, their relative positions in accordance with flooding tolerances inferred from the studies cited above.

Another study transected 200 m of a Seminole County hydric hammock (Table 5), descending 80 cm to river swamp dominated by bald cypress, red maple, and sweetgum (G. R. Best and P. Wallace, pers. comm.). The first half of the transect probably was slightly above average high water, whereas the second half was slightly below. Sugarberry and hornbeam were found only in the first 50 m, while swamp laurel oak extended to 150 m. Sweetgum and Florida elm ranged throughout the two hammock sections and into the swamp. Cabbage palm, the dominant tree in this hydric hammock (Table 5), also was ubiquitous, but its abundance declined greatly in the swamp. Red maple occurred in swamp and hydric hammock, though only as saplings in the latter. No live oaks were sampled, although this species was observed in other, generally drier, parts of the hydric hammock.

Some of the differences in composition of plant species among hydric hammocks also result from variable patterns of flooding and drydown. The Seminole County hammock probably floods more often and for a longer period than many others, which was reflected in the vegetation: Florida elm was an important species, red maple and swamp laurel oak saplings were abundant, no live oaks were sampled, and bald cypresses were present. Live oak was absent also from the Wekiva Springs and Tiger Creek hydric hammocks, both of which receive seepage and are almost always moist. In the Wekiva Springs hammock, a high water table is maintained by discharge from a deep aquifer (see Figure 9). The hydrology of the Tiger Creek hammock was discussed in Chapter 2.4; this wetland receives upland seepage depending on the season. The profusion of shrubs and ground vegetation in these hammocks probably results from the nearly constant saturation of the soils. The influence of seepage on plant species composition is especially pronounced at Wekiva Springs. Numerous bay trees, needle palm, and cinnamon fern make this forest intermediate in composition between "typical" hydric hammock and bayhead, a community characterized by constant seepage. The relatively constant moisture regime of the Wekiva Springs and Tiger Creek hammocks contrasts with the extremes of drought and flooding experienced by other hydric hammocks. We suggest that hydric hammocks low in species diversity and dominated by cabbage palm and live oak exist where long, dry periods are interrupted by occasional episodes of flooding. Examples are found in the upper St. Johns and Myakka River basins, where river overflow only sporadically floods the hydric hammocks. In Myakka River State Park, hydric hammock has expanded into freshwater marsh during the past 30 years (Figure 31), at the same time as river levels have declined due to upstream diversions (Robert Dye, Florida Department of Natural Resources; pers. comm.). Whereas the old part of the hydric

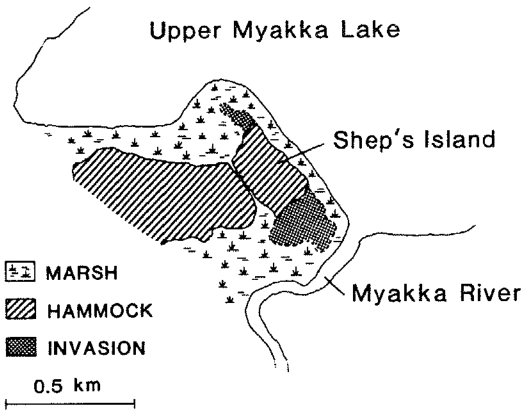


Figure 31. Expansion of hydric hammock (Shep's Island) into freshwater marsh, Myakka River State Park, 1957-1972.

hammock is composed of cabbage palm and live oak, the invading vegetation consists of swamp laurel oak, Florida elm, and, closer to the marsh, water locust and pop ash (Figure 32). Severe flooding during the summer of 1982 killed many swamp laurel oaks, but not live oaks. Apparently the latter species can withstand occasional deep inundation but not prolonged soil saturation.

3.3.3 Edaphic Conditions

Particular plant species may be favored in some hydric hammocks because of variations in soil type. Changes in soil texture, organic content, and pH can markedly affect drainage and nutrient availability, and therefore, the growth and survival of various species. For example, sweetbay generally is associated with organic soils (Wharton *et al.* 1976). This species is most abundant in hydric hammocks such as the Wekiva Springs forest (Table 5) that are characterized by seepage of ground water and organic-rich soils. The abundance of loblolly pine in the northern gulf coastal hammocks is negatively correlated with soil pH (Thompson 1980). Among the hydric hammocks sampled in Table 5, loblolly pine was most important in the Silver Springs forest; the clayey soils in that region are more acid than the fine sands common to most hydric hammocks. The abundance patterns of water oak, both within the northern Gulf Hammock and among hydric hammocks, parallel those of loblolly pine, suggesting that growth of both species is favored by similar conditions.

Figure 32. Profile of expanding hydric hammock, Myakka River State Park.

The salt concentration of hydric-hammock soils strongly influences community structure. Hydric hammocks immediately adjacent to salt marshes of the central gulf coast are composed almost entirely of cabbage palm, southern red-cedar, and live oak (Figure 21). These forests were termed coastal hammocks by Swindell (1949), the Florida Game and Fresh Water Fish Commission (1976), and Clewell (1981), but we consider them to be an extreme type of hydric hammock that is simplified by ocean spray and floodwater. The dominance of cabbage palm in association with live oak and red-cedar continues for about 2 km inland (Figure 33). As distance from the saltmarsh boundary increases, the forest is enriched with additional species. Loblolly pine is the first addition, sometimes occurring at the forest edge. Cedar elm occurs as scattered trees beginning perhaps 200-300 m from the coast. At about 1 km, Florida elm, sugarberry, and Florida maple become common in some places. Sweetgum, swamp laurel oak, and hornbeam are abundant at 2 km. Average

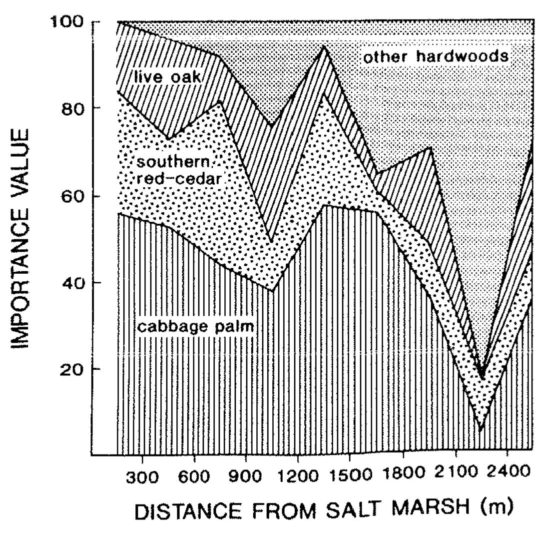


Figure 33. Change in tree-species composition of a hydric hammock with increasing distance from its salt-marsh boundary. The point-quarter method was used, at 50-m intervals, to sample the trees along a transect in Gulf Hammock.

maximum height of trees increases from 12-14 m at the marsh edge to 18-20 m inland 1.5 km. Thompson (1980) noted that the structure of hydric-hammock stands in the northern Gulf Hammock also varied with distance from tidal marsh. Cabbage palm and southern red-cedar decreased in relative importance and sweetgum increased, as stands were located farther from the marsh and soil concentrations of soluble salts decreased. Cabbage palm, live oak, and southern red-cedar are very salt-tolerant (Kurz and Wagner 1957). The last species has been termed a calciphile (calcium-loving) because it almost always is associated with limestone outcrops or coastal (salty) regions. However, southern red-cedar does not require salt; it may be restricted to salt-influenced hydric hammocks because it is excluded from others by less salt-tolerant species. Absent from many hydric hammocks, southern red-cedar is most abundant at the seaward edge of the gulf coastal hammocks and in hydric hammocks of the upper St. Johns River basin (Table 5). The species composition of hydric hammocks in these two areas is very similar: almost exclusively cabbage palm, live oak, and southern red-cedar. The hydric-hammock soils adjacent to the marshes of the St. Johns River are bathed by occasional river overflow containing salts originating as upstream artesian flow of fossil sea water (see Chapter 2.3).

3.3.4 Fire

Hammocks commonly are thought to be free of fire and, indeed, to owe their existence to protection from this disturbance (e.g., Wells 1942). Harper (1915) noted of hydric hammocks: "The humus probably seldom or never gets dry enough to burn, so that fire does not need to be reckoned with." He emphasized two features of this community that tend to reduce fire frequency and intensity: wet soils and (usually) the lack of a substantial litter layer. However, we observed fire scars in virtually every hydric hammock we visited. Almost all of the charred trunks were of cabbage palms. Fire marks are preserved on these trees for many years because they do not slough off the trunks (Laessle 1942). No doubt hydric hammocks burn much less often than fire-adapted communities such as pine flatwoods, but we propose that fires are sufficiently frequent and intense in some stands to influence plant composition (Figure 34).

The effects of fire on hydric-hammock vegetation are mediated by differences in susceptibility among the plants. Seedlings and sapling-sized trees are more likely to be killed by fire than larger trees, because the bark tends to be less thick and the crowns can be reached by the flames. However, even large trees of some hydric-hammock species, especially hardwoods, can be injured by fire, making them subject to attacks by fungi and insects (Fowells 1965). Bark thickness varies among species, accounting for some, but not all, of the differences in fire susceptibility (Table 6). When bark thickness was held constant, fourteen species of southern trees still varied in fire resistance, presumably due to differences in the structure, composition, density, and moisture content of the bark (Hare 1965). Generally, conifers were more resistant than hardwoods, and field observations support these findings. Pine flatwoods (and planted pine plantations) are maintained by regular fires that kill hardwood reproduction. Two severely burned cypress swamps experienced 18% and 23% declines in the abundance of the dominant tree, pond cypress (*Taxodium distichum* var. *nutans*, a conifer), but 98% and 83% decreases in the hardwoods (mainly swamp tupelo, sweetgum, and sweetbay) (Ewel and Mitsch 1978). Loblolly pine is among the most fire-tolerant species in hydric hammocks, and almost all the hardwoods are susceptible to fire. However, one conifer, southern red-cedar, is quite fire-susceptible (Putnam *et al*. 1960).

Figure 34. Fire in the cabbage palm edge of hydric hammock, Seminole Ranch, Brevard County; top, June 1977, bottom, May 1978 (photo at top by G. Kenneth Scudder).

Table 6. Fire sensitivity in five tree species common to hydric hammocks. A standardized flame was applied to living bark and the mean time in seconds for cambium to reach a lethal temperature of 60 °C was recorded (from Hare 1965).

	Bark thickness (cm)		
Species	0.5	0.8	1.0
Sweetgum	25.6	48.6	101.8
Red maple	29.0	56.8	117.6
Water oak	30.2	61.0	136.0
Sweetbay	30.8	67.0	152.0
Loblolly pine	35.6	84.2	179.2

Cabbage palm is the most fire-tolerant tree in hydric hammocks, surviving even severe fires. An intense burn in a cabbage palm/live oak/southern redcedar stand in Tosohatchee State Reserve killed all trees except cabbage palms (Randall E. Hester, Florida Department of Natural Resources; pers. comm.). Harlow (1959) ascribed nearly monospecific stands of cabbage palm to frequent fires (every 2-3 years). Fires favor cabbage palm, and their production of flammable litter in turn promotes fire. Less frequent and intense fires probably favor live oak in addition to cabbage palm. Though many authors (e.g., Putnam *et al.* 1960; Fowells 1965) have claimed that live oak is fire-susceptible, Laessle and Monk (1961) observed signs of fire in all eight of the live-oak-dominated forests they examined in northeastern Florida. Because coastal and inland stands featured similar vegetation and fire scars, Laessle and Monk (1961) concluded that salt spray was less important than occasional fire, coupled with the tenacity and longevity of live oak, in maintaining live oak forest. More frequent and intense fires resulted, in coastal areas, in a low thicket of vegetation containing saw palmetto and dwarfed forms of several oak species (Laessle and Monk 1961).

Some of the variation in species composition among hydric hammocks (Table 5) also may result from differences in fire frequency and intensity. The domination of loblolly pine in hydric hammocks along Silver Springs run probably is favored by occasional light fires as well as soil conditions. If fire (and cattle grazing) were prevented, the forest would converge toward more "typical" hydric hammock with an abundance of cabbage palm, oaks, and sweetgum (Florida Game and Fresh Water Fish Commission 1976). Hydric hammocks highly dominated by cabbage palm, and some live oak, are found in the Myakka and St. Johns River basins (Table 5). In these areas, hammocks often are bounded both up- and down-slope by communities characterized by frequent fire--pine flatwoods and freshwater marsh. Geographical location plays a role in the low diversity of hydric hammock in the Myakka region (see section 3.31), but other factors also may be important. Figure 35 contrasts the tree species composition of two hydric hammocks within Myakka River State Park. The

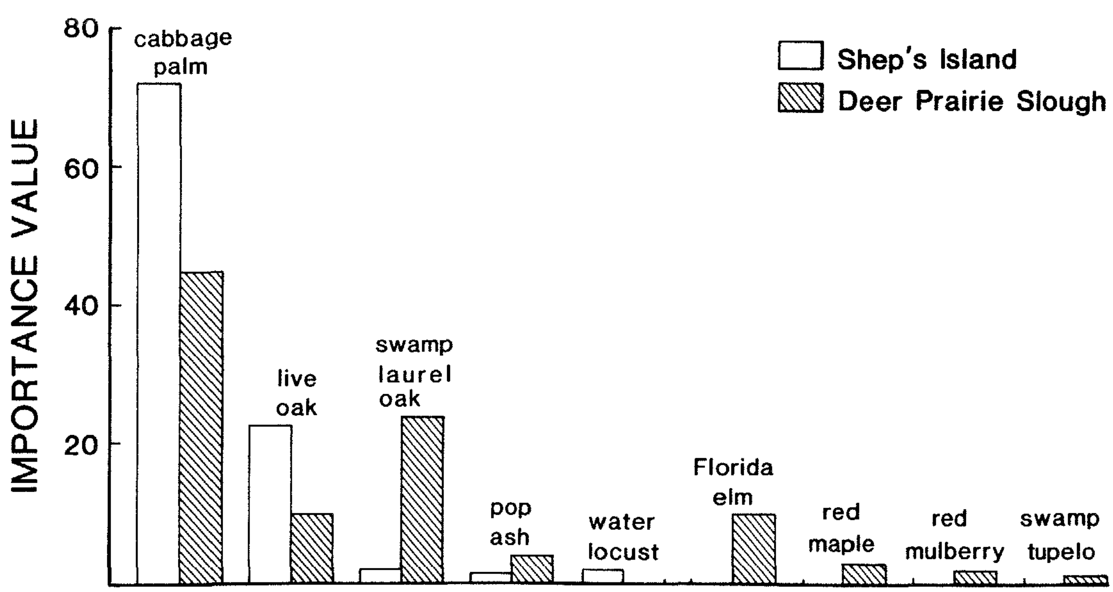


Figure 35. Tree-species composition of two hydric hammocks in Myakka River State Park: Shep's Island, adjacent to Upper Myakka Lake and Deer Prairie Slough, about 20 km to the east.

first, Shep's Island (Table 5), adjacent to Upper Myakka Lake, consists of cabbage palm and live oak and has little shrub and ground vegetation. The second hammock, located about 20 km to the east in Deer Prairie Slough, contains a number of hardwoods absent from Shep's Island, as well as copious shrubs and herbs. The hydric hammock in Deer Prairie Slough occupies a slightly elevated area that is completely surrounded by mixed hardwood swamp. We suggest that this contrast in hammock vegetation is due to a difference in fire frequency and intensity. Presumably fires that sweep the vast marshes of the Myakka region also burn Shep's Island but are damped by the swamp in Deer Prairie Slough and only rarely reach the hammock there. It also is possible that the hydrological conditions of the two hammocks differ enough to account for some of the differences in species composition. The swamp may modulate the flooding regime of the Deer Prairie Slough hammock such that the duration of flooding is less than in the Shep's Island hammock and drydowns are not as severe.

The plant composition of the Tosohatchee hydric hammock (upper St. Johns River) varies greatly on a local scale (Figure 36). Portions of the hammock immediately adjacent to freshwater marsh (Figure 36c, d) are the least diverse. Fire scars are pervasive, signalling more frequent burns in these sites than in hammock portions next to a mixed hardwood swamp (Figure 36b) and a creek (Figure 36a). The low basal area of forest (d) and its short stature (the average height of the canopy is 12 m, in contrast to 17 m in site (b)) probably are due to

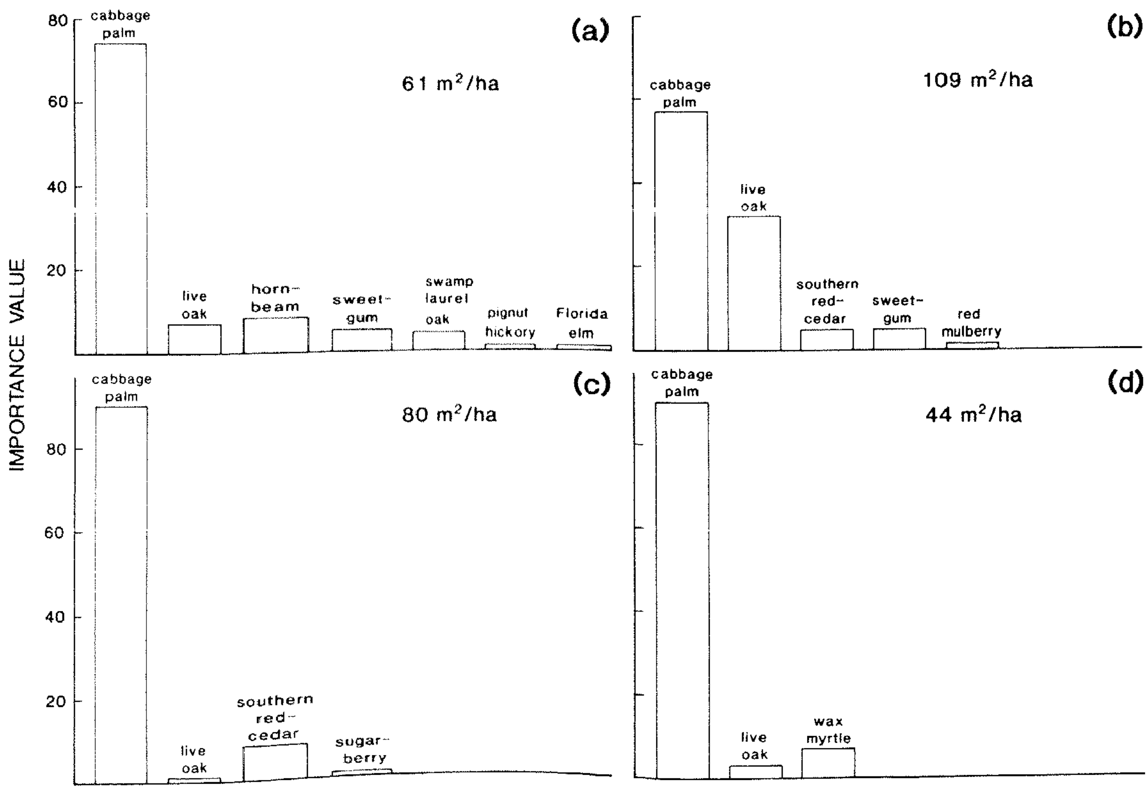


Figure 36. Species composition of four nearby portions of a hydric-hammock stand in the northern part of Tosohatchee State Preserve, Orange County. Total basal area is listed for each site.

frequent fires, although timber harvesting (evident from stumps of southern red-cedar) also may be significant. It is likely that sites (a) and (b) are more diverse not only because of less frequent fire, but because of less extreme hydrological regimes--their soils probably are kept more constantly saturated. The low diversity at sites (c) and (d) may also result, in part, from higher salt concentrations that exclude salt-intolerant species.

The boundaries of hydric hammocks, as well as their species composition, may be affected by fire. When fire is suppressed in an adjoining community, often by human actions, hydric hammock may expand. In the Alafia River system of west-central Florida, Clewell *et al.* (1982) documented the movement of wetland hardwoods (live oak, swamp laurel oak, water oak, and sweetgum) into pine flatwoods. They attributed the extension to a reduction in fire frequency brought about by agricultural activities in the uplands. Though the expansion of hydric hammock into freshwater marsh in Myakka River State Park is related partly to changes in the hydrological regime (see section 3.32), fire suppression also may be responsible. Fire suppression within the park has accompanied increased recreational use; frequency also has decreased in the watershed due to land-use changes.

3.3.5 Other Disturbances

Hydric hammocks have a long history of human use and disturbance that is chronicled in the accompanying management handbook (Simons *et al.* 1989). Probably few areas have remained untouched by human activities. Timber harvesting and livestock grazing probably have had the greatest influence on the plant composition of contemporary hydric hammocks.

Logging of hydric-hammock forests has greatly varied in intensity and scale, from selective cuts of scattered individuals to clearcutting of hundreds of acres. Until the twentieth century, the cuts generally were selective; the chosen species changed with market demand. Live oak was highly valued in the era of wooden ships, especially in the early and mid-1800's when the United States built its navy. Pencil production in the late 1800's was dominated by southern red-cedar, resulting in the over-exploitation of this species in Gulf Hammock. The large stumps that have endured in the hydric hammocks show that regenerated southern red-cedars have not yet reached their former size. In the 1800's and 1900's, sweetgum and some other hardwoods of hydric hammocks were cut selectively for manufacture of furniture and crates, and these harvests too are manifested in present size distributions. Sweetgum trees between 50 and 75 cm dbh are common in the Tiger Creek hydric hammock, long protected from harvesting, and in remote areas of the gulf coastal hammocks, but elsewhere the trees are rarely greater than 50 cm dbh. Where past harvesting is particularly evident, for example in the Orange Lake palm/oak hammock (Table 5), sweetgums are less than 25 cm dbh. Highgrading, the practice of harvesting all merchantable trees while leaving species and individual trees of low value, became popular in the twentieth century. This type of logging in hydric hammocks generally retains all cabbage palm, live oak, and an assortment of crooked and decayed trees. The dominance of cabbage palm and live oak in some hydric hammocks, for example the Orange Lake forest, must in part be due to highgrading and selective harvesting practices that bypassed these species. Clearcutting became the predominant mode of harvest in hydric hammock in the past 20 years. Sometimes the clearcuts are allowed to regenerate naturally, but more often, and particularly in the gulf coastal hammocks, they are planted with loblolly pine.

Spanish explorers brought cattle and hogs to Florida in the sixteenth century, and wild hogs have roamed hydric hammocks and many other habitats ever since. Cattle still are grazed in some hydric hammocks where ground vegetation is relatively lush, such as the inland reaches of the gulf coastal hammocks and in loblolly pine-dominated hammocks. Grazing by cattle or feral hogs can greatly influence the plant species composition of hydric hammock. Hogs avidly consume mast, influencing oak regeneration, and their rooting for tubers, roots, and small invertebrates severely disturbs the soil. Cattle compact the soil and reduce browse and groundcover vegetation, including hardwood regeneration (Figure 37). Where cattle density is high, hydric hammock may resemble a manicured lawn with an occasional tree (often live oak). The dominance of cabbage palm and live oak in some hydric hammocks, for example the Orange Lake forest, probably is perpetuated by preferential consumption of hardwood seedlings and saplings by grazers.

The major natural disturbances in hydric hammocks are flooding, fire, grazing, and wind. Browsing by native wildlife, mainly deer, influences the abundance and composition of groundcover, tree seedlings, and shrub vegetation. Gaps from fallen trees are found in all hydric hammocks, but they are especially common in coastal areas vulnerable to hurricanes (Figure 38).

Succession, whether on naturally cleared or on harvested sites, has not been documented in hydric hammocks. However, some trends can be predicted based upon species differences in shade tolerance, relative growth rate, longevity, requirements for seedling establishment, and ability to sprout following disturbance (Putnam *et al.* 1960; Fowells 1965; McKnight *et al.* 1981). The composition of the regenerating forest is affected by a number of factors including the type, severity, and extent of disturbance, the composition of the pre-disturbance

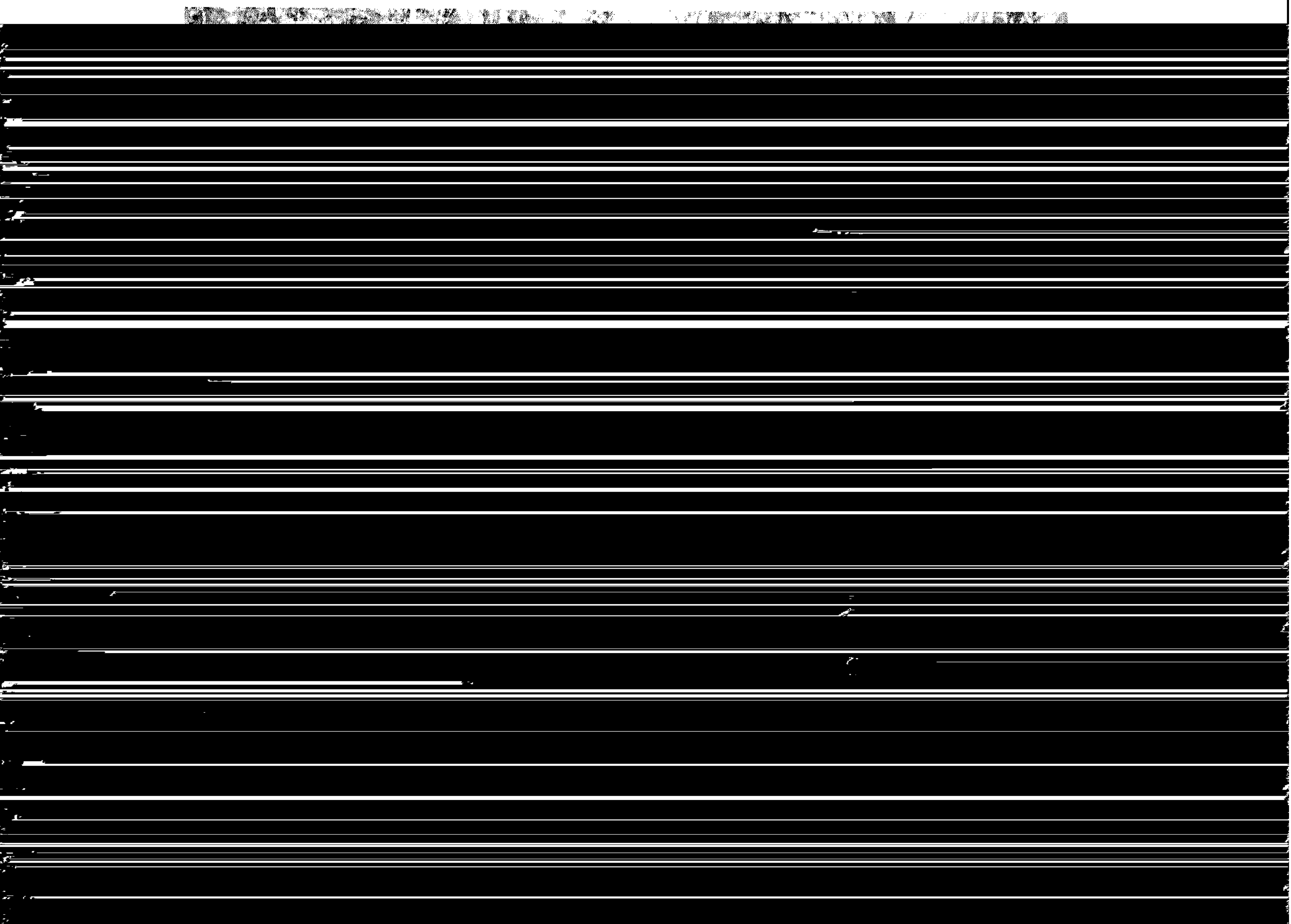


Figure 38. Tree blowdowns due to hurricanes are a common sight in gulf coastal hammocks. This southern red-cedar was located in a patch of hammock surrounded by salt marsh.

stand (especially ages and species of trees), and seed sources. If the disturbance (fire, hurricane, logging, etc.) is relatively moderate, removing mainly canopy trees, then the new forest will be dominated by the growth of remaining seedlings and saplings and sprouts from vigorous sprouters such as sweetgum and persimmon. More severe disturbances favor sprouting or new regeneration; the outcome probably depends on the original composition of the stand. Virtually all hardwoods common to hydric hammock are capable of sprouting, but in many species this ability is inversely related to the size of the tree. Therefore, if young hardwoods are present in the pre-disturbance stand and the disturbance is not so intense as to destroy their roots, they may then sprout vigorously to produce a new canopy. The new forest is likely to contain sweetgum and hornbeam, but also oaks, sugarberry, and other hardwoods. On the other hand, if the canopy contained mostly older hardwoods and little understory was present prior to the disturbance, then severe disturbance will initiate new regeneration in which loblolly pine and sweetgum are dominant species. Sweetgum is the major colonizer following most disturbances in hydric hammock because usually it is an abundant member of the forest, it is a prolific producer of seeds, and it vigorously sprouts from roots and stumps. However, loblolly pine is more favored by severe, large-scale disturbances, such as clearcuts with the slash removed. Loblolly pine requires mineral soil and the absence of competing vegetation for good seed germination and growth, and it regenerates and grows very rapidly when these conditions are present in hydric hammock. The development of "mature" hydric hammock, with its abundance of oaks and uncluttered, park-like appearance, takes about 100 years. Live oak grows more slowly than colonizers such as sweetgum and loblolly pine, but once established, it is extremely tenacious and long-lived.

3.3.6 Summary

Hydric-hammock vegetation typically is dense and evergreen, containing one or more species of oaks, cabbage palm, and, often, sweetgum and Florida elm in the overstory. Hydric hammocks vary considerably in plant composition, particularly in the degree of dominance of cabbage palm and live oak. Stands almost exclusively composed of cabbage palm, live oak, and, sometimes, southern red-cedar, abut the salt marshes of the gulf coast and the freshwater marshes of the St. Johns and Myakka River basins. Dominance of cabbage palm and live oak is favored by one or more factors. Cabbage palm is highly fire-resistant, flood-tolerant, and salt-tolerant, and it is avoided by grazers and timber cutters. Live oak is moderately tolerant of fire, very long-lived, and salt-tolerant; it withstands occasional floods but not constant saturation, and at present is not valued as timber. Thus, several combinations of environmental extremes promote the predominance of these two species and the elimination of others. Conversely, species richness in hydric hammocks is favored by the absence of fire, salt, timber harvest, and excessive drydown and flooding. Cabbage palm is absent only from hydric hammocks situated outside of its geographical range. Live oak is sparse or missing in hammocks, or parts of hammocks, with soils that are nearly always wet.

Subtle variations in hydrological regime, soil conditions, and fire frequency probably account for the differences in abundance of many plant species among hydric hammocks. Abundance of loblolly pine and water oak in hydric hammocks appears to be related to soil pH and clay content; sweetbay is associated with moist soils relatively enriched with organic matter. Interactions among plant species must also be considered. For example, southern red-cedar probably is restricted to salt-influenced hydric hammocks not because it requires salt, but because it is excluded from other hammocks by competition with less salt-tolerant species. At present we can only speculate as to the forces influencing the species composition of hydric hammocks. Causes of such variation within and among these forests are difficult to determine because of the interactions among factors; the longevity of many hydric-hammock species (they can persist long after favorable conditions for establishment and growth are past); and human disturbances. Correlations of species composition and environmental variables suggest some of the forces at play, but they do not establish causal mechanisms; only experiments can do that.

3.4 PRIMARY PRODUCTION AND ITS FATE

Plant biomass and its rate of production have not been measured in hydric hammock. Basal areas of hydric-hammock forests (Table 5) fall within the range of the high values reported for swamps in the southeastern United States (15-92 m^2/ha, mean = 49 m^2/ha; Connor and Day 1982); plant standing-crop probably is similarly large. From known and predicted relationships between the productivity of forested wetlands and hydrological regime, we infer that the productivity of hydric hammock also is at least moderately high.

Net primary productivity of southeastern forested wetlands is variable but often very great (Brinson *et al.* 1981; Connor and Day 1982; Wharton *et al.* 1982). Highest productivities occur in forests that experience seasonal flooding by flowing water, such as bottomland hardwood forests. Hydrological effects on productivity may be mediated by nutrient inflow. Brown (1981) found a strong positive correlation between phosphorus input and productivity of cypress-dominated wetlands. Highly productive floodplain forests received a large volume of phosphorus-rich water; less productive cypress domes obtained little phosphorus because their water was stagnant and derived mainly from rainfall. Hydric hammocks probably are more productive than cypress domes (956 gm dry wt/m^2; Brown 1981), and less productive than bottomland hardwood forests (1,374 gm dry wt./m^2/yr in a Louisiana stand; Connor and Day 1976). Hydric hammocks are considered to be still-water wetlands in contrast to those dominated by river flow; however, surface water may move across the gentle slopes of hammocks during and following floods. Flooding frequency varies among hydric hammocks, but in many, inundation occurs at the height of the rainy season(s)--either once or twice per year. Unlike cypress domes, hydric hammocks receive water from a variety of sources, including rainfall, river overflow, and upland seepage.

In forested wetlands, the two components of above-ground production, stem growth and the production of leaves, fruit, and flowers (measured as litter fall), are about equally important (Connor and Day 1982). Litter-fall production in wetlands is positively related to the movement of water (Brinson *et al.* 1981), but the relationship with flooding frequency is less clear. In Florida's Apalachicola River floodplain, annual litter-fall in swamp communities is less than in high-ground, levee stands (760 versus 874 gm dry wt./m^2/yr respectively; Elder and Cairns 1982). The levee soils are saturated only during the flood season, and their forests are dominated by sweetgum, sugarberry, and swamp laurel oak. The first two species are especially high producers of leaf litter; grape vines also contribute heavily to leaf fall in the levee forests. Litter production differed only slightly between an upland terrace forest and its adjacent floodplain forest in the South Carolina coastal plain (606 versus 667 gm dry wt./m^2/yr respectively; Shure and Gottschalk 1985). Situated just beyond the flooding margin, the terrace forest contained water oak, swamp chestnut oak, poplar, and pignut hickory. The floodplain swamps of both rivers were composed largely of tupelos and ash; the Apalachicola swamp also had abundant bald cypress, and the South Carolina forest included sweetgum and red maple. The drier forests of the two systems have tree species in common with hydric hammock and their flooding frequencies probably circumscribe the range among hammocks. Litter production in hydric hammock is likely to be on the same order as the levee and upland terrace forests, but the seasonal pattern may be quite different. In the Apalachicola River floodplain, litter fall peaks sharply in autumn (Elder and Cairns 1982). Most of the tree species, including sweetgum, American elm, and hornbeam, follow this phenology, but swamp laurel oak sustains high leaf-fall production from October through March. Whereas floodplain swamps typically are dominated by deciduous species, hydric hammocks contain an abundance of evergreens. Still, evergreen leaves are not permanent. In some cases, leaf fall is pulsed; live oak and sweetbay drop their leaves at the same time as new ones emerge in spring. Other species, such as cabbage palm, lose leaves throughout the year.

Litter must decompose slowly within the hydric-hammock community. The rate of decomposition is likely to be less than in wetlands with flowing water and with a higher frequency and greater duration of flooding. Leaves immersed in the Apalachicola River decomposed significantly faster than those set on an unflooded levee site (Elder and Cairns 1982). No doubt water flow enhanced the fragmentation and leaching of the material, a composite of five major floodplain species. On the levee, even the most rapidly decomposing leaves lost less than half their mass in six months. Rate of leaf decomposition that decreased across floodplain transects correlated with reduced flooding; however, changes in the species composition of the litter probably were the proximate cause (Elder and Cairns 1982; Shure *et al.* 1985). In the South Carolina floodplain system described in the preceding paragraph, locally collected litter lost 85% of its mass in one year at a streambank site, but only 58% annually in the terrace forest dominated by oaks (Shure *et al.* 1985). The leaf decomposition rates of most floodplain species, including tupelo, ash, black gum, red maple, and sweetgum, were very rapid, but those of bald cypress and swamp laurel oak were considerably slower (Elder and Cairns 1982; Shure *et al.* 1985). Leaves that were recalcitrant to decomposition tended to have higher carbon:nitrogen ratios and greater concentrations of lignin and cellulose. Decomposition rates of oak leaves besides swamp laurel were not measured, but they also are likely to be slow because of similar chemical characteristics. Although litter decomposition is likely to be slow in hydric hammocks because of plant species composition, low flooding frequency, and the absence of strong water flow, probably only a small amount of litter and decomposed material is washed out by occasional floods. The amount and form (particulate, dissolved) of export from a hammock depends on current velocity, the timing of floods in relation to the seasonal pattern of litter fall, and uptake rates of dissolved nutrients by hammock plants.

CHAPTER 4. ANIMALS

4.1 INTRODUCTION

Virtually nothing has been published about invertebrates inhabiting hydric hammock. This habitat is important to certain butterflies (John A. Fluno, Department of Entomology, Ohio State University, retired; pers. comm.). Sugarberry is the sole host plant for the snout butterfly (*Libytheana bachmanii*), the hackberry butterfly (*Asterocampa celtis*), and the tawny emperor (*Asterocampa clyton*). Sugarberry and water elm (*Planera aquatica*) are primary hosts for the questionmark butterfly (*Polygonia interrogationis*), with false nettle as an occasional host. Caterpillars of the eastern tiger swallowtail (*Papilio glaucus*) feed on *Fraxinus*, *Liriodendron*, and *Magnolia virginiana*.

Very few animals are endemic to hydric hammock. The crayfish *Procambarus geodytes*, a primary burrower, appears to have an endemic distribution in the hydric hammock along Silver River and in other forested wetlands of the Oklawaha River watershed (Franz 1976). A subspecies of the southeastern shrew (*Sorex longirostris eionis*) was described by Davis (1957) from the hydric hammock around Homosassa Springs, Citrus County, Florida. However, the actual distribution of this form and its validity as a taxon are uncertain (Humphrey *et al*. 1986). Despite their common names, neither the Gulf Hammock rat snake nor the Gulf Hammock dwarf siren are restricted to hydric hammock, though the rat snake occurs there; the siren occurs in ponds in and beyond hydric hammock.

Though the biology of most vertebrates found in hydric hammock is fairly well known, very few have been studied there. The vertebrate fauna of hydric hammock is not unique to the habitat, resembling faunas of most other forested habitats in peninsular Florida. However, the hydric-hammock fauna is luxuriant. Compared with other types of forest in the region, hydric hammock has a highly diverse vertebrate fauna and a high abundance of selected species.

4.2 REPTILES AND AMPHIBIANS

The herpetofauna has no species unique to hydric hammock and is representative of the region (Table 7). Characteristic species include southern black racer, rat snake, Florida box turtle, green anole, ground skink, broad-headed skink, southern toad, green treefrog, squirrel treefrog, and eastern narrow-mouth toad. The coastal variant of hydric hammock lacks many species found in the inland variants of hydric hammock where floodwater is fresh rather than brackish. The blue-striped ribbon snake and blue-striped garter snake are widespread in several habitats of the gulf coastal region, but they were found only in the coastal sample of hydric hammock shown in Table 7. Inland hydric hammock has an association of reptiles and amphibians that appears to be ecotonal between mesic hammock and swamp forest. Loblolly pine-dominated hydric hammock includes a number of species characteristic of pine flatwoods (pinewoods snake, scarlet king snake, pinewoods treefrog).

Some quantitative data are available on the reptile and amphibian community

Table 7. Occurrence of reptiles and amphibians in three variants of hydric hammock along the route of the proposed Cross-Florida Barge Canal, including associated aquatic habitats such as ponds and streams (Florida Game and Fresh Water Fish Commission 1976).

Species	Coastal hydric hammock[a]	Inland hydric hammock	Loblolly pine hydric hammock
Eastern mud snake (*Farancia abacura abacura*)		P-O	P-O
Southern ringneck snake (*Diadophis punctatus punctatus*)	P-F	P-F	P-F
Pinewoods snake (*Rhadinaea flavilata*)			C-O
Rough green snake (*Opheodrys aestivus*)	P-F	P-F	P-F
Southern black racer (*Coluber constrictor priapus*)	P-F	P-F	P-F
Eastern coachwhip snake (*Masticophis flagellum flagellum*)	P-O	P-I	
Eastern indigo snake (*Drymarchon corais couperi*)	P-O	C-F	P-O
Red rat snake (*Elaphe guttata guttata*)	P-O	P-O	
Yellow rat snake (*Elaphe obsoleta quadrivittata*)		P-F	P-O
Gulf Hammock rat snake (*Elaphe o. q.* x *E. o. spiloides*)	C-O	P-F	
Scarlet kingsnake (*Lampropeltis triangulum elapsoides*)	P-O		C-F
Eastern kingsnake (*Lampropeltis getulus getulus*)		P-O	P-I
Florida scarlet snake (*Cemophora coccinea coccinea*)	P-O	P-O	
Rough earth snake (*Virginia striatula*)			C-I
Florida water snake (*Nerodia fasciata pictiventris*)		P-O	P-F
Peninsula ribbon snake (*Thamnophis sauritus sackeni*)		P-F	P-F
Blue-striped ribbon snake (*Thamnophis sauritus nitae*)	C-F		
Eastern garter snake (*Thamnophis sirtalis sirtalis*)		P-O	P-F
Blue-striped garter snake (*Thamnophis sirtalis similis*)	C-F		
Striped crayfish snake (*Regina alleni*)			P-I
Northern Florida swamp snake (*Seminatrix pygaea pygaea*)		P-O	P-O
Florida brown snake (*Storeria dekayi victa*)	P-O	P-O	P-I
Florida red-bellied snake (*Storeria occipitomaculata obscura*)		P-F	
Eastern coral snake (*Micrurus fulvius fulvius*)	P-O	P-O	P-O
Florida cottonmouth (*Agkistrodon piscivorous conanti*)		P-F	P-O
Dusky pigmy rattlesnake (*Sistrurus miliarius barbouri*)	P-F	P-O	P-O
Eastern diamondback rattlesnake (*Crotalus adamanteus*)	P-O	P-O	P-O
Stinkpot turtle (*Sternotherus odoratus*)		P-C	P-F
Striped mud turtle (*Kinosternon baurii*)		P-F	P-F
Florida mud turtle (*Kinosternon subrubrum steindachneri*)			P-I
Florida box turtle (*Terrapene carolina bauri*)	P-O	P-F	C-F
Peninsula cooter (*Pseudemys floridana peninsularis*)		P-O	P-O
Green anole (*Anolis carolinensis carolinensis*)	P-F	P-F	P-F
Southern fence lizard (*Sceloporus undulatus undulatus*)		P-O	P-O
Eastern glass lizard (*Ophisaurus ventralis*)	P-F		P-F
Island glass lizard (*Ophisaurus compressus*)	P-I		
Ground skink (*Scincella laterale*)	P-F	P-F	P-F
Broad-headed skink (*Eumeces laticeps*)	P-I	C-F	P-O
Southeastern five-lined skink (*Eumeces inexpectatus*)	P-F		P-F
Two-toed amphiuma (*Amphiuma means*)		P-O	
Striped newt (*Notophthalmus perstriatus*)		P-O	P-I
Peninsula newt (*Notophthalmus viridescens piaropicola*)		P-F	P-O
Mole salamander (*Ambystoma talpoideum*)		P-O	
Slimy salamander (*Plethodon glutinosus glutinosus*)		C-F	P-I
Dwarf salamander (*Eurycea quadridigitata*)		P-O	P-O
Southern dusky salamander (*Desmognathus auriculatus*)		P-O	
Greater siren (*Siren lacertina*)		P-O	
Eastern spadefoot toad (*Scaphiophus holbrooki holbrooki*)		P-O	
Oak toad (*Bufo quercicus*)			P-O
Southern toad (*Bufo terrestris*)	P-F	P-F	P-F
Florida cricket frog (*Acris gryllus dorsalis*)	P-O	P-F	P-F

(Continued)

Table 7. (Concluded).

Species	Coastal hydric hammock[a]	Inland hydric hammock	Loblolly pine hydric hammock
Little grass frog (*Limnaoedus ocularis*)		P-F	P-F
Florida chorus frog (*Pseudacris nigrita verrucosa*)			P-F
Green treefrog (*Hyla cinerea*)	P-F	P-F	P-F
Southern spring peeper (*Hyla crucifer bartramiana*)		P-F	P-O
Pinewoods treefrog (*Hyla femoralis*)			P-F
Barking treefrog (*Hyla gratiosa*)		P-O	P-F
Squirrel treefrog (*Hyla squirella*)	P-F	P-F	P-F
Cope's gray treefrog (*Hyla chrysoscelis*)		P-F	
Greenhouse frog (*Eleutherodactylus planirostris*)			P-F
Bullfrog (*Rana catesbeiana*)		P-O	P-I
Southern leopard frog (*Rana sphenocephala*)	P-F	P-F	P-F
Bronze frog (*Rana clamitans clamitans*)		P-O	
River frog (*Rana heckscheri*)		P-I	
Pig frog (*Rana grylio*)			P-F
Eastern narrow-mouth toad (*Gastrophryne carolinensis*)	P-F	P-F	P-F
Total number of species	28	51	50

[a] The coastal hammock sampled here was topographically diverse and included some mesic and xeric hammock. The sample also included the eastern hognose snake (*Heterodon platyrhinos*), Florida crowned snake (*Tantilla relicta relicta*), Peninsula mole skink (*Eumeces egregius onocrepis*), and Florida worm lizard (*Rhineura floridana*), which do not occur in hydric hammock. Other species characteristic of mesic or xeric hammock may also have been over-represented in this sample.

C = characteristic
P = present
F = frequent
O = occasional
I = infrequent

of hydric hammocks. In a permanent plot in loblolly pine hydric hammock (Table 8), more than 97 individuals of 8 species of reptiles and amphibians were found in quadrat sampling, and more than 245 individuals of 17 species were found in time-constrained sampling. Compared with seven other habitats so sampled in the region, hydric hammock ranked second in the number of species present and had more than twice as many individuals as in any other habitat. The two methods together produced more than 342 individuals of 18 species, more than in any other habitat. The most abundant species were the green anole, ground skink, Florida cricket frog, little grass frog, squirrel treefrog, and greenhouse frog. The little grass frog and squirrel treefrog reached their maximum abundance in this habitat.

Arrays of drift fences fitted with pit-fall traps and funnel-traps captured a different set of reptiles and amphibians (Table 9). Compared with ten other habitats sampled by this technique, hydric hammock ranked second in number of species and third in number of individuals captured (with captures of the greenhouse frog deleted because of its selection of traps for shelter). The most common species in hydric hammock were the narrow-mouth toad, spadefoot toad, and ground skink. The spadefoot toad

Table 8. Occurrence of reptiles and amphibians in a loblolly pine hydric hammock on the route of the proposed Cross-Florida Barge Canal (Florida Game and Fresh Water Fish Commission 1976).

Species	Spring	Summer	Autumn
Area-limited search of a 1000-m^2 quadrat without time limits			
Scarlet kingsnake		3 eggs	
Green anole	2		3
Ground skink	2	1 egg	10
Oak toad	2	4	
Little grass frog	1	>20	
Pinewoods treefrog		1	14
Squirrel treefrog	2	5	7
Greenhouse frog		>20	
Total species/individuals	5/9	7/>54	4/34
Time-limited search for 6 man-hours without marked boundaries			
Pinewoods snake			1
Black racer	2		
Florida cottonmouth		1	
Florida box turtle			1
Green anole	2	6	21
Ground skink	18	1	5
Southeastern five-lined skink		3	
Unidentified skink	1		2
Oak toad		3	
Southern toad		2	
Florida cricket frog			>20
Little grass frog	>20	>20	2
Pinewoods treefrog		3	
Squirrel treefrog		35	10
Greenhouse frog	18	>20	2
Southern leopard frog	1	4	>20
Eastern narrow-mouth toad		1	
Total species/individuals	7/>62	12/>99	10/>84

reached its maximum abundance in this habitat.

During intensive sampling of the loblolly pine variant of coastal hydric hammock in St. Marks National Wildlife Refuge, Wakulla County, Florida, 12 species of reptiles and amphibians were found (U.S. Fish and Wildlife Service [1980]): pigmy rattlesnake, ribbon snake, black racer, box turtle, green anole, ground skink, broad-headed skink, southern toad, green treefrog, squirrel treefrog, southern leopard frog, and narrow-mouth toad. In continuous sampling in this habitat (Table 10), the community of reptiles and amphibians ranked second in number of individuals and ninth in number of species, compared with similar samples from 11 other habitats in that region. The most common

Table 9. Occurrence of reptiles and amphibians in two drift fence arrays with pit-fall traps and funnel-traps from 31 March to 18 October 1975, in a hydric hammock on the route of the proposed Cross-Florida Barge Canal (Florida Game and Fresh Water Fish Commission 1976).

Species	Number
Southern ringneck snake	3
Eastern coachwhip snake	3
Eastern garter snake	2
Florida red-bellied snake	1
Dusky pigmy rattlesnake	1
Striped mud turtle	1
Green anole	7
Ground skink	20
Broad-headed skink	1
Slimy salamander	3
Eastern spadefoot toad	18
Southern toad	5
Little grass frog	1
Southern spring peeper	1
Southern leopard frog	4
Bronze frog	2
Eastern narrow-mouth toad	47
Total species	17
Total individuals	120

species were garter snake, red-bellied snake, ground skink, broad-headed skink, green treefrog, squirrel treefrog, southern leopard frog, and narrow-mouth toad.

Studies of particular species of reptiles or amphibians specifically in hydric hammock are almost non-existent. The lone exception is the eastern indigo snake, a threatened species. This species spends most of the winter in dens in hollow root channels and rodent burrows at the bases of large live oaks; other den sites are armadillo burrows, hollow logs, solution holes in limestone outcrops, and windrows of debris from lumbering operations (Moler [1985]).

Table 10. Occurrence of reptiles and amphibians in two drift fence arrays with pit-fall traps and funnel-traps from 9 December 1978 to 25 July 1979, in coastal hydric hammock, loblolly pine variant, in St. Marks National Wildlife Refuge, Wakulla Co., Florida (U.S. Fish and Wildlife Service 1980).

Species	Number
Southern ringneck snake	6
Southern black racer	7
Scarlet kingsnake	1
Eastern kingsnake	1
Florida scarlet snake	8
Florida water snake	1
Ribbon snake	8
Garter snake	12
Florida red-bellied snake	6
Florida mud turtle	1
Green anole	1
Ground skink	65
Broad-headed skink	27
One-toed amphiuma (*Amphiuma pholeter*)	1
Slimy salamander	1
Dwarf salamander	2
Southern toad	9
Cope's gray treefrog	1
Green treefrog	8
Squirrel treefrog	7
Bullfrog	1
Southern leopard frog	100
Eastern narrow-mouth toad	94
Total species	23
Total individuals	368

Indigo snakes breed in late autumn and winter (Speake *et al.* 1978), when males make brief trips away from dens apparently in search of females (Moler [1985]). During summer, indigo snakes are often found in association with ponds. Animals with access to both clearcuts and uncut hammock seem to prefer the former, frequently occurring near the ecotone of clearcut and hammock. Home ranges in winter average 6.5 ha in size; in summer, they average 158 ha (Moler [1985]).

4.3 BIRDS

4.3.1 Community Structure

More is known about the community of birds of hydric hammocks than about other groups of animals living there, but very little is known about specific bird populations in this habitat. The most common year-round residents are the red-shouldered hawk, barred owl, red-bellied woodpecker, pileated woodpecker, northern flicker, American crow, fish crow, blue jay, Carolina wren, tufted titmouse, Carolina chickadee, and northern cardinal. The most common summer residents are the great crested flycatcher, northern parula warbler, and summer tanager. The most common winter residents are the eastern phoebe, American robin, house wren, ruby-crowned kinglet, yellow-rumped warbler, American goldfinch, and white-throated sparrow.

Three variants of this habitat were included in the study of flora and fauna of the route of the proposed Cross-Florida Barge Canal (Florida Game and Fresh Water Fish Commission 1976). Raw data from that study have been analyzed by Humphrey and Nesbitt [1989] and are summarized in Table 11. Coastal hydric hammock was characterized by the highest absolute number of kingfishers, fish crows, hermit thrushes, yellow-rumped warblers, northern cardinals in winter, and white-throated sparrows. This was the only habitat in which gray kingbirds were recorded. Inland hydric hammock was characterized by the highest absolute number of red-shouldered hawks, mourning doves, pileated woodpeckers, Carolina wrens, blue-gray gnatcatchers, and black-and-white warblers. The loblolly pine variant of hydric hammock was characterized by the highest absolute number of black vultures, downy woodpeckers, hairy woodpeckers, American crows in winter, wood pewees, brown-headed nuthatches, yellow-throated vireos, and summer tanagers. Large, rare species for which hydric hammock was important included nesting ospreys and American swallow-tailed kites (*Elanoides forficatus*) and post-breeding wood storks (*Mycteria americana*), an endangered species. Hydric hammock supported large numbers of overwintering passerines. Not recorded in these samples but very abundant, especially foraging over the edge of hydric hammock with marsh and with flatwoods, were flocks of overwintering tree swallows (*Iridoprocne bicolor*).

Bird communities in the three types of hydric hammock (Table 11) were consistently among the most diverse of those of 14 habitats in the region. In the breeding season, the diversity index H′(Shannon and Weaver 1949) was highest in loblolly pine hydric hammock, second in rank in coastal hydric hammock, and fifth in inland hydric hammock. As measured by number of species, diversity in the breeding season ranked fourth, fifth, and sixth in the three types of hydric hammock. In winter, diversity as measured by number of species was higher in the three types of hydric hammock than in any other habitat, and diversity as measured by H′ was highest in inland hydric hammock, fourth in rank in hydric loblolly pine hammock, and eighth in coastal hydric hammock. Abundance of birds, as measured by number of individuals, was intermediate in the three types of hydric hammock.

Although each of the three types of hydric hammock can be differentiated by a few species of birds occurring only or in highest number there, the similarity of these bird communities is much more striking than their differences (Humphrey and Nesbitt [1989]). This similarity is not limited to hydric hammocks; it extends to all types of forests sampled in the region, suggesting that bird communities do not differentiate among types of forests nearly as finely as do foresters and ecologists. Instead of being habitat-specific entities, these bird associations appear to form according to the adaptations of individual species in response to gradients of various features of the environment. Humphrey and Nesbitt suggested two such gradients on the basis of the available data--three-dimensional

Table 11. Bird populations and community characteristics along the route of the proposed Cross-Florida Barge Canal. The sampling unit was the sum of counts made on a day at a site in a habitat; the duration of these counts ranged from 105 to 330 minutes in one day. Tabular values are averages of the one-day counts expressed as birds per hour. For species significantly affected by season in analysis of variance across 14 habitats, counts are shown separately for winter and summer; otherwise, they are combined. Some species were not observed anywhere in some seasons.

Variable	Season	Coastal hydric hammock	Inland hydric hammock	Loblolly pine hydric hammock
Population counts				
Green-backed heron (*Butorides striatus*)	winter	0.4	0	0
Killdeer (*Charadrius vociferus*)	winter*	0	0	0.4
Turkey vulture (*Cathartes aura*)	both	1.2	0	0
Black vulture (*Coragyps atratus*)	winter*	0	0	1.4
Red-shouldered hawk (*Buteo lineatus*)	winter*	0	2.8	0.9
Osprey (*Pandion haliaetus*)	breeding	2.7	0	0
Northern bobwhite (*Colinus virginianus*)	breeding*	0	0	1.4
Mourning dove (*Zenaida macroura*)	breeding*	0	3.3	0
Yellow-billed cuckoo (*Coccyzus americanus*)	both*	0	0.2	0
Barred owl (*Strix varia*)	breeding	0	1.8	0
Belted kingfisher (*Ceryle alcyon*)	both*	1.4	0	0
Red-bellied woodpecker (*Melanerpes carolinus*)	breeding*	5.0	17.8	10.6
Northern flicker (*Colaptes auratus*)	both*	0.6	1.6	0.2
Yellow-bellied sapsucker (*Sphyrapicus varius*)	winter*	0.4	0.8	0.4
Downy woodpecker (*Picoides pubescens*)	winter*	0	1.2	2.3
Hairy woodpecker (*Picoides villosus*)	breeding*	0	0	2.4
Pileated woodpecker (*Dryocopus pileatus*)	both*	2.0	3.6	0.5
Gray kingbird (*Tyrannus dominicensis*)	breeding	1.0	0	0
Great crested flycatcher (*Myiarchus crinitus*)	breeding*	0	1.5	0.4
Eastern wood-pewee (*Contopus virens*)	breeding	0	0	8.8
Eastern phoebe (*Sayornis phoebe*)	winter	0.4	0	1.9
Acadian flycatcher (*Empidonax virescens*)	breeding	0	0.4	0
Purple martin (*Progne subis*)	breeding	1.0	0	1.8
Blue jay (*Cyanocitta cristata*)	breeding*	0	3.3	3.6
American crow (*Corvus brachyrhynchos*)	breeding*	0	9.8	6.6
American crow (*Corvus brachyrhynchos*)	winter*	0	3.2	12.8
Fish crow (*Corvus ossifragus*)	breeding*	11.7	3.6	2.0
Tufted titmouse (*Parus bicolor*)	both	2.6	4.2	4.2
Carolina chickadee (*Parus carolinensis*)	both*	1.0	0.6	2.4
Brown-headed nuthatch (*Sitta pusilla*)	breeding*	0	0	2.6
Carolina wren (*Thryothorus ludovicianus*)	breeding*	8.0	15.6	7.8
Carolina wren (*Thryothorus ludovicianus*)	winter*	1.2	9.6	3.3
House wren (*Troglodytes aedon*)	winter	0	4.8	1.3
Ruby-crowned kinglet (*Regulus calendula*)	winter*	3.2	6.0	7.6
Blue-gray gnatcatcher (*Polioptila caerulea*)	winter*	0.4	6.8	0.9
Eastern bluebird (*Sialia sialis*)	breeding*	0	0	1.4
Hermit thrush (*Catharus guttatus*)	winter*	0.8	0	0
American robin (*Turdus migratorius*)	winter	5.6	6.0	13.6
Loggerhead shrike (*Lanius ludovicianus*)	winter*	0	0	0.4
Gray catbird (*Dumetella carolinensis*)	winter*	0.4	0.4	0
Northern mockingbird (*Mimus polyglottos*)	breeding*	1.3	0	0.2
Northern mockingbird (*Mimus polyglottos*)	winter*	0.4	0	0
Brown thrasher (*Toxostoma rufum*)	both	0.4	0.6	0

(Continued)

Table 11. (Concluded).

Variable	Season	Coastal hydric hammock	Inland hydric hammock	Loblolly pine hydric hammock
White-eyed vireo (*Vireo griseus*)	breeding*	2.0	1.5	0.6
Yellow-throated vireo (*Vireo flavifrons*)	breeding*	0	0	3.2
Solitary vireo (*Vireo solitarius*)	winter*	0.4	0	0.3
Red-eyed vireo (*Vireo olivaceus*)	breeding*	0	0.7	0
Northern parula warbler (*Parula americana*)	breeding	1.0	1.1	1.2
Black-and-white warbler (*Mniotilta varia*)	winter*	0	6.0	0.1
Yellow-rumped warbler (*Dendroica coronata*)	winter	19.6	0.4	8.6
Yellow-throated warbler (*Dendroica dominica*)	both	0	0	1.2
Prairie warbler (*Dendroica discolor*)	breeding	0.3	0	0
Pine warbler (*Dendroica pinus*)	winter*	0	0	9.6
Common yellowthroat (*Geothlypis trichas*)	both	0.6	1.0	0.9
Eastern meadowlark (*Sturnella magna*)	winter*	0	0	0.4
Redwinged blackbird (*Agelaius phoeniceus*)	breeding*	1.0	0	0.2
Boat-tailed grackle (*Quiscalus major*)	both	0.4	0	0
Common grackle (*Quiscalus quiscula*)	breeding*	9.3	0	0
Summer tanager (*Piranga rubra*)	breeding*	0	1.5	6.0
Northern cardinal (*Cardinalis cardinalis*)	breeding*	5.7	13.5	14.6
Northern cardinal (*Cardinalis cardinalis*)	winter*	8.8	4.8	0.7
American goldfinch (*Carduelis tristis*)	winter	4.0	0	8.4
Rufous-sided towhee (*Pipilo erythrophthalamus*)	breeding*	0	0.4	0
Rufous-sided towhee (*Pipilo erythrophthalamus*)	winter*	0	1.6	0
Savannah sparrow (*Passerculus sandwichensis*)	winter	1.6	0	0
Bachman's sparrow (*Aimophila aestivalis*)	breeding*	0	0	0.2
White-throated sparrow (*Zonotrichia albicollis*)	winter*	1.6	0.4	0
Swamp sparrow (*Melospiza georgiana*)	winter	0	0.8	0
Community characteristics				
Number of species	breeding	24.0	22.0	23.5
Number of species	winter*	23.0	29.0	23.3
Diversity index (H')	breeding*	2.74	2.55	2.77
Diversity index (H')	winter*	2.30	2.96	2.60
Number of individuals	breeding*	70.2	95.0	92.2
Number of individuals	winter	57.6	80.0	94.4

* Significant habitat effect for the season indicated ($P < 0.05$).

structure of the vegetation ranging from homogeneous to heterogeneous, with hydric hammocks being near the multistratal extreme, and tree composition ranging from all hardwood to including substantial numbers of conifers, with the loblolly pine variant of hydric hammock forming one extreme of this gradient. Several species most strongly associated with the conifer end of this gradient (yellow-throated warbler, yellow-throated vireo, brown-headed nuthatch, and summer tanager) occur only or in highest numbers in forests with co-dominant conifers.

The importance of hydric hammock to overwintering passerines can be surmised from the high number of certain species in Table 11 (American robin, ruby-crowned kinglet, black-and-white warbler, yellow-rumped warbler), but this phenomenon has not been described adequately. The best information is from censuses of a 13.5-ha hydric hammock in Hillsborough River State Park, Hillsborough Co., Florida (Woolfenden 1967; 1968). This site supported 366 individuals of 16 species per 40.5 ha during breeding versus 411 individuals of 33 species during winter. Species of overwintering migrants identified on this site (in addition to those just listed) include eastern phoebe, hermit thrush, yellow-bellied sapsucker, solitary vireo, ovenbird, orange-crowned warbler, palm warbler, common yellowthroat, and American goldfinch. Much attention has been given recently (e.g., Pasquier 1982) to the role of Neotropical forests in supporting populations of migrant passerines that breed in eastern North America, but the same role of forests of the southeastern United States, and hydric hammock in particular, is less widely recognized. This role needs to be much better documented and publicized.

Long-term trends in populations of breeding birds in Florida, based on breeding bird survey counts from 1969 to 1983 in all habitats, revealed significant changes in the number of several species occurring in hydric hammock (Cox 1987). These included increases in number of the mourning dove and osprey and decreases in number of the northern flicker, brown-headed nuthatch, northern mockingbird, eastern bluebird, loggerhead shrike, yellow-throated warbler, prairie warbler, common yellowthroat, red-winged blackbird, and eastern meadowlark. Three of the declining species are cavity-nesters.

4.3.2 Selected Species

The wood duck (*Aix sponsa*) usually forages elsewhere but nests in cavities of live trees, including those in hydric hammock. This habitat may be important to wood ducks because of its abundance of den trees and its proximity to water. Acorns and other mast are important fall and winter foods of wood ducks (Landers *et al.* 1976). Wood ducks prefer to forage for mast fallen into shallow water or on the forest floor adjacent to water, and we have observed this behavior in flooded hydric hammocks.

Wild turkey (*Meleagris gallopavo*) were subject to market hunting in Florida until that commerce was banned in 1901. The population in Gulf Hammock in 1948-49 was considered "reasonably good" (estimated at 500 to 600 birds, or one per 71 ha of suitable habitat) but far below carrying capacity (Swindell 1949). Major pressures on the population were considered to be hunting, which increased after World War II, and reduction of habitat quality by succession and canopy closure following lumbering. The lowest densities of turkeys in the area are in extensive hammock unbroken by clearings, which would provide poults with a suitable abundance of insects. Turkeys shift to the hammocks in autumn when acorns are available and to hammock edges, flatwoods, and clearings in late winter and early spring when new herb growth becomes available.

The ivory-billed woodpecker (*Campephilus principalis*) once inhabited hydric hammock, as well as its modal habitat of river swamp and cypress swamp. Records of original distribution of this bird in "marl hammocks" (Tanner 1942) were up the St. Marks River (Wakulla County); Pumpkin and California Swamps (Dixie County); Suwannee Hammock, Rosewood, Otter Creek, Gulf Hammock, and Sim's Ridge (Levy County); Crystal River (Citrus County); Tampa (Hillsborough County); Manatee County; Enterprise and Turnbull Hammock (Volusia County); Jim Creek (Orange County); Taylor Creek and Wolf Creek (Osceola County); Highlands Hammock (Highlands County); and Caloosahatchee region (Lee County). The available density estimates are that one pair of ivory-bills needed 15.5 to 44 square kilometers of good habitat; the same stands supported roughly 72 pileated woodpeckers and 252 red-bellied woodpeckers. Virgin hydric hammock is characterized by very old and standing dead trees, which supported the woodpeckers' main diet of larvae of borers (buprestid and cerambycid beetles). Unlike larvae of other types of borers, these occur only between the bark and sapwood; hence they are available only for a few years after death of the tree, and their overall density is quite low, even in virgin forest. The near extinction of this woodpecker is attributed mainly to cutting of virgin forest, accelerated by hunting by Indians for ornaments, by scientists and collectors for specimens, and by local residents for curiosity and for food. The ivory-bill disappeared from most of Florida by 1900-15. By 1935 only a few remnant populations were left; the last reliable report from Gulf Hammock was in 1934 (Tanner 1942).

The Carolina parakeet (*Conuropsis carolinensis*) also occupied hydric hammock (McKinley 1985), but the recorded observations are too vague to provide a sense of the importance of this association. Apparently this species occurred primarily in cypress swamps and pine flatwoods, where it fed on conifer seeds. However, there are several specific references to Carolina parakeets seen or collected in hydric hammock: Gulf Hammock, Levy County (Laurent 1906; Gordon 1909); hammock woods and cypress swamps around Orlando and Sanford (Nehrling 1896); and numerous localities that are near both hydric hammock and primary feeding habitats.

Although it did not appear in the samples reported in Table 11 (perhaps due to the highly clumped dispersion and nomadic travels of its flocks), the cedar waxwing (*Bombycilla cedrorum*) is quite abundant in hydric hammock, especially in autumn and winter. The species is named for its preference for cedar berries (Martin *et al.* 1951); cedar berries may be exceptionally nutritious because of their high lipid content. A flock of waxwings usually feeds until satiated and then rests in a group on bare limbs of a tree near the food source. Most seeds pass rapidly through the digestive system and are deposited with the feces near but not under the parent tree, after which the birds often feed again. This association of seed-disperser and fruit-producer may be a primary force in maintaining the red-cedar component of the hydric hammock community.

4.4 MAMMALS

4.4.1 Community Structure

The mammals occurring in hydric hammock have been identified (Table 12), but the status designation provides poor resolution of abundance. In pitfall trapping directed at reptiles and amphibians, the small mammals captured in hydric hammock or bayhead (data pooled) per 1,000 pit-nights were 2.70 short-tailed shrews, 0.74 southeastern shrews, 0.25 least shrews, and 0.25 golden mice (Florida Game and Fresh Water Fish Commission 1976). In pitfall trapping directed at shrews in coastal hydric hammock, the small mammals captured in 772 pit-nights were three southeastern shrews, eleven short-tailed shrews, and one least shrew (Humphrey *et al.* 1986). Mammal tracks counted per mile in loblolly pine hydric hammock (Florida Game and Fresh Water Fish Commission 1976) included 11.33 for white-tailed deer, 2.00 for armadillo, and 0.67 for feral hogs. Individual mammals observed while night-lighting along 91 miles travelled in loblolly pine hydric hammock (Florida Game and Fresh Water Fish Commission 1976) included 34 white-tailed deer, 20 armadillos, 5 rabbits, 4 raccoons, and 3 opossums. Miscellaneous observations of mammals made per 100 hours in a habitat type (Florida Game and Fresh Water Fish Commission 1976) included: coastal hydric hammock--4 white-tailed deer and 4 long-tailed weasels; inland hydric hammock--3 white-tailed deer; and loblolly pine hydric hammock--22 armadillos, 8 white-tailed deer, 5 raccoons, 4 opossums, and 3 gray squirrels. The number of squirrels seen or heard per hour while conducting point-counts of birds (Florida Game and Fresh Water Fish Commission 1976) was highest among 18 habitat types in inland hydric hammock (2.40) and third highest in coastal hydric hammock (1.67), but none were detected in

Table 12. Occurrence of mammals in three variants of hydric hammock along the route of the proposed Cross-Florida Barge Canal, compiled from all sources (Florida Game and Fresh Water Fish Commission 1976).

Species	Coastal hydric hammock	Inland hydric hammock	Loblolly pine hydric hammock
Virginia opossum (*Didelphis virginiana*)	P-I	P-F	P-O
Southeastern shrew (*Sorex longirostris*)		P-I	
Short-tailed shrew (*Blarina carolinensis*)		P-I	
Least shrew (*Cryptotis parva*)		P-I	
Red bat (*Lasiurus borealis*)		P-I	
Seminole bat (*Lasiurus seminolus*)		P-I	
Yellow bat (*Lasiurus intermedius*)			P-O
Evening bat (*Nycticeius humeralis*)		P-I	
Southeastern big-eared bat (*Plecotus townsendii*)	P-I		
Nine-banded armadillo (*Dasypus novemcinctus*)			P-F
Eastern cottontail (*Sylvilagus floridanus*)			P-O
Marsh rabbit (*Sylvilagus palustris*)			P-O
Gray squirrel (*Sciurus carolinensis*)	C-F	C-F	P-I
Sherman's fox squirrel (*Sciurus niger shermani*)			P-I
Southern flying squirrel (*Glaucomys volans*)	P-O	C-F	
Eastern woodrat (*Neotoma floridana*)		P-I	
Cotton mouse (*Peromyscus gossypinus*)	P-F	P-F	P-I
Golden mouse (*Ochrotomys nuttalli*)		P-I	
Eastern harvest mouse (*Reithrodontomys humulis*)			P-I
Marsh rice rat (*Oryzomys palustris*)	P-O		
Hispid cotton rat (*Sigmodon hispidus*)	P-O	P-I	
Gray fox (*Urocyon cinereoargenteus*)			P-O
Long-tailed weasel (*Mustela frenata*)	P-I	P-I	
Striped skunk (*Mephitis mephitis*)			P-I
Raccoon (*Procyon lotor*)	P-F	P-O	P-I
Florida panther (*Felis concolor coryi*)		P-I	
Feral hog (*Sus scrofa*)			P-O
White-tailed deer (*Odocoileus virginianus*)	P-I	P-O	P-F

C = characteristic
P = present
F = frequent
O = occasional
I = infrequent

loblolly pine hydric hammock. The only small mammals trapped in coastal hydric hammock and inland hydric hammock in the St. Marks Wildlife Refuge, Wakulla County, Florida, were cotton mice, golden mice, and eastern woodrats (U.S. Fish and Wildlife Service [1980]).

Considering all the available information, at least the following species of mammals are characteristic of hydric hammock: opossum, southeastern shrew, short-tailed shrew, armadillo, gray squirrel, flying squirrel, cotton mouse, raccoon, feral hog, and white-tailed deer. The Florida panther has no specific habitat preference; it has been reported in coastal hammock (Pearson 1951) and hydric hammock (Layne 1970). The panther probably was characteristic of hydric hammock before the elimination of most breeding populations from northern Florida by man. Like the panther, the Florida black bear (*Ursus floridanus floridanus*) has no specific habitat preference. Instead, the preferred habitat of bears is a mosaic of wetland and upland forests (Harlow 1961), including hydric hammocks. Bears are still relatively common in and near the Ocala and Osceola National Forests, which include some hydric hammock habitat. Specific bear sightings were reported for the Ocala National Forest by Florida Game and Fresh Water Fish Commission (1976) and for the Osceola National Forest (U.S. Fish and Wildlife Service 1978). The southeastern brown bat (*Myotis austroriparius*) and bobcat (*Lynx rufus*) also occur in hydric hammocks (Pearson 1954).

4.4.2 Selected Species

Armadillos have been studied extensively in Florida, though not with reference to specific habitats. The diet of armadillos in Florida (Nesbitt *et al.* 1977) consists mostly of insects (78% by volume) and includes small quantities of earthworms (5%), reptiles and amphibians (1%), and birds and mammals (<1%). Though a variety of vertebrates are included in the diet, these account for <0.01% of the items eaten (Wirtz *et al.* 1985). Presumably an abundance of macroinvertebrates in the leaf litter of hydric hammock is responsible for the abundance of armadillos there. Armadillos dig burrows and den underground; in regularly flooded areas, burrows are placed in patches of high ground.

Gray squirrels occur at densities of roughly 5 per ha in inland hydric hammock and 2.5 per ha in coastal hydric hammock in autumn (Jennings 1951). Staple foods of the gray squirrel in hydric hammock and adjacent forests are the seeds of loblolly pine and the seeds, buds, and flowers of hickories, oaks, elms, magnolias, and red maples. The abundance of staple foods shifts seasonally among local plant communities, affecting the local distribution of squirrels. From September to mid-January, acorns and hickory nuts are available in all habitats, squirrels are widely distributed, and they become fat. By mid-January the supply of hard mast is exhausted, but buds and seeds of elm and maple become abundant in hydric hammock and river swamp, and squirrels (perhaps the entire population) become concentrated in these communities, with a density of 13.8 per ha recorded by Jennings. At this time squirrels abandon coastal hydric hammock, because cedar berries are no longer available; little food is produced and no squirrels are present there until autumn. In spring and summer, squirrels are dispersed throughout river swamp, hydric hammock, and mesic hammock. Green nuts of hickories, oaks, and loblolly pines are eaten in July and August. Usually a gray squirrel can find at least two of these plant communities by moving only a few hundred feet, because many hydric hammocks are small and ecotonal or, if large, are interspersed with dendritic swamps and mesic ridges. Squirrels scatterhoard acorns in the soil, especially at elevated sites near the bases of trees and stumps. Acorns buried during drought periods may be covered subsequently by standing water before they are consumed. The supply of stored food helps support the squirrel population through the winter and may be an essential resource for the spring breeding season. While lack of an acorn crop in one or a few species of oak is normal, a complete failure of acorn mast in all species is uncommon. In such a mast failure, the few available acorns were completely harvested by wildlife by mid-October; thereafter the squirrels survived by recovering stored acorns (Jennings 1951). Gray squirrels nest in tree cavities (usually in live oaks) during winter, and in the spring they build nests made of leaves and twigs or of cabbage palm fibers. Ordinarily a spring and a fall breeding season occur, but spring breeding does no specific habitat preference; it has been reported in coastal hammock (Pearson 1951) and hydric hammock (Layne 1970). The panther probably was characteristic of hydric hammock before the elimination of most breeding populations from northern Florida by man. Like the panther, the Florida black bear (*Ursus floridanus floridanus*) has no specific habitat preference. Instead, the preferred habitat of bears is a mosaic of wetland and upland forests (Harlow 1961), including hydric hammocks. Bears are still relatively common in and near the Ocala and Osceola National Forests, which include some hydric hammock habitat. Specific bear sightings were reported for the Ocala National Forest by Florida Game and Fresh Water Fish Commission (1976) and for the Osceola National Forest (U.S. Fish and Wildlife Service 1978). The southeastern brown bat (*Myotis austroriparius*) and bobcat (*Lynx rufus*) also occur in hydric hammocks (Pearson 1954).

4.4.2 Selected Species

Armadillos have been studied extensively in Florida, though not with reference to specific habitats. The diet of armadillos in Florida (Nesbitt *et al.* 1977) consists mostly of insects (78% by volume) and includes small quantities of earthworms (5%), reptiles and amphibians (1%), and birds and mammals (<1%). Though a variety of vertebrates are included in the diet, these account for <0.01% of the items eaten (Wirtz *et al.* 1985). Presumably an abundance of macroinvertebrates in the leaf litter of hydric hammock is responsible for the abundance of armadillos there. Armadillos dig burrows and den underground; in regularly flooded areas, burrows are placed in patches of high ground.

Gray squirrels occur at densities of roughly 5 per ha in inland hydric hammock and 2.5 per ha in coastal hydric hammock in autumn (Jennings 1951). Staple foods of the gray squirrel in hydric hammock and adjacent forests are the seeds of loblolly pine and the seeds, buds, and flowers of hickories, oaks, elms, magnolias, and red maples. The abundance of staple foods shifts seasonally among local plant communities, affecting the local distribution of squirrels. From September to mid-January, acorns and hickory nuts are available in all habitats, squirrels are widely distributed, and they become fat. By mid-January the supply of hard mast is exhausted, but buds and seeds of elm and maple become abundant in hydric hammock and river swamp, and squirrels (perhaps the entire population) become concentrated in these communities, with a density of 13.8 per ha recorded by Jennings. At this time squirrels abandon coastal hydric hammock, because cedar berries are no longer available; little food is produced and no squirrels are present there until autumn. In spring and summer, squirrels are dispersed throughout river swamp, hydric hammock, and mesic hammock. Green nuts of hickories, oaks, and loblolly pines are eaten in July and August. Usually a gray squirrel can find at least two of these plant communities by moving only a few hundred feet, because many hydric hammocks are small and ecotonal or, if large, are interspersed with dendritic swamps and mesic ridges. Squirrels scatterhoard acorns in the soil, especially at elevated sites near the bases of trees and stumps. Acorns buried during drought periods may be covered subsequently by standing water before they are consumed. The supply of stored food helps support the squirrel population through the winter and may be an essential resource for the spring breeding season. While lack of an acorn crop in one or a few species of oak is normal, a complete failure of acorn mast in all species is uncommon. In such a mast failure, the few available acorns were completely harvested by wildlife by mid-October; thereafter the squirrels survived by recovering stored acorns (Jennings 1951). Gray squirrels nest in tree cavities (usually in live oaks) during winter, and in the spring they build nests made of leaves and twigs or of cabbage palm fibers. Ordinarily a spring and a fall breeding season occur, but spring breeding does not take place in years of mast failure. Deaths due to starvation or disease have not been recorded in this habitat.

The eastern woodrat is most abundant in the ecotone between mesic and hydric hammocks (Pearson 1952). Breeding occurs year-round. Nests are marked only by very small piles of sticks, and they are found in barns, hollow logs, and subterranean chambers under stumps or the bases or roots of trees.

The golden mouse is most plentiful in areas having a dense thicket or shrub layer and a sparse herbaceous ground cover. Nests are in dense shrubs or subterranean chambers. Golden mice use shrubs, hollow logs, and underground tunnels as escape cover (Pearson 1954). It is important to note that although Pearson (1954) found golden mice only in adjacent mesic hammocks, the Florida Game and Fresh Water Fish Commission (1976) and the U.S. Fish and Wildlife Service [1980] found them in hydric hammock.

The cotton mouse is the most abundant mammal in Gulf Hammock (Pearson 1953, 1954). Cover and nest sites are more common in hydric hammock than in adjacent mesic hammock. Males have larger home ranges than females. Home ranges of males overlap one another, but those of females do not. Home ranges are smaller when population density is high than when it is low. Breeding takes place during most of the year, but females seldom are pregnant in summer (May through August). Nests are in logs, stumps, and bases of trees; often they contain caches of live oak and swamp laurel oak acorns. The most important factor affecting populations probably is the quantity of acorn mast--high densities of cotton mice decline after a mast failure. Potential competitors in poor mast years include wild turkeys, blue jays, common grackles, gray squirrels, eastern woodrats, opossums, white-tailed deer and (most importantly) feral hogs. Potential predators include bobcats, barred owls, and several species of snake. Parasitism by cuterebrid fly larvae (Cuterebridae) in this habitat is heavy and may be fatal. Cotton mice readily swim, climb vegetation, and jump to the ground from considerable heights.

The raccoon is an opportunist and generalist in both habitat and diet. Raccoons occur in every terrestrial and wetland habitat within their overall range. Plants (mostly nuts, drupes, and berries) make up 50%-80% of the raccoon diet. The drupes and berries have seeds that probably are dispersed rather than destroyed, including beautyberry, blackberry, blueberies, cabbage palm, palmettos, elderberry, grapes, greenbriars, hollies, pepper vine, persimmon, red cedar, sugarberry, swamp tupelo, and viburnum (F. Harper 1927; Ivey 1947; Caldwell 1963; Johnson 1970; Halls 1977).

The black bear population of Gulf Hammock was exterminated by about 1950, because the local people considered bears destroyers of property (Pearson 1954). The remaining fragments of bear distribution include extensive areas of hydric hammock along the gulf coast of Pasco and Hernando Counties and Taylor and Wakulla Counties (Brady and Maehr 1985). Extant populations in the Osceola and Ocala National Forests also include local hydric hammocks in their ranges. Like other large mammals, the black bear has broad habitat requirements and can live wherever sufficient foraging areas, denning sites, and escape cover are available. Areas in Florida occupied by black bears consist of large tracts of undeveloped forests containing diverse vegetation types (Harlow 1961). No seasonal movements among habitats by Florida black bear are known, but they probably occur, especially in spring when mast supplies are exhausted.

The black bear is an omnivore, but most of its diet is plant material, and mast is the prominent component. Examination of stomach contents and scats of black bears in a variety of Florida habitats (Maehr and Brady 1984) showed that the diet of black bears in spring is dominated by cabbage palm hearts, early growths of alligator flag (*Thalia geniculata*) and saw palmetto, and other non-fruit plant parts, plus honeybees (*Apis mellifera*) and carpenter ants (*Campanotus*). In summer the diet shifts from soft vegetative parts to ripening soft mast and early hard mast, including blueberries, gallberries, blackberries, saw palmetto berries, honeybees, bess beetles (*Odontotaenius disjunctus*), carpenter ants, walkingsticks (*Anisomorpha buprestoides*), paper wasps (*Polistes*), and bumblebees (*Bombus bimaculatus*). In autumn and winter the diet consists of hard mast and fruits of oaks, saw palmetto, swamp tupelo, cabbage palm, needle palm, gallberries, honeybees, and yellow jackets (*Vespula*). Bears feed on acorns both on the ground and arboreally. Vertebrates account for only about 5% of the diet; species include gopher tortoise (*Gopherus polyphemus*), armadillo, feral hog, and white-tailed deer. Black bears actively maintain certain species in the plant communities they occupy by dispersing undigested seeds of the fruits they eat (Rogers and Applegate 1983; Maehr 1984). Major species involved in this mutualism include saw palmetto, cabbage palm, needle palm, swamp tupelo, blueberry, and raspberry. Probably numerous other species (see Maehr and DeFazio 1985) also gain this advantage as minor dietary components of bears.

Sites preferred by black bears for winter denning are cavities in large trees, which provide protection from weather and disturbance (Hamilton and Marchinton 1980; Pelton *et al.* 1980). Denning is especially important for sows with cubs. The smaller size of sows and the tendency of sows to den earlier than boars (Pelton *et al.* 1980) may give females access to smaller cavities and the best-protected den sites. Large, dense thickets provide escape cover from most dangers (U.S. Fish and Wildlife Service 1978), but hunters' dogs are deterred only by very large water-filled areas. In Florida the best such escape cover is bayheads, titi swamps, and hardwood swamps (Layne 1976; Williams 1978). The home ranges of black bears overlap broadly, but individuals avoid one another. Subadult males may be killed or driven away by adult males. Dispersing subadults often move out of suitable habitat and are shot by humans. Home ranges of black bears in the Osceola National Forest (which contains many very small patches of hydric hammock) are large and variable relative to those in other areas of the United States, probably because of low quality of the habitat (James Mykytka, Reynolds, Smith and Hills, Tampa; pers. comm.).

The Florida panther inhabited hydric hammock near the town of Gulf Hammock (Levy County) and east of Cedar Key until about 1950 (e.g., Pearson 1954). Now it is widely thought that all breeding populations have been extirpated from northern Florida. However, occasional reports like the confirmed sighting near the northern edge of the Ocala National Forest (Table 12) and regular reports in the 1970's and 1980's in and near hydric hammock on the west bank of the St. Johns River in Orange and Seminole Counties indicate that a few individuals remain in this habitat.

Domestic hogs were first introduced into Florida in 1539 by Hernando De Soto (Lewis 1907). Although now abundant in hydric hammock, feral hogs have not been studied there. In South Carolina, feral hogs usually avoid salt marsh but make heavy use of fresh- and brackish-water marsh and of cypress-gum swamps (except during autumn); they use upland pine habitats in proportion to availability, and they use upland hardwood forests lightly except when acorns are available (Wood and Brenneman 1980). Feral hogs feed in oak stands in autumn and winter as long as acorns are available, and at other times they feed on grasses, roots, and tubers on the margins of marshes and swamps (Wood and Roark 1980). Where fewer habitats are present and individual hogs compete intensely for food (e.g., on Ossabaw Island, Georgia), feral hogs frequently use salt marsh (Graves and

Graves 1977). These observations suggest that the supply of mast, particularly acorns, is a key resource for feral hogs in hydric hammock. In some seasons or during mast failures, roots are a dietary staple; feral hogs also eat tree seedlings, chewing the roots, swallowing the sap and starches, and rejecting the woody tissue (Wood and Roark 1980). This destruction of roots and seedlings can deter forest regeneration. Feral hogs are intense competitors with native wildlife for the supply of fallen mast. During a year of mast failure, they may have serious impacts on turkey, deer, and (to a lesser extent) bear populations.

White-tailed deer were studied in a very general way in Gulf Hammock by Swindell (1949). According to Bartram (1791) and early residents, deer were very abundant in the region. Market hunting was intense in the late 1800's, and by 1925 the population was so reduced that sightings of deer sign in Gulf Hammock were unusual. Subsequently the deer population increased to an estimated 100-325 animals for the entire area by 1948-49. The legal harvest that year was documented as one deer per 900 acres of suitable habitat. Swindell judged that hunting (which legally allowed harvest of bucks only) continued to be the primary limiting factor, based on the prevailing buck:doe ratio of 1:2.5 to 1:4, with illegal "fire hunting" (with headlights at night) of both sexes accounting for at least 25% of the legal kill. Legal hunting usually employed dogs; this method was very effective and caused survivors to abandon their home ranges temporarily to move to remote portions of the hammock. Swindell considered the habitat to be excellent in quality but underused by deer. Deer foraged mainly in hydric hammock in the dry springtime and moved to the higher mesic hammocks in summer when hydric hammock flooded. In autumn, deer sought acorns wherever they occurred, preferring acorns from live oak > swamp chestnut oak > laurel and water oaks. Diet of deer in the Gulf and Richloam Hammocks in late fall and winter was 58% acorns, 30% woody plants, 6% forbs, and 6% mushrooms (Harlow 1965).

Subsequently 122,000 acres of Gulf Hammock became the Gulf Hammock Wildlife Management Area. Kill data from the period 1953-56 indicated a population of 1,400 to 1,800 deer for the area. Along with an estimated 3,000 cattle and 6,000 feral hogs, the total density of ungulates was approximately one per 11 acres--among the heaviest concentrations in Florida (Harlow 1959).

CHAPTER 5. PLANT-ANIMAL INTERACTIONS

A primary value of hydric hammocks for wildlife is the numerous tree cavities used by many species of wildlife for nesting or cover. Den trees (live cavity-bearing trees) remain standing much longer (Carey 1983) than snags (dead cavity-bearing trees). In a survey of den trees in various habitats in Florida and South Carolina, McComb *et al.* (1986) found that old forest stands (>60 years) had 3 to 20 times more dens than in young stands. The survey classified forest types into groups found in both states (hydric hammock does not occur in South Carolina; Florida hammmocks either were included in another group or were not sampled). The oak-tupelo-bald cypress and palm categories had respectively the highest and second-highest number of den trees and dens among 12 forest types in Florida. Loblolly pine plantations, to which hydric hammocks often are converted, had among the lowest number of den trees and dens--roughly 10% as many as in palm forest and 5% as many as in oak-tupelo-bald cypress forest.

Another feature of hydric hammock of great significance to wildlife is the abundance and character of the seeds and fruits it produces. Seasonally abundant seeds and fruits are important sources of protein and phosphorus (Short and Epps 1976), which frequently are in limited supply in forage available in southern forests (Blair and Epps 1969). The phosphorus requirement in the diet of growing and developing wild turkeys is 0.75%-0.80%, 1.0% for the northern bobwhite, 0.5% for tree squirrels, and >0.25% for white-tailed deer (Halls 1970). Average values show that legume seeds are the best source of both nutrients (31.2% and 0.54% of dry matter, respectively; Short and Epps 1976), but the only common species of legume in hydric hammock is water locust, which occurs on the marsh edge of some stands. Water locust seeds are consumed by black bears, cattle, and feral hogs. Numerous other seeds, including those of pines and sweetgum, average lower in protein (17.6% of dry matter) and phosphorus (0.37%) than legumes, but higher than acorns and fleshy and dried fruits. Pine seeds are used by squirrels and apparently were a dietary staple of Carolina parakeets. Sweetgum seeds are a mainstay for overwintering American goldfinches. Dried fruits, including the samaras of maple, elm, and ash, also are intermediate in content of protein (11.9% of dry matter) and phosphorus (0.24%), and they are important foods when fresh. At that time, they are heavily eaten by animals such as the northern cardinal and gray squirrel. However, when dried, the high fiber content of these seeds makes their digestibility very low. Despite relatively low content of protein and phosphorus, acorns (5.9% and 0.09% of dry matter, respectively) and fleshy fruits (8.4% and 0.22% of dry matter, respectively) are extremely valuable because of their palatability, seasonal abundance, and accessibility to a wide variety of wildlife species. In particular, acorns are available for a long period in autumn and winter. Acorns and fleshy fruits are dietary staples of numerous species of birds and mammals, including the important game species (wild turkey, gray squirrel, raccoon, black bear, feral hog, and white-tailed deer).

Consumption of fleshy fruits by resident and migrant birds has not been examined in hydric hammock, but it has been studied in mesic hammock in Florida (Skeate 1987). Most species of frugivorous birds are mutualistic seed-dispersers; only three species (northern cardinal, summer tanager, and rose-breasted grosbeak, *Pheucticus ludovicianus*) are fruit "thieves" that ate the pulp and dropped the seed, undispersed, below the parent plant. Consequently the support of this segment of the avifauna has reciprocal implications for the reproduction and resilience of a subset of the plant community. In mesic hammock this mutualism involves 22 species of birds and 45 species of plants, dominated by migrant species of birds and plants that fruit in fall or fall-to-winter. The greatest proportions of fruits are eaten by wintering American robins (57%) and cedar waxwings (20%); the greatest diversity of fruits are eaten by wintering robins (18 species) and hermit thrushes (*Catharus guttatus*, 16 species). The pace of seed-dispersal quickens in September and October, beginning with arrival of four transient species of thrushes and continuing with the arrival of wintering robins, waxwings, hermit thrushes, and yellow-rumped warblers (Figure 39). By the peak of seed-dispersal activity in December, 28 species of bird-dispersed plants are in fruit, being consumed by 10 winter and 4 year-round resident species of bird. Seed-dispersal activity diminishes in March, and by April-May only 3 species of bird-dispersed plants are in fruit, and the disperser association diminishes to 4 summer and 4 year-round resident species of bird. This forest has proportionately less summer fruiting (a total of 9 species) and more winter fruiting (4 species in addition to the 19 fall-winter fruiting species) than in a forest in Illinois.

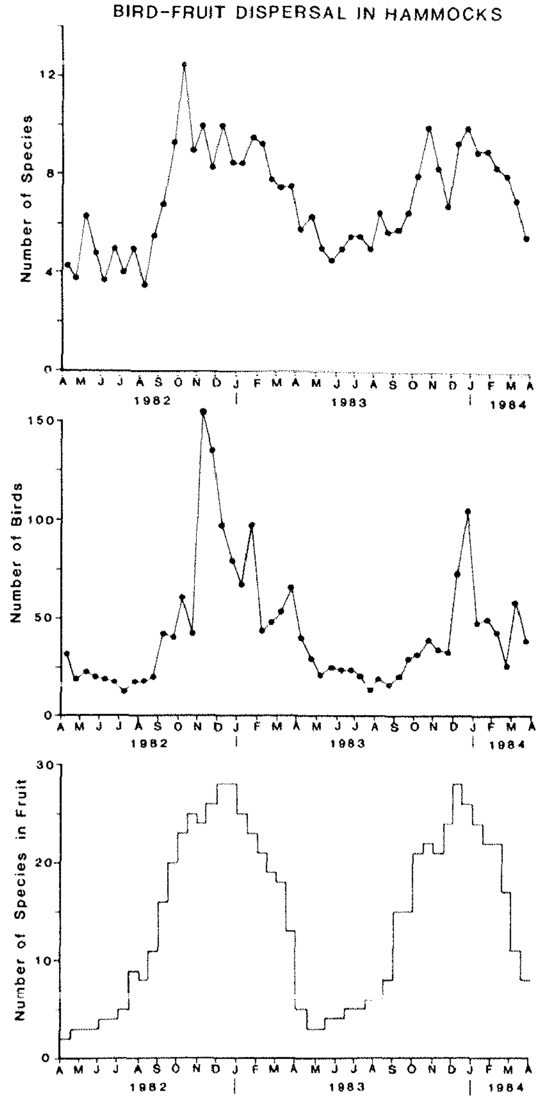


Figure 39. Phenology of bird diversity and abundance and the number of species of plants producing fruits edible to birds in a mesic hammock in San Felasco State Preserve, Alachua County, Florida (Skeate 1987).

Maintenance and elaboration of the association of bird and plant mutualists is thought to be driven by a few pairs of strongly interacting birds and plants (Skeate 1987). These are the veery (*Catharus fuscescens*) with Virginia creeper (*Parthenocissus quinquefolia*), *Aralia spinosa*, and flowering dogwood (*Cornus florida*); robins with dogwood, red bay (*Persea borbonia*), and cherry laurel (*Prunus caroliniana*); and waxwings with mistletoe (*Phoradendron serotinum*). All these plants provide excellent food because their fruits are unusually rich in lipids. Consumption of these primary dietary items indirectly favors seed-dispersal of other species that are less common or have less rewarding fruits, because the primary frugivores have varied diets. At the same time, less abundant or effective species of frugivorous birds, each with its own varied diet, are encouraged in the association by the predictably timely resource of a variety of fruits. Wide-ranging species of primary plants with high-lipid fruit (creeper, dogwood) supply migrating frugivores with a high-quality supply of food continuously during migration southward through the Atlantic flyway, and similar species with ranges restricted to the southeastern United States offer resources to support the bird populations during winter.

Another mutualism that may be important in succession or invasion of hydric hammock is an association of tree swallows and yellow-rumped warblers with wax-myrtle and a microorganism (the soil bacterium *Frankia*). This interaction is important because of the aggressive pioneering of wax-myrtle, made possible by the nitrogen-fixing of its actinomycete-nodulated roots, its allelopathy to young competitors, and its broadcast dispersal by large flocks of overwintering, omnivorous birds (Schnoes and Humphrey 1987).

Generalized consumers (such as raccoons and bears) and scatter-hoarders (such as blue jays and gray squirrels) also are prominent dispersers of seeds of plants of hydric hammock. Seedlings of cabbage palm and red bay have been observed growing in bear scats (Maehr 1984). The diversity of drupes and berries eaten by bears and raccoons suggests the size of the assemblage of mutualists involved. Although generalized consumers usually kill nuts by eating them and hence do not benefit oak trees, acorns nonetheless are crucial to the interactive roles of generalized consumers by attracting them to the sites where drupes and berries also are eaten and dispersed. In contrast, jays and squirrels store nuts (especially acorns) individually in the soil for later consumption. Nuts forgotten or left because of death or departure of the consumer contribute to reproduction of the mature forest or succession after disturbance or lumbering of the forest.

The diversity of mast-producing species in southern forests produces a composite phenology yielding food year-round for generalized consumers capable of eating both hard and soft mast (Harris *et al*. 1979). However, the continuity of this supply is incomplete within specific types of forest. For example, little hard mast is produced in hydric hammock in winter, and duration of the hiatus between consumption of the last acorns and availability of the first elm and maple seeds varies according to the volume of the year's acorn crop. To bridge discontinuities in the seasonal food supply, juxtaposition or interspersion of two or more types of forest is critically important to many mobile or large species of wildlife that move to find food. Documented examples are given in the discussion of individual species of mammals and birds, Chapter 4.

CHAPTER 6. LINKAGES WITH OTHER ECOSYSTEMS

Hydric hammocks are interconnected with upland and downslope communities by flows of water and movements of animals. Because of high ground-water level and, sometimes, discharge from deep aquifers, a hammock may be connected to recharge areas, such as the sandy uplands of the central Florida ridge, which are located far beyond the watershed defined by surface drainage. Hydric hammocks often intercept surface and ground water before it enters rivers and estuaries, perhaps altering the pattern and quality of flow. Some animals merely pass through hydric hammocks en route to preferred habitat, but for others, this forested wetland provides critical shelter and food during part of their life cycles. Movements of animals, and their transport of fruits and seeds, link both the plant and animal components of hydric hammocks to adjacent and distant communities.

6.1 WITH ESTUARIES

The extensive band of hydric hammocks along the gulf coast of Florida (Figure 1) links upland and salt marsh/estuarine systems. The most important feature of this coupling is the modification, by passage of water through hydric hammock, of the quantity, timing, and quality of freshwater that reaches the estuaries. Changes in one or more of these parameters can greatly alter estuarine structure and productivity.

The flow of freshwater into estuaries has numerous consequences (Snedaker and deSylva 1977), of which the major ones are the reduction of salinity; the induction of freshwater and saltwater mixing; the establishment of horizontal and vertical gradients of salinity; and the addition of nutrients, dissolved and particulate organic matter, and sediments derived from the watershed. The quantity and timing of freshwater delivery determine, in part, seasonal changes in physico-chemical regimes that in turn are reflected in regular patterns of estuarine use by animals. Year-round inhabitants, mainly invertebrates, are plentiful, but the great number and variety of part-time residents distinguish estuaries. In the southeastern United States, most fish and invertebrate species of commercial importance use estuaries and their fringing salt marshes as nurseries, entering and leaving the shallow waters in a regular seasonal progression from late fall through early summer (Sheridan and Livingston 1979; Rogers *et al.* 1984). Temporal and spatial distributions of species within estuaries are associated with physico-chemical and biotic factors, many of which are influenced by freshwater inflow (e.g., salinity and food availability). In coastal waters, annual freshwater input is correlated with production of some invertebrate and fish species, but the mechanisms generally are not well understood (Meeter *et al.* 1979; Sinclair *et al.* 1986). The effect of freshwater discharge on the abundance of oysters is mediated by changes in salinity. The optimal salinity range for oyster growth in Apalachicola Bay is 15%-25%, but a more important role of salinity is indirect in that low salinity excludes important predators of oysters (Menzel *et al.* 1966).

How forested wetlands influence the delivery of freshwater to estuaries can be inferred from the consequences of timber harvesting in swamps within the drainage area of Apalachicola Bay, in northwestern Florida (Livingston and Duncan 1979). Normally the Apalachicola River's flow into the bay peaks in winter-spring, whereas local rainfall is highest in summer. The discrepancy in seasonal patterns of river flow and rainfall is due to the higher evapotranspiration of watershed vegetation in summer. In contrast, runoff from clearcut swamps is pulsed and timed with bouts of rain. Hydric hammocks also are likely to stabilize the timing of freshwater inflow to adjoining estuaries and to attenuate peak flows that, unchecked, cause abrupt changes in salinity. How forested wetlands influence the quality of freshwater inflow to estuaries is less clear. Both the magnitude and timing of flooding affect the amounts and forms of materials transported from forested wetlands to estuaries (Livingston 1984). Nutrient and pollutant assimilation by wetlands is enhanced by slow passage of water over these flat, densely vegetated areas. On the other hand, materials can be transferred from wetlands to receiving waters during periods of high flow. A strong positive correlation between rate of flow and concentration of detritus was observed during winter and spring in the lower Apalachicola River (Livingston 1984). No correlation was found in summer; then, even occasional high flows contained low levels of detritus. Particulate organic matter was transferred from the floodplain to the estuary primarily during winter and spring floods because river flow rates were high and because the floods occurred soon after the litter-fall peak (Elder and Cairns 1982). Considered over an annual cycle, the floodplain forest of the Apalachicola River exported nutrients to the estuary (Mattraw and Elder 1982). Hydric hammock is flooded less frequently and severely than river-dominated floodplain forest, so net export of nutrients is likely to be small. Floods due to hurricanes may occasionally flush detritus from coastal hydric hammocks into estuaries, although their timing (late summer) is such that the standing crop of litter is likely to be small.

6.2 WITH ADJACENT AND DISTANT HABITATS

Many kinds of animals move among habitats to find essential support during the annual cycle or in different stages of their life cycles. Local movements of resident animals within their home ranges can link hydric hammock with upslope habitats. However, this phenomenon has seldom been documented because of the paucity of research on animals inhabiting hydric hammocks. The reports of movements of eastern indigo snakes between hydric hammocks and clearcuts [Moler 1985] and of seasonal shifts in density of gray squirrels between hydric and mesic hammock (Jennings 1951) are exceptions that prove the rule.

Longer movements of non-sedentary passerine birds that spend much of the winter in hydric hammock likewise link this habitat with upland forests in Florida. While on winter range, these birds are nomadic and non-specific in their habitat requirements. In late winter and early spring, large numbers of normally forest-dwelling passerines appear in various upland and disturbed habitats to take advantage of isolated and newly available food resources. Unfortunately, this movement is so complex and variable among places and years as to seem chaotic; it probably will never be documented adequately without a massive investment of funding for research. Some of the most common species involved are seed-dispersing mutualists (tree swallow, cedar waxwing, American robin, yellow-rumped warbler); this linkage presumably also maintains similarities in composition of the various plant communities.

Finally, long-distance, seasonal migrations of these same species between breeding and non-breeding ranges (Figure 40) link otherwise unrelated habitats through support of the birds over their annual reproductive cycles. Especially for strongly mutualistic species, these linkages set up interdependencies, the scope of which can only dimly be envisaged. The tree swallow, for example, is omnivorous during winter and strikingly involved in plant succession of Florida habitats because of its great numbers and wide dispersal of seeds of the pioneering wax-myrtle. On breeding range, the tree swallow population is limited by a declining resource, cavities made in trees by other animals (Erskine 1979). Possibly a decline in nesting of tree swallows in eastern North America may affect succession of hydric hammocks.

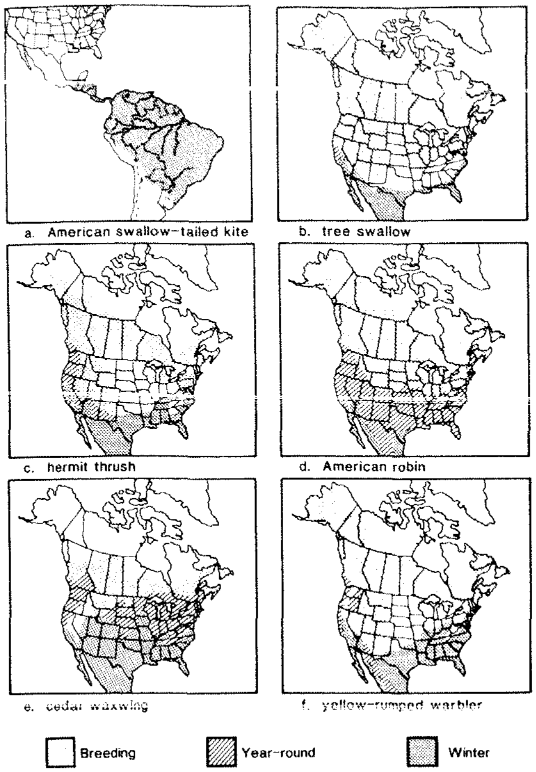


Figure 40. Breeding and winter ranges of selected migrant birds that live in hydric hammock for part of the year: (a) American swallow-tailed kite; (b) tree swallow; (c) hermit thrush; (d) American robin; (e) cedar waxwing; and (f) yellow-rumped warbler.

REFERENCES

Applin, P.L. 1951. Preliminary report on buried pre-Mesozoic rocks in Florida and adjacent states. U.S. Geol. Surv. Inf. Circ. 47. 15 pp.

Barry, J.M. 1980. Natural vegetation of South Carolina. University of South Carolina Press, Columbia. 214 pp.

Bartram, W. 1791. Travels through North and South Carolina, Georgia, East and West Florida. Q.M. van Doren, ed. Dover Publications, New York (1928 reprint). 414 pp.

Bechtold, W.A., and H.A. Knight. 1982. Florida's forests. U.S. Dep. Agric. For. Serv. Resour. Bull. SE-62. 84 pp.

Bedinger, M.S. 1978. Relation between forest species and flooding. Pages 427-435 *in* P.E. Greeson, J.R. Clark, and J.E. Clark, eds. Wetland functions and values: the state of our understanding. American Water Resource Association, Minneapolis, Minn.

Blair, R.M., and E.A. Epps, Jr. 1969. Seasonal distribution of nutrients in plants of seven browse species in Louisiana. U.S. Dep. Agric. For. Serv. Res. Pap. SO-51. 35 pp.

Brady, J.R., and D.S. Maehr. 1985. Distribution of black bears in Florida. Florida Field-Nat. 13:1-7.

Brinson, M.M., A.E. Lugo, and S. Brown. 1981. Primary productivity, decomposition, and consumer activity in freshwater wetlands. Annu. Rev. Ecol. Syst. 12:123-161.

Brown, K.E. 1973. Biological life history and geographical distribution of the cabbage palm, *Sabal palmetto*. Ph.D. Dissertation. North Carolina State University, Raleigh. 101 pp.

Brown, M.T., and E.M. Starnes. 1983. A wetlands study of Seminole County: identification, evaluation and preparation of development standards and guidelines. Cent. Wetlands Tech. Rep. No. 41. University of Florida, Gainesville. 284 pp.

Brown, S. 1981. A comparison of the structure, primary productivity, and transpiration of cypress ecosystems in Florida. Ecol. Monogr. 51:403-427.

Caldwell, J.A. 1963. An investigation of raccoons in north-central Florida. M.S. Thesis. University of Florida, Gainesville. 107 pp.

Carey, A.B. 1983. Cavities in trees in hardwood forests. Pages 167-184 *in* J.W. Davis, G.A. Goodwin, and R.A. Ockenfels, eds. Snag habitat managment: proceedings of the symposium. U.S. For. Serv. Gen. Tech. Rep. RM-99.

Clewell, A.F. 1981. Natural setting and vegetation of the Florida panhandle. Contract No. DACW01-77-C-0104. U.S. Army Corps of Engineers, Mobile, Ala. 773 pp.

Clewell, A.F., J.A. Goolsby, and A.G. Shuey. 1982. Riverine forests of the south prong Alafia River system, Florida. Wetlands 2:21-72.

Conner, W.H., and J.W. Day, Jr. 1976. Productivity and composition of a baldcypress-water tupelo site and a bottomland hardwood site in a Louisiana swamp. Am. J. Bot. 63:1354-1364.

Conner, W.H., and J.W. Day, Jr. 1982. The ecology of forested wetlands in the southeastern United States. Pages 69-87 *in* B. Gopal, R.E. Turner, R.G. Wetzel, and D.F. Whigham, eds. Wetlands--ecology and management. National Institute of Ecology and International Scientific Publications, Jaipur, India.

Conover, C.S., J.J. Geraghty, and G.G. Parker. 1984. Ground water. Pages 36-53 *in* E.A. Fernald and D.J. Patton, eds. Water resources atlas of Florida. Florida State University, Tallahassee.

Cooke, C.W. 1939. Scenery of Florida as interpreted by a geologist. Fla. Geol. Surv. Bull. No. 17. 118 pp.

Cowardin, L.M., V. Carter, F.C. Golet, and E.T. LaRoe. 1979. Classification of wetlands and deepwater habitats of the United States. U.S. Fish Wildl. Serv., Biol. Serv. Program FWS/OBS-79/31. 103 pp.

Cox, J. 1987. The breeding bird survey in Florida: 1969-1983. Fla. Field Nat. 15:29-56.

Davis, J.H., Jr. 1943. The natural features of southern Florida. Fla. Geol. Surv. Bull. No. 25. 311 pp.

Davis, J.A., Jr.. 1957. A new shrew (*Sorex*) from Florida. Am. Mus. Novit. 1844:1-9.

Dohrenwend, R.E., and L. Harris. 1975. A climatic change impact analysis of peninsular Florida life zones. Pages 107-122 *in* Impacts of climatic change on the biosphere. Climatic Impact Assessment Program, Monogr. 5, Part 2, U.S. Dep. Transp., Washington, D.C.

Dunn, W.J. 1982. Plant communities and vascular flora of San Felasco Hammock, Alachua County, Florida. M.S. Thesis. University of Florida, Gainesville. 134 pp.

Elder, J.F., and D.J. Cairns. 1982. Production and decomposition of forest litter fall on the Apalachicola River flood plain, Florida. U.S. Geol. Surv. Water Supp. Pap. 2196-B. 42 pp.

Erskine, A.J. 1979. Man's influence on potential nesting sites and populations of swallows in Canada. Canad. Field-Nat. 93:371-377.

Ewel, K.C., and W.J. Mitsch. 1978. The effects of fire on species composition in cypress dome ecosystems. Fla. Sci. 41:25-31.

Faulkner, G.L. 1973. Geohydrology of the Cross-Florida Barge Canal area with special reference to the Ocala vicinity. U.S. Geol. Surv. Water-Resour. Invest. 1-73. 117 pp.

Florida Game and Fresh Water Fish Commission. 1976. Cross Florida Barge Canal restudy report. Wildlife study. Vols. 1-5. Wildlife Research Laboratory, Gainesville, Fla.

Florida Game and Fresh Water Fish Commission. 1987. Official lists of endangered and potentially endangered fauna and flora in Florida. Tallahassee, Fla. 19 pp.

Florida Natural Areas Inventory. 1984. Florida natural communities. The Nature Conservancy, Tallahassee, Fla. 12 pp.

Fowells, H.A. 1965. Silvics of forest trees of the United States. U.S. Agric. Handb. No. 271. 762 pp.

Franz, R. 1976. Freshwater crustaceans: their distribution in the Cross Florida Barge Canal area. Pages J-1 to J-19 *in* Florida Game and Fresh Water Fish Commission, Cross Florida Barge Canal Restudy Report. Wildlife study, Vol. 5.

Gill, C.J. 1970. The flooding tolerance of woody species--a review. For. Abstr. 31:671-688.

Godfrey, R.K. 1979. Pink-root. Pages 160-161 *in* D.B. Ward, ed. Plants. Rare and endangered biota of Florida, Vol. 5. University of Florida Presses, Gainesville.

Gordon, T. 1909. Ivory-billed woodpecker. For. & Stream 72:972.

Gosselink, J.G., S.E. Bayley, W.H. Conner, and R.E. Turner. 1981. Ecological factors in the determination of riparian wetland boundaries. Pages 199-219 *in* J.R. Clark and J. Benforado, eds. Wetlands of bottomland hardwood forests. Developments in Agricultural and Managed-forest Ecology, Vol. 11. Elsevier Scientific, New York.

Graves, H.B., and K.L. Graves. 1977. Some observations on biobehavioral adaptations of swine. Pages 103-110 in G.W. Wood, ed. Research and management of wild hog populations. Belle W. Baruch Forest Science Inst., Clemson University, Georgetown, S.C.

Greller, A.M. 1980. Correlation of some climate statistics with distribution of broadleaved forest zones in Florida, U.S.A. Bull. Torrey Bot. Club 107:189-219.

Halls, L.K. 1970. Nutrient requirements of livestock and game. Pages 10-18 *in* Range and wildlife habitat evaluation--a research symposium. U.S. Dep. Agric. For. Serv. Misc. Publ. 1147.

Halls, L.K., editor. 1977. Southern fruit-producing woody plants used by wildlife. U.S.D.A. For. Serv. Gen. Tech. Rep. SO-16. 235 pp.

Hamilton, R.J., and R.L. Marchinton. 1980. Denning and related activities of black bears in the coastal plain of North Carolina. Pages 121-126 *in* C.J. Martinka and K.L. McArthur, eds. Bears--their biology and management. Bear Biol. Assoc. Conf. Ser. 3. U.S. Gov. Print. Off., Washington, D.C.

Hampson, P.S. 1984. Wetlands in Florida. Fla. Bur. Geol. Map Ser. No. 109.

Hare, R.C. 1965. Contribution of bark to fire resistance of southern trees. J. For. 63:248-251.

Harlow, R.F. 1959. An evaluation of white-tailed deer habitat in Florida. Fla. Game Fresh Water Fish Comm. Tech. Bull. 5. 64 pp.

Harlow, R.F. 1961. Characteristics and status of Florida black bear. Trans. 26th North Am. Wildl. Conf., pp. 481-495.

Harlow, R.F. 1965. Food habits. Pages 74-109 *in* R.F. Harlow and F.K. Jones, Jr., eds. The white-tailed deer in Florida. Fla. Game Fresh Water Fish Comm. Tech. Bull. No. 9. 240 pp.

Harms, W.R., H.T. Schreuder, D.D. Hook, and C.L. Brown. 1980. The effects of flooding on the swamp forest in Lake Ocklawaha, Florida. Ecology 61:1412-1421.

Harper, F. 1927. The mammals of the Okefinokee swamp region of Georgia. Proc. Boston Soc. Nat. Hist. 38:191-396.

Harper, R.M. 1905. "Hammock," "hommock", or "hummock"? Science, New Series 22:400-402.

Harper, R.M. 1914. Geography and vegetation of northern Florida. Fla. Geol. Surv. Annu. Rep. 6:163-437.

Harper, R.M. 1915. Vegetation types. Pages 135-188 *in* E.H. Sellards, R.M. Harper, E.N. Mooney, W.J. Latimer, H. Gunter, and E. Gunter, eds. Natural resources survey of an area in central Florida. Fla. Geol. Surv. Annu. Rep. 7:117-251.

Harper, R.M. 1927. Natural resources of southern Florida. Fla. Geol. Surv. Annu. Rep. 18:27-192.

Harris, L.D., D.H. Hirth, and W.R. Marion. 1979. The development of silvicultural systems for wildlife. Pages 65-82 *in* C.L. Shilling and J.R. Tolliver, eds. Recreation in the South's third forest. Proc. 28th Annu. La. State Univ. For. Symp., Baton Rouge.

Healy, H.G. 1975. Terraces and shorelines of Florida. Fla. Bur. Geol. Map Ser. No. 71.

Hook, D.D., and R.M.M. Crawford, eds. 1978. Plant life in anaerobic environments. Ann Arbor Science Publ., Ann Arbor, Mich. 564 pp.

Hosner, J.F. 1960. Relative tolerance to complete inundation of fourteen bottomland tree species. For. Sci. 6:246-251.

Hosner, J.F., and S.G. Boyce. 1962. Tolerance of water saturated soil of various bottomland hardwoods. For. Sci. 8:180-186.

Huffman, R.T., and S.W. Forsythe. 1981. Bottomland hardwood forest communities and their relation to anaerobic soil conditions. Pages 187-196 *in* J.R. Clark and J. Benforado, eds. Wetlands of bottomland hardwood forests. Developments in Agricultural and Managed-forest Ecology, Vol. 11. Elsevier Scientific, New York.

Humphrey, S.R., and S.A. Nesbitt. [1989]. The community approach to wildlife conservation: characteristics of bird communities in northern Florida.

Humphrey, S.R., R.W. Repenning, and H.W. Setzer. 1986. Status survey of five Florida mammals. Florida Coop. Fish and Wildlife Res. Unit, Tech. Rep. No. 22. 117 Newins-Ziegler Hall, University of Florida, Gainesville. 38 pp.

Ivey, R.D.W. 1947. The mammals, excluding bats, of Palm Valley, Florida. M.S. Thesis. University of Florida, Gainesville. 129 pp.

Jennings, W.L. 1951. A study of the life history and ecology of the gray squirrel (*Sciurus c. carolinensis* Gmelin) in Gulf Hammock. M.S. Thesis. University of Florida, Gainesville. 151 pp.

Johnson, A.S. 1970. Biology of the raccoon (*Procyon lotor varius* Nelson and Goldman) in Alabama. Ala. Coop. Wildl. Res. Unit, Auburn Univ. Bull. No. 402. 148 pp.

Jones, R.H. 1981. A classification of lowland forests in the northern coastal plain of South Carolina. M.S. Thesis. Clemson University, Clemson, S.C. 177 pp.

Jordan, C.L. 1984. Florida's weather and climate: implications for water. Pages 18-35 *in* E.A. Fernald and D.J. Patton, eds. Water resources atlas of Florida. Florida State University, Tallahassee.

Kozlowski, T.T. 1984*a*. Extent, causes, and impacts of flooding. Pages 1-7 *in* T.T. Kozlowski, ed. Flooding and plant growth. Academic Press, Orlando, Fla.

Kozlowski, T.T. 1984*b*. Responses of woody plants to flooding. Pages 129-163 *in* T.T. Kozlowski, ed. Flooding and plant growth. Academic Press, Orlando, Fla.

Kurz, H., and K. Wagner. 1957. Tidal marshes of the Gulf and Atlantic coasts of northern Florida and Charleston, South Carolina. Fla. State Univ. Stud. 24. 168 pp.

Laessle, A.M. 1942. The plant communities of the Welaka area. Univ. Fla. Biol. Sci. Ser. 4(1). 143 pp.

Laessle, A.M., and C.D. Monk. 1961. Some live oak forests of northeastern Florida. Q. J. Fla. Acad. Sci. 24:39-55.

Landers, J.L., A.S. Johnson, P.H. Morgan, and W.P. Baldwin. 1976.

Duck foods in managed tidal impoundments in South Carolina. J. Wildl. Manage. 40:721-728.

Laurent, P. 1906. Bird notes from a Florida porch. Bird-Lore 8:67.

Layne, J.N. 1970. Terrestrial wildlife of the Oklawaha regional ecosystem. Pages 33-41 *in* Environmental impact of the Cross-Florida Barge Canal with special emphasis on the Oklawaha regional ecosystem. Florida Defenders of the Environment, Gainesville. 115 pp.

Layne, J.N. 1976. Introduction. Pages 8-11 *in* J.N. Layne, ed. Mammals. Rare and endangered biota of Florida, Vol. 1. University Presses of Florida, Gainesville.

Leitman, H.M., J.E. Sohm, and M.A. Franklin. 1983. Wetland hydrology and tree distribution of the Apalachicola River flood plain, Florida. U.S. Geol. Surv. Water Supp. Pap. 2196-A. 52 pp.

Lewis, T.H. 1907. Spanish explorers in the southern United States 1528-1543. Charles Scribner's Sons, New York. 411 pp.

Lichtler, W.F., W. Anderson, and B.F. Joyner. 1968. Water resources of Orange County, Florida. Fla. Geol. Surv. Rep. Invest. No. 50. 150 pp.

Little, E.L., Jr. 1978. Florida. Atlas of United States trees, Vol. 5. U.S.D.A. Misc. Publ. 1361. 22 pp., 268 maps.

Little, E.L., Jr. 1979. Checklist of United States trees (native and naturalized). Agric. Handb. No. 541. U.S.D.A. For. Serv., Washington, D.C. 375 pp.

Livingston, R.J. 1984. The ecology of the Apalachicola Bay system: an estuarine profile. U.S. Fish Wildl. Serv. FWS/OBS 82/05. 148 pp.

Livingstone, R.J., and J. Duncan. 1979. Short- and long-term effects of forestry operations on water quality and epibenthic assemblages of a north Florida estuary. Pages 339-382 *in* R.J. Livingstone, ed. Ecological processes in coastal and marine systems. Plenum Press, New York.

Maehr, D.S. 1984. The black bear as a seed disperser. Fla. Field Nat. 12:40-42.

Maehr, D.S., and J.R. Brady. 1984. Food habits of Florida black bears. J. Wildl. Manage. 48:230-235.

Maehr, D.S., and J.T. DeFazio, Jr. 1985. Foods of black bears in Florida. Fla. Field Nat. 13:8-12.

Martin, A.C., H.S. Zim, and A.L. Nelson. 1951. American wildlife and plants. McGraw Hill Book Co., New York. 500 pp.

Martin, R.A., and S.D. Webb. 1974. Late Pleistocene mammals from the Devil's Den fauna, Levy County. Pages 114-145 *in* S.D. Webb, ed. Pleistocene mammals of Florida. University of Florida Press, Gainesville.

Mattraw, H.C., and J.F. Elder. 1982. Nutrient and detritus transport in the Apalachicola River, Florida. U.S. Geol. Surv. Water Supply Pap. 2196-C.

McComb, W.C., S.A. Bonney, R.M. Sheffield, and N.D. Cost. 1986. Den tree characteristics and abundance in Florida and South Carolina. J. Wildl. Manage. 50:584-591.

McKinley, D. 1985. The Carolina parakeet in Florida. Fla. Ornithol. Soc., Spec. Publ. No. 2. 65 pp.

McKnight, J.S., D.D. Hook, O.G. Langdon, and R.L. Johnson. 1981. Flood tolerance and related characteristics of trees of the bottomland forests of the southern United States. Pages 29-69 *in* J.R. Clark and J. Benforado, eds. Wetlands of bottomland hardwood forests. Developments in Agricultural and Managed-forest

Ecology, Vol. 11. Elsevier Scientific, New York.

Meeter, D.A., R.J. Livingston, and G. Woodsum. 1979. Short and long-term hydrological cycles of the Apalachicola drainage system with application to Gulf coastal populations. Pages 315-338 *in* R.J. Livingstone, ed. Ecological processes in coastal and marine systems. Plenum Press, New York.

Menzel, R.W., N.C. Hulings, and R.R. Hathway. 1966. Oyster abundance in Apalachicola Bay, Florida, in relation to biotic associations influenced by salinity and other factors. Gulf Res. Rep. 2:73-96.

Milliman, J.D., and K.O. Emery. 1968. Sea-levels during the past 35,000 years. Science 162:1121-1123.

Moler, P.E. [1985]. Home range and seasonal activity of the eastern indigo snake, *Drymarchon corais couperi*, in northern Florida. Fla. Game Fresh Water Fish Comm. Unpubl. MS. 25 pp.

Monk, C.D. 1965. Southern mixed hardwood forest of north central Florida. Ecol. Monogr. 35:335-354.

Monk, C.D. 1966. An ecological study of hardwood swamps in north-central Florida. Ecology 47:649-654.

Monk, C.D., and J.T. McGinnis. 1966. Tree species diversity in six forest types in north central Florida. J. Ecol. 54:341-344.

Nash, G.V. 1895. Notes on some Florida plants. Bull. Torrey Bot. Club 22:141-147.

Nehrling, H. 1889, 1896. Our native birds of song and beauty. Brumder, Milwaukee. 2 vols.

Nesbitt, S.A., W.M. Hetrick, L.E. Williams, Jr., and D.H. Austin. 1977. Foods of the nine-banded armadillo in Florida. Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies 31:57-61.

Olmsted, I., and L.L. Loope. 1984. Plant communities of Everglades National Park. Pages 167-184 *in* P. Gleason, ed. Environments of south Florida--past and present. Memoir II, Miami Geological Society, Coral Gables, Fla.

Oxford English Dictionary. 1933. Vol. V. Oxford University Press, Oxford, England.

Pasquier, R.F. 1982. Whose birds are they? Nat. Conservancy News 32(4):12-15.

Pearson, P.G. 1951. Mammals of Gulf Hammock, Levy County, Florida. M.S. Thesis. University of Florida, Gainesville. 155 pp.

Pearson, P.G. 1952. Observations concerning the life history and ecology of the Florida wood rat, *Neotoma floridana floridana* (Ord). J. Mammal. 33:459-463.

Pearson, P.G. 1953. A field study of Peromyscus populations in Gulf Hammock, Florida. Ecology 34:199-207.

Pearson, P.G. 1954. Mammals of Gulf Hammock, Levy County, Florida. Am. Midland Nat. 51:468-480.

Pelton, M.R., L.E. Beeman, and D.C. Eagar. 1980. Den selection by black bears in the Great Smoky Mountains National Park. Pages 149-151 *in* C.J. Martinka and K.L. McArthur, eds. Bears--their biology and management. Bear Biol. Assoc. Conf. Ser. 3. U.S. Gov. Print. Off., Washington, D.C.

Ponnamperuma, F.N. 1984. Effects of flooding on soils. Pages 9-45 *in* T.T. Kozlowski, ed. Flooding and plant growth. Academic Press, Orlando, Fla.

Puri, H.S., and R.O. Vernon. 1964. Summary of the geology of Florida and a guidebook to the classic exposures. Fla. Geol. Surv. Spec. Publ. 5, rev. 312 pp.

Puri, H.S., J.W. Yon, and W.R. Oglesby. 1967. Geology of Dixie and Gilchrist Counties, Florida. Fla. Geol. Surv. Bull. 49. 155 pp.

Putnam, J.A., G.M. Furnival, and J.S. McKnight. 1960. Management and inventory of southern hardwoods. U.S.D.A. For. Serv. Agric. Handb. No. 181. 102 pp.

Riggs, S.R. 1984. Paleoceanographic model of Neogene phosphorite deposition, U.S. Atlantic continental margin. Science 223:123-131.

Rogers, L.L., and R.D. Applegate. 1983. Dispersal of fruit seeds by black bears. J. Mammal. 64:310-311.

Rogers, S.G., T.E. Targett, and S.B. VanSant. 1984. Fish-nursery use in Georgia salt-marsh estuaries: the influence of springtime freshwater conditions. Trans. Am. Fish Soc. 113:595-606.

Schnoes, R.S., and S.R. Humphrey. 1987. Terrestrial plant and wildlife communities on phosphate-mined lands in central Florida. Bull. Fla. State Mus., Biol. Sci. 30:53-116.

Shannon, C.E., and W. Weaver. 1949. The mathematical theory of communication. University of Illinois Press, Urbana. 125 pp.

Sheridan, P., and R.J. Livingston. 1979. Cyclic trophic relationships of fishes in an unpolluted, river-dominated estuary in north Florida. Pages 143-161 *in* R.J. Livingstone, ed. Ecological processes in coastal and marine systems. Plenum Press, New York.

Short, H.L., and E.A. Epps, Jr. 1976. Nutrient quality and digestibility of seeds and fruits from southern forests. J. Wildl. Manage. 40:283-289.

Shure, D.J., and M.R. Gottschalk. 1985. Litter-fall patterns within a floodplain forest. Am. Midl. Nat. 114:98-111.

Shure, D.J., M.R. Gottschalk, and K.A. Parsons. 1986. Litter decomposition processes in a floodplain forest. Am. Midl. Nat. 115:314-327.

Simons, R.W., and J.H. Hintermister. 1984. Native plant and animal communities, northern phosphate resource district. Pages 76-81 *in* H. Hood and R.M. Palmer, eds. Phosphate mining in Florida, a source book. Florida Defenders of the Environment, Gainesville and the Environmental Service Center, Tallahassee.

Simons, R.W., W.R. Marion, and J.H. Hintermister. 1984. Native plant and animal communities, central and south phosphate resource districts. Pages 52-58 *in* H. Hood and R.M. Palmer, eds. Phosphate mining in Florida, a source book. Florida Defenders of the Environment, Gainesville and the Environmental Service Center, Tallahassee.

Simons, R.W., S.W. Vince, and S.R. Humphrey. [1989]. Hydric hammock: a guide to management. U.S. Fish Wildl. Serv. In press.

Sinclair, M., G.L. Bugden, C.L. Tang, J.C. Therriault, and P.A. Yeats. 1986. Assessment of effects of freshwater runoff variability on fisheries production in coastal waters. Pages 139-160 *in* S. Skreslet, ed. The role of freshwater outflow in coastal marine ecosystems. Springer-Verlag, Berlin.

Skeate, S.T. 1987. Interactions between birds and fruits in a northern Florida hammock community. Ecology 68:297-309.

Snedaker, S.C., and D.P. de Sylva. 1977. Role of freshwater in estuarine ecosystems. Volume One: Summary. Southwest Fla. Water Manage. Dist. Plann. Rep. No. 1977-2.

Speake, D.W., J.A. McGlincy, and T.R. Colvin. 1978. Ecology and management of the eastern indigo snake in Georgia: a progress report. Pages 64-73 *in* R.R. Odom and L. Landers, eds. Proceedings rare and endangered wildlife symposium, Ga. Dept. Nat. Res., Game Fish Div. Tech. Bull. WL 4.

Stringfield, V.T., and H.E. LeGrand. 1966. Hydrology of limestone terranes in the coastal plain of the southeastern United States. Geol. Soc. Am. Spec. Pap. 93. 46 pp.

Swindell, D.E., Jr. 1949. Plant communities and other factors affecting the deer and turkey populations in Gulf Hammock. M.S. Thesis. University of Florida, Gainesville. 150 pp.

Tanner, J.T. 1942. The ivory-billed woodpecker. Nat. Audubon Soc. Res. Rep. No. 1. 111 pp.

Tanner, W.F., and I.M. Smith. 1981. Natural environment. Pages 14-73 *in* E.A. Fernald, ed. Atlas of Florida. Florida State University, Tallahassee.

Teskey, R.O., and T.M. Hinckley. 1977. Impact of water level changes on woody riparian and wetland communities. Vol. 2: The southern forest region. U.S. Fish Wildl. Serv. FWS/OBS-77/59.

Thompson, S.K.S. 1980. Hammock vegetation in the northern Gulf Hammock region of Florida. M.S. Thesis. Florida State University, Tallahassee. 49 pp.

U.S. Fish and Wildlife Service. 1978. Osceola National Forest phosphate extraction and processing: impacts on federally listed threatened or endangered and other species of special concern. National Ecology Center, Gainesville, Fla. 414 pp.

U.S. Fish and Wildlife Service. [1980]. St. Marks National Wildlife Refuge: forestry management and non-game wildlife. Unpubl. rep. 119 pp.

U.S. Fish and Wildlife Service. 1985. Endangered and threatened wildlife and plants; review of vertebrate wildlife; notice of review. Fed. Reg. 50:37958-37967.

U.S. Soil Conservation Service. 1960. Soil survey of Orange County, Florida. Washington, D.C.

U.S. Soil Conservation Service. 1974. Soil survey of Brevard County, Florida. Washington, D.C.

U.S. Soil Conservation Service. 1977. Soil survey of Hernando County, Florida. Washington, D.C.

U.S. Soil Conservation Service. 1979. Soil survey of Marion County, Florida. Washington, D.C.

U.S. Soil Conservation Service. 1980. Soil survey of Volusia County, Florida. Washington, D.C.

U.S. Soil Conservation Service. 1981. 26 Ecological communities of Florida. Washington, D.C.

Vernon, R.O. 1951. Geology of Citrus and Levy Counties, Florida. Fla. Geol. Surv. Bull. 33. 256 pp.

Vernon, R.O., and H.S. Puri. 1965. Geologic map of Florida. Fla. Geol. Surv. Map Ser. No. 18.

Watts, W.A. 1971. Postglacial and interglacial vegetation history of southern Georgia and central Florida. Ecology 52:676-689.

Watts, W.A. 1980. The late Quaternary vegetation history of the southeastern United States. Annu. Rev. Ecol. Syst. 11:387-409.

Watts, W.A., and M. Stuiver. 1980. Late Wisconsin climate of northern Florida and the origin of species-rich deciduous forest. Science 210:325-327.

Wells, B.W. 1942. Ecological problems of the southeastern United States coastal plain. Bot. Rev. 8:533-561.

Wharton, C.H. 1977. The natural environments of Georgia. Office of Planning and Research, Georgia Department of Natural Resources, Atlanta, Ga. 227 pp.

Wharton, C.H., H.T. Odum, K. Ewel, M. Duever, A. Lugo, R. Boyt, J. Bartholomew, E. DeBellevue, S. Brown, M. Brown, and L. Duever. 1977. Forested wetlands of Florida - their management and use. Center for Wetlands, University of Florida, Gainesville.

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 Wildl. Serv. FWS/OBS-81/37. 133 pp.

White, W.A. 1970. The geomorphology of the Florida peninsula. Fla. Geol. Surv. Bull. 51. 164 pp.

Whitlow, T.H., and R.W. Harris. 1979. Flood tolerance in plants: a state-of-the-art review. U.S. Army Engineers Waterways Experiment Stn. Tech. Rep. E-79-2. Vicksburg, Miss. 161 pp.

Williams, L.E., Jr. 1978. Florida black bear. Pages 23-25 *in* J.N. Layne, ed. Mammals. Rare and endangered biota of Florida, Vol. 1. University Presses of Florida, Gainesville.

Winker, C.D., and J.D. Howard. 1977. Plio-Pleistocene paleogeography of the Florida gulf coast interpreted from relict shorelines. Trans. Gulf Coast Assoc. Geol. Soc. 27:409-420.

Wirtz, W.O., D.H. Austin, and G.W. Delke. 1985. Food habits of the common long-nosed armadillo *Dasypus novemcinctus* in Florida, 1960-61. Pages 439-451 *in* G.G. Montgomery, ed. The evolution and ecology of armadillos, sloths, and vermilinguas. Smithsonian Institution Press, Washington D.C. 451 pp.

Wood, G.W., and R.E. Brenneman. 1980. Feral hog movements and habitat use in coastal South Carolina. J. Wildl. Manage. 44:420-426.

Wood, G.W., and D.N. Roark. 1980. Food habits of feral hog in coastal South Carolina. J. Wildl. Manage. 44:506-511.

Woolfenden, G.E. 1967. Live oak-cabbage palm hammock. Audubon Field Notes 21:635-637.

Woolfenden, G.E. 1968. Live oak-cabbage palm hammock. Audubon Field Notes 22:488.

50272-101

REPORT DOCUMENTATION PAGE

1. REPORT NO.	Biological Report 85(7.26)
2.	
3. Recipient's Accession No.	
4. Title and Subtitle	The Ecology of Hydric Hammocks: a Community Profile
5. Report Date	September 1989
6.	
7. Author(s)	Susan W. Vince, Stephen R. Humphrey, and Robert W. Simons
8. Performing Organization Rept. No.	
9. Performing Organization Name and Address	Author Affiliation: Florida Museum of Natural History, University of Florida, Gainesville, FL 32611
10. Project/Task/Work Unit No.	
11. Contract(C) or Grant(G) No.	(C) (G)
12. Sponsoring Organization Name and Address	U.S. Department of the Interior, Fish and Wildlife Service, National Wetland Research Center, Washington, DC 20240
13. Type of Report & Period Covered	
14.	
15. Supplementary Notes	

16. Abstract (Limit: 200 words)

This publication describes the nature and dynamics of a type of forested wetland called hydric hammock. Hydric hammock has not been carefully defined or studied, and it often is ignored or lumped with other mixed hardwood forests. Hydric hammock occurs at low elevations along the gulf coast of Florida from Aripeka to St. Marks and at various inland sites in Florida. The largest contiguous tracts occur along the gulf coast and the St. Johns River. Sites typically are gentle slopes between mesic hammock or pine flatwoods and river swamp, wet prairie, or marsh. Hydric hammocks occur on soils that are poorly drained or have high water tables, and occasional flooding saturates the soils long enough to restrict or modify species composition. Hydric hammocks typically contain live and swamp laurel oaks (*Quercus virginiana* and *Quercus laurifolia*), cabbage palm (*Sabal palmetto*), southern red-cedar (*Juniperus silicicola*), sweetgum (*Liquidambar styraciflua*), and hornbeam (*Carpinus caroliniana*). Hydric hammocks lack certain tree species while sharing others with both upslope mesic forests and downslope swamp forests. The vertebrate fauna contains no unique species but has a high diversity of species and high abundance of selected species. Hydric hammocks are particularly important habitat for game species and for overwintering passerine birds.

17. Document Analysis a. Descriptors

forested wetland, Florida, inundation, water table, limestone, fire, game animals, passerine birds, linkage, plant-animal interactions

b. Identifiers/Open-Ended Terms

c. COSATI Field/Group

18. Availability Statement	Unlimited distribution
19. Security Class (This Report)	Unclassified
20. Security Class (This Page)	Unclassified
21. No. of Pages	ix + 81
22. Price	

(See ANSI-Z39.18)

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