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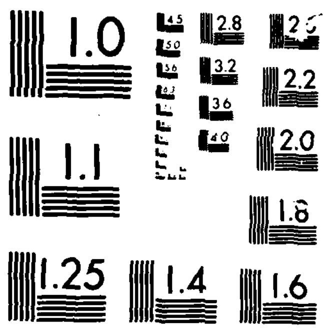

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NATURAL SETTING AND VEGETATION OF THE FLORIDA PANHANDLE

Prepared Under Contract —

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JANUARY 1986

US Army Corps of Engineers
Mobile District

NATURAL SETTING AND VEGETATION OF THE FLORIDA PANHANDLE

An Account of the Environments and Plant Communities of Northern Florida West of the Suwannee River

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LIST OF COMMON NAMES AND THEIR BINOMIALS

Alder, hazel	Alnus serrulata
Ash	Fraxinus
green	F. pennsylvanica
popash	F. caroliniana
pumpkin	F. profunda
white	F. americana
Basswood	Tilia spp.
Bay	
loblolly	Gordonia lasianthus
red	Persea borbonia
sweet	Magnolia virginiana
swamp	Persea palustris
Beech, American	Fagus grandifolia
Birch, river	Betula nigra
Blackberry	Rubus spp.
Blackgum	Nyssa biflora
Blackhaw	Bumelia lanuginosa
Blueberry, dwarf	Vaccinium myrsinites
Bluestem	Andropogon, Schizachyrium spp.
Bracken	Pteridium aquilinum
Broomsedge	Andropogon virginicus
Buckwheat-tree	Cliftonia monophylla
Buttonbush	Cephalanthus occidentalis
Cattails	Typha spp.
Cedar	
red (southern red)	Juniperus silicicola
white	Chamaecyparis henryae
Cherry	Prunus
black	P. serotina
laurel	P. caroliniana
Cottonwood, swamp	Populus heterophylla
Cordgrass	Spartina alterniflora
big	S. cynosuroides
smooth	S. alterniflora
saltmeadow	S. patens
Corkwood	Leitneria floridana
Couchgrass	Spartina patens
Crab-apple	Malus angustifolius
Cypress	Taxodium
bald	T. distichum
pond	T. ascendens
Cyrilla	Cyrilla
little-leaf	C. parvifolia
swamp	C. racemiflora
Dahoon	Ilex cassine
Dog-fennel	Eupatorium capillifolium, E. compositifolium

Dogwood	Cornus florida
Elm, American	Ulmus americana
Fetterbush	Lyonia lucida
Gallberry	Ilex glabra
large	I. coriacea
Glasswort	Salicornia spp.
Hackberry	Celtis laevigata
Hercule's-club	Aralia spinosa
Hickory	Carya
mockernut	C. tomentosa
pignut	C. glabra
water	C. aquatica
Holly	Ilex
American	I. opaca
myrtle-leaf	I. myrtifolia
Horse-sugar	Symplocos tinctoria
Ironwood	Carpinus caroliniana
Lizzard's-tail	Saururus cernuus
Locust, water	Gleditsia aquatica
Magnolia	Magnolia grandiflora
southern	M. grandiflora
Manateegrass	Syringodium filiforme
Maple	Acer
red	A. rubrum
silver	A. saccharinum
sugar	A. saccharum
Mountain-laurel	Kalmia latifolia
Mulberry, red	Morus rubra
Needlerush	Juncus roemerianus
Oak	Quercus
black	Q. velutina
blackjack	Q. marilandica
bluejack	Q. incana
bluff	Q. austrina
Chapman	Q. chapmanii
diamond-leaf	Q. laurifolia
dwarf-live	Q. minima
laurel	Q. hemisphaerica
live	Q. virginiana
myrtle	Q. myrtifolia
overcup	Q. lyrata
post	Q. stellata
red	Q. flacata
running	Q. pumila
sand-live	Q. geminata
sand-post	Q. margaretta
Shumard	Q. shumardii
Spanish	Q. falcata
swamp-chestnut	Q. michauxii
turkey	Q. laevis
water	Q. nigra

white	Q. alba
willow	Q. phellos
Olive, wild	Osmanthus americanus
Palm	
cabbage	Sabal palmetto
needle	Rhapidophyllum hystrix
Panic-grass	Dichanthelium spp.
Persimmon	Diospyros virginiana
Pine	Pinus
loblolly	P. taeda
longleaf	P. palustris
pond	P. serotina
sand	P. clausa
shortleaf	P. echinata
slash	P. elliottii
spruce	P. glabra
Planer-tree	Planera aquatica
Poison-ivy	Rhus toxicodendron
Popash	Fraxinus caroliniana
Possum-haw	Ilex decidua
Redbud	Cercis canadensis
Reedgrass	Phragmites australis
Rosemary	Ceratiola ericoides
Saltgrass	Distichlis spicata
Sassafras	Sassafras albidum
Sawgrass	Cladium jamaicense
Saw-palmetto	Serenoa repens
Sea-oats	Uniola paniculata
Shoalgrass	Halodule wrightii
Soapberry	Sapindus marginatus
Sourgum	Nyssa sylvatica
Sparkleberry	Vaccinium arboreum
St. John's-wort	Hypericum spp.
Staggerbush	Lyonia ferruginea, L. fruticosa
Sumac, winged	Rhus copallina
Sweetbay	Mangolia virginiana
Sweetgum	Liquidambar styraciflua
Sycamore	Platanus occidentalis
Tapegrass	Vallisneria americana, Sagittaria kurziana
Titi	Cliftonia, Cyrilla spp.
black	Cliftonia monophylla
Tulip-poplar	Liriodendron tulipifera
Tupelo	Nyssa
ogeechee	N. ogeche
swamp	N. biflora
water	N. aquatica
Turtlegrass	Thalassia testudinum
Virginia-creeper	Parthenocissus virginiana
Water-lily	Nymphaea odorata
Wax-myrtle	Myrica cerifera

White-cedar	Chamaecyparis thyoides (or henryae?)
Widgeongrass	Ruppia maritima
Willow	Salix
black	S. nigra
Carolina	S. caroliniana
Wiregrass	Aristida stricta
Witch-hazel	Hamamelis virginiana
Yaupon	Ilex vomitoria

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20. ABSTRACT (Continue on reverse side if necessary and identify by block number) This report is a comprehensive treatise on the natural setting of the Florida Panhandle including geology, physiology, soils, climate and other physical features which collectively comprise and define the habitats and physical environments. The natural plant communities that are found in these various habitats are described. Ruderal vegetation and other semi-natural communities that have developed in response to distrubance and land management practices are also described. Successional trends are discussed and a number of physical factors are identified which must be maintained if a given plant communitiy is to persist indefinitely. Changes

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expected in community physiognomy and floristic composition are enumerated which are caused by agriculture and forestry practices, wetlands modifications and other habitat management practices. A limited discussion is also included on paleoecology and endemism in the Florida Panhandle area.

1. INTRODUCTION

Objectives. This report has eight objectives:

1. To describe the natural setting of the Florida panhandle, including geology, physiography, soils, climate, and other physical features which collectively comprise and define the habitats and physical environments.

2. To describe the natural plant communities of these habitats.

3. To describe the ruderal vegetation and other, semi-natural communities that developed in response to disturbance and land management.

4. To identify the physical factors which must be maintained if any given plant community is to persist indefinitely.

5. To identify successional trends, if any, within and between plant communities.

6. To indicate the changes expected in community physiognomy and floristic composition, caused by agriculture and forestry practices, wetlands modifications, and other habitat management.

7. To classify the vegetation ecologically according to structural and functional criteria.

8. To assess what little is known about paleoecology and endemism in our area.

Previous Studies. There were two previous attempts to make comprehensive descriptions of the natural setting and vegetation of the panhandle, one by Williams (1827) and the other by Harper (1914). Both contain valuable observations. Neither benefits from the many subsequent studies which are basic to a contemporary understanding of our region and to the sound stewardship of its resources.

Applicability. Nearly all of the plant communities of the Atlantic Coastal Plain from the Carolinas to the Mississippi River are represented in the panhandle. As a result, this report is applicable to this greater region with only a few species substitutions from place to place. The literature reviewed for this report includes those references which described the vegetation from this greater region.

Status of Vegetational Knowledge. The written history of the southeastern coastal plain dates back 450 years. The earliest Spanish explorers described the natural scenery and vegetation, as did several naturalists in later centuries. In the first half of the present century several perceptive ecologists made substantial contributions to our knowledge of the plant communities and habitats of the coastal plain. Included among these investigators were R. M. Harper, H. H. Chapman, and B. W. Wells. The region is fortunate to contain representative stands of nearly all plant communities that are preserved in their original state and many more that are only slightly altered by man's activities.

In light of the long history of vegetational observations and in spite of the availability of natural habitats for study, the vegetation of the coastal plain is incompletely described and poorly understood. Most of the rest of the North American continent is much better known. Braun (1950) summarized the vast deciduous forest formation of eastern North America, yet no comparable work treats the adjacent coastal plain in its entirety.

There are several reasons for this void in knowledge for the coastal plain. First, prior to about 1950 there were few research-oriented universities on the coastal plain and therefore few resident botanists and ecologists. Investigators from other regions who made forrays to study the coastal plain contributed to its knowledge but often misinterpreted their observations, reflecting a lack of familiarity with the complexities of the region.

Second, until recently very few ecologists appreciated the role of fire in shaping natural vegetation. A national campaign to prevent all fires began about 1920 in response to disasterous forest fires in other regions of the country. It seems probable that the national mood against fire influenced a generation of ecological thought. Fire was considered a destructive force in natural systems. This view was reinforced by the location of many universities where ecologists were taught, the eastern deciduous forest region. This is one of the few regions in the world where fire is not important is shaping vegetation. Students were trained where they could not observe natural fire as a regulator of plant processes.

Third, American ecologists have been preoccupied by the theoretical concepts of succession and climax, which were developed in this country in the early 1900's. These concepts gave a philosophical framework to the young field of ecology and legitimized it as an academic discipline. These concepts also generated some chauvinistic pride by setting American ecology apart from the European schools of ecology. Ecologists became obsessed by these concepts. The results of ecological investigations were interpreted so as to comply with the new orthodoxy of succession and climax. Unfortunately, these concepts are not particularly compatible with much of the vegetation of the coastal plain, except in river valleys and on sites disturbed by man's activities.

Potential Audiences. This report is more than a monograph on the plant communities and the physical parameters that affect the vegetation. It is also a text, because the various topics are often introduced with general background information. These introductory comments are included as a service to those readers whose expertise lies in other disciplines. In this age of specialization, very few people are familiar with all the disciplines that contribute to an understanding of the vegetation.

The report was written for several audiences. One includes the personnel of those governmental agencies charged with environmental protection. Another audience consists of those planners, resource managers and engineers, both in public agencies and with private firms, whose activities impact the vegetation. A third includes those university students and other individuals who wish to become familiar with the regional vegetation. Finally, this report is intended to entice researchers to investigate the many problems that await solution in our region.

Research Summaries. A unique feature of this report is the inclusion of brief, 1 to 4 page research summaries. These are presented as supplementary information without much comment in the text. The report would become unwieldy if the data in the research summaries were incorporated in the text. On the other hand, the research summaries document many of the points made in the text. Some research summaries were taken from published papers. Most consist of unpublished data, some my own and others from the research projects of my students.

Conceptualization of Communities. The plant communities are defined as broadly as possible, so as to emphasize vegetational relationships rather than differences. Natural zones or phases within each community are indicated, so that users of this report can subdivide these communities to suit their specific needs. The communities are arranged in a system of classification based on physiognomic and functional criteria, rather than on preconceived notions that fit a particular climax theory.

Floristics. Two factors which likely retarded ecological work on the coastal plain are the complexity of the flora and the lack of local field manuals for plant identification. The most important floristic works have been Small's flora (Small 1903) and its updated version, Small's manual (Small 1933). These books were difficult to use, because they contained all of the species from the Southeast, including those of the southern Appalachians. Small's manual has been outdated for many years, both in terms of nomenclature and of the delimitation of many taxa.

More modern manuals have been published recently for parts of the coastal plain. These are Radford, Ahles and Bell (1968) for the Carolinas, Correll and Johnston (1970) for Texas, and Long and Lakela (1971) for Tropical Florida. Most plants of the panhandle may be identified using these books. Kurz and Godfrey (1962) treated the trees of northern Florida, and Duncan (1967) treated the woody vines of the Southeast.

Wildflowers may be identified from photographs in volumes prepared by Rickett (1967) and Duncan and Foote (1975). Mitchell (1963) listed the flora at Florida Caverns State Park. Ward (1968) listed the ferns, conifers and monocots of Florida. D. B. Ward recently began publishing a series of papers in Phytologia which give keys and notes on selected families and genera as they occur in Florida.

The panhandle contains a number of rare, endangered and threatened species (US Fish and Wildlife Service 1980). Most of these are endemic to the Apalachicola River region and were noted by Clewell (1977).

Several books are in preparation. R. K. Godfrey has in press a manual for the identification of wetland plants of the Southeast. R. Kral is preparing a manual of the flora of Alabama and central Tennessee. A. Radford is editing a flora for the entire Southeast, which will essentially modernize Small's manual. I am preparing a companion volume to the present report, which gives keys for the identification of all vascular plants of the panhandle.

Two public herbaria contain large collections of specimens from the panhandle. These are the herbaria of Florida State University and of the University of Florida.

Bryophytes, which are not treated in this report nor in the above-cited references, are identifiable in the panhandle using the publications of Breen (1963) and Briel (1970).

The first botanist in residence in the panhandle was Alvin Wentworth Chapman, a physician who lived many years in Chattahoochee and Apalachicola. He collected extensively and described many new species. He published a flora for the Southeast in 1860 which is an excellent work and is still an important taxonomic reference.

Acknowledgements. I thank C. L. Coultas for his critical review of the chapter on soils and R. S. Murali for those on geology, physiography, rivers, lakes, and aquifers. Many of the studies which led to this work were funded by the Tall Timbers Research Station. Other studies were funded through contracts from the U. S. Forest Service, The Florida Department of Transportation, and the Florida Department of Environmental Regulation. This report was written with the support from the Army Corps of Engineers.

I am indebted to many naturalists who introduced me to the region, who answered my many questions, and who reacted to my ideas. Among them were R. K. Godfrey (subtlties of vegetational zonation, lakes, wiregrass), Ed and Roy Komarek and Leon Neel (fire, habitat management), Charles Wharton (river swamps), Herman Kurz and Red Gidden (tidal marshes), Steven Leonard (coastal dunes and ridges), W. F. Tanner and R. S. Murali (Geology), C. L. Coultas and P. E. Avers (soils), and E. A. Hebb (sandhills). With regret my knowledge of savannahs was enhanced by only a single day in the field with B. W. Wells.

<u>Some Abbreviations</u>

BA	basal area
BP	years before present
cfs	cubic feet per second
dbh	diameter at breast height (4.5 ft above the ground)
ft	feet
ha	hectare (10,000 m^2)
in	inch
km	kilometer
m	meter
mi	mile
mm	millimeter
msl	mean sea level
Rel	relative

SCS Soil Conservation Service, USDA

USDA U. S. Department of Agriculture

USGS U. S. Geological Survey, Dept. of the Interior

Some Definitions.

Plant Community. A floristic assemblage that occurs within particular habitats or under particular conditions. Interspecific competition and other interactions may occur but are not implied in this definition. Successional and climax connotations are likewise excluded from this definition.

Basal Area. The area of the cross section of a tree trunk 4.5 feet above the ground, usually expressed as the collective basal areas of all trees of a species in a given area.

Relative Basal Area. Percent basal area. The basal area of the trees of one species divided by the total basal area of all species.

Density. Number of plants per unit area.

Relative Density. Percent density or percentage composition. The density of the plants of one species divided the total density of all plants.

Frequency. The number of sample units (e.g., quadrats) in which one or more plants of a species occur. Sometimes expressed in terms of 100 sample units.

Quadrat. A sample area of any size or shape in which basal area, density, or frequency are determined.

Interception. Sampling method employing a line or tape measure. Any plant touching the line or crossing over or under it is tallied. Relative density is obtained by dividing the total number of tallies into those for each species. Frequency is obtained by counting the number of meter-long intervals (or other length) in which a species is tallied.

Physiognomy. The structure or architecture of a community as determined by habit and life form, rather than by species composition.

Some Conversion Factors.

To Convert	To	Multiply By
acres	ha	0.405
acres	km^2	0.004
acres	mi^2	0.0016
^oC	^oF	$1.8(^oC) + 32$
^oF	^oC	$(^oF - 32)0.556$
cfs	10^7 gal/day	0.646
cfs	m^3/second	0.028
ft	m	0.305
ft^2	m^2	0.093
ft^3	gallons	7.481
ha	acres	2.471
ha	mi^2	0.004
in	cm	2.54
km^2	acres	247.105
km^2	mi^2	0.386
m	ft	3.281
m^2	ft^2	10.764
m^2	km^2	2.590
mi	km	1.609
mi^2	acres	640.000
mi^2	ha	258.399

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2. GEOGRAPHY

The panhandle of Florida is defined as that part of the state between the Suwannee River to the east and the Perdido River to the west. The state lines of Alabama and Georgia form the northern and western boundaries. The Gulf of Mexico defines the southern boundary. The Florida Department of Transportation road map for 1978 shows the geographical features of the panhandle (Figs. 1, 2). Figure 3 outlines the 21 counties of the panhandle. The more important streams, lakes, and coastal features are shown in Figure 4. The total area of the panhandle is 14,915 $miles^2$ or 38,628 km^2 (Knight 1969, McClure 1970). Of this area 4.6% is water.

Figures 5-14 are portions of USGS topographic maps, 1:250,000, with contour intervals of 25 feet (7.6 m). The scale on Figure 12 applies to all of these maps. The maps copied were NH 16-5 (Pensacola), NH 16-9 (Apalachicola) NH 17-4 (Valdosta), and NH 17-7 (Gainesville). Not all of the panhandle is represented in these figures, but those regions which are emphasized in later chapters are shown.

The physiographic regions of the panhandle are mapped in Figure 15 and will be discussed in Chapter 7. Additional background information for the region is compiled in SCS (1977) and in several publications cited in the next chapter.

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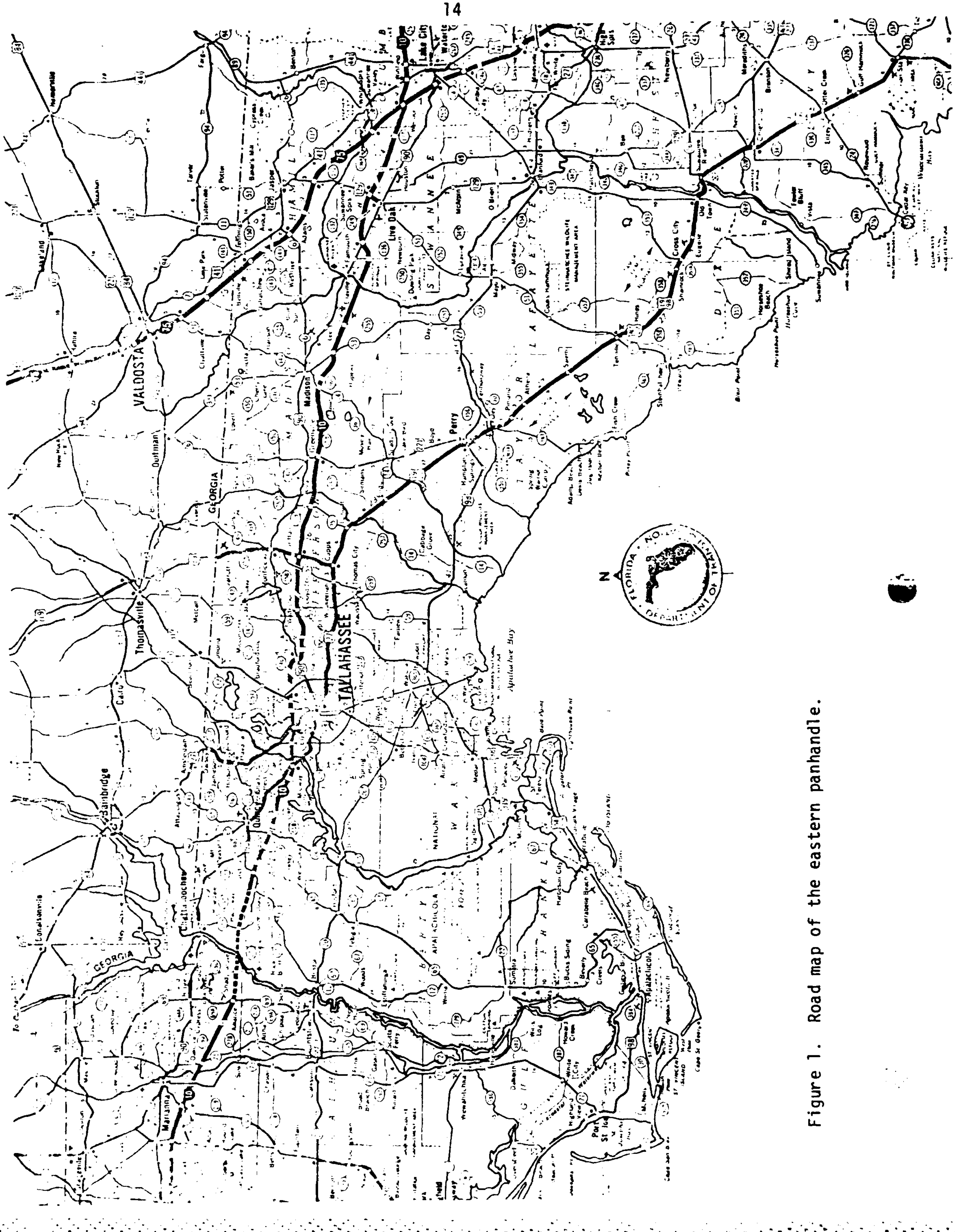


Figure 1. Road map of the eastern panhandle.

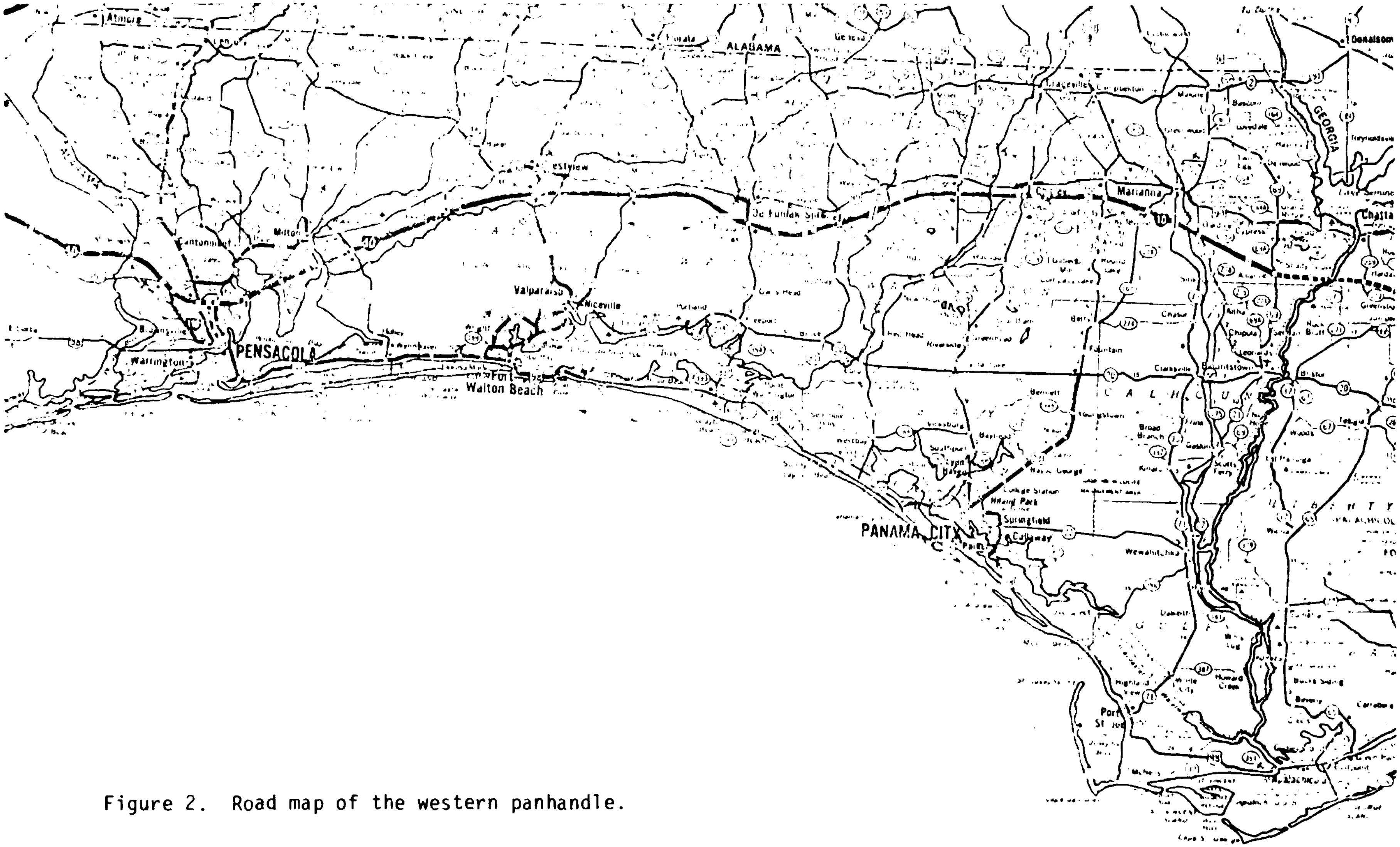
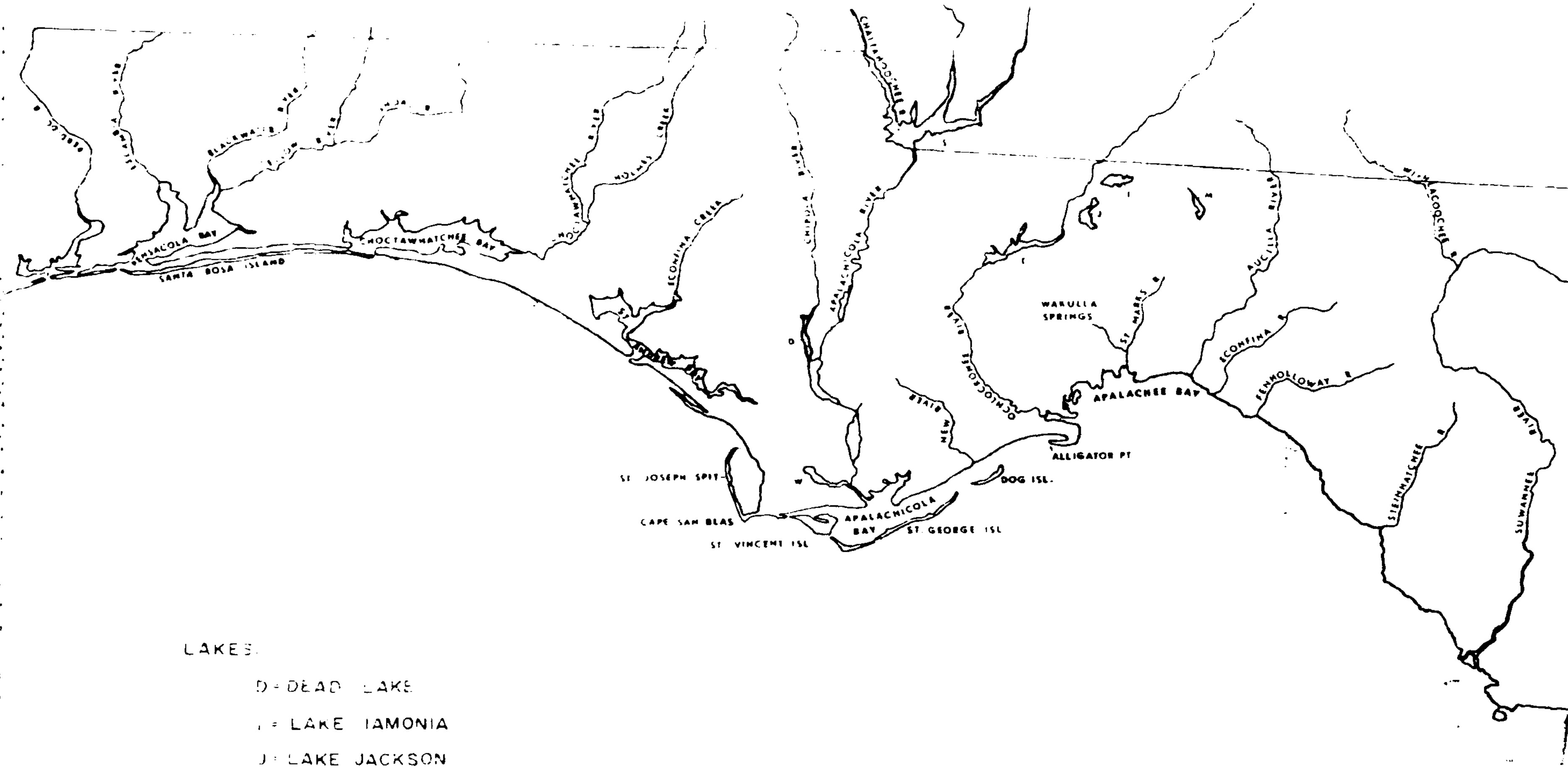


Figure 2. Road map of the western panhandle.

Figure 3. Counties of the Florida panhandle.



LAKES:

D = DEAD LAKE
I = LAKE IAMONIA
J = LAKE JACKSON
M = LAKE MICCOSUKEE
S = LAKE SEMINOLE
T = LAKE TALQUIN
W = LAKE WIMICO

Figure 4. Major lakes, rivers, and coastal features.

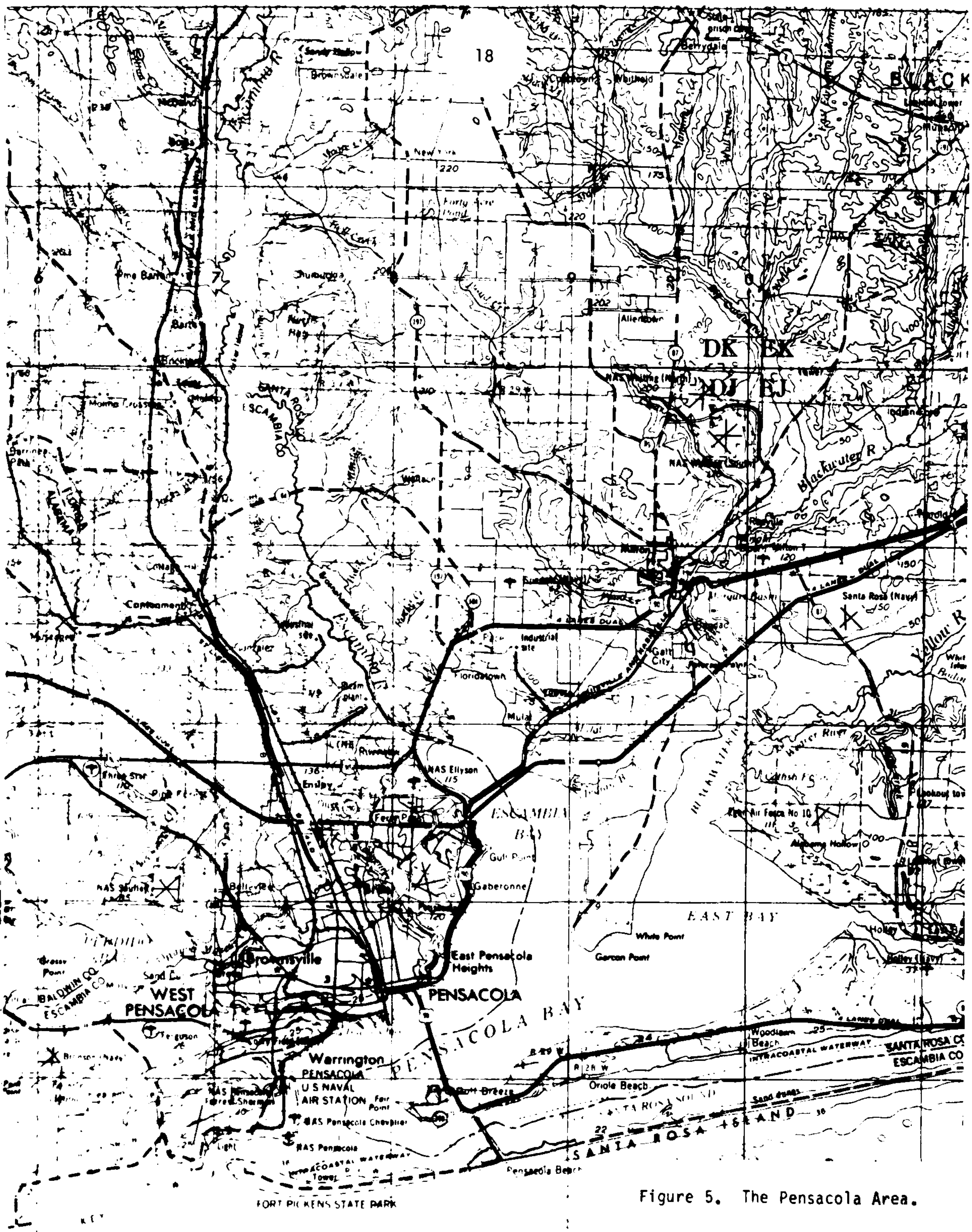


Figure 5. The Pensacola Area.

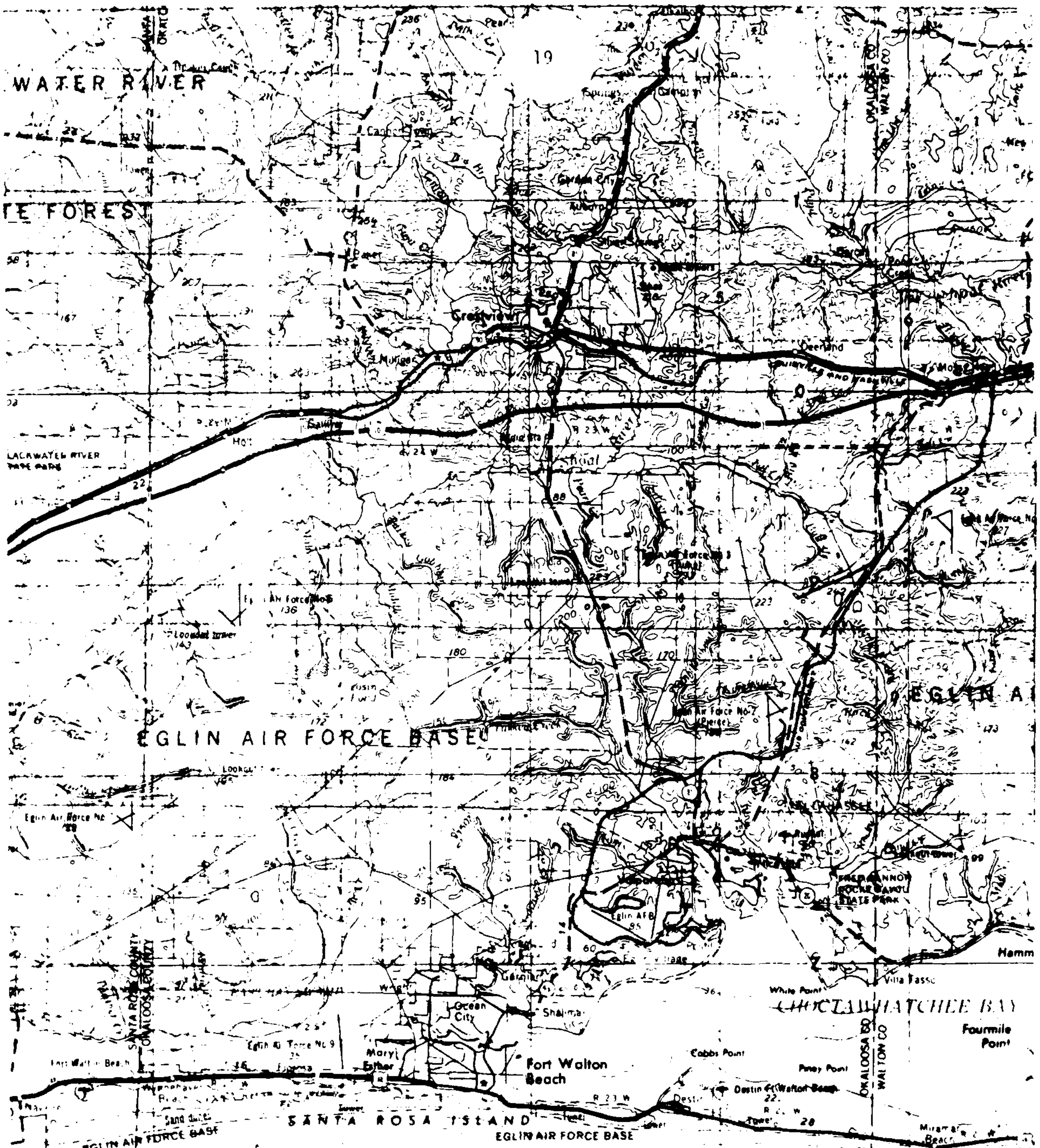


Figure 6. The Fort Walton Beach Area.

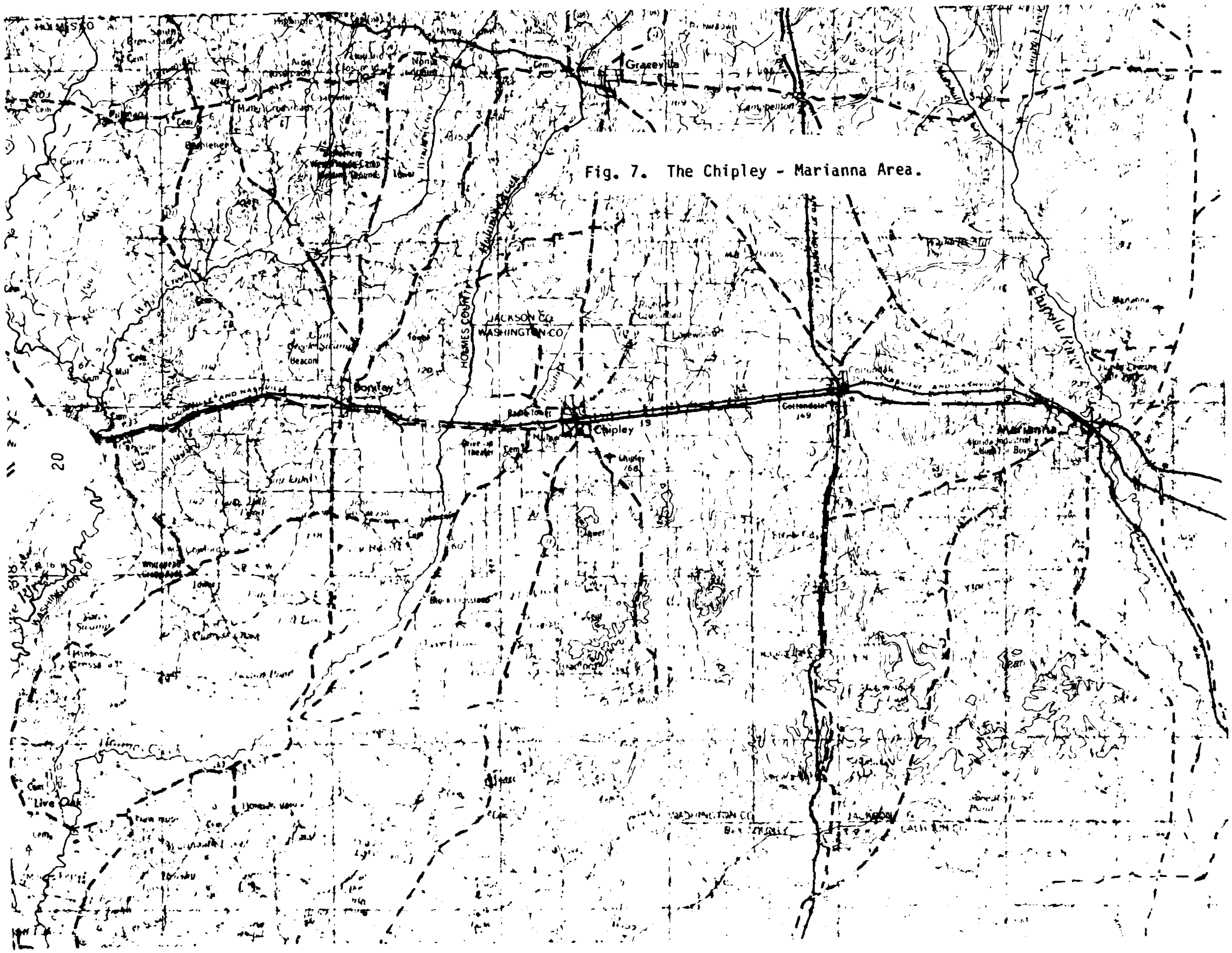


Fig. 7. The Chipley - Marianna Area.

Figure 8. The Panama City Area.

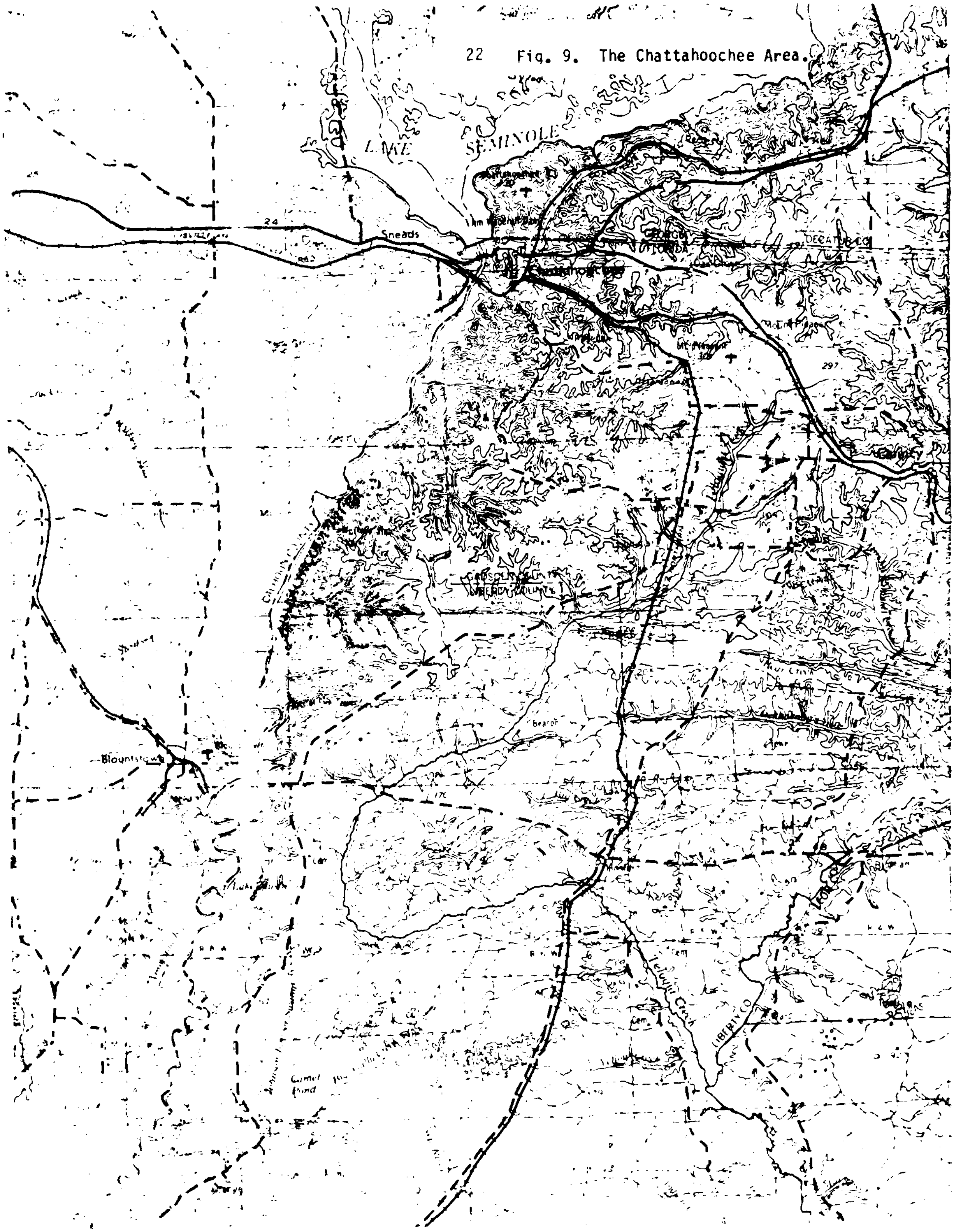
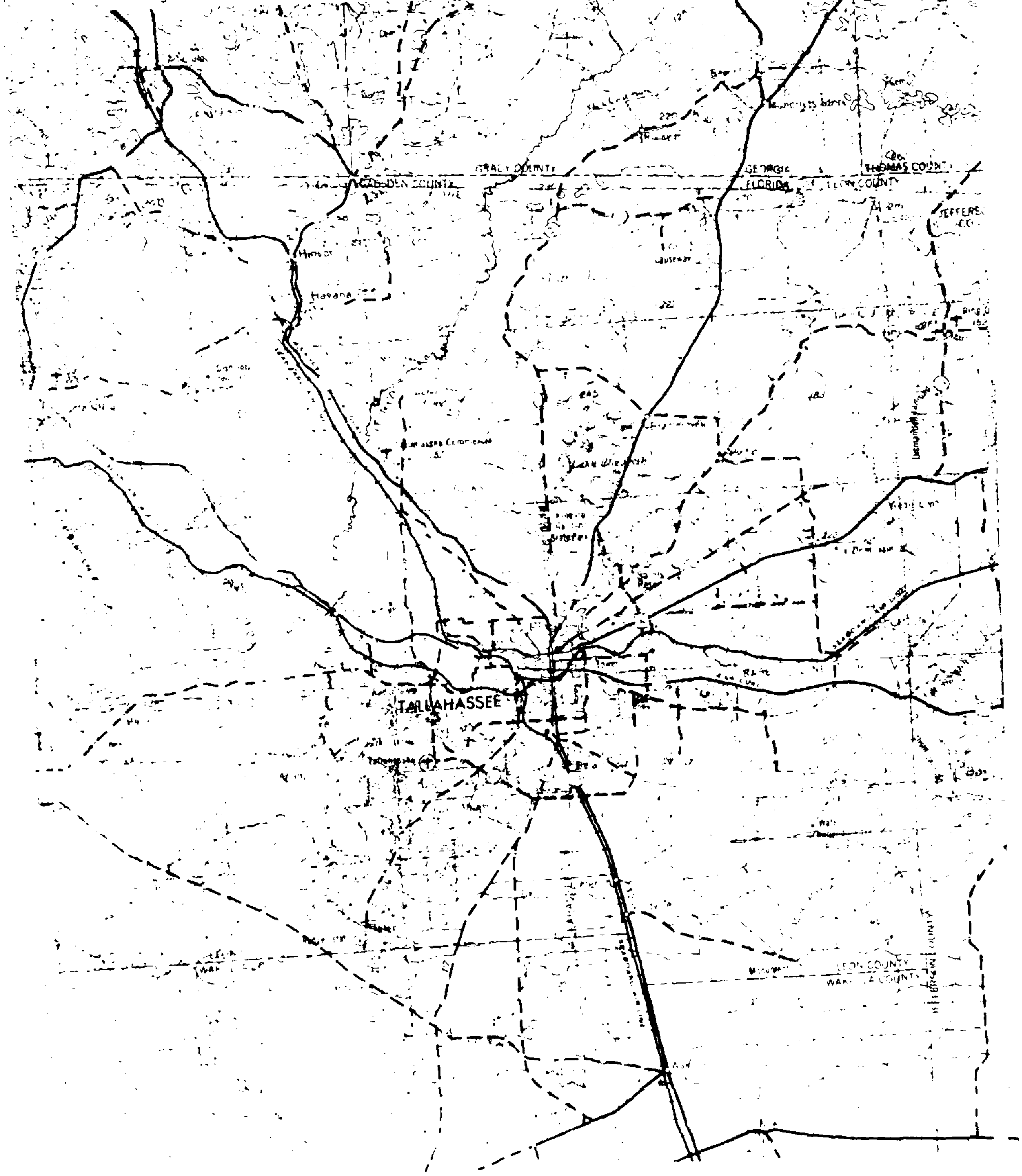


Fig. 9. The Chattahoochee Area.

Fig. 10. The Tallahassee Area.



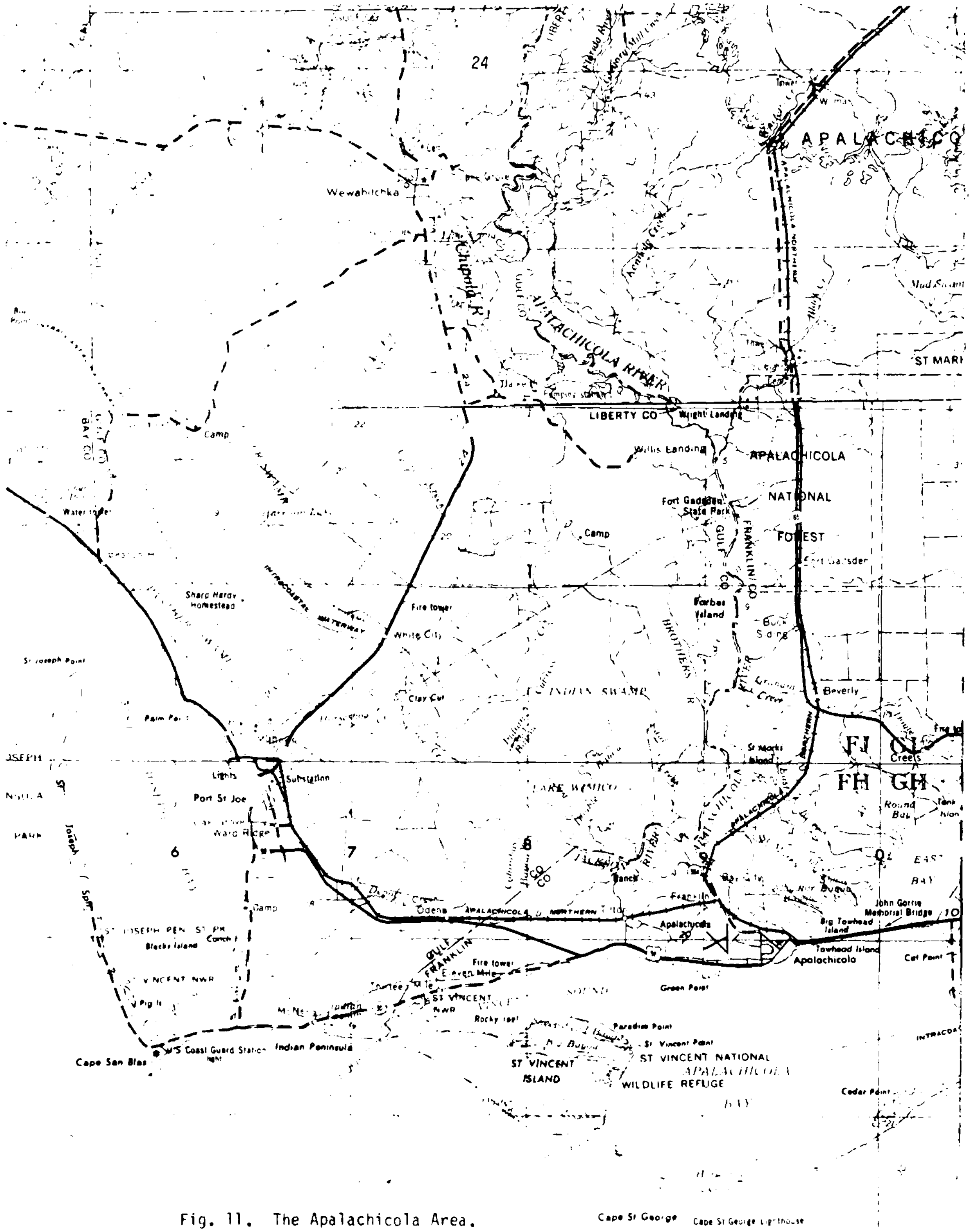


Fig. 11. The Apalachicola Area.

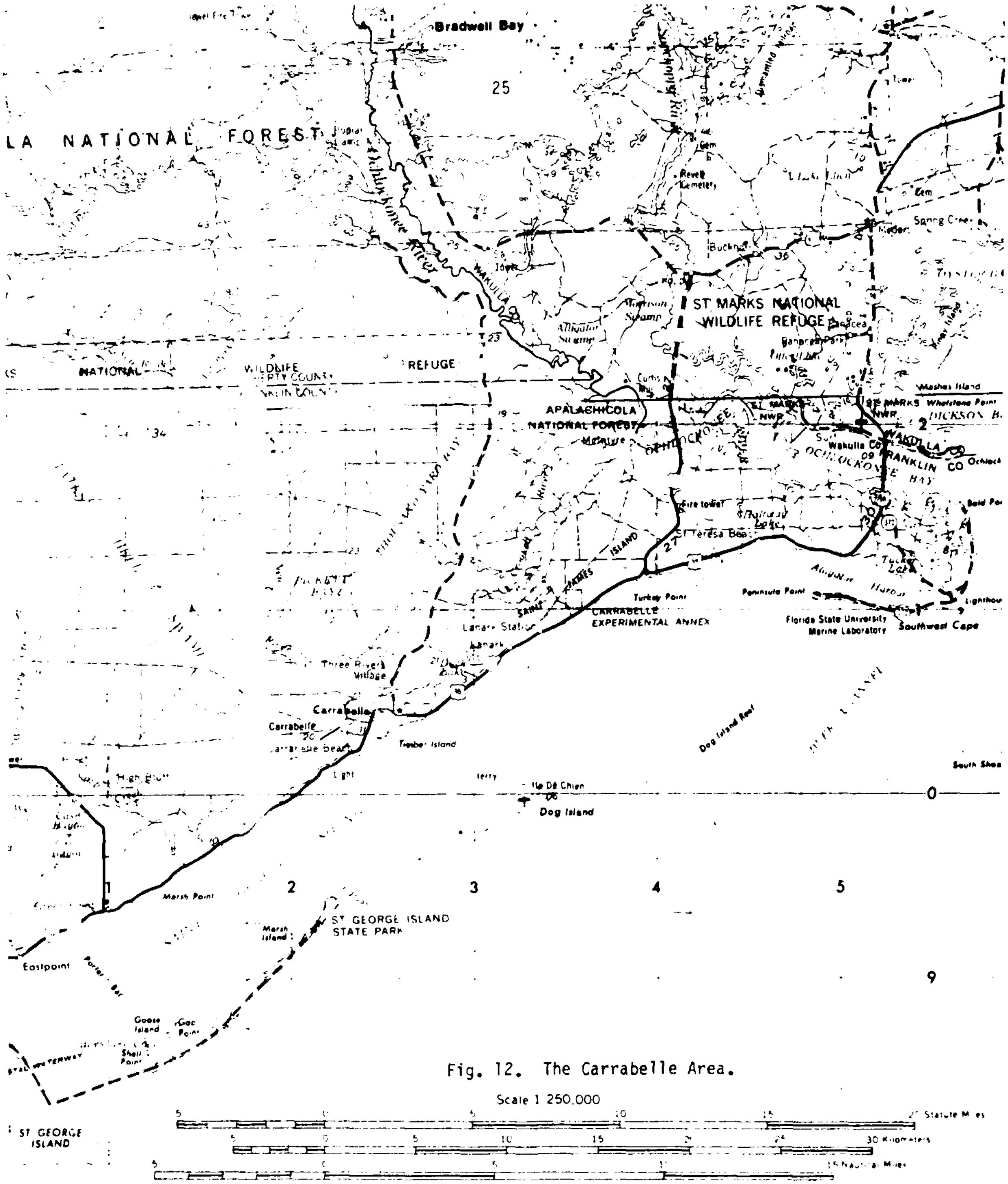


Fig. 12. The Carrabelle Area.

CONTOUR INTERVAL 50 FEET
WITH SUPPLEMENTARY CONTOURS AT 25 FOOT INTERVALS

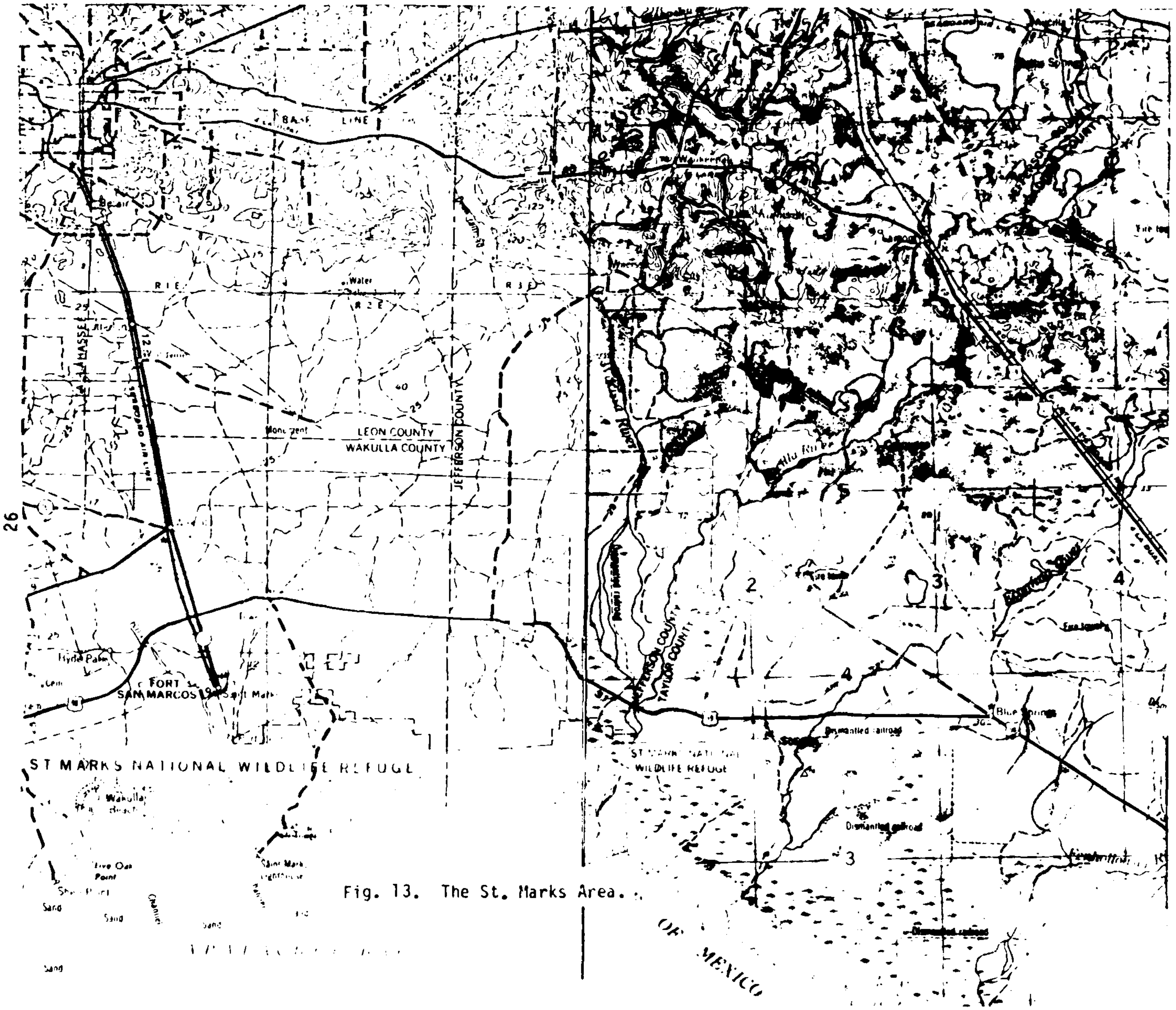


Fig. 13. The St. Marks Area.

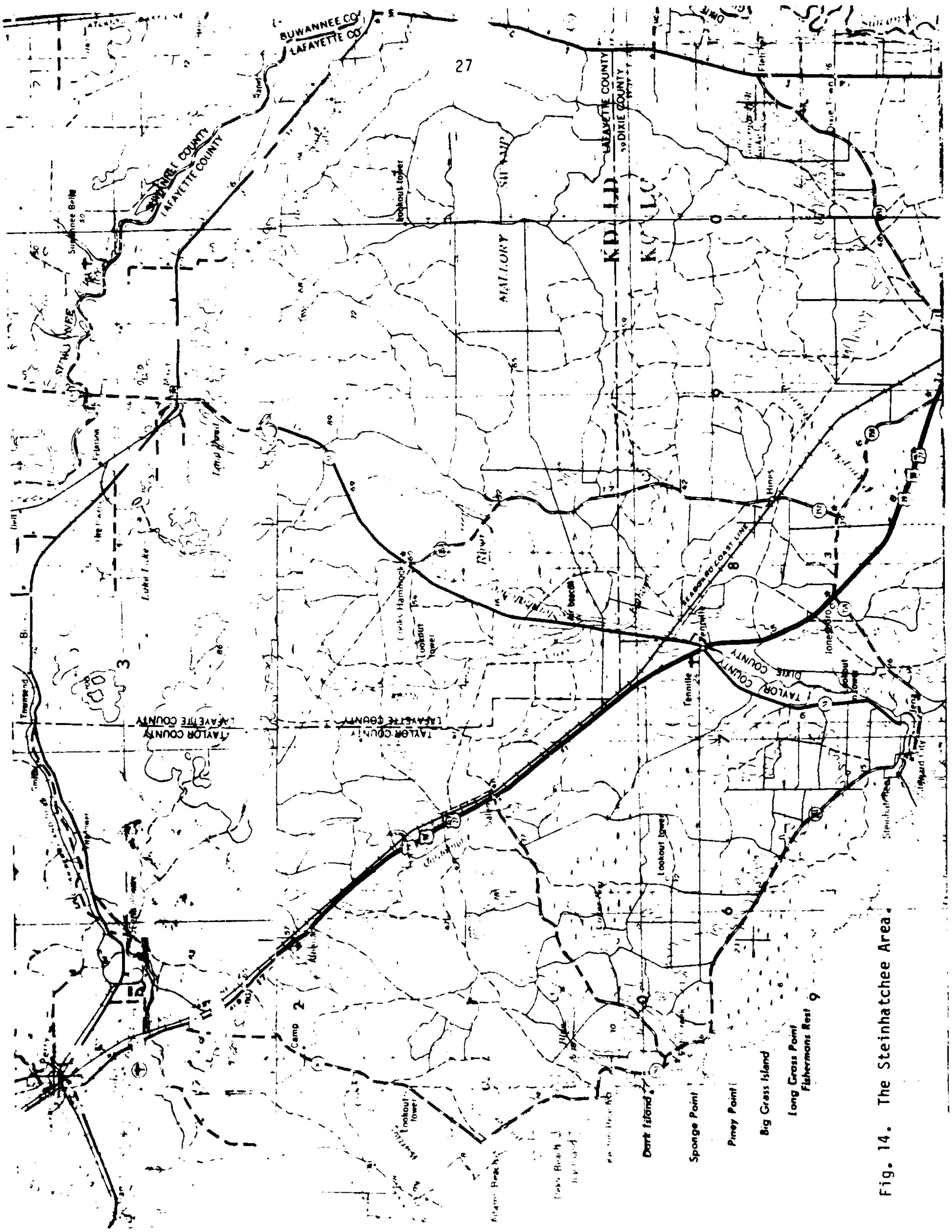


Fig. 14. The Steinhatchee Area.

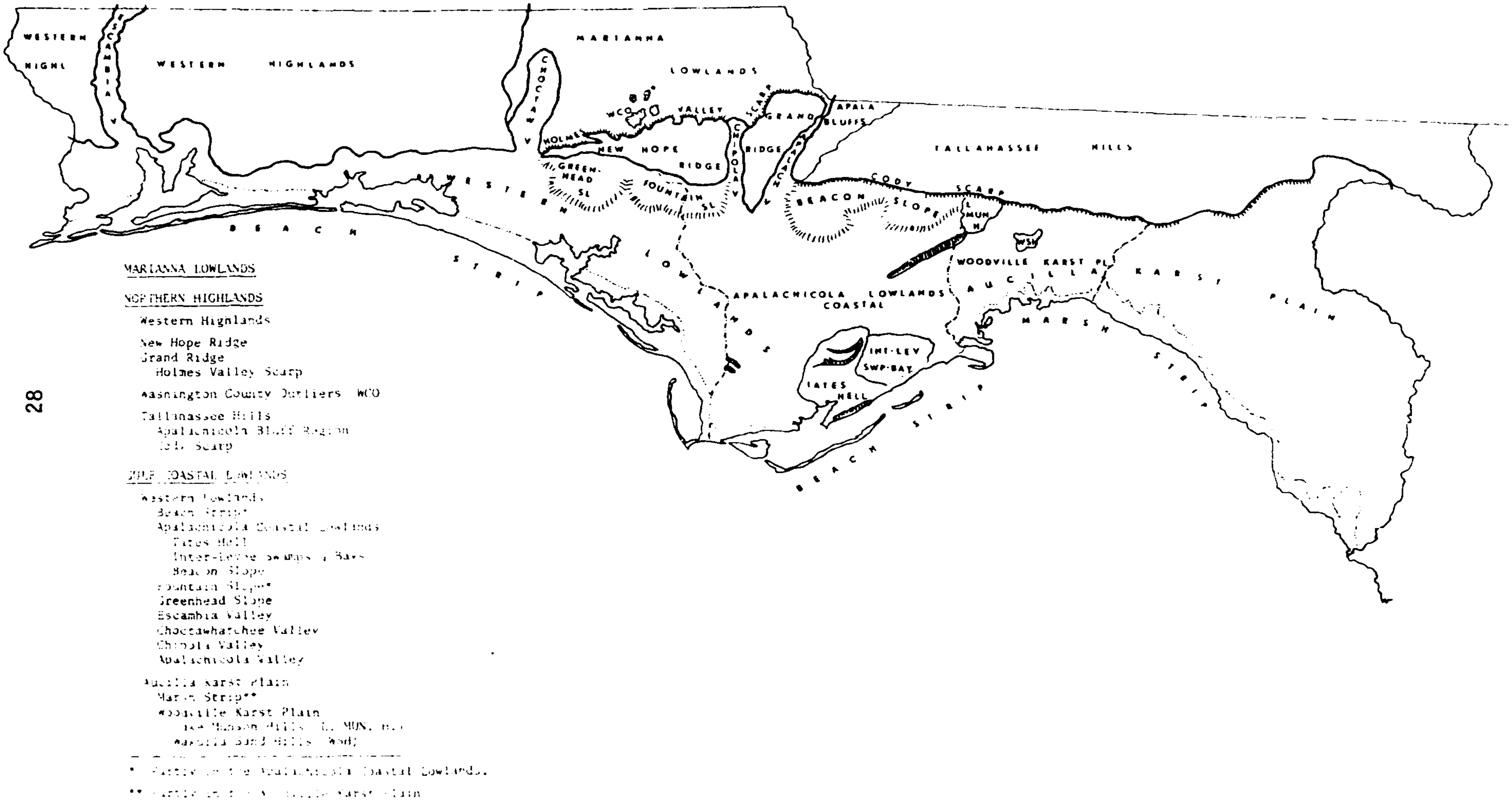


Figure 15. Physiographic regions of the Florida panhandle.

3. HISTORY

The vegetation of most of the panhandle has been modified by the activities of man, both Indians and their European successors. A full understanding of the vegetation requires an introduction to the history of the region. We are fortunate in that a written history of our region dates to the early 16th century, including notes on the vegetation and on land use. Some of the earlier botanical descriptions are given in this chapter, and others are noted in subsequent chapters in relation to specific topics. Historical events in this chapter were taken largely from Tebeau (1971) unless otherwise cited.

Indian Occupation. The earliest artifactual evidences of occupation by Indians date back more than 10,000 years BP (before present). The earlier Indians were hunters and gatherers who lived along rivers and near the coast. The outstanding evidences of their presence are the vast kitchen middens along the coast. These are piles of oyster shells which were discarded after the contents were eaten. The shells of conch and other molluscs are intermixed, along with an abundance of potsherds. The vegetation on middens is often distinctive.

Much of the northeastern shoreline of St. Vincent Island (Fig. 11) consists of a continuous midden which is nearly 2 meters deep in places. Most any disturbance of the soil in coastal regions is likely to expose oyster shells that have been covered shallowly by sand or vegetation. Many such shell middens are either many meters inland from the shore or are buried beneath the peats of tidal marshes. This range of occurrence is evidence for minor fluctuations in mean sea level (msl) during recent millenia.

The Indians of the panhandle began growing maize, beans, and other crops approximately 1,000 years BP (Hale Smith, personal communication 1974), Evidence for the most intensive agriculture comes from the Tallahassee Hills region (Fig. 15), particularly in northern Leon and Jefferson counties. This region was occupied by the Apalachee Indians at the time of Spanish contact in the 16th century. Agriculture was absent from the Gulf Coastal Lowlands with the possible exceptions of a few sites along rivers and behind tidal marshes. The soils of the lowlands are sterile and usually either too wet, too dry, or too acid for agriculture.

Spanish Exploration. The first European to explore the panhandle was Panfilo de Narvaez who marched with a small force from Tampa Bay to near present-day Tallahassee in 1528. Ships that were to meet him somewhere along the coast south of Tallahassee never arrived. His men were forced to build crude ships which were later lost in a storm with nearly everyone lost. The expedition was chronicled by one of several survivors, Cabeza de Vaca, whose writings were translated by Hodge and Lewis (1907). Cabeza de Vaca described the Apalachee territory as wooded and sparsely settled. He said that they took 640 bushels of maize from one town. In light of the poor-yield varieties of maize of that day and in light of the lack of any metal implements for farming, that quantity of maize suggests extensive fields under cultivation.

The next explorer in the panhandle was Hernando de Soto, who landed at Tampa Bay and marched his large army to the Apalachee territory. They spent five months during the winter of 1539-1540 in a town near present-day Tallahassee. In the spring of 1540 the expedition continued into Georgia. A chronicler of the expedition, Garcilaso de la Vega, described the terrain as follows (in Irving 1835):

> "The spaniards had now arrived at the commencement of a fertile region covered with those villages and fields of grain for which the province of Apalachee was famous throughout the country....At daybreak the Spaniards resumed their march through extensive fields of maize, beans, pompions, and other vegetables, extending on each side of the road as far as the eye could reach, interspersed with small cabins, showing a numerous, but scattered population....After contending for two leagues through the fields of corn, the Spaniards came to a deep stream bordered by deep forests....The stream forded, they marched two more leagues.... through the same kind of fertile and cultivated country....The province was reputed to be pleasant, the soil fertile, producing maize, cucumbers, beans, and wild plums....The governor remained five months in winter quarters; and such was the fertility of the province of Apalachee, and the quantity of maize, beans, pumpkins and various other kinds of grain, pulse and vegetables, besides a variety of fruits, that there was no need of foraging more than a league and a half around the village to find food in abundance, though the force consisted of fifteen hundred persons, including Indians and above three hundred horses."

Spellman (1948) reviewed the historical documents pertaining to Apalachee agriculture. He noted that one field extended 10 miles around a town of 200 houses. These fields supported an Indian population estimated at 6,000-12,000 in the hills of northern Leon and Jefferson counties in the mid-1600's.

The Mission Era. Beginning about 1633 Spanish missions were established in the Apalachee territory and elsewhere in the eastern panhandle. These missions were placed on hilltops at Indian village sites. Maize and other commodities were grown by Indians and transported to the Spanish colony of St. Augustine on the Atlantic coast. The Apalachee territory was the bread basket for St. Augustine after the delivery of provisions from Cuba became undependable. The Tomucuan Indians who occupied the panhandle east of the Aucilla River were also agricultural.

The English colony in South Carolina was wary of the Spanish in Florida. Colonel James Moore of South Carolina brought an army to the Apalachee territory in 1704, reinforced it with Creek Indians of central Georgia and Alabama, and raided the Spanish missions. Moore's raid drove the Spanish to St. Augustine. The Apalachees, whose population had been reduced by previous skirmishes with the Creeks and by diseases of European origin, were nearly all driven out. Some escaped to Mobile, and others were captured and sold as slaves in New England.

For the next 125 years the fertile Apalachee territory was nearly unpopulated, and the former fields lay fallow. During these years the Lower Creeks or Seminoles drifted southward and established a few agricultural communities, notably at Lake Miccosukee in northeastern Leon County (Fig. 10). Their small population did not have nearly the effect on the land as did the much larger population of Apalachees. Maps by two explorers, Gauld (1767) and Purcell (1778) both showed extensive Indian old fields in northern Leon County. Romans (1775) traveled through the area in 1771 and wrote:

> "Another curiosity...are the marks of former improvement of this country; particularly the vestiges of the regular maize hills (even in woods where, since the area of culture, trees of twelve to eighteen inches diameter have grown up) and the nails and spikes drove into some very large trees, apparently at ancient Spanish cowpens; add to these, the reliques of old fences, huts, houses and churches, particularly a church bell in the fields, at Santa Fe....A country once nobly and extensively settled...reduced again to a wilderness."

The only other settlement of importance in the panhandle was Pensacola. Tristan de Luna y Arellano tried to colonize the Pensacola area with 1,600 people in 1559, but the venture failed after two years. A Spanish garrison was established in 1696. It was attacked by the French in 1719 and later taken by the English in 1763, who laid out the city as it presently exists. The Spanish recaptured Pensacola in 1781. A fort was constructed by the Spanish at the confluence of St. Marks and Wakulla rivers in 1679 (Fig. 13). San Marcos de Apalache, as it was called, was occupied discontinuously until the founding of the Territory of Florida, but the small garrisons stationed there were of little consequence to the land and the vegetation.

Territory of Florida. The Spanish ceded Florida to the United States in 1821. Florida was a territory of the U.S. until statehood was granted in 1846. Representatives from Pensacola and St. Augustine, the only settlements in Florida, agreed to found a capital city at Tallahassee. The first house was constructed there in 1824. In the next dozen years other towns were founded, including Quincy, Monticello, Marianna, Apalachicola, and Port St. Joe.

William's Descriptions. One of the founders of Tallahassee was John Lee Williams of Pensacola. He traveled extensively through the panhandle by boat and horseback and summarized his observations in two books (1827, 1837). His descriptions of the landscape give valuable information on the plant communities. His remarks were augmented by lists of important or conspicuous plants for each general habitat type.

Williams (1837) described the panhandle as follows.

"The soils of West Florida may, perhaps, all be comprised in five kinds, to wit: Pine barrens, uplands, hammocks, swamps, and marshes. If we estimate the quantity of land at 10,560,000 acres, and deduct one fourth part for bays, lakes, rivers, &c., there will remain 7,920,000. Of this quantity, two thirds, or 5,280,000 acres may be covered with pine barrens; 800,000 with tillable upland; 600,000 with hammocks; 500,000 with swamps; and 400,000 with marsh."

Williams' calculations are off by 340,000 acres, but better this error than no record at all.

The pine barrens are essentially of longleaf pine with some slash pine near the coast and in boggy sites. Habitats of the pine barrens include pine-palmetto flatwoods, upland longleaf pine woods, and longleaf pine-turkey oak sandhills and ridges. Williams (1837) described them as follows:

"The pine barrens are composed, principally, of silicious sand, more or less mixed with calcareous and vegetable matter, and often divested of every fertilizing principle, by the frequent fires which run over them. Barrens are found on the seacoast, and on the ridges, between the large water courses. All the lands covered with pine timber,

> are by no means barren; on the contrary, some of the best uplands are wholly, or nearly all, covered with yellow pines. And some of the burnt barrens will not produce even pine or scrub oaks, but are usually partially covered with clumps of savin."

Yellow pine is another name for longleaf pine. Savins are cedars; however, Williams did not give any cedars in the check list of species that followed his narrative. He alluded to the pine barrens of the panhandle elsewhere in his book as follows:

> "A large portion of the country is covered with forests, the trees usually at a considerable distance apart, without underbrush; while the surface of the ground presents a carpet of verdant grass and flowers most of the year."

The grassy parklike appearance of these barrens is the result of frequent surface fires that consume the undergrowth but do not harm the thick-barked pine trees. The less fire-resistant hardwoods are essentially excluded. The grasses and many other perennial herbs resprout after fire, much as a lawn resprouts after mowing.

Williams (1837) described the uplands as follows:

> "Uplands are formations of clay, which arise gradually on the subtending limestone; they usually commence about twenty miles from the coast....The trees, on this soil, are abundant, and form the pleasantest groves imaginable."

His check list began primarily with longleaf pine and the hardwoods of the pine-oak-hickory community, including black oak, laurel oak, Spanish oak, post oak, white oak, and mockernut hickory. The list continued with species more commonly associated with other mixed hardwood forests, including magnolia, beech, and a few species of bottomlands. The latter species occur along creeks in the uplands.

He said that the hammocks were similar to the uplands but contained a greater variety of species. Some of those not found in the uplands were sweetbay, the coastal cabbage palm, red cedar, sweetgum, live oak, and several trees of floodplains.

He divided swamps into three types, these were (1) alluvial swamps along rivers, (2) "pine barren swamps" dominated by cypress, "which are natural basins, containing the waters of the surrounding country", (3) "galls" covered by titi. From the species and notes in his check list, it is obvious that Williams included the more open bogs and savannahs in his general category of swamps.

Williams divided marshes into fresh and salt marshes and emphasized the diversity of species and soils associated with both types. These descriptions of the vegetation were printed in both books (Williams 1827, 1837); the latter also contained brief descriptions of mangrove swamps and tropical hammocks from peninsular Florida.

Williams (1837) also described each county, including occasional references to the vegetation. He said the following of Jackson County.

> "The western part of Jackson, with the exception of Holmes Valley, and Oak and Hickory Hills, is poor pine barren land. The Marrianna Lowlands contains from eight to ten sections of good land, sunk nearly one hundred feet below the surface of the surrounding country. The soil is a dark sandy loam, covered with white, black, and yellow oak, white ash, black gum, wild cherry, red bay, magnolia, with sassafras, pawpaw, witch-hazle, and haw shrubs; the whole being

mixed with wild cane."

The Oak and Hickory Hills are the Washington County Outliers (Fig. 15).

"They stand insulated in the midst of extensive pine barrens, above which they are elevated some hundreds of feet. The land on them is excellent upland, similar to the rich red clays of Leon County; they are clothed with heavy forests of oak, hickory, chestnut, gum, sorel tree, and magnolia."

Leon County then extended from the coast to Georgia and from the Ochlockonee River to the Suwannee River. Williams said:

"There are many rich hammocks on the borders of the Appalachee bay, and much of the pine land, for some distance from the coast, has a rich soil, and is very productive....To the distance of fifteen or twenty miles from the coast, the rock is but slightly covered with sand; the small streams are rather scarce....This tract of country is generally covered with excellent yellow pine timber, under which the wild grass grows luxuriantly....From the level tract of pine land, as described, the country rises over gentle swells of red and white clay, covered with an excellent brown soil, and crowned with spreading oaks and tall hickories, mixed with liriodendron, magnolia and gum....This kind of land, in some places, extends into Georgia; in other parts, the pine barrens make large indentations from various directions."

Cotton Era. The Cotton Era began with the founding of Tallahassee in 1824. Stoddard (1969) estimated that 75-90% of the red hill country between Tallahassee and Thomasville, Georgia, was cleared by slave labor before the Civil War. Historical accounts of this era were written by Groene (1971) and Rogers (1963). Large cotton plantations were established which thrived until the Civil War. These plantations and other agricultural lands of the panhandle were distributed almost exclusively in the Northern Highlands and Marianna Lowlands.

This era ended about 1875 with the deterioration of the plantation system and with depressions in the cotton market (Paisley 1968). Smaller farms persist to the present, but great acreages of former plantation lands were lain fallow (Brubaker 1956). The trees that invaded these fields now provide forest cover. Sharecropping became a major mode of subsistence for the relatively large population of rural blacks and other poor people. A family would farm one or few acres of land, depending on how much land could be tilled behind a mule or ox. Part of the crop was "shared" with the land owner in lieu of rent. These small fields and accompanying homesites were widespread throughout the former plantation lands and elsewhere in the agricultural belt. Other small farms and homesteads were established in the coastal lowlands, even in droughty sandhills. When jobs became plentiful in the cities during World War II, sharecropping quickly disappeared. Fallow fields of sharecroppers have either grown over with native vegetation or have been preempted for other uses.

A significant development in the Tallahassee-Thomasville region was the purchase of most former cotton plantations by northern industrialists during the late 1800's for use as hunting preserves. These large, privately owned tracts are still used for that purpose. Quail is the favored quarry.

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4. LAND USE AND LAND MANAGEMENT

Table 1 shows that 79.7% of the panhandle is used for commercial forestry. Only 5.4% of the region is planted to crops, and 4.6% consists of lakes, bays, and other bodies of water. The remaining 10.3% of the land is used for other uses, including municipalities, highway corridors, and pastures. Jackson County, centered in the Marianna Lowlands (Fig. 15), leads in harvested croplands. Industrial forests cover 35.3% of the panhandle. The large majority of industrial forest lands are owned by several large pulp mills that manufacture paper goods and chemical cellulose from pine wood (Table 2). Many forests are in public ownership in the form of national and state forests, military reservations, parks and preserves.

Grazing. Cattle, hogs, and other domestic animals were first introduced in the panhandle by de Soto. These animals foraged in the pine barrens which served as open range. They were tended by Indians and later by American settlers during territorial times. The abundant wiregrass was a major source of food for cattle, but only the new sprouts were nutritious. As a result, the Indians and their European successors burned the pine barrens at all seasons to promote the sprouting of tender shoots. Livestock would congregate on fresh burns, thereby eliminating the need for fences except as exclosures around cultivated fields.

This practice continued until the passage of the fence law in the 1940's, which prohibited grazing on open range. Thereafter pastures were fenced and improved by the planting of bahia grass and other exotics. Many forested lands continue to be converted to improved pastures. An

TABLE 1. Surface Area ($Miles^2$) by County of Waters and Some Land Uses.

	1 County Area	2 Waters	3 Commercial Forests	4 Harvested Croplands	5 All Other Uses
Bay	773	106	660	7	0
Calhoun	566	10	484	24	48
Dixie	713	21	615	5	72
Escambia	652	105	437	37	73
Franklin	544	21	478	0	45
Gadsden	512	15	359	58	80
Gulf	567	21	519	1	26
Hamilton	514	1	394	49	70
Holmes	483	1	318	64	100
Jackson	939	6	529	184	220
Jefferson	600	11	430	66	93
Lafayette	550	11	460	22	57
Leon	672	11	497	41	123
Liberty	844	7	819	2	16
Madison	714	6	506	85	117
Okaloosa	917	54	735	26	102
Santa Rosa	1,015	121	830	64	0
Taylor	1,044	20	948	5	71
Wakulla	618	21	545	5	47
Walton	1,073	89	840	41	103
Washington	605	14	479	25	87
TOTAL	14,915	672	11,882	811	1,541
Percent	100	4.6	79.7	5.4	10.3

Columns 1 and 3 from Knight (1969) and McClure (1970). Column 2 from Marth and Marth (1978). Column 4 from Raisz (1959). Data in column 5 are column 1 minus columns 2+3+4. Column 5 data are approximate, because the estimates of county size differed between authors.

TABLE 2. Commercial Forest Areas (Miles^2) by Ownership.

	Public	Forest Industry	Farmer	Misc. Corporate	Private Individuals
Bay	43	373	0	0	244
Calhoun	5	253	93	12	122
Dixie	1	601	2	2	8
Escambia	7	133	118	18	160
Franklin	45	417	0	0	17
Gadsden	3	115	117	39	84
Gulf	0	345	123	10	41
Hamilton	0	225	36	0	134
Holmes	1	81	141	0	94
Jackson	10	76	247	5	192
Jefferson	7	189	52	0	182
Lafayette	1	347	43	22	47
Leon	161	88	62	15	171
Liberty	402	299	37	0	81
Madison	0	248	191	0	68
Okaloosa	424	66	109	5	132
Santa Rosa	285	252	55	12	226
Taylor	1	786	14	40	108
Wakulla	307	84	16	0	137
Walton	214	220	153	0	253
Washington	3	60	116	0	300
TOTAL	1,920	5,258	1,725	180	2,801
Percent of Entire County	12.9	35.3	11.6	1.2	18.8

Data from Knight (1969) and McClure (1970). Forest Industry lands are owned by companies or individuals operating wood-using plants.

example is the M-K Ranch which extends at least 15 miles along the Apalachicola River in Gulf County.

Hogs were less easily controlled on the open range, and many became feral. They are common today throughout all types of moist and wet woods, in spite of programs to trap and shoot them. They cause substantial damage by eating pine seedlings and by rooting for food in parks and other natural preserves.

Turpentining. The extraction of resins from pines for the production of turpentine and other naval stores began early and has been widely practiced for at least 150 years. As a rule, the trees were turpentined for two or three years before being logged. Pine needles and other combustible vegetation were raked away from each tree to prevent damage to the face (slashed surface) during the near-annual fires in the pine barrens. Turpentine stills were operated at small camps throughout the pine barrens.

Stumps of the original growth pines persist today, in spite of being cut at least fifty years ago. The high resin content in these stumps acts as a preservative. These stumps are being pulled from the ground systematically in great numbers and are chipped and distilled for their naval stores. Since 1950 94% of the naval stores in Florida came from old stumps of the original timber (Marcus and Fernald 1975).

Logging. Longleaf pines were logged and exported from Pensacola in 1761. Pensacola and Apalachicola were important ports for exporting timber in the late 1800's. Timber near the Apalachicola River was high graded (the best trees selectively cut) and rafted to saw mills along the Gulf coast as early as 1830 (Clewell 1971). Harper (1911) reported that a good deal of cypress had been removed from the floodplain of the lower Apalachicola River, much of which was exported to Europe.

The timber boom in Florida lasted from about 1870 to 1925 and resulted in the harvesting of virtually all original-growth trees, particularly pines. Peak production was reached in 1923 (Marcus and Fernald 1975). Large scale cutting began in the panhandle in the early 1900's (C. H. Coulter, personal communication 1978), including Jefferson County (Shofner 1976). Lands now in the Apalachicola National Forest were cut mainly between 1913 and 1927. The timber of the sandhills near Tallahassee may have been harvested in the late 1800's (Clewell 1971). Virtually all tracts of virgin timber in the panhandle were cut by 1930. Stoddard (1931) said, "The last virgin pine flatwoods passed into the hands of turpentine operators and will be lumbered soon."

The logging, turpentining, and grazing operations had no consequential effect on the grasses and other undergrowth in the pine barrens. Stoddard (1931) mentioned, though, that in the sandhills of West Florida, "after the original stand of pine is cut, a dense growth of scrub oak develops." Once the land was clear cut, it often reverted to public ownership. The Apalachicola National Forest, the St. Marks National Wildlife Refuge, and other public forests, parks, military bases, and wildlife preserves were created in these lands, primarily in the 1930's.

Burning. Indiscriminant burning of the open range retarded natural reforestation on cut-over lands. Major forest fires elsewhere in the United States led to a massive national campaign to prevent all forest fires, even prescribed burning. Stoddard (1969) recalled attempts in the 1920's by overzealous federal officials to censor the chapter in his book on bobwhite quail, which endorsed prescribed fires. The book (Stoddard 1931) was written in cooperation with the U.S. Department of Agriculture. In spite of anti-burning campaigns, annual burning continued in most of the panhandle, including the game plantations of Leon County. Indiscriminant burning was reduced, though, in favor of prescribed burning. Fire was excluded from some large areas to promote forest regeneration.

Effective fire protection began following the creation of the State Division of Forestry in 1928. Prescribed burning began on the Apalachicola National Forest about 1944, and the pinelands have been winter-burned about every fifth year thereafter. Periodic prescribed winter-burns are standard practice in much of the pinelands of the panhandle today.

Commercial forestry. Since the last of the original growth pines were harvested, most sites have been reforested with second growth pines. These grew from seedlings and saplings that were already established at the time of clear cutting or from natural reseeding by the few remaining mature trees. Compared with the original growth stands, the second growth forests are more densely stocked and the trees are not quite as large, particularly in girth. Many of these stands, if left to grow, will be difficult to distinguish from original growth by the end of this century.

Most of these second growth stands, though, are being harvested at a rapid pace to support wood-utilizing industries, including pulp mills at Panama City, Pensacola, Port St. Joe, and Perry. The Panama City installation was built in 1931 and was the first in the panhandle. Since about 1950 most lands that have been clear cut are planted to pine, usually following treatment of the habitat to insure full stocking and rapid growth. Such treatment is called site preparation.

Site preparation may involve any or all of the following, burning, draining, tilling, root raking, fertilizing, the application of herbicides, and other practices. Tillage often consists of disking, chopping, and bedding. Disking is accomplished by disk-harrows that slice the soil but do not turn it completely. Chopping consists of turning the soil with blades fixed to a heavy drum pulled by a tractor or larger vehicle. Smaller trees are pushed over and their trunks severed by choppers. Bedding plows make the soil surface corrugated by throwing the soil into broad ridges separated by equally broad furrows. Bedding is a widespread technique on wet sites. Pine seedlings are planted on the ridges where the soil is better drained. Root rakes push plants and brush into windrows. Careless operators often push much of the topsoil into the windrows as well. Fertilizers, such as dimmonium phosphate, are broadcast from aircraft.

Since about 1960 the mechanical disturbance of the soil is almost always involved in site preparation. Disturbance effectively reduces competition from the native vegetation. The term, intensive management usually infers soil disturbance during site preparation. Intensive management is almost universally practiced in the vast commercial forests owned by large pulp companies. Genetically improved pine seedlings are row-planted in densely stocked stands. A thinning operation is sometimes required to reduce the density of the saplings. The trees are clear cut in about 25-30 years. The span of time between site preparation and harvest is called a rotation. Rotations of 60 years or more are prescribed for the production of saw timber and poles, but the great majority of pines are grown for pulp.

Periodic fires are sometimes prescribed in tree farms during the rotation but not in stands where the trees are intended for the production of pure cellulose. Flecks of charred materials sometimes contaminate the processed cellulose and are expensive to remove.

Public lands are under less intensive management. Nonetheless about 2,000 acres per year of natural pinelands are being chopped or bedded and row-planted to pine seedlings in the Apalachicola National Forest west of the Ochlockonee River. Some public lands and private holdings are less intensively managed by the seed tree and shelter wood methods. The seed tree method of regeneration consists of clear cutting with the exception of a few scattered trees that serve to produce seeds which restock the stand naturally. Site preparation usually consists only of prescribed burning just before seed fall and fire suppression until the saplings are large enough to tolerate fire.

The seed tree method as practiced on game plantations usually consists of selective cutting rather than clear cutting. Regeneration consists of ringing open areas with a firelane to protect seedlings from annual fires. When these grow into fire-tolerant saplings, the firelanes are allowed to revegetate, and fires burn across them. The rotation is very long, often exceeding 100 years. The great height of the trees allows their sale as poles and pilings, which brings a much higher price than that for saw timber and particularly for pulpwood. In contrast to intensive management, this method of silviculture requires little labor, machinery, fossil fuels, chemicals, and fertilizers. Intensive management, though, realizes a greater volume of timber per unit area within the same span of time.

The shelterwood method usually involves two thinnings before the final harvest (Croker and Boyd 1975). Trees remaining after the second thinning serve as sources of seed and are not cut until after the saplings growing from these seeds are well established.

About one of six acres of commercial forest land is artificially planted to pine, mostly slash pine (Knight 1969). More than a third of the longleaf pine-turkey oak sandhills of the panhandle have been converted to pine plantations. The average stand density is increasing. Trees of at least 5 inches of dbh comprised 36 ft^2 basal area/acre in 1949 and 41 ft^2 20 years later. Pulpwood harvest doubled during the 1960's. Farm forests are decreasing and industrial forests increasing, particularly in northeastern Florida (McClure 1970). The timber harvest is greater per acre on industrial forest lands than in other commercial forests. There is an overall increase of 48% (northeast Florida) and 56% (northwest Florida) of growing stock over the timber harvested.

Vegetational Preserves. Portions of the lands in public ownership have been set aside as natural preserves. Some other portions of these lands are not intensively managed and conserve native vegetation in a more-or-less natural state. The private game plantations also largely serve as natural preserves.

The public lands include two huge holdings. These are the Apalachicola National Forest (557,000 acres or 870 mi^2) in Liberty and Wakulla counties (Fig. 2), and Eglin Airforce Base (464,000 acres, formerly the Choctawahatchee National Forest), centered in Okaloosa and Walton counties (Fig. 1). The Blackwater River State Forest (183,153 acres) in Santa Rosa County is also a large holding. Pine Log State Forest in Bay County is much smaller (6,911 acres).

The St. Marks National Wildlife Refuge (65,000 acres) spans most of the coastal areas in Wakulla and Jefferson counties and includes some forested uplands. St. Vincent National Wildlife Refuge occupies all of St. Vincent Island in Franklin County. Other coastal regions are preserved in the form of Gulf Islands National Seashore on Santa Rosa Island, St. Josephs Peninsula State Park in Gulf County, and recently acquired state lands on either end of St. George Island in Franklin County. There are several other state parks, the most notable of which is Torreya Park on the bluffs of the Apalachicola River in Liberty County. This park was established to preserve the unique flora of that area. The Florida Caverns State Park in Jackson County preserves the unique vegetation of the Marianna Lowlands. The Blackwater River State Park and the Ochlockonee River State Park are located in Santa Rosa and Wakulla counties, respectively. Other recreation areas, historic sites, and gardens are maintained under the State Park System.

There are two sites in the National Wilderness Preservation System. One is the St. Marks Wilderness, which consists mostly of tidal marshes in St. Marks Refuge. Most of the wilderness lies between the St. Marks and the Aucilla rivers (Fig. 13). The other is the Bradwell Bay Wilderness in the Apalachicola National Forest north of Sopchoppy in Wakulla County (Fig. 12). Bradwell Bay is an acid swamp fringed with pine flatwoods. Each of these wilderness areas encompasses about 20,000 acres.

The State of Florida is also purchasing preserves in an Environmentally Endangered Lands Program, initiated in 1972. A 30,000 acre area in the floodplain of the lower Apalachicola River is now being acquired (Pearce 1977).

The privately endowed Tall Timbers Research Station, which is north of Lake Iamonia in Leon County (Fig. 10) serves as a preserve of old growth timber and as an experimental area for the study of environmentally compatible techniques of habitat management. It was founded in 1957 at Tall Timbers Plantation and staffed initially by H. L. Stoddard, Sr., and some of the colaborators in his investigations of the bobwhite quail. Station activities have had considerable influence in bringing about the acceptance of controlled burning as a tool for forest and wildlife management (Komarek 1977).

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5. CLIMATE

The climate of the panhandle is mild, moist, and relatively uniform. The annual rainfall ranges from about 48-64 inches (Fig. 16), although it is quite variable at a given place from year to year (Fig. 17) and for the same month in different years (Table 3). The growing season or freeze-free period ranges from about 265 to 310 days (Fig. 18). The annual temperature is quite variable at a given place from year to year and for the same month in different years (Table 3). The climate is slightly warmer along the coast. The mean annual number of days with temperatures at or below freezing is 20 along the Alabama-Georgia border and 5 at Cape San Blas. The mean annual number of days with temperature at or above 90°F is 90 for most of the panhandle but only 20 at Cape San Blas (ESSA 1968). Mean annual lake evaporation is about 46 inches and mean annual pan evaporation about 60 inches throughout the panhandle (ESSA 1968, Visher and Hughes 1969, Dohrenwend 1977).

The following discussion was abstracted largely from the narrative climatological summary for Tallahassee (NOAA 1976): There is a definite march of the four seasons with considerable winter rainfall and reduced sunshine. The average year-round temperature is 68°F (20°C) and has varied from 65° to 71°. During the winter topographic effects and cold air drainage into lower elevations give a wide variation of minimum temperatures on cold, calm nights. Freezing temperatures at the airport average about 35 occurrences each winter, but freezing temperatures in the city are about half that number. Temperatures of 25° or lower occur about three times per winter, and once every third winter temperatures below 20° can be expected. The lowest ever recorded was -2° (-19°C) in 1899, and since then the lowest was 10° in 1962.

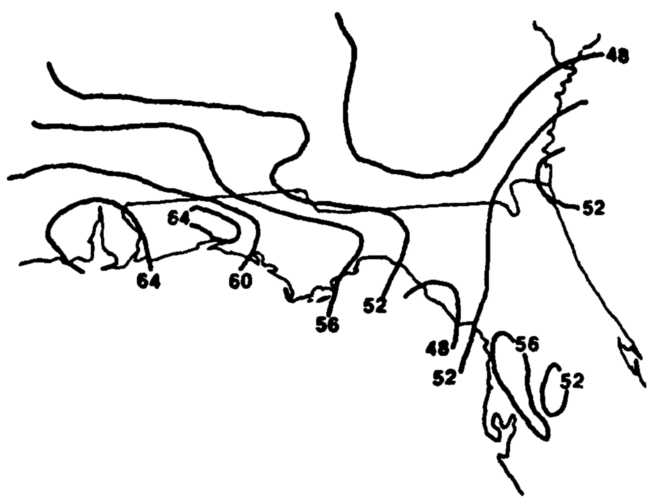

Figure 16. Normal annual rainfall in inches (redrawn from ESSA, 1968).

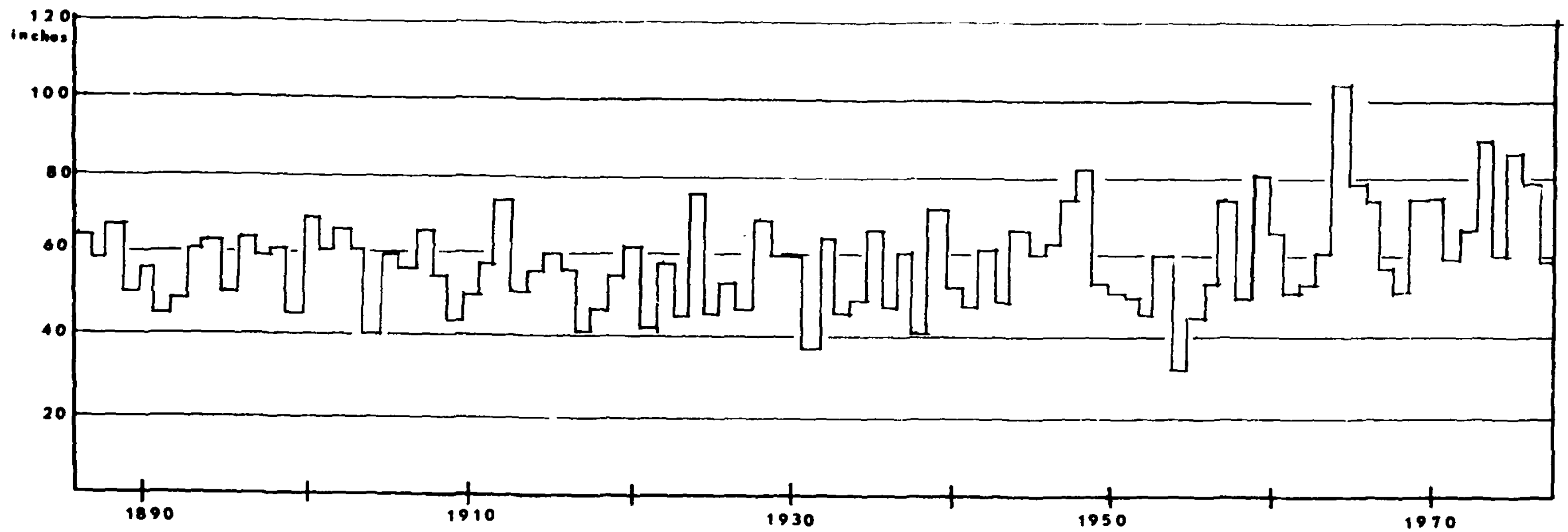

Figure 17. Annual rainfall at Tallahassee. From Hughes (1969) and NOAA records at the Tallahassee airport.

TABLE 3. Average Temperature and Precipitation at Tallahassee (NOAA 1976).

Average Temperature

Year	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec	Annual
1937	65.0	55.0	59.9	66.6	76.2	80.6	81.5	80.7	75.6	67.1	57.3	53.2	68.3
1938	54.2	60.6	67.0	68.2	77.0	78.8	80.3	83.4	76.8	67.2	63.0	54.0	69.2
1939	57.4	60.6	64.7	67.6	73.8	80.2	81.0	78.9	79.6	70.7	58.4	54.8	69.0
*1940	41.8	51.4	58.8	65.2	71.0	79.0	80.4	81.3	74.2	66.7	58.8	56.8	65.4
1941	51.2	48.2	53.5	68.8	75.0	80.1	80.8	82.6	79.2	75.0	58.8	54.6	67.5
1942	49.6	48.8	57.5	66.8	73.2	79.7	82.2	80.4	76.6	69.2	61.2	54.6	66.6
1943	54.0	53.0	60.2	66.2	76.4	81.8	82.2	82.2	76.8	66.2	55.0	50.8	67.1
1944	51.0	61.2	63.0	66.8	74.6	82.6	79.8	80.9	79.1	66.3	58.0	49.8	67.7
1945	50.8	58.8	68.4	69.8	72.8	80.6	80.2	80.2	79.6	68.2	59.2	48.2	68.1
*1946	55.0	55.2	63.4	69.2	74.4	79.4	81.6	80.6	77.2	70.7	66.7	57.0	69.2
1947	59.8	49.0	56.0	71.6	75.2	80.0	80.0	81.6	78.6	72.2	59.6	55.6	68.3
1948	48.4	59.6	64.3	72.0	77.6	81.4	81.0	80.8	76.7	66.3	65.6	60.2	69.5
1949	61.4	63.3	60.8	68.5	76.7	79.7	81.2	80.8	77.6	74.8	57.2	58.8	70.1
1950	65.4	59.5	58.7	63.5	76.4	80.8	79.1	81.1	77.0	71.9	55.3	50.7	68.3
1951	53.2	54.9	62.1	66.0	74.1	80.7	82.2	83.5	79.9	72.7	56.5	58.5	68.7
1952	59.7	57.3	61.5	65.4	75.1	83.8	82.8	80.4	77.2	67.2	58.9	52.5	68.5
1953	55.1	56.8	65.3	65.4	78.1	80.4	81.0	80.3	77.3	68.8	57.5	54.3	68.4
1954	54.9	56.9	59.9	72.1	71.6	80.8	82.7	83.9	80.9	68.3	56.7	50.2	68.3
1955	51.2	55.6	63.9	69.8	76.2	77.4	80.3	81.7	79.1	67.4	58.0	52.9	67.9
1956	48.8	59.8	59.7	64.7	75.8	78.2	79.6	80.7	75.0	69.1	56.7	58.5	67.2
1957	58.4	62.1	59.2	68.7	75.4	79.7	81.4	80.4	77.7	65.6	61.3	53.0	68.7
1958	46.6	46.3	59.1	68.2	74.0	80.4	81.0	80.9	79.4	68.1	62.7	51.7	66.5
1959	50.7	59.4	58.8	66.3	75.7	79.0	81.0	81.3	78.5	72.9	58.9	53.1	68.0
1960	52.0	51.8	54.5	68.1	71.4	78.0	81.0	80.1	78.0	71.1	61.4	49.0	66.4
*1961	47.8	58.0	63.8	62.1	71.8	77.3	80.2	79.2	77.9	66.9	61.7	54.4	66.8
1962	51.0	62.2	57.4	65.1	78.1	79.9	82.4	80.6	78.3	69.4	56.2	50.6	67.6
1963	49.2	49.3	61.9	68.8	75.5	79.7	81.4	82.3	77.1	67.9	57.1	45.3	66.3
1964	49.5	49.0	60.2	68.4	73.9	80.6	80.5	81.2	78.2	64.6	60.6	55.7	66.8
1965	50.3	53.3	59.8	69.4	75.1	79.0	81.2	81.6	80.1	69.3	63.3	53.9	68.0
1966	49.1	52.6	58.7	66.2	74.0	77.0	82.5	80.2	78.3	70.0	60.1	51.7	66.7
1967	53.8	52.0	64.1	72.1	74.0	80.7	79.9	80.7	74.8	66.4	58.6	58.8	68.0
1968	51.9	47.0	56.6	70.4	74.3	82.1	81.8	82.9	77.9	69.3	54.8	50.0	66.6
1969	51.8	51.9	53.4	68.0	73.4	82.4	82.1	80.2	77.1	72.1	55.6	49.9	66.5
1970	46.0	49.6	60.7	69.1	73.2	78.0	80.6	80.4	79.9	70.9	52.3	53.5	66.2
1971	51.2	53.3	54.6	62.9	69.5	77.4	79.1	80.1	78.5	71.5	58.2	62.8	66.8
1972	59.0	53.4	59.8	68.2	73.0	78.0	80.2	82.0	79.3	70.2	59.2	57.2	68.3
1973	52.1	50.7	64.7	64.1	72.3	79.9	82.7	80.8	80.7	70.0	63.8	52.1	67.8
1974	66.6	53.7	64.2	64.9	74.5	77.9	80.3	80.6	78.8	64.9	56.7	52.3	68.0
1975	56.8	57.8	60.0	65.5	76.4	80.1	79.4	81.3	76.5	70.1	59.8	51.5	67.8
1976	47.4	56.8	62.9	66.8	72.4	78.0	82.1	81.7	76.9	63.4	53.3	50.2	66.0
RECORD MEAN	53.3	55.0	61.1	67.5	74.6	79.7	80.8	80.7	77.9	69.3	59.5	53.8	67.8
MAX	63.8	65.9	72.4	79.2	85.9	89.8	90.0	89.7	87.0	79.6	70.6	64.3	78.2
MIN	42.8	44.1	49.8	55.7	63.2	69.5	71.6	71.6	68.7	58.9	48.4	43.3	57.3

Precipitation

Year	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec	Annual
1937	2.35	4.78	4.23	5.52	3.44	9.74	6.41	10.54	6.52	1.65	4.03	1.58	60.79
1938	2.63	0.68	2.13	2.39	2.94	6.09	6.72	3.71	5.21	2.32	1.20	2.28	40.30
1939	3.33	6.01	2.81	9.25	4.66	14.64	10.86	10.80	3.77	1.24	0.93	3.14	71.44
*1940	1.16	5.21	3.27	4.18	2.39	7.88	10.12	6.84	0.88	0.02	3.37	6.50	51.82
1941	1.10	1.66	4.63	1.82	1.24	6.75	6.33	7.22	4.88	5.16	0.81	4.75	46.45
1942	5.00	6.72	10.06	0.37	3.78	10.26	4.17	6.44	8.26	1.18	0.73	4.88	61.85
1943	4.31	2.61	7.70	2.29	4.52	6.70	5.32	4.95	5.15	0.06	1.40	3.40	48.41
1944	3.91	4.95	10.29	3.79	2.64	1.16	14.42	10.66	9.21	1.55	2.18	0.81	65.57
1945	2.64	3.40	0.91	4.46	2.47	5.91	10.35	8.09	3.91	4.74	0.64	9.06	56.58
*1946	5.29	3.42	9.09	1.27	10.38	3.75	9.09	7.04	8.50	0.59	1.89	0.81	61.12
1947	6.11	3.25	5.73	9.95	8.28	11.42	4.59	5.22	5.37	4.05	12.64	4.72	81.53
1948	6.26	0.85	16.48	8.20	1.28	5.73	17.88	7.09	4.19	5.50	3.96	6.10	83.52
1949	1.03	3.71	4.54	6.56	0.81	6.82	15.50	4.54	3.81	2.98	1.68	1.36	53.34
1950	0.28	3.40	4.70	9.35	5.53	5.51	6.56	10.63	0.73	1.65	0.91	2.75	52.00
1951	1.96	1.79	7.43	.44	4.14	4.60	5.57	3.21	6.68	0.62	8.44	4.77	50.65
1952	1.68	7.50	6.85	4.39	3.28	2.50	5.57	6.32	4.77	0.16	1.27	1.44	45.71
1953	3.89	6.15	1.08	7.26	0.80	8.26	5.77	9.71	6.14	1.41	2.64	7.89	61.00
1954	0.79	1.69	2.22	1.02	3.12	5.26	5.97	3.26	2.82	1.79	1.20	1.84	30.98
1955	5.21	2.65	0.99	3.67	0.85	5.99	10.51	3.82	5.41	1.44	0.97	2.60	44.11
1956	5.09	5.47	2.00	1.90	3.71	7.32	9.78	5.40	4.20	4.34	0.42	2.28	53.91
1957	0.21	0.82	3.65	5.26	8.01	9.69	8.89	6.72	20.32	1.63	5.18	2.01	74.39
1958	2.88	3.72	5.44	8.76	5.45	5.15	6.91	3.59	1.58	1.85	1.97	2.98	50.28
1959	4.55	6.15	11.15	3.65	9.73	8.99	7.41	9.40	6.31	12.27	0.46	1.76	81.83
1960	2.77	9.00	4.03	7.19	3.25	9.65	5.59	5.07	9.83	3.28	4.12	3.34	67.12
*1961	2.58	5.29	4.43	2.36	2.40	4.55	6.48	10.07	3.00	T	1.70	4.23	47.09
1962	1.68	2.43	10.66	2.41	0.98	6.98	4.87	5.95	6.72	0.45	7.42	2.44	52.99
1963	5.30	5.81	2.76	1.68	5.49	9.23	7.13	7.70	6.60	0.45	2.88	7.06	62.07
1964	9.27	11.50	4.08	5.61	2.63	8.16	20.12	9.32	6.51	10.48	3.87	12.65	104.18
1965	3.86	10.03	7.86	7.14	T	12.62	8.09	8.16	10.25	3.49	2.54	4.75	78.79
1966	9.25	9.95	3.24	2.21	8.23	8.09	6.54	8.89	10.67	2.89	1.15	3.99	75.08
1967	6.38	5.60	1.29	1.44	5.43	5.00	8.31	9.03	1.71	3.39	3.06	6.28	56.92
1968	2.15	3.76	2.10	1.06	4.00	2.96	4.89	5.40	8.91	4.70	4.07	6.72	50.72
1969	0.60	5.17	9.13	2.02	4.38	4.88	18.83	4.88	15.92	1.21	1.93	5.77	74.52
1970	6.50	4.62	11.49	3.57	2.41	4.80	16.13	8.93	6.85	4.63	2.31	3.23	75.47
1971	3.04	5.48	4.81	1.85	4.08	7.64	10.80	10.75	1.57	3.46	0.88	4.11	58.27
1972	6.52	7.05	5.80	0.35	9.08	11.13	4.13	5.23	0.11	1.75	9.86	4.85	66.06
1973	4.96	7.16	13.57	13.13	8.38	7.09	4.61	10.78	5.30	2.35	3.21	7.46	87.80
1974	3.38	2.87	3.00	3.97	8.59	3.84	7.60	9.38	10.43	0.93	1.64	3.80	59.43
1975	11.68	2.85	6.18	7.17	10.34	4.77	17.52	6.80	4.88	4.41	1.50	7.83	85.93
1976	5.52	1.21	5.30	1.65	11.66	11.02	4.19	7.35	2.79	11.79	10.46	4.09	77.02
RECORD MEAN	4.01	4.65	5.01	3.88	4.14	6.61	7.97	7.00	5.52	2.87	2.77	4.30	58.73

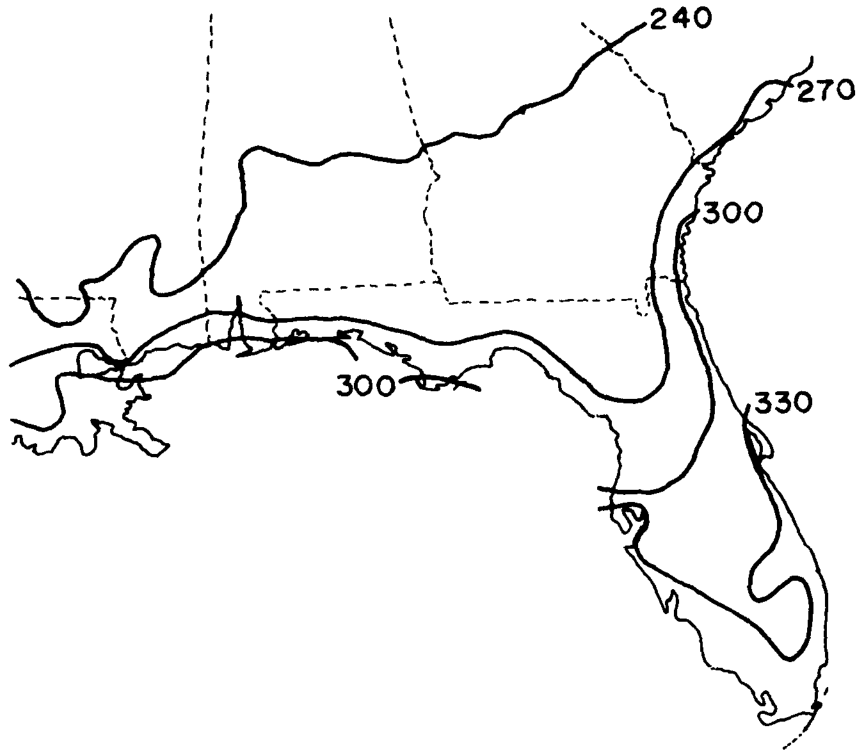

Figure 18. Average growing season (days). Redrawn from ESSA (1968).

The average date for the last occurrence of 32^o is February 28, but it has been as late as April 8. The average date of the first occurrence of 32^o in the fall is November 25, but it has been as early as October 21. The average growing season is 270 days.

Thunderstorms occur on the average of every other day in the summer. Summer humidities are very high. Maximum summer temperatures of 95^o occur on about 22 days. Temperatures of 100^o (38^oC) occur once or twice in less than half of the years. Summertime cloudiness holds the maximum temperatures to about 91^o.

The average yearly rainfall is near 61 inches (155 cm) with variations from as low as 30.98 inches (79 cm) to 104.18 inches (265 cm). July is the wettest month followed by August, September, and June. The driest months are October and November. A secondary but significant maximum rainfall occurs during the early spring months when evapotranspiration is low and water storage in the soil is considerable at the start of the growing season.

Extended droughts are infrequent and shorter droughts rather common. Droughts when extended over months or years cause the disappearance of large lakes and cypress ponds. Droughts of shorter duration create fire danger in the nearby forests. These shorter droughts, when coupled with an extended period of less than normal rainfall, can give cause to very large forest fires. In 65 years there have been six (not consecutive) months with less than 0.1 inch of rain, and three instances in the same period when the total for two consecutive months was less than one inch. In the four-month period ending January, 1934, the total was 2.74 inches (7 cm), making the worst drought of record. The most recent wet periods were in 1964, 1973, and 1975 and caused large lakes to overflow. The most recent dry period was 1954-55 when most lakes disappeared completely.

High winds are infrequent and of short duration, usually associated with strong cold fronts in the late winter and early spring months. The likelihood of a hurricane occurrence in our coastal area is about once every 17 years with fringe effects felt about once every five years. The last hurricane to do appreciable damage was in 1941. The frequency of hurricanes increases westward in the panhandle. There were more than 21 damaging tropical storms from Apalachicola westward, 1901 to 1955, but only 11-15 from St. Marks eastward (U.S. Forest Service 1969). Hurricanes strike Pensacola about once in 10 years and Apalachicola once in 15 years (Marcus & Fernald 1975).

Traces of snow are recorded every few years. Small but measurable amounts of snow are recorded several times a century.

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6. GEOLOGY

Introduction. The panhandle is an uneven platform of carbonate bedrock over which has been deposited one or more layers of less consolidated clastics. The bedrock consists mainly of limestone ($CaCO_3$) and sometimes of dolomite ($CaCO_3 \cdot MgCO_3$). Some of the limestone contains impurities of sand, silt and clay, particularly in the western panhandle. Other limestone has been silicified into layers or veins of chert or flint. The superficial strata of bedrock date to the Eocene, Oligocene, and early Miocene. The bedrock of the panhandle has been subjected to considerable solution activity, forming numerous caverns, lime sinks, and other karst features. One geologist speculated that if the overburden of clastics were removed, the bedrock would look like Swiss cheese.

The clastics consist of sand, silt, clay, shell marl, gravel, rock fragments, phosphatic matrix, and fuller's earth. Fossils, including petrified wood, are abundant in some deposits and absent in others. Sand, silt, and clay are defined as mineral particles with particular diameters (Table 4).

Layers of shells and their degradation products are often common. Clastics with shell marl are mostly thought to represent the sediments of shallow seas and estuaries. These sediments became terrestrial clastics when sea level dropped. The abundance of oyster shells in many shell marls suggests that oyster bars in bays and lagoons were often covered by sediments which later became terrestrial clastics.

Rock fragments have various origins. Some were localized layers of carbonates in mid-Miocene clastics which consolidated into limestone.

TABLE 4. Particle Size Classes (Soil Survey Staff, 1960).

Name of Separate	Diameter (mm)
Very coarse sand	2.00 - 1.00
Coarse sand	1.00 - 0.50
Medium sand	0.50 - 0.25
Fine sand	0.25 - 0.10
Very fine sand	0.10 - 0.05
Silt	0.05 - 0.002
Clay	under 0.002

Particle size distribution is determined by mechanical analysis. A soil sample is sifted through a series of increasingly smaller sieves. The fractions held by each sieve are weighed and the weights expressed as percentages of the total weight of the sample.

Some others were layers of sand cemented by limonite ($Fe_2O_3 \cdot 3H_2O$) which was leached from the upper layer of the soil. Plates up to a meter thick of the resultant sandstone are common in the western panhandle (Marsh 1966).

Phosphate-rich clays and other crusty or pebbly clastics are common in some deposits. These are sufficiently pure and thick to be strip-mined in Hamilton County for the production of agricultural fertilizer. Fuller's earth consists largely of the silicified walls of diatoms that accumulated in marine sediments. Such deposits are also know as pipe clay, diatomaceous earth, and attapulgite. Thick beds are mined commercially in Gadsden County for the production of abrasives and other products. Veins of fuller's earth shrink and swell considerably with changes in moisture. This movement requires special foundations for structures built on terrain containing fuller's earth.

The various strata of clastics were deposited beginning in the Miocene after the bedrock had formed. Some of these clastics were once marine sediments of near-shore environments. These were exposed when the panhandle was uplifted geologically with respect to sea level. Others were transported by rivers (fluvial deposits) and were deposited as alluvium in valleys or as deltaic or estuarine deposits near river mouths. Others were wind-blown (aeolian deposits) such as dunes. Still others were sediments in lake bottoms (lacustrine deposits).

The clastic deposits form terraces which slope gently towards the Gulf and which are either separated from each other by step-like escarpments or by subtler changes in relief. Since their deposition the terraces have been subjected to considerable erosion and dissection by streams and rivers.

Entire strata have been removed from some areas, and the materials of other strata have been reworked (rearranged) by erosional processes. Since the beginning of the Pleistocene there have been several drastic fluctuations in sea level. These were eustatic changes, caused by changes in the volume of water in the ocean basins rather than by uplifts and other tectonic movements. When much of the world's water was locked in continental ice sheets, sea level dropped, exposing the continental shelf. The land surface of the panhandle was more than doubled in area. Sea level rose during the interglacial stages to approximately 8 meters above present sea level. Minor eustatic fluctuations continued since the end of the Pleistocene, reflecting either the volume of water frozen in polar ice caps or the capacity of the ocean basins of the world, which probably changes constantly to some extent.

As a result of post-Pleistocene fluctuations in sea level, coastal regions less than about 33 ft or 10 m in elevation have experienced a complicated history of erosion, deposition, and reworking of sediments in conjunction with coastal processes. Dunes, bars, spits, beach ridges, and other topographic expressions of coastal processes were stranded inland as seas receded. Some of these were eroded or reworked until their origin is only speculative, while others are easily discernable. Some pre-Pleistocene escarpments are even recognizable as former coast lines. Several submerged features have been located. Submerged beach ridges and drowned valleys are topographic features dating to glacial stages when sea level was lower than at present.

Peat. Peat deposits are common. Peat consists of dead vegetable matter which may persist for several millenia or longer without appreciable decomposition. Peats aggrade in marshes, swamps, and lake bottoms, wherever anaerobic conditions prevail, inhibiting organisms of decay. High acidity and low levels of nitrogen may reinforce this inhibition. The oldest peat occurs at the bottom of a deposit, and new peat forms at the surface as dead plant materials accumulate. Microscopic examinations of peat in paraffin sections reveal well preserved plant tissues (Cohen and Spackman 1972). The anatomical details of these tissues often allow the identification of the plants from which the peat was formed. Many peats are fibrous. Other, non-fibrous peat is greasy when rubbed between the fingers and is generally called muck. Most peats contain some sand, silt, or clay that was transported by water or wind from other areas. Well preserved wood is of common occurrence in peat. Florida peat deposits and associated vegetation were surveyed by Harper (1910) and Davis (1946). Peat deposition in the Okefenokee Swamp was studied by Cohen (1973, 1974a, 1974b, 1975).

<u>Karst</u>. Karst topography is a term applied to a regional landform which has been modified by the solution of limestone. The limestone usually lies near the surface and is covered with sands or other permeable clastics. Rainwater percolates easily through the surficial stratum to the limestone and filters into the crevices or fractures that characterize most limestones. This water is charged with CO_2 from the ambient atmosphere and from the soil where roots, soil fauna, and microorganisms give off CO_2 in their metabolism CO_2 forms carbonic acid in solution, which is capable of dissolving limestone.* Some solution of limestone is attributable to the organic acids which are leached from decomposing organic matter in the soil.

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*$CO_2 + H_2O \longrightarrow (H^+ + HCO_3^-)$ carbonic acid

$H^+ + HCO_3 + CaCO_3$ (limestone) $\longrightarrow Ca(HCO_3)_2$ calcium bicarbonate (soluble)

Solution is more rapid in pure limestone than in dolomitic limestone or limestone that contains sand, silt, or clay. It is more rapid in soft, chalky limestone than in hard limestone. Solution features are often initiated near the water table where acidized water accumulates. The water table varies seasonally with rainfall. It has also varied widely over the millenia in response to changes in sea level. Sellards (1910) estimated that a foot of limestone dissolves in about 5,000-6,000 years (1 meter per 15-18,000 years). This general rate of solution is apparent on old marble tombstones on which the incised lettering is becoming obscure.

Figure 19 diagrams some of the more common karst features of the panhandle. These features are described further by Puri et al. (1967). An overburdon of sand (1) covers limestone bedrock (2). The surface of the bedrock is uneven because of localized differences in the solubility of the limestone. If the surface is divided into pinnacles or narrow ridges of limestone, it is termed karrenfeld. These irregularities may be masked by the sandy overburden, or they may cause an uneven soil surface. Vertical and horizontal crevices permeate the limestone. A horizontal solution channel (3) forms as limestone is dissolved along a horizontal fracture. This channel may serve as a passage for an underground river.

A vertical solution channel called a funnel sink (4) forms by the enlargement of a vertical fracture. After a fracture is enlarged by solution, percolating water in the sandy overburden may enter the fracture in an eddying swirl. Sand carried by this water acts as an abrasive agent on the limestone. Some funnel sinks have been polished by this abrasion, while others have been enlarged considerably by it. Some vertical

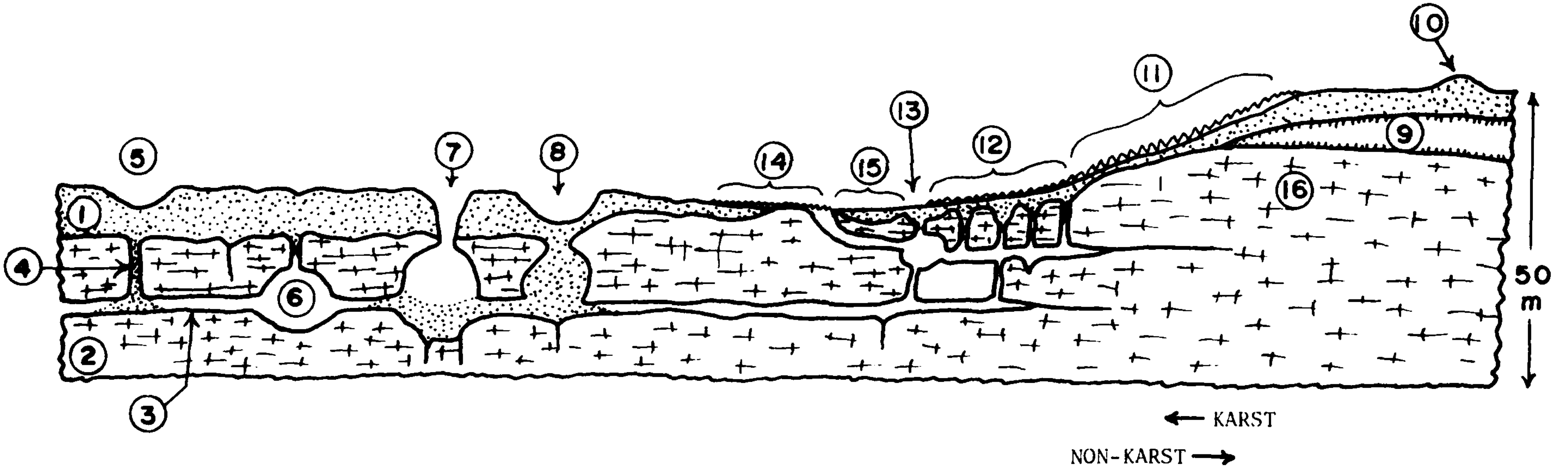

Figure 19. Karst topography. See text for explanation.

solution channels are many meters deep but only a few centimeters wide. These are called solution pipes or natural wells. They are thought to have formed by the upward movement of swirling water under artesian pressure. A depression (5) forms on the land surface when sand from the overburden filters into the funnel sink.

A cave (6) forms where a horizontal solution channel enlarges. The funnel sinks and solution pipes in the vicinity help carry acidized water into the developing cave. Solution is rapid when acidized waters move freely through the crevices and channels. This movement is reduced if the ground-water level is high, saturating the limestone and permanently filling the channels and caves with water.

A sinkhole (7) forms when the thin roof of a cave collapses, allowing the sandy overburden to fall into the cave. The sandy sides of the sinkhole are often wet just above the limestone. Rainwater percolates through the sand around the sink to the limestone. Some of this water moves laterally on top of this limestone and seeps out along the sides of the sink. The sandy sides of the sink eventually erode, causing the cave beneath to fill with sand (8). What was once a narrow steep-sided sink is now a broad shallow depression. This depression may contain standing water, depending on the position of the water table.

An impermeable stratum of clay or other fine-textured clastics (9) prevents the percolation of rain water to the limestone beneath. As a result, the ground water is perched, and the sandy overburden is poorly drained, except where thickened into a sandhill (10). A stream (11) drains these wet uplands, but it becomes merely a creek (12), because vertical solution channels and fractures capture most of its flow. The creek is essentially two-tiered with part of the flow above ground and part beneath. This area was once a series of small sinkholes that developed along a prominent vertical fracture or joint. These sinks later coalesced by solution and erosion and formed a relatively deep creek bed. The surface creek flows into a sink (13) and becomes entirely subterranian. The creek reappears at the surface (14). The intervening terrain is called a natural bridge (15).

The original limestone surface persists at (16), because acids cannot percolate through the impervious clastics. Solution lowers the limestone surface to the left of (16).

The entire panhandle is underlain by karst configurations, but their topographic expressions are masked to at least some extent by the overburden of clastics. The Marianna Lowlands and the Aucilla Karst Plain are the most obvious karst regions of the panhandle (Fig. 15). Active solution continues in these regions and to some extent in most other regions. Sinks and some lakes serve as conduits for acidized waters to reach limestone buried beneath deep or impermeable clastics. The effects of this activity are obscured by the clastic beds. Nonetheless, lake basins may form or enlarge or hydrological changes may occur which affect soil moisture or drainage. These effects influence vegetation.

A final karst feature, not shown in Figure 19, is known in Florida as a prairie. A prairie is a broad, flat, marshy depression which contains shallow water in wet seasons. This water either evaporates or drains underground during dry seasons. Vernon (1942) said that, "Prairies are formed by solution activity dissolving limestone down to the average ground water level and then spreading laterally." The percolation of acidized water is inhibited by the ground water which saturates all but the uppermost stratum of limestone in wet seasons. Percolation above the water table is not inhibited, allowing lateral solution.

Coastal Features. Shoreline topography is marked by beach ridges, dunes, dune ridges, swales, sloughs, flats, barrier islands, spits, lagoons, estuaries, and wave-cut cliffs and notches.

Beach ridges are of marine origin. They may form as offshore bars, shaped by littoral drift (longshore currents). If sea level drops, these bars emerge as terrestrial features. Beach ridges are also formed by the swash of waves which pushes sand into a berm high on a beach. They often occur side by side, making the terrain appear corrugated.

Cotton (1949) explained the formation of such a series of parallel ridges. Sand is constantly transported by rivers and spread by littoral drift along a gently sloping coast. Waves become overloaded by this sand and deposit it as an exposed beach ridge on the shore. As more sand enters the system, a new ridge is formed seaward of the first ridge. Subsequent ridges continue to be built (prograded) as long as the sand source is constant, the bottom is sufficiently shallow, and strong offshore currents do not upset the system.

Beach ridges are straight or slightly curved and oriented parallel to the coast. The sand grains are angular, because they are protected from abrasion by a film of water during fluvial and marine transport. (Gravel and larger rock fragments are too large to maintain a tight film. They are chipped and become rounded.) The grains are poorly sorted into size classes, and the smaller grains fill the spaces between the larger grains, making the beach ridge compact. Shell fragments constitute part of the sand and contribute carbonates which coat the quartz grains, causing them to adhere slightly to each other. This compaction and cementing of sand grains tends to protect beach ridges from wind and water erosion.

Dunes are of aeolian origin and may assume most any shape or orientation. Drifting sand causes the abrasion of individual grains. The grains become rounded and their surfaces scratched or frosted. The sand grains are well sorted into various size classes by the winnowing effect of the wind. At any given part of a dune the grains tend to be of the same size. As a result, the grains are poorly packed, and the dunes are loose and well drained. Shell fragments are less common than on beach ridges. The lack of a carbonate adhesive and the rounded surfaces of the grains allows dunes to be eroded or reworked much more easily than beach ridges.

Figure 20 diagrams two segments of shoreline as occur commonly on spits and barrier islands. Figure 20a shows tall foredunes nearest the Gulf. Sand from these dunes has drifted some distance inland, making a low dune field on the flats to the interior. Figure 20b shows a coastal foredune behind which lies a series of parallel beach ridges.

In spite of their cohesive properties, exposed beach ridges are subjected to aeolian forces. The surface layers may be reworked by the wind (wind-decorated) into dune-like masses, or drifting sand may form dunes on top of beach ridges. Such features are called dune ridges. Most of the beach ridges along the coast of the panhandle have been converted to some extent into dune ridges.

A swale is any small or narrow moist depression in which the vegetation is more rank than on the surrounding terrain. Swales generally occur as the

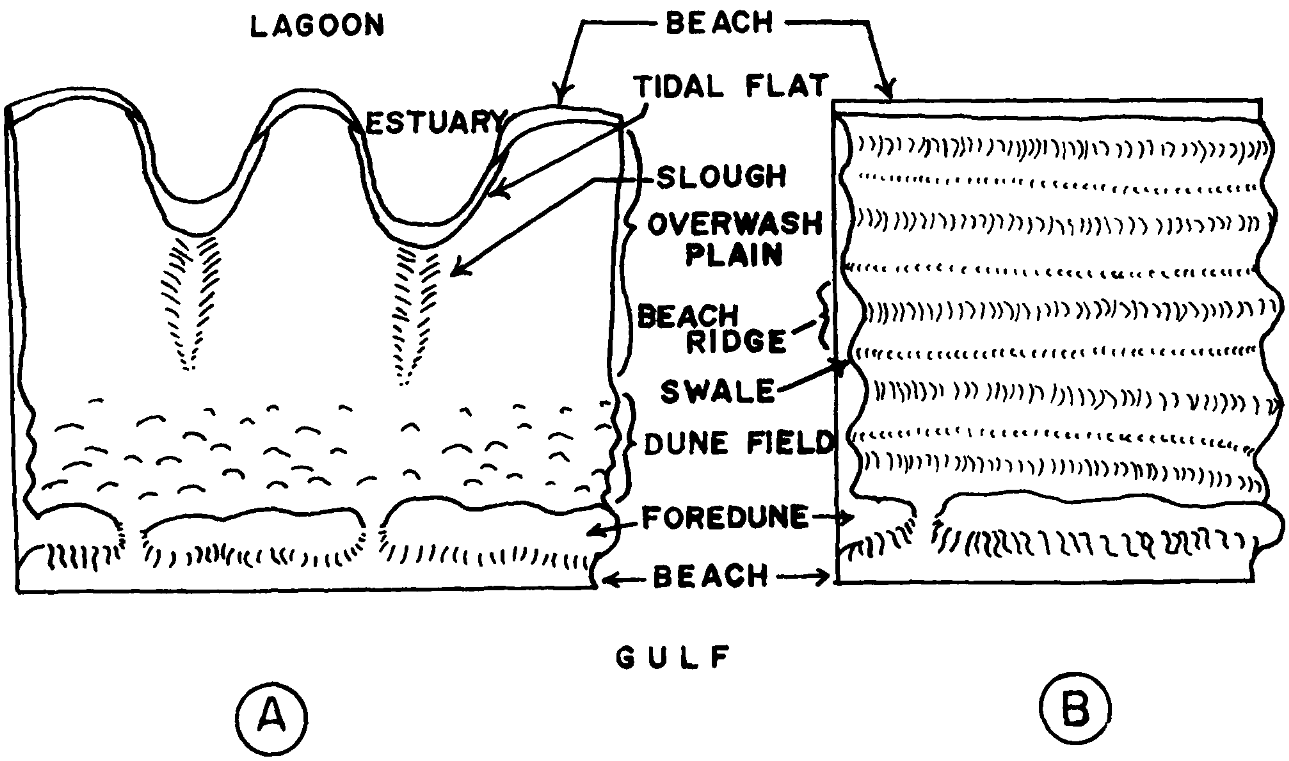

Figure 20. Coastal topography.

troughs or depressions between ridges or dunes. A slough is a shallow and often intermittent water course which is so densely vegetated that the flow of water is obstructed to some degree. The channel is often poorly defined. The vegetation may be of aquatic plants but is often of emergent marsh species or even of shrubs and trees. Sloughs are often nothing more than swales that serve as shallow water courses, as shown in Figure 20. Swales and sloughs are not necessarily confined to coastal topography and may occur inland, often associated with bogs and savannahs.

Coastal flatlands include tidal flats and overwash plains. The tidal flats occupy the intertidal region which is flooded by predicted tides. Included are sites that are inundated only a few times a year during the particularly high spring tides. Overwash plains are those flats which occur above the high tide zone. They may be flooded during storm tides or hurricanes. They may occur independently of dunes and beach ridges, or they may occur as flats between widely separated dunes or ridges.

Barrier islands are common along the coast of the panhandle west of the Ochlockonee River (the Beach Strip of Figure 15). These generally run parallel to the coast and consist of beach ridges, dunes, swales, sloughs, and flats. Examples are Dog Island, St. George Island, St. Vincent Island, and Santa Rosa Island. Spits are similar to barrier islands, but they are connected at one end to the mainland. Examples are Alligator Point and Cape San Blas. A lagoon is a narrow, shallow body of water between a barrier island and the mainland, such as St. George Sound and Santa Rosa Sound.

A widely accepted explanation for the origin of barrier islands is given by Cotton (1949). Assuming a static sea level and a nearly flat terrain, waves break near the shore, eroding a trough which becomes the lagoon. The eroded sediment is deposited partly on the beach and the rest is carried seaward. The sediment carried seaward is deposited behind the turbulent zone of the breakers and accumulates to form the barrier island. This model seems simplistic for our coast where sea level has fluctuated constantly for several million years. Barrier islands along the coast of the panhandle may have once begun as beach ridge systems which were covered and somewhat reworked as sea level rose and later were exposed as sea level dropped again. The exposed bar became an axis upon which new beach ridges were built and reworked into dunes and flats. Sand contributing to the growth of the barrier island did not come from the lagoon but rather from rivers or from deep sediments carried upwards by strong currents.

Wave-cut cliffs are formed by the erosion of a steeply grading shoreline by waves. A sea cliff can also be somewhat undercut or notched by wave action, forming a wave-cut notch. Tall dune-lines on barrier islands are subject to wave cutting and notching in the panhandle. Many of the various escarpments in the panhandle are thought to have developed as cut or notched shorelines that subsequently were stranded inland as sea level dropped.

From the Ochlockonee River westward the present shoreline is characterized by barrier islands, spits, lagoons, dunes, beach ridges, and other prominent topographic features. Dunes up to 10 meters high occur on St. George Island, St. Joseph Spit (Fig. 11), and elsewhere. This region is recognized in Figure 15 as the Beach Strip. The Gulf of

Mexico is relatively deep offshore from the Beach Strip. Moderate wave action and littoral drift carry sand onshore where it is reworked into dunes and other topographic configurations. Barrier islands and spits developed where the gradient of the bottom was not steep. No such features occur where the Gulf is about 98 feet (30 m) deep within 1.9 mi (3 km) offshore (Tanner 1960).

Eastward the shoreline is characterized by extensive marsh-covered intertidal flats. Low beaches up to about 1.5 m above mean sea level (msl) form the seaward limit of the marshes in Wakulla County. These probably developed on beach ridges that formed in the Holocene. Farther eastward these beaches are lower or absent. The coastal zone east of the Ochlockonee River is recognized in Figure 15 as the Marsh Strip. Apalachee Bay lies offshore from the Marsh Strip and is characterized by shallow water. The relief is less than 1 meter per kilometer offshore from Taylor County. Waves encounter friction from the shallow bottom far offshore in Apalachee Bay and lose their energy. As a result, no topographically prominent features have developed.

The Marsh Strip from St. Marks southeastward to Tarpon Springs is called a "zero energy shoreline" (Tanner 1960, Tanner and Bates 1965), because wave breakers average less than 4 cm in height and are unable to carry enough sand to form beaches and other shoreline features. Littoral drift is nearly absent. Beach ridges lie well offshore which are still preserved in this zero energy environment. The ridges may have formed when sea level was lower and wave energy higher. These ridges occur at the following depths and were dated tentatively by Tanner and Bates (1965) as follows:

Depth in meters	BP (Years Before Present)
-2	6,000 or younger
-6	6,000 - 7,000
-8	7,000
-10	7,200
-12	7,500

Tanner (1975) presented evidence that the panhandle coast is generally eroding. Of the 135 km of open Gulf beaches from Mexico Beach (north of St. Joseph Spit, Fig. 2) to a point due south of Tallahassee, 52% have been eroding in historical times, 35% have been stable, and 14% have been aggrading. Maximum erosion was recorded at Cape San Blas where the beach has retreated 11.2 meters per year between 1875 and 1942. Dog Island (Fig. 12) has eroded at about 1 meter per year. The eroded materials have been deposited as spits at either end of the island, extending its length. St. George Island has been lengthening on its eastern tip at 19.4 meters per year, but the beach face nearby has been retreating 1.34 meters per year for the interval 1934-1970. The middle of St. George Island has been stable.

The easternmost 5 kilometers of St. Vincent Island has been unstable, being influenced by the growth of a bar attached to adjacent St. George Island. The rest of St. Vincent Island was stable until a few decades ago. Erosion since 1970 was spectacular at some localities, leaving many trees standing in the surf zone. The non-synchronous changes in the shoreline of the panhandle suggest that fluctuations in msl cannot account for the recent changes alone but that local erosional and depositional processes are also responsible.

Tanner (1975) stated that the history of the coast was of general deposition up until a time no earlier than 500 BP, followed by severe erosion over the last century or two and more moderate erosion in the last 20-40 years. He predicted severe erosion in the near future along the Beach Strip but no essential change along the Marsh Strip.

Terraces. The Florida panhandle is generally described as a stepwise series of terraces which progress in elevation with increasing distance from the coast. Each terrace supposedly was once a sea bottom when sea level was higher than at present. Each step between adjacent terraces is called a scarp and is often interpreted as an ancient shoreline. The highest terrain of the panhandle is considered by some not to be technically a terrace but instead the eroded remnants of the original Miocene uplands. The panhandle has undergone an uplift since the Miocene. As a result, sea level has dropped relative to the surface of the land. This drop was not constant. Whenever sea level remained static for a long time, shoreline features developed, such as dunes, beach ridges, and wave-cut scarps. Some of those features still persist in varying degrees of preservation, allowing the deliniation of ancient shorelines and their corresponding terraces. The terrace nearest the coast was the most recent to emerge from the sea and is the lowest in elevation. Each successive terrace inland is presumably older and higher.

Matson and Sanford (1913) recognized 3 terraces, based on the meager maps and the few geological studies of that day for Florida. As the geological information increased over the years, so did the number of papers which attempted to delineate terraces and shorelines. Cooke (1945), MacNeil (1949), and others collectively recognized 8 terraces that were mapped by Healy (1975) and redrawn with modification as Figure 21. Healy included a concordance which correlated the terraces and shorelines

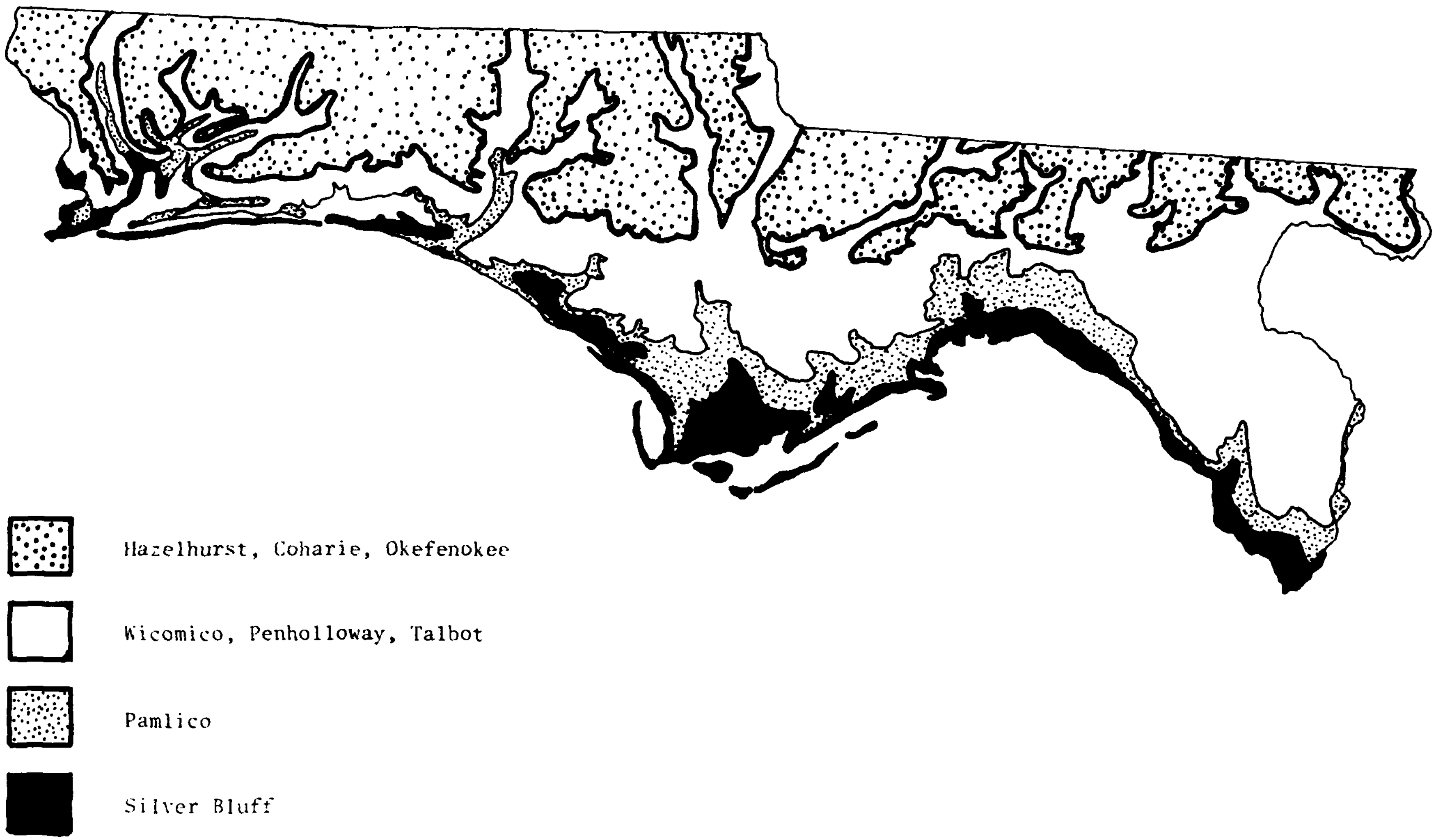

Figure 21. Terraces (redrawn from Healy, 1975).

recognized in nine previously published studies. The lack of agreement as to the delimitation of terraces was emphasized by Winker and Howard (1977), who recognized only three major shorelines based on topographic data. They elected to designate these shorelines by names which had never been used by previous authors.

The lack of agreement between authors reflects in part the discontinuity of features along a given shoreline. Physiographic discontinuity is seen along the present coast. The Beach Strip contrasts sharply with the Marsh Strip (Figure 15). If today's shoreline had been formed a million years ago and were stranded many miles inland by a drop in sea level, it would be difficult to delineate in its entirety.

Secondary processes further obscure the integrity of ancient shorelines. These processes include dissection by streams and rivers, erosion, solution of underlying limestone with a subsequent depression of the terrain, and localized warping of the bedrock. Warping has altered the older highlands but not substantially (Winker and Howard 1977). Erosion by wind and water has been significant in leveling ancient dunes and ridges and in filling swales, lagoons, and other depressions. Minor shoreline features that are geographically unrelated to others complicate interpretations. They may have formed during relatively brief periods of static sea levels.

Doering (1956) argued that the Gulf Coastal Plain has undergone continuous seaward tilting. He defined the terraces not on the basis of elevation but on the steepness of their seaward slopes. The older terraces have the steepest slopes, while younger surfaces are more nearly level. Doering's hypothesis has been partially substantiated but lacks general acceptance.

Sea Level. Sea level fluctuated drastically several times in the Pleistocene. During glacial maxima, when much of the world's water was bound in glaciers and polar ice caps, sea level dropped as much as 135 m below its present level. Florida essentially doubled in area and extended approximately to the edge of the continental shelf. Martin and Webb (1974) argued that the terrain which was then exposed was covered by prairies and savannahs. Mammals and other organisms used this terrain as a corridor for migration between peninsular Florida and Middle America.

During glacial advance the climate was cooler than at present. The terrain of the present-day panhandle was drier because of depressed water tables and perhaps lower rainfall. Martin and Webb (1974) concluded that the coldest climate during the Pleistocene occurred in the most recent glaciation, the Wisconsin, about 17,000 BP. Their conclusion was based on the study of fossil mammal faunas of different ages in Florida and from other paleoecological studies that they reviewed. Extinction of animals was most severe then, and fossil animals and plants of northern affinity were represented for the first time in Pleistocene deposits.

Ice caps and glaciers melted and sea level rose during the warm, moist interglacial periods. The older literature assumes that nearly all of Florida was inundated by interglacial seas. Alt and Brooks (1965) dispelled this contention and argued that much of Florida has not been inundated by seas since the Miocene. Current evidence argues that sea level rose approximately to a maximum height of 8-11 m above sea level during Pleistocene interglacial stages. When present sea level was exceeded, it is widely assumed that the climate was warmer and more moist than at present. Recent references to Pleistocene high sea level stands include Milliman and Emery (1968), Scholl, Craighead and Stuiver (1969), Pirkel *et al.*(1970), Rosenberg (1970), Alexander (1974), and Fairbridge (1974).

Figure 22 portrays changes in sea level from the Miocene to the present with respect to present sea level. This figure was compiled from the often contradictory literature cited in this chapter and from several conversations with W. F. Tanner and R. S. Murali (personal communication 1975-7). It is likely that most any geologist or paleoecologist will dispute some aspects of Figure 22. For example, the mid-Wisconsin interglacial stage may not have been as extreme as shown. Nonetheless, Figure 22 illustrates the magnitude of sea level fluctuation and infers drastic vegetational changes in nearly all parts of the panhandle in the not too distant past.

Figure 22 shows that sea level fluctuated a few meters above and below present sea level over the past several millenia. There is convincing evidence that these fluctuations indeed occurred. The times of fluctuation are subject to the vagaries of the radio carbon dating method. The extent of eustatic change in sea level is also in doubt because of differences reported in studies at different locations. These differences may be attributable to local effects of solution, warping, and erosion.

Geological Formations. Figure 23 shows the predominant superficial geological formations of the panhandle and Figure 24 their stratigraphic relationships. Those formations consisting of clastics tend to be variable in composition and structure, reflecting the complexities of the ever-changing coastal, fluvial, and sometimes lacustrine environments in

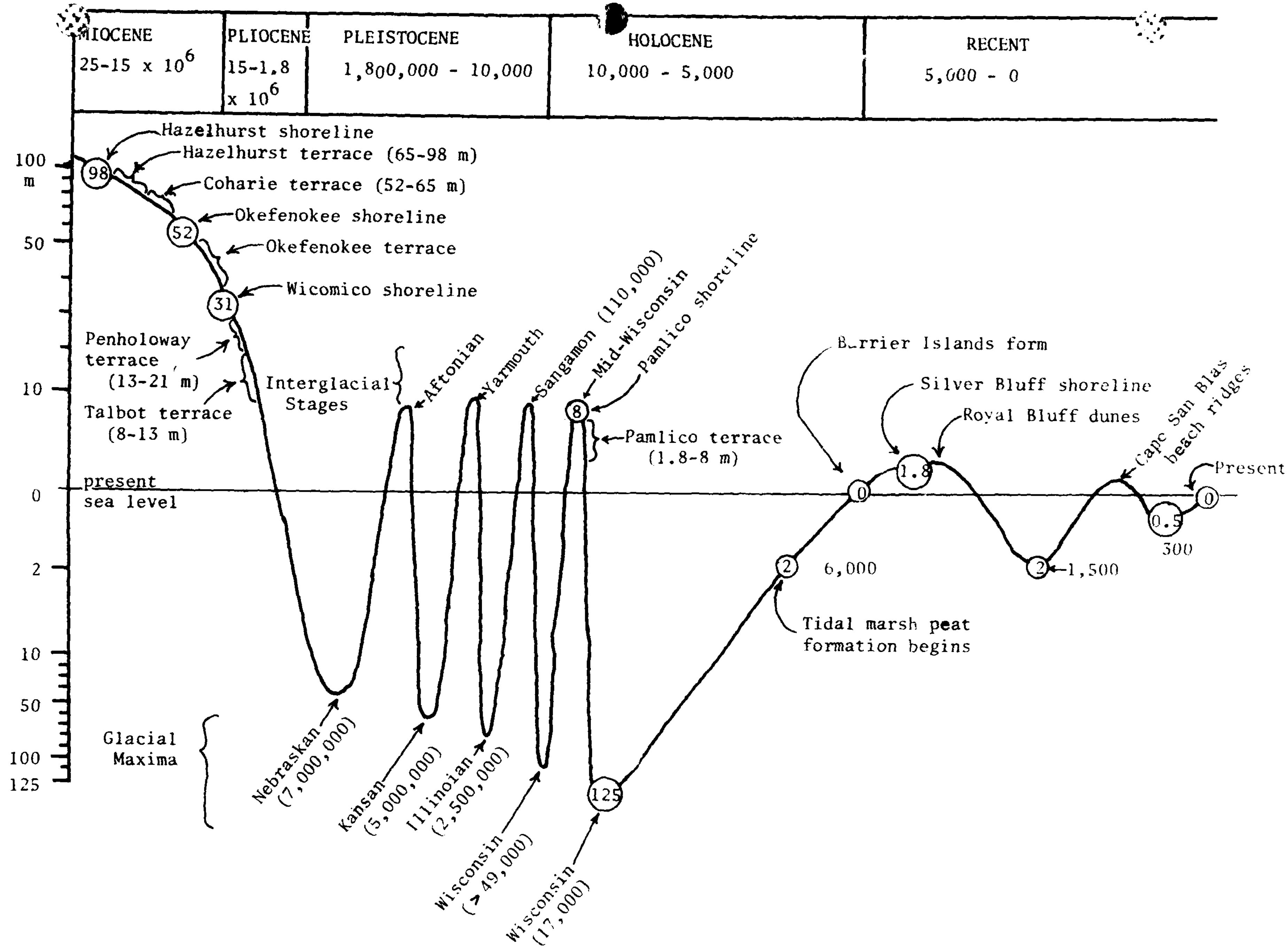

Figure 22. Approximate changes in sea level since the Miocene.

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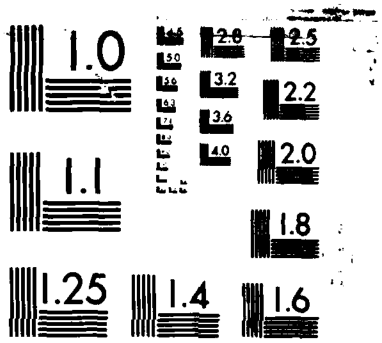

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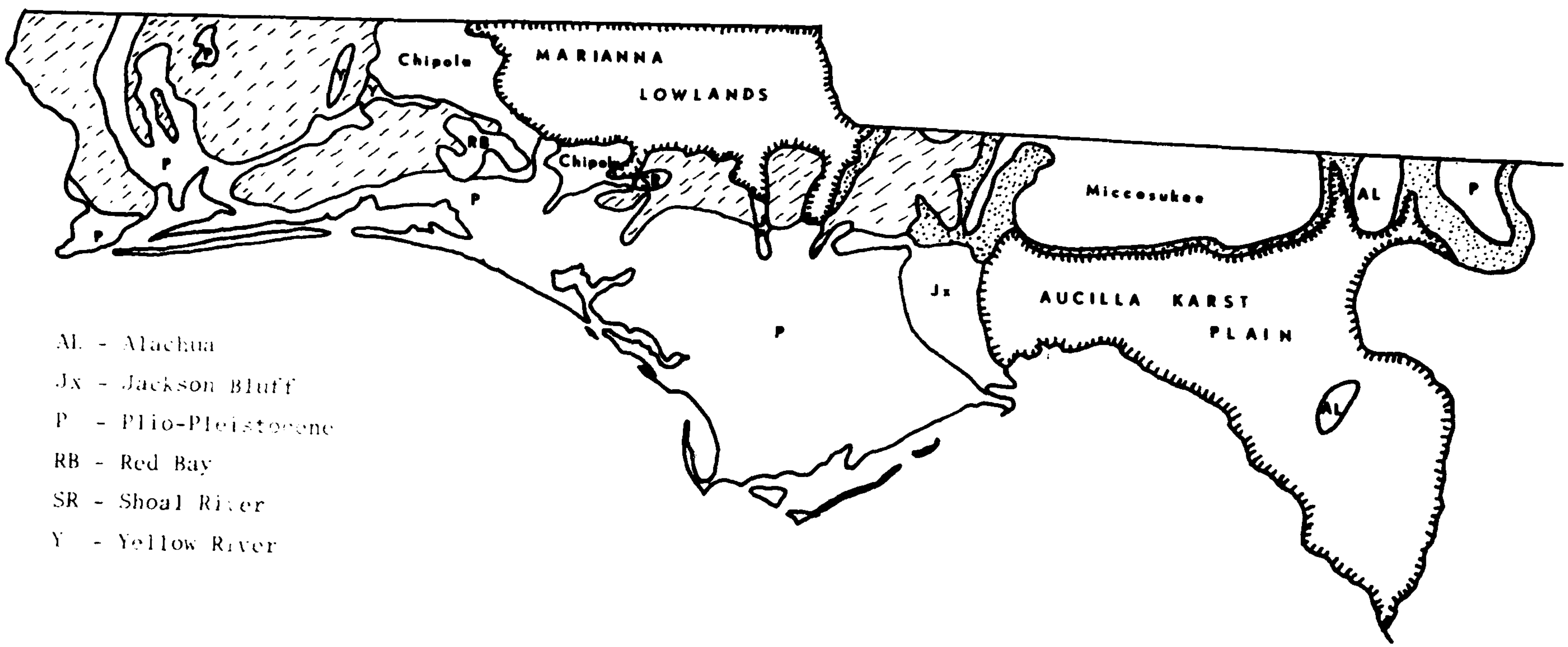


Figure 23. Surficial geology (modified from Puri and Vernon, 1964).

	Escambia to Walton counties	Walton County to the Apalachicola River	Apalachicola River to the Suwannee River
RECENT HOLOCENE	Surficial peats	Unnamed alluvial, deltaic and lacustrine deposits and buried peats	Marine sands deposited on sea bottoms when sea level was higher than at present, and present shoreline features, including beach ridges, dunes, spits, barrier islands, etc.
PLEISTOCENE			
PLIOCENE	These deposits are usually indistinguishable as to age and are referred to here as Plio-Pleistocene Sands.		
	Citronelle (some may date to the early Pleistocene. Mainly sandy alluvium with lenses of clay & gravel. Includes the Fort Preston deposits.)		
LATE MIOCENE (Choctawhatchee Stage)	Coarse Clastics	(Citronelle, continued)	Miccosukee (deltaic loams & sands)
	Pensacola Upper Clay Member	Red Bay (loamy shell marl) Yellow River (micaceous sand)	Jackson Bluff (sandy loam & shell marl)
MID-MIOCENE (Alum Bluff Stage)	Escambia Sand Member Pensacola Lower Clay Member	Shoal River (micaceous sandy loam & shell marl) Chipola (shell marl or sandy limestone with clay lenses)	Hawthorn (Phosphatic marine sand, clay, marl, sandy limestone with veins of fullers earth) Alachua (irregular deposits of sand & clay)
EARLY MIOCENE (Tampa Stage)	Chattahoochee (limestone)		St. Marks (limestone)
OLIGOCENE	(Deep limestone formations)	Suwannee (limestone)	
EOCENE		Marianna (limestone) Crystal River (limestone)	

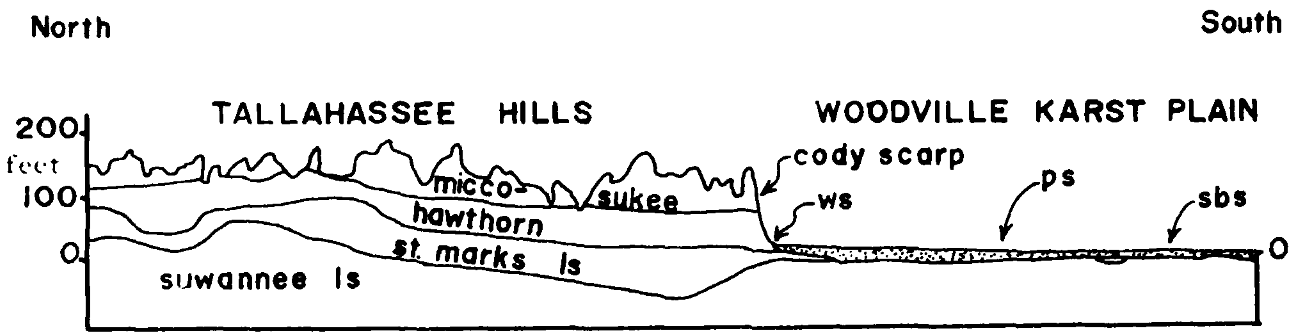
Figure 24. Approximate stratigraphy of those deposits that influence the physiography.

which they were deposited. Some clastic formations are poorly differentiated from each other. Certain deposits, some of them extensive, are only tentatively identifiable with respect to their age of deposition and to their strategraphic relationship with other better defined formations.

The Citronelle Formation exemplifies these problems. This deposit, which is about 13-240 m thick in Escambia and Santa Rosa Counties, consists mostly of yellowish to reddish or brown sand, some of it white or grey. The sands are frequently interrupted by lenses of gravel, silicified limestone, siltstone, clay (up to 20 m thick), and sandstone. The latter consists of sand cemented by limonite. There has been considerable disagreement as to how far east the formation extends and whether it is of Pliocene or early Pleistocene in age (Marsh 1966). It is thought to represent an alluvial deposit primarily (Puri and Vernon 1964). It rests on Miocene clays and sands in the western panhandle that are not as yet identifiable in terms of stratigraphy with other Miocene clastics of the central panhandle.

Plio-Pleistocene sands are comprised of various marine sediments which were deposited during high sea level stands during the Pliocene and the interglacial stages of the Pleistocene. Coastal marine sands of Holocene deposition are also included in this catch-all category. The Plio-Pleistocene deposits form a thin mantle over the Aucilla Karst Plain, the Jackson Bluff Formation, the lower part of the Citronelle Formation, and perhaps other formations mapped in Figure 23 that lie at lower elevations. This mantle is so thin that it is not considered to represent the predominant formation at the surface. It is mapped in Figure 23 only where it consists of a deep deposit.

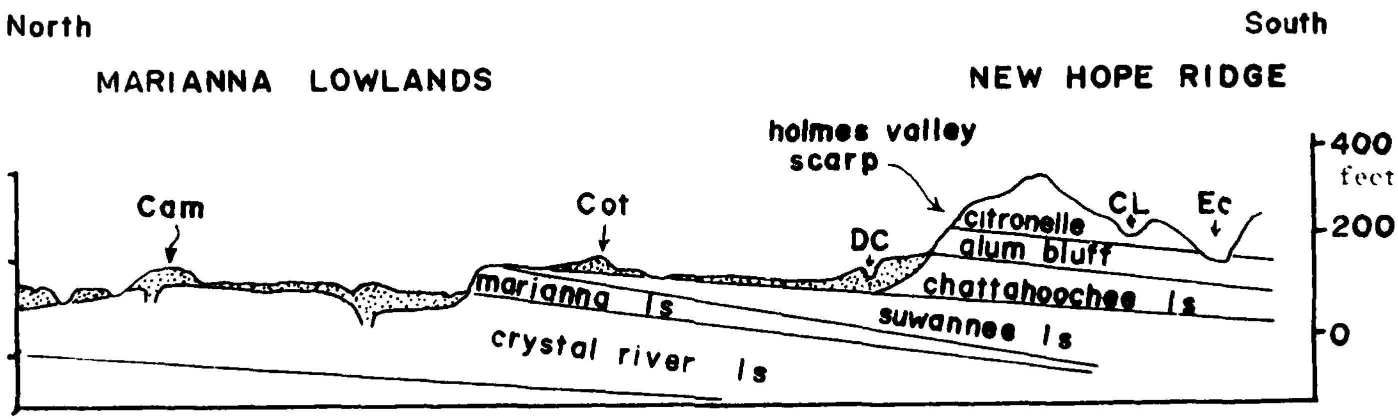
Figures 25-28 show the vertical relationships of the formations at selected localities. Only a few of the formations shown in Figure 24 occur



ws - Wicomico Shoreline
ps - Pamlico Shoreline
sbs - Silver Bluff Shoreline

stippled - Plio-Pleistocene sands

Figure 25. Cross-section of Jefferson County. Modified from Yon (1966).



Cam - City of Cambleton
Cot - City of Cottondale
DC - Dry Creek
CL - Compass Lake
EC - Econfina Creek

stippled - Post-Miocene or reworked clastics

Figure 26. Cross-section of Jackson County. Modified from Moore (1955).

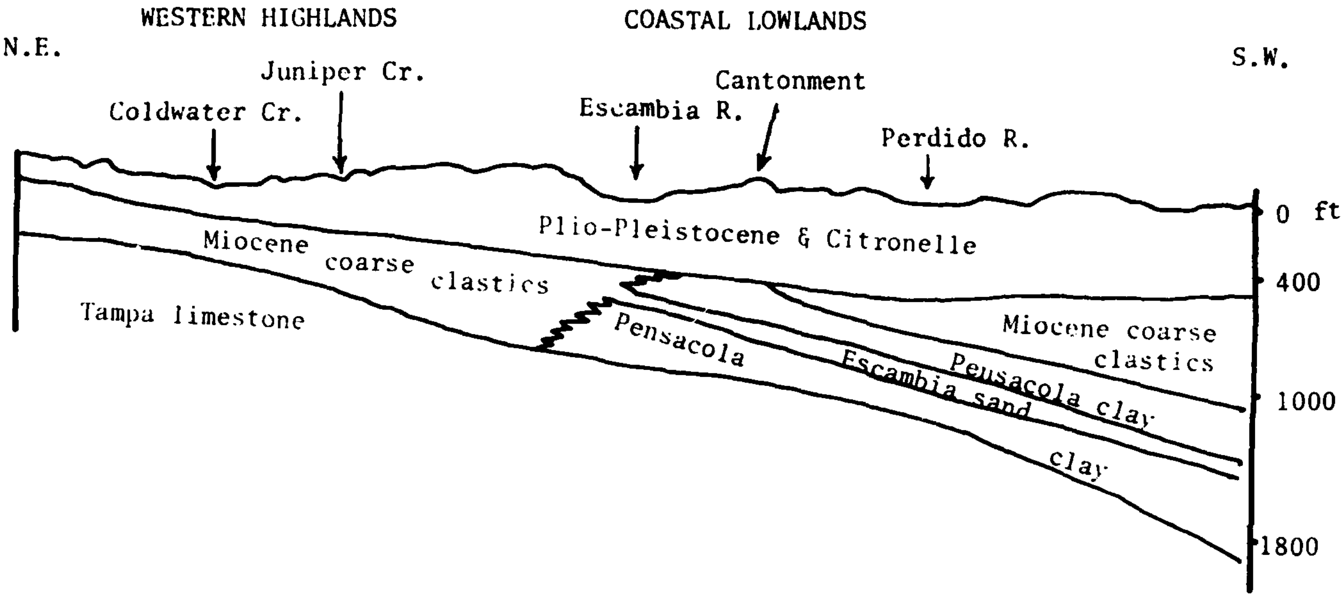


Figure 27. Cross-section from n.e. Santa Rosa Sounty to s.w. Escambia County and adjacent Alabama. Modified from Marsh (1966).

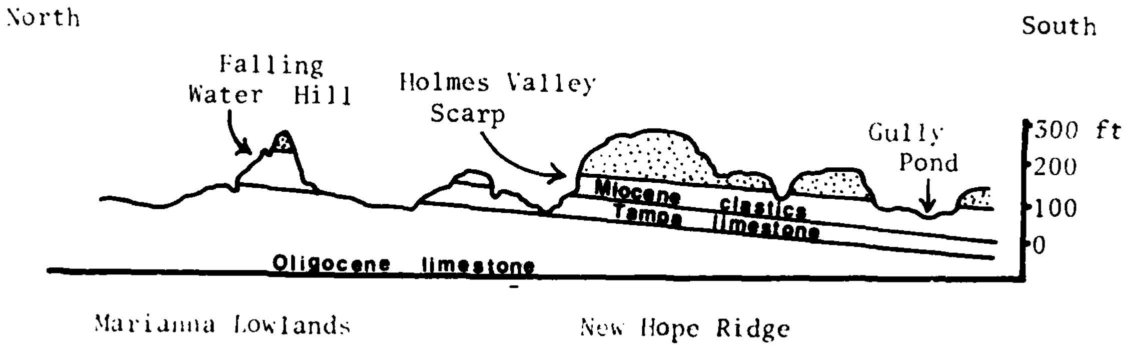


Figure 28. Cross-section of Holmes and Washington counties. Modified from Vernon (1942).

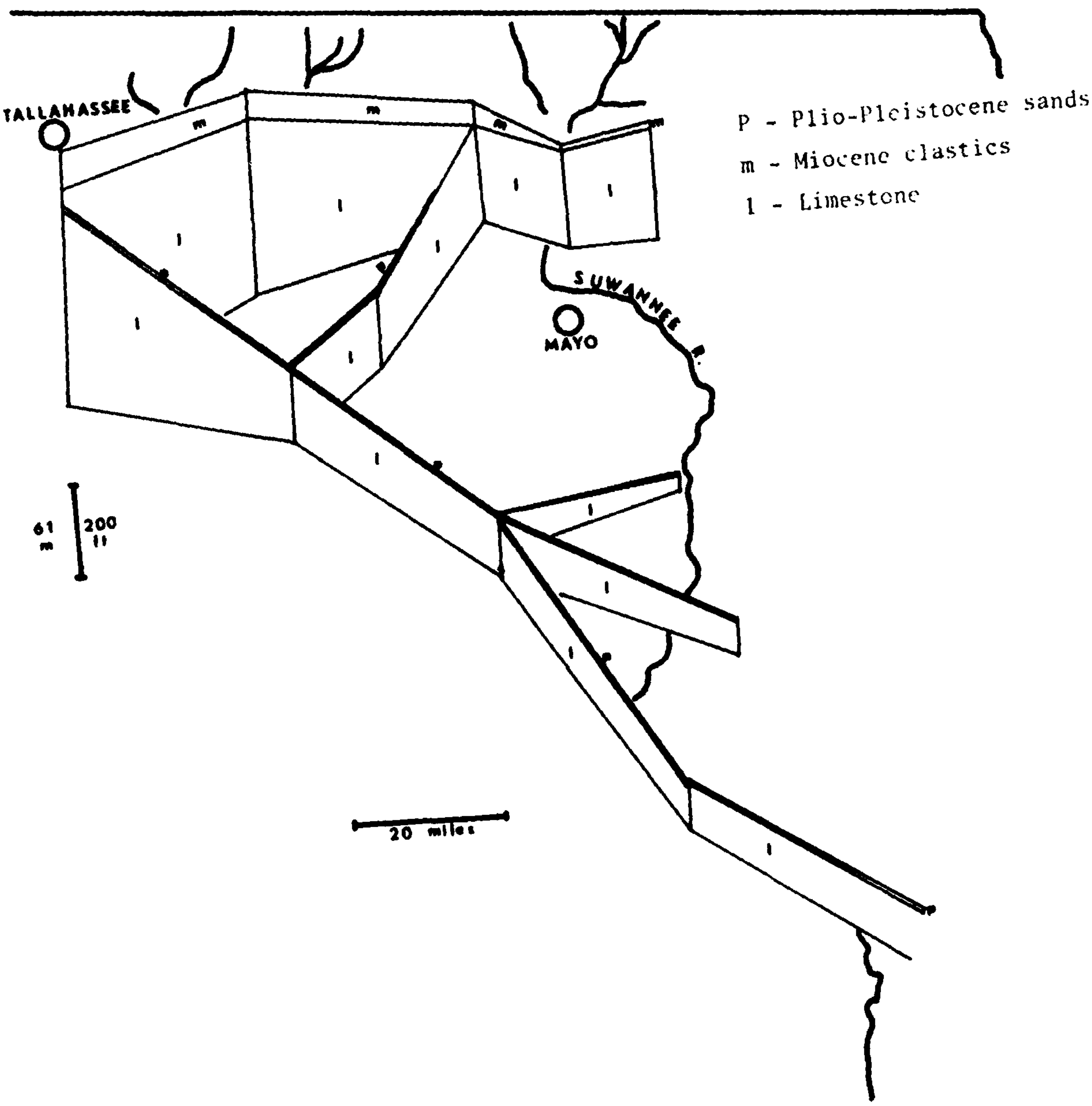


Figure 29. Cross-section of the eastern panhandle. Modified from Puri and Vernon (1964).

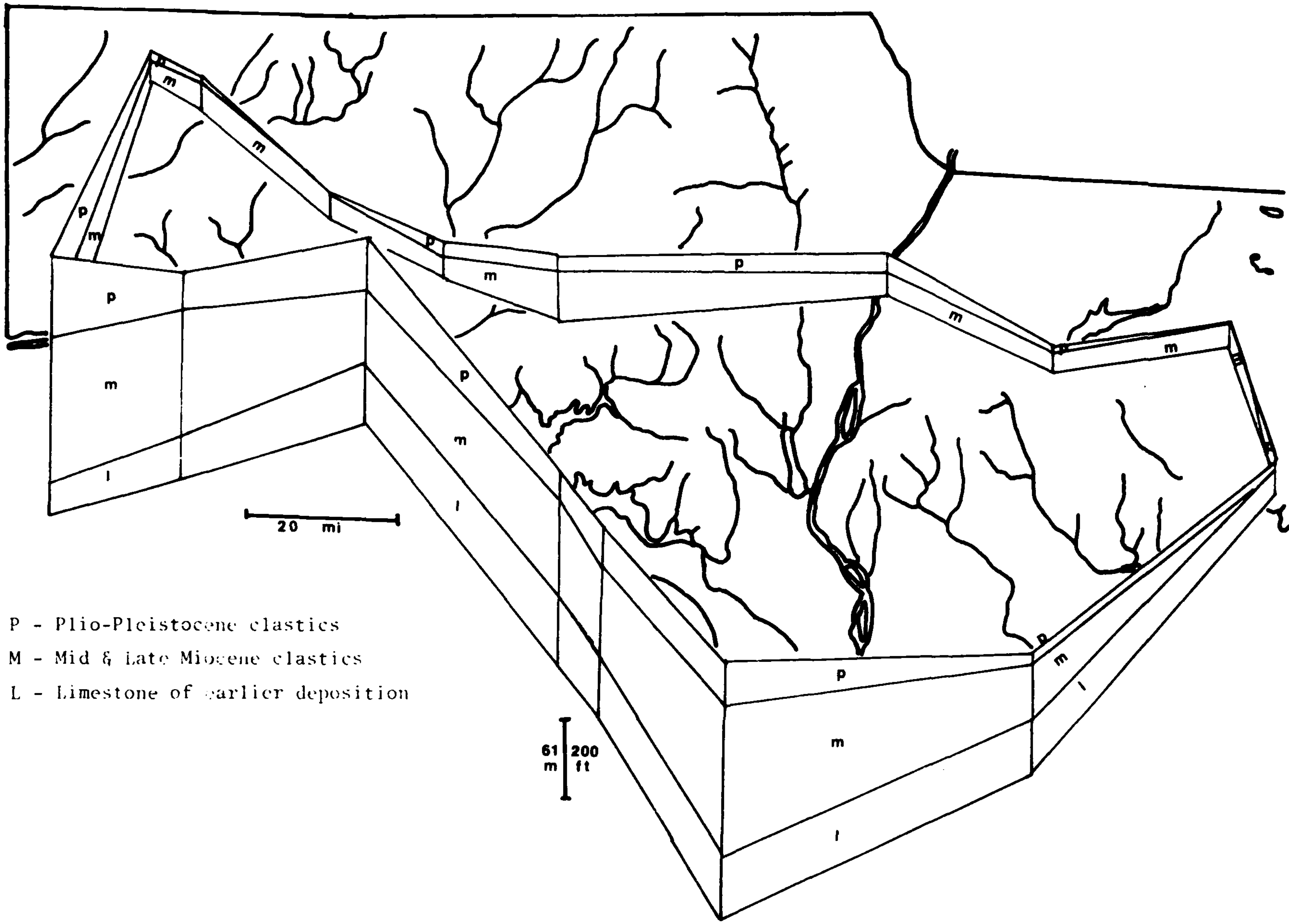


Figure 30. Cross-section of the central panhandle. Modified from Puri and Vernon (1964).

in vertical sequence at any given location. Not all formations were deposited uniformly across the panhandle, and some formations have been removed by erosion in places. Figures 29 and 30 show that the bedrock becomes deeply buried by less consolidated clastics west of the Ocklockonee River with the exception of the Marianna Lowlands. The veneer of Plio-Pleistocene sands is very thin over the Aucilla Karst Plain. Miocene clastics are essentially absent on the Aucilla Karst Plain but replace the Plio-Pleistocene sands to the north and underlie them to the west.

Severe (1966) described the geology of adjacent Thomas County, Georgia.

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7. PHYSIOGRAPHY

Introduction. The physiographic provinces of the panhandle are mapped in Figure 15. This map was based largely on the map of Puri and Vernon (1964), which was the most current attempt to delineate the physiographic provinces for the entire panhandle. The previous maps of Harper (1914) and Fenneman (1938) bear little resemblance to that of Puri and Vernon (1964) or to each other. The reasons for disagreement are that (1) topographic expressions are not always correlated with geological formations; (2) these formations are sometimes scarcely distinguishable from each other and are imprecisely known; and (3) the vegetation, which in many parts of the world conforms to physiographic and geological boundaries, often crosses these boundaries, making them indistinct.

Figure 15 incorporates some physiographic features proposed in local studies by Hendry and Sproul (1966) and Yon (1966). The major departure in Figure 15 from previous studies is the separation of the Gulf Coastal Lowlands into the Western Lowlands and the Aucilla Karst Plain. These two divisions are heterogeneous but are useful in respect to the characterization of lowland vegetation types.

There are three principal provinces in the panhandle. These are the Northern Highlands, the Mariana Lowlands, and the Gulf Coastal Lowlands (Fig. 15). The Northern Highlands consist primarily of the Western Highlands and the Tallahassee Hills. These provinces are interrupted by the Marianna Lowlands, but the continuity of the Northern Highlands is maintained by New Hope Ridge and Grand Ridge which skirt the Marianna Lowlands to the south. Grand Ridge has suffered considerable erosion and is closer in average elevation to the Marianna Lowlands than to the Tallahassee Hills.

Much of the Tallahassee Hills is capped by the fine-textured Miccosukee Formation, which was deposited as a delta plain in the late Miocene (Fig. 23). This formation rests on the similar Hawthorn Formation which outcrops at lower elevations (Fig. 25). Solution of the underlying limestone (St. Marks Formation) is retarded by the deep and often impermeable clastics above. Karst features are not nearly as prominent as on the adjacent Aucilla Karst Plain.

The surface of the Miccosukee Formation is often of sand or loamy sand on the hilltops and ridges. The removal of vegetation through agricultural practices allowed considerable sheet erosion. The more clayey subsoils were often exposed, and such sites are locally called gall spots.

West of the Ochlockonee River the Tallahassee Hills are capped primarily by the deep sands of the Citronelle Formation (Ft. Preston of Puri and Vernon 1964), rather than by the finer textured Miccosukee Formation. The Citronelle is thought to be primarily alluvial in origin. The Tallahassee Hills end abruptly as tall, steep bluffs along the Apalachicola River (Fig. 9). A series of trelised creeks (creeks branching at right angles) interrupt these bluffs and flow from deep ravines in western Gadsden and Liberty counties. This westernmost portion of the Tallahassee Hills is shown on Figure 15 as the Apalachicola Bluff Region which includes the lands dissected by the trelised creeks.

The Tallahassee Hills are separated from the Gulf Coastal Lowlands by the often steep and prominent Cody Scarp. This scarp cuts across the southern part of the City of Tallahassee and can be seen dramatically from the campus of Florida A. and M. University (Fig. 10). The Leon County Fairgrounds are near the base of the scarp, and the Tallahassee

Municipal Airport is in the lowlands just below the scarp. Hendry and Sproul (1966) equated the scarp with the Okefenokee shoreline in Leon County. They identified an upland west of Tallahassee as an Okefenokee dune field. These ancient dunes essentially lie between State Routes 20 and 267, U.S. Route 90, and the eastern portion of Lake Talquin (Figs. 1, 10). The Cody Scarp was equated with the Wicomico shoreline in Jefferson County, the scarp having been lowered there by the solution of underlying limestone (Yon 1966).

Grand Ridge, New Hope Ridge, and the western portion of the Tallahassee Hills are included as the southernmost portion of the Tifton Uplands by Fenneman (1938). These uplands continue northeastward through Georgia. The eastern part of the Tallahassee Hills was assigned by Fenneman to those marine terraces above the Wicomico shoreline (Fig. 22). These terraces parallel the Tifton Uplands on the east in Georgia.

The Holmes Valley Scarp separates the Marianna Lowlands from New Hope Ridge to the south (Figs. 15, 25, 28, also 7). The lowlands extend into adjacent Alabama and Georgia as a karst plain. The entire region is called the Dougherty Plain by Fenneman (1938), and the Marianna Lowlands is that portion of the Dougherty Plain in Florida. This plain borders the Tifton Uplands on the west in Georgia.

The Gulf Coastal Lowlands comprise roughly the southern half of the panhandle. Included in these lowlands are the valleys of the Escambia, Choctawhatchee, Chipola, and the Apalachicola rivers, which extend northward and interrupt the Northern Highlands. The Gulf Coastal Lowlands are divisible into the Aucilla Karst Plain and the Western Lowlands.

The Aucilla Karst Plain consists of a thin mantle of Plio-Pleistocene sands over limestone. The sand deposits are mostly less than 10 meters deep, and limestone often outcrops, particularly along streams and near the coast. The rivers are fewer and smaller than in the Western Lowlands. Much of the surface water seeps through the sands and into the limestone where it flows underground. The few surface streams are largely fed by springs which emanate from crevices or channels in the limestone. Natural bridges are common.

The western portion of the Aucilla Karst Plain, exclusively of the coastal region, was called the Woodville Karst Plain by Hendry and Sproul (1966), and occurs from Jefferson County westward (Yon 1966). Whether or not this province continues eastward has not been determined. The Woodville Karst Plain is distinguished by ancient dune fields now stabilized by vegetation. These dunes appear to have been shaped by prevailing winds from the northeast. A prominent dunal area is distinguished as the Wakulla Sand Hills (Fig. 15) and may represent the Pamlico Shoreline. Most streams are subterrainian, and the region is remarkable free of creeks.

The northwestern portion of the Woodville Karst Plain is distinguished as the Lake Munson Hills (Hendry and Sproul 1966). Lake Bradford, Lake Munson, and the Dismal Sink area are included in this region. These sand-hills are 10-17 meters higher than the rest of the Woodville Karst Plain. Impermeable clastics separate to some extent the sands from the limestone. As a result, the land surface has not been lowered by solution, as was the case for most of the Aucilla Karst Plain. Circular lakes of sinkhole origin are common here but not elsewhere in the Woodville Karst Plain. The Lake Munson Hills may represent the highly modified remnants of barrier islands from Wicomico times.

The coastal region of the Aucilla Karst Plain is distinguishable as the Marsh Strip. The limestone is mostly within 2 meters of the surface and is covered by sand and/or peat derived from tidal marsh vegetation.

Many circular and presumably sinkhole ponds interrupt the tidal marshes and are often connected by tidal creeks. A dragline once cracked through the limestone while constructing dikes near the St. Marks lighthouse (Fig. 13) in the 1930's. A spring has since emanated from this crack.

The Citronelle Formation caps most of the Western Highlands, New Hope Ridge, and Grand Ridge (Fig. 23). In the western panhandle the bedrock is particularly deep (Figs. 27, 30). Solution and resultant karst features are nearly precluded by the great depth of the Citronelle, by the lenses of clay and other impermeable materials embedded within the sands of the Citronelle, and by older impermeable clastics between the Citronelle and the limestone.

The Marianna Lowlands were once highlands with elevations comparable to those of the Northern Highlands (Fig. 15). Streams severely dissected and eroded the Miocene clastics, substantially lowering the elevation of the region and exposing bedrock in many places. Several isolated hills, shown in Figure 15 as the Washington County Outliers, are remnants of the former upland, which were spared from erosion. One of these, Falling Water Hills, is shown in Figure 28. Removal of the Miocene clastics was initiated by the Chattahoochee River which once crossed the region. Its flow was captured and its valley abandoned. This valley was in excess of 70 meters deep but is now completely filled by sediments. The terrain is essentially flat, and the valley was discovered after examining cores obtained by well drillers (Moore 1955). The Flint and Apalachicola rivers removed additional clastics. These rivers once flowed through the region but later migrated in a southeasterly direction to their present position.

The rate of solution of limestone was probably slow until the limestone was exposed by the removal of Miocene clastics. The lowering of the Marianna Lowlands by solution is thought to have been of minor significance with respect to the removal of clastics.

The Marsh Strip is limited inland by a wave cut scarp and other dune and beach ridge features which constitute the Silver Bluff shoreline. This shoreline is 1.7-2 m above present mean sea level and was formed about 5,000 BP when sea level was higher (Murali 1976). Wave energy was greater when sea level was higher. Marine sands were carried by waves to the shore and were reworked into the Silver Bluff features. The fire tower on State Route 59 near the St. Marks lighthouse was built on the Silver Bluff Shoreline (Fig. 13).

The rest of the Aucilla Karst Plain from Taylor County eastward lacks prominent or easily distinguishable physiography. Harper (1914) recognized the near-coastal region as Gulf Hammock, which is definable more by its swamps and wet flatwoods than by its physiography. Like much of the panhandle, the eastern part of the Aucilla Karst Plain needs physiographic clarification.

The Western Lowlands are characterized by flat terraces of Plio-Pleistocene sands and by an absence of karst features. The eastern portion of these lowlands is called the Apalachicola Coastal Low lands (Fig. 15). This region was named by Hendry and Sproul (1966) and encompasses the lower Apalachicola River Basin and the lower Ochlockonee River Basin. Impermeable Miocene clastics separate the surficial sands from the limestone beneath, or the limestone lies at such depths that solution is negligible and its effects are masked by the thickness of the overburden.

In contrast to the Aucilla Karst Plain, the Western Lowlands have not been lowered noticably by solution. Going from the western edge of the Aucilla Karst Plain onto the Western Lowlands involves a rise in elevation of 17 meters in as little as 3 kilometers (or about 50 feet in 2 miles). This change in elevation is readily appreciated by driving northwestward on State Route 267 from the intersection of State Route 369 in Wakulla County (Fig. 10). This journey begins on flat dry well drained sands. Soon one ascends gradually. After 6 miles one is about 80 feet higher in elevation. The terrain is moist and swampy. Drainage is inhibited by impermeable clastics of the Jackson Bluff Formation which underlie the surficial sands.

The route of this journey would be comparable to traversing those portions of Figure 19 labeled "11" and "12". Streams that drain eastward from the Western Lowlands go underground upon reaching the Aucilla Karst Plain, also as shown in Figure 19.

Water that is not removed from the Western Lowlands by evapotranspiration either remains trapped in irregular basins containing acid swamps or ponds, or it moves downhill through the porous sands above the impermeable stratum. The rate of movement is slow because of the absence of appreciable slope. The water may eventually reach steeper hillsides, ravines, or river bluffs where it seeps to the surface and evaporates or emanates as springs. It may also enter a river, lake, or swamp.

Puri and Vernon (1964) recognized Greenhead Slope, Fountain Slope, and Beacon Slope in the northern portion of the Western Lowlands (Fig. 15). Although recognizable as landforms, these slopes contain the same vegetation as elsewhere in the lowlands.

Coastal topography associated with the present shoreline constitutes the Beach Strip of the Western Lowlands (Fig. 15). This strip conforms somewhat to the Silver Bluff terrace but not as nicely as in the Marsh Strip. Sands of the Silver Bluff Shoreline in Franklin County drifted closer to the coast and now form high dunes. This dune formation is called Royal Bluff and is traversed by U.S. Route 98 east of Carrabelle. Peats dated at 6,000 BP underlie Royal Bluff and suggest its aeolian deposition over these peats shortly thereafter.

The topography diagrammed in Figure 20a is typical for much of the coast. A tall foredune rises abruptly not far from the high tide mark. A low dune field lies behind the foredune. These dunes become smaller with distance from the beach and finally grade into an overwash plain. This description fits much of Santa Rosa Island, Alligator Point, and central St. George Island. Beach ridges are most prominent in the general vicinity of Cape San Blas. Figure 20b portrays the topography of St. Josephs Spit off Cape San Blas. St. Vincent Island consists primarily of groups of beach ridges, the oldest of which are nearest the mainland and the youngest towards the Gulf (Tanner 1974).

St. George Island exemplifies the topographic diversity of the present barrier islands and spits. The western tip consists mainly of beach ridge systems, much like St. Vincent Island. Dune fields characterize the middle portion. The eastern tip is a large overwash plain. A spit angles northwestward from near the eastern end and encloses Rattlesnake Cove. This spit consists of an abrupt, central beach ridge flanked by an overwash plain.

The physiographic diversity of St. George Island and other barrier islands and spits suggests a complicated history of development. They may have formed initially during the Pleistocene. With the great fluctuations in Pleistocene sea levels, they must have been alternately submerged and stranded far inland. They must have been subjected to aggradation, erosion, and reworking of materials during these cycles. Differences in currents, wave energy, wind strength, wind direction, availability of sediments, and type of sediments all would have contributed to the physiographic diversity.

Much of Franklin County interior from the Beach Strip constitutes a topographic low which Healy (1975) mostly mapped as Silver Bluff terrace. The western portion of this region is known as Tates Hell (Figs. 11, 12). It lies roughly between the towns of Carrabelle and Sumatra and consists of bogs and shallow swamps. The topographic low northeast of Carrabelle was mapped by Puri and Vernon (1964) as Interlevee Swamps and Bays (Fig. 15). Two relict bars are shown in Tates Hell in Figure 15. These were once barrier islands dating to the Sangomon interglacial period when sea level was higher (Brenneman 1957).

Puri and Vernon (1964) mapped another relict bar about 20 miles long in northwestern Wakulla County. It begins at the edge of the Lake Munson Hills (Fig. 15) and extends southwestward to the Ochlockonee River at Smith Creek. It may represent a barrier island associated with the Wicomico shoreline. It forms the northern border of Bradwell Bay, a large circular acid swamp about 6 miles in diameter.

Early Literature. The older publications of the Florida Geological Survey include some general descriptions, including Sellards (1917), Sellards and Gunter (1918) and Cooke (1939). Some of these are valuable for their photographs of habitats containing original vegetation.

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8. RIVERS

River Types. There are three basic types of rivers in the panhandle. Each river either represents one of these types or shares characteristics of two or all three types. The first type is the large, alluvial river which carries a heavy load of sediments. The water is turbid and brown from the silt-clay fraction of the sediments. This silt-clay fraction is contributed by the erosion of fine-textured formations in the watershed. This fraction is augmented by the relative rapid erosion of agricultural fields in hilly terrain. The watersheds are generally large, compared to those of the other river types. The pH is circumneutral. The discharge varies seasonally, and substantial flooding occurs annually. The Apalachicola River and the Choctawhatchee River are the best examples.

The second type is the black water river which assumes the color of strong tea from the high concentration of tannins and other organic acids. These substances are leached from the sandy pinelands and particularly the peaty swamps that border these rivers. The pH often falls between 3.4 and 5.9. These rivers are mostly small to moderate in size, both from the standpoint of discharge and watershed. They may carry a sandy alluvium during periods of high discharge. The silt-clay fraction is virtually absent, owing to the sandy consistency of the watershed and to the flat, well vegetated terrain in which erosion is minimal. The upper Suwannee River, the Sopchoppy River, and New River are examples.

The third type is the clear, calcareous spring run, which is fed by springs emanating from caves or fractures in the limestone channel. Environmental conditions are usually constant because of the continuous flow of subterrainian water from springs. The pH is slightly alkaline, the water temperature is cool year around, the water is hard, and the water level fluctuates relatively little. The sediment load is generally small in spite of the sometimes swift currents. Erosion of sediments into spring runs is minimal, owing to gentle, well vegetated slopes and only nominal flooding in wet seasons. The sandy bottoms are stabilized by dense growths of rooted aquatic plants; however, much of the bottom consists of exposed limestone. The Wakulla River and the Wacissa River are prime examples.

Most rivers in the panhandle are black water, but many of these are partially spring-fed, either by short spring runs that enter as tributaries or as spring-boils along the bottom. The Suwannee River has its head waters in the Okeefenokee Swamp in southeastern Georgia, and it drains the western part of that swamp. Highly acid, darkly stained waters characterize the upper Suwannee. Approaching the town of White Springs (Hamilton Co.), the bottom consists mostly of limestone, from which clear spring water boils in many places. This spring water is at least partially responsible for the increase in pH downstream. Near White Springs the pH drops as low as 3.5 but increases to 6.8 near the mouth (USGS 1973). During the dry seasons when the discharge is minimal, much of the water flowing into the Suwannee comes from springs. During wet seasons the river is charged with highly acid and deeply colored water that enters as runoff. The Ochlockonee River combines the features of all three river types: brown water, black water, and spring runs.

The factors that determine the type of river are water quality (pH, conductance, color, hardness, Kaufman 1970, 1975, Slack and Kaufman 1975), quantity and type of sediment load (sand, silt, clay), and discharge. Discharge is defined as the volume of water that passes a given point within a given period of time. It is often expressed as cubic feet per second (cfs). Both the size of the sediment load and the erosional properties of a river are proportional to its discharge. Beck (1965) commented further on Florida streams. Conover and Leach (1975) mapped the river basins of Florida.

Discharge. Table 5 gives the mean monthly discharge for five rivers in the panhandle for one year. The values for April are unusually high because of heavy rains. There is considerable variation in discharge from month to month on each river. Discharge tends to be low in all rivers in the autumn and high in the spring. The autumn season is usually marked by low rainfall and high temperatures. Much of the water from rain is removed by evapotranspiration before it can reach streams as runoff. Heavy rains in the late winter and in early spring, coupled with cool temperatures and low evapotranspiration, account for the high discharges in the spring. Low stream flow data were compiled by Stone (1974) for Florida rivers. Snell and Kenner (1974) elaborated further on discharge.

Monthly changes in mean discharge are not necessarily parallel from river to river. The Apalachicola River is the only river in Florida with its headwaters in the Piedmont and southern Appalachians. All other rivers begin in the coastal plain. As a result, the volume of water in the Apalachicola River channel reflects hydrological conditions in northern Georgia and Alabama and is little affected by local rainfall. The Aucilla River and other small streams with limited watersheds are

TABLE 5. Mean Monthly Discharge (cfs) in 1972-73 (USGS, 1973).

River:	APALACHICOLA	SUWANNEE	ESCAMBIA	YELLOW	AUCILLA
Nearby City:	Blountstown	Wilcox	Century	Milligan	Lamont
October	10,010	5,552	868	229	6
November	10,710	5,203	1,654	464	10
December	33,440	5,775	10,410	2,730	59
January	46,380	7,595	10,690	2,677	172
February	63,360	15,040	14,330	2,502	1,028
March	45,230	18,410	21,060	3,175	625
April	73,970	38,790	31,410	3,109	6,000
May	39,760	28,690	11,500	2,007	774
June	42,410	20,500	10,540	2,114	921
July	19,640	17,550	4,323	823	333
August	19,590	13,760	4,372	749	209
September	15,020	10,240	3,589	585	128

especially prone to widely fluctuating discharges because of localized rainfall and sometimes because of the hydrological vagaries of karst topography. Hurricanes cause record discharges in small streams during the autumn when flow is normally minimal.

Table 6 gives discharge data for the larger rivers of the panhandle. These data apply only to the positions of the gaging stations and not to entire rivers. The first column gives the average monthly discharge, based on at least 16 years of data. The next two columns give the highest and the lowest monthly discharges tallied during the years of record. The extremes in discharge for a river are striking. These extremes are least in the Wakulla River, which is spring-fed.

River Stage. River level or "stage" changes with discharge. The vertical distance between the maximum and minimum stages recorded for each river is given in Table 6. These values are also striking for their magnitude. There is little correlation, though, between these values and average discharge, the area of the watershed, or any other statistic in the table. The height of the water column in the river channel is largely a function of not only absolute discharge, but also the width of the floodplain, the steepness of the valley, and the rapidity of change in discharge rates. The percentage of the time during a year that a river is at any given height can be plotted against height to give a stage-duration curve. Figure 31 is the stage-duration curve for the Apalachicola River at Blountstown.

Rivers are at flood stage when they overflow their banks and spread onto adjacent terraces called floodplains. Both discharge and sediment load are highest at flood stage. Upon overflowing the water soon loses its

TABLE 6. River Discharge Data.

River and Nearby City	Discharge (cfs) Average	Maximum	Minimum	Extremes in River Level (ft.)	Drainage Area (mi^2)	Feet Above msl
APALACHICOLA Blountstown	24,190	162,500	6,280	22	17,600	27
SUWANNEE Wilcox	10,610	84,700	3,270	21	9,730	0
CHOCTAWHATCHEE Bruce	6,985	69,600	1,290	17	4,384	4
ESCAMBIA Century	6,016	77,200	578	20	3,817	28
SUWANNEE White Springs	1,888	38,100	5	39	2,390	49
OCHLOCKONEE Bloxham	1,614	89,400	107	30	1,720	25
CHIPOLA Altha	1,481	25,000	330	26	781	20
YELLOW Milligan	1,124	28,000	131	15	624	45
SHOAL Crestview	1,051	21,700	240	13	474	47
PERDIDO Barrineau	729	39,000	188	23	394	26
HOLMES CREEK Vernon	668	10,900	234	13	386	11
ST. MARKS Newport	666	4,750	310	8	535	17
ECONFINA CREEK Bennett	527	4,860	307	8	122	1
WAKULLA Wakulla Springs	386	1,910	25	5	0	4
AUCILLA Lamont	362	11,500	0	12	747	43
STEINHATCHEE Cross City	330	17,600	3	17	350	8
BLACKWATER Baker	305	26,200	60	24	205	61

Data are from USGS (1973) and represent 16-48 years of records at each site, except Wakulla Springs where data are based on 271 readings taken since 1907. The minimum discharge at Bloxham is based on 1973 data.

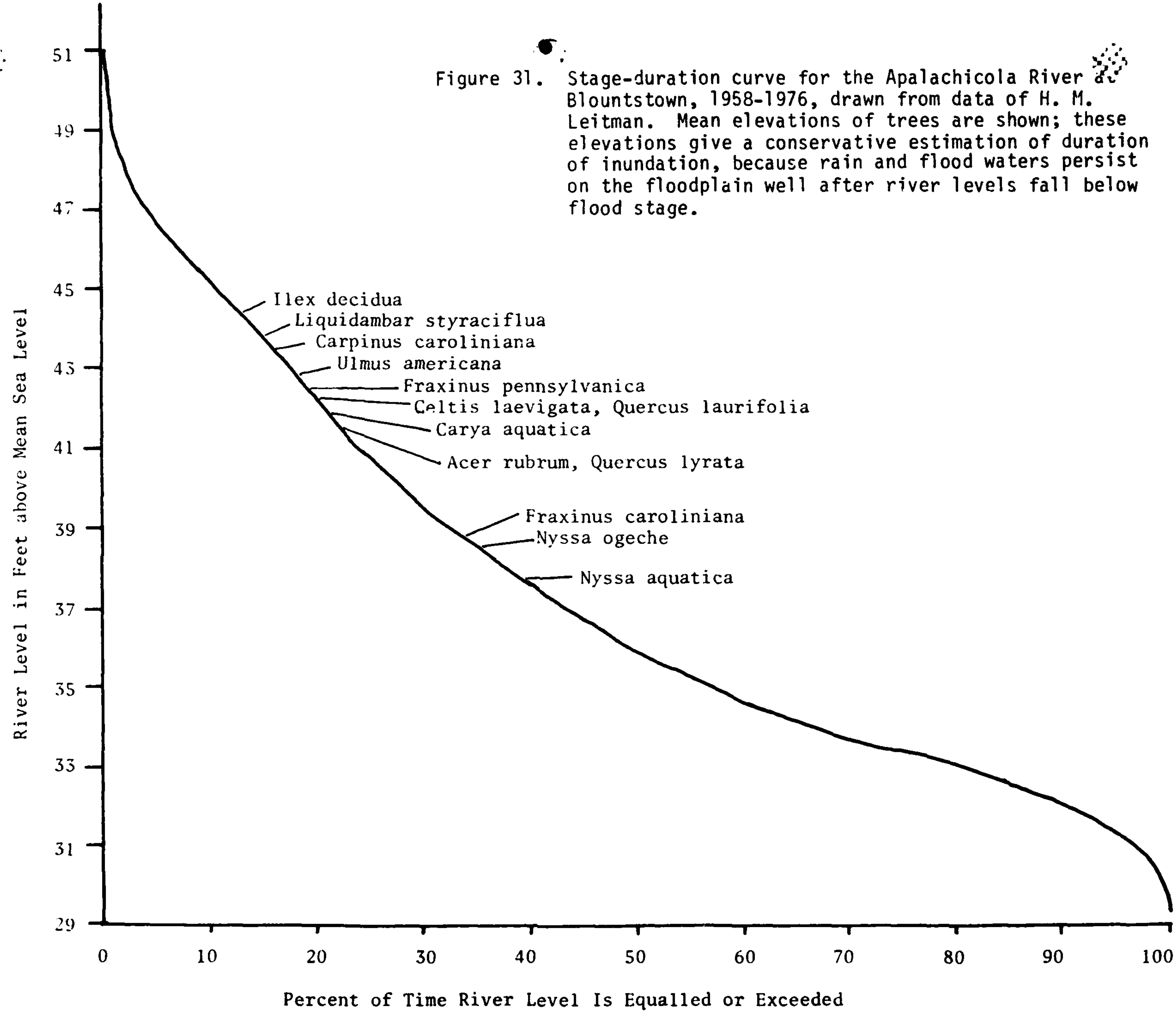


Figure 31. Stage-duration curve for the Apalachicola River at Blountstown, 1958-1976, drawn from data of H. M. Leitman. Mean elevations of trees are shown; these elevations give a conservative estimation of duration of inundation, because rain and flood waters persist on the floodplain well after river levels fall below flood stage.

velocity from friction with the soil and with the vegetation. With loss in velocity the heaviest particles of the sediment, mainly sand grains, settle and are deposited on the floodplain near the river bank. Successive flood stages allow the aggradation of sediments into ridges called levees which parallel the river on either side. Levees are typically the tallest and best drained land forms on floodplains.

The best developed levees are along the Apalachicola River. The enormous discharge of the river has produced many levees 2-3 meters tall and 30 or more meters wide. In contrast, the levees along the St. Marks River in southern Leon County are a few centimeters tall and about a meter wide.

Silts and clays remain in suspension and are carried beyond the levees across the floodplain. If the velocity is sufficient, these sediments are swept back into the channel. If the discharge is more moderate, these sediments either settle out evenly across the floodplain, or the water becomes trapped in depressions, allowing the deposition of sediments in these depressions.

Leitman (personal communication of thesis research data, 1978) discovered that channel stage often varied independently of water depth on the floodplain of the Apalachicola River. At flood stage the water's surface in the channel was essentially at the same elevation as the surface of the water on the floodplain. When the water level fell below flood stage in the channel, higher water levels were retained on the floodplain for days or weeks because of the slow return of water back into the channel. The return of water was hindered by friction with the soil and with the vegetation, obstruction by levees and other topographic highs, retention in temporary ponds and other topographic lows, and retention as capillary water in the mostly fine-textured soils. Local rains also kept water levels high on the floodplain. In the mean time, the river level stayed below flood stage in the channel but fluctuated widely, reflecting hydrological conditions far away in Georgia and Alabama rather than local conditions.

Leitman's study showed that soils are flooded or saturated longer on floodplains than a stage-duration curve for the river channel would indicate. The duration of flooding and saturation varies widely from place to place on a floodplain, depending on elevation, topographic irregularities that affect drainage, and the drainage characteristics of the soil.

Geology of Valleys. There is a general tendency for the rivers of the panhandle to run from northeast to southwest. Hendry and Sproul (1966) assumed that river channels follow fractures in the underlying rock formations. The fractures are mostly in a northeast-southwest direction, as is revealed by linear trends on topographic maps and aerial photo mosaics. They also noted that rivers tend to have higher and steeper bluffs on the east side and more gentle slopes on the west side. Marsh (1966) explained that tendency as follows. "The regional south to southwestward dip of the rocks has apparently caused many streams to erode their banks more strongly in that direction, making these banks much steeper than those on the opposite side." This process is called homoclinal shifting.

The larger rivers of the panhandle are characterized by broad valleys through which meandering channels traverse well developed floodplains. The valleys are commonly defined by relatively steep slopes or bluffs on the east side and gentler slopes on the west side. The bluffs and slopes are interrupted occasionally by the ravines of tributary creeks. These mature valleys presumable began as narrow, steep-sided upland valleys, in which the water flowed swiftly in a straight channel. Upon reaching the flat lowlands, the channel became ill defined, and the flow fanned out over a broad area. Such youthful streams are common on the Cody Scarp, and some are traversed by State Route 20 in western Leon County (Figs. 9, 10).

In time, the upland valley became deeper and the channels became better defined in the lowlands. Moving water deepened the channels by removing clastics. Acids in the water dissolved channels through limestone. The bedload of rocks and gravel bounced along the bottom, further gouging out the channel.

Later the channel widened from side cutting. Further widening resulted from the erosion of the slopes (mass wasting) and the transport of the eroded materials as part of the sediment load and the bedload. Finally the base level was reached, below which further erosion was impossible without a drop in sea level. Extensive side cutting continued after the base level was attained, further broadening the valley.

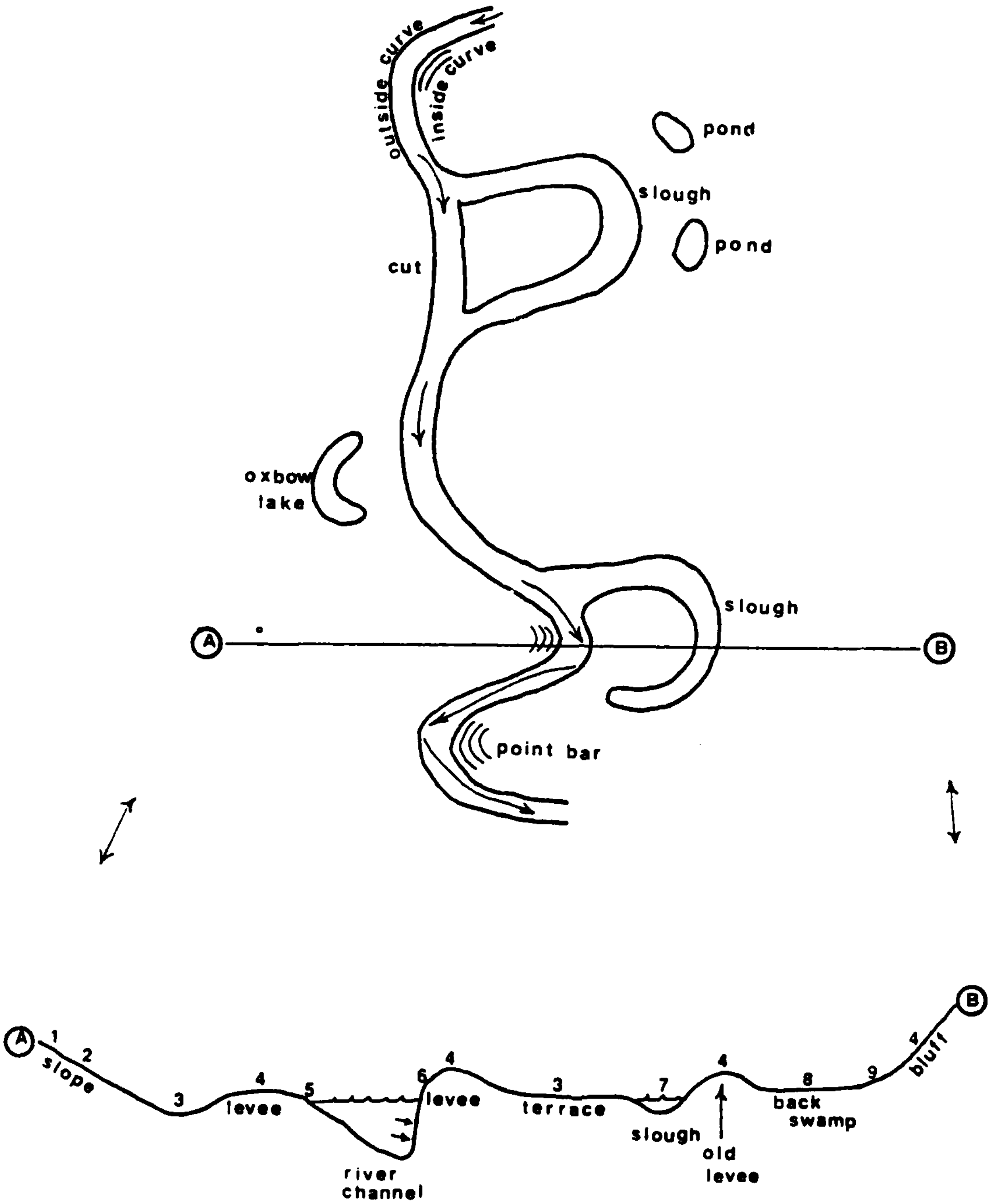
The formerly straight channel became sinuous and later began to meander in broad curves on the widening floodplain. This meandering was in response to differences in elevation and erodability of the floodplain. The length of the channel more than doubled from the head of the river to its mouth because of this meandering. The increased length created more surface along the bottom for friction with the flowing water.

Additional friction was caused by currents directed against the sides of the channel at the outside curves. Even more friction was caused at flood stage when flood waters passed over the floodplain. Because of increased friction, the kinetic energy of the water, and thus its velocity, was considerably reduced upon reaching the Gulf, as compared to times when the channel was straight.

The current tends to zigzag across the river, striking the outside curves and avoiding the inside curves (Fig. 32). The sides of the outside curves are subject to erosion and undercutting. The eroded materials are transported to the next inside curve, where slack water causes their deposition. A shoal aggrades as these sediments accumulate and extend the inside curve into an elongated point bar. This process continues until a sinuous channel becomes one of broad, "S" shaped curves.

Eventually the point bar becomes so elongated that the angle of flow is too great to divert the current around the bar. The current erodes a cut across the base of the bar, and that part of the channel looping around the point bar is abandoned. This loop is now called a slough. A levee eventually seals the upstream entrance to the slough and later the downstream entrance, forming what is called an ox-bow lake. This lake gradually fills with sediments and assumes the level of the surrounding floodplain. In the meantime, the new cut begins to meander because of differential erosion and aggradation.

Steepheads. The tributary creeks are either dendritic or trellised. From the Ochlockonee River westward many creeks are trellised and occupy deep, narrow ravines. These creeks begin as springs issuing from the



1 - Pine flatwoods
2 - Loblolly pine-sweetgum
3 - Hardwood swamp
4 - Mesic hardwoods
5 - Willow
6 - Birch
7 - Cypress-tupelo
8 - Blackgum
9 - Sweetbay

Figure 32. Topographic aspects of floodplains.

base of a steep slope at the head of a ravine. This slope is called a steephead (Sellards and Gunter 1918, Vernon 1942a, Marsh 1966, Means 1977). Steepheads form only in flat regions with deep, porous sands which absorb rain before it can runoff. The water percolates to a less permeable formation and moves laterally until it emerges as a spring at the base of a ravine. The spring undercuts the ravine, causing the sand above to slump into the spring. This sand is transported by the creek, and undercutting and slumping continue.

Repeated slumping increases the steepness of the slope of the steephead. This slope may exceed 30 meters in vertical relief in some streams, such as the Little Sweetwater Creek and other tributaries of the Apalachicola River in Liberty and Gadsden counties (Fig. 9). The angle of the steephead is steepest where the sand is most cohesive or compacted and thus resistant to erosion. The valleys continue to elongate as the face of the steephead is eroded. Since the erosion is from a near-vertical surface, it appears as if the floor at the head of a creek is nearly at the same elevation as at its mouth.

Tributary Valley Lakes. The Apalachicola and Choctawhatchee rivers have the highest discharges of the panhandle rivers and carry a heavy sediment load. Alluviation of their valleys is rapid. Levees and floodplains aggrade continually. Their tributary creeks have a much reduced discharge and scarcely any sediment load. As a result, the mouths of some tributaries have been partially sealed by levees. Water backs up and drowns the lower ends of their valleys to form what are called tributary valley lakes. The largest and best known example is Dead Lake which formed when levees of the Apalachicola River sealed the mouth of the

Chipola River (Fig. 11).

Vernon (1942b) said that the bottom of Dead Lake is 5-10 feet deeper than the bottom of the Apalachicola River. The lake basin is as much as 25 feet lower than the floodplain of the Apalachicola River. These figures show the magnitude of aggradation in the Apalachicola Valley.

Since the formation of Dead Lake, the main channel of the Apalachicola River migrated eastward to its present position. A new series of levees were aggraded during this migration, obliterating the former lower end of the Chipola River below Dead Lake. An overflow channel from Dead Lake now occupies abandoned channel segments of the Apalachicola River and also some inter-levee lowlands. This channel ultimately joins the Apalachicola River.

Later the Apalachicola River formed a new cut between its present channel and the overflow channel where it joins Dead Lake. This distributary is called the Chipola Cutoff. It is forming a levee which is encroaching on the lower end of Dead Lake. Vernon (1942a) suggested that the Chipola Cutoff may become the main channel of the Apalachicola River.

Williams (1827) wrote, "Thirty miles below this spring, an arm of the Apalachicola has lately burst into the Chipola, and formed a lake twenty miles in length, and seven miles wide, in which the forests are yet standing." Living cypress trees still persist in the lake today. A low dam was placed at the lower end of Dead Lake to maintain minimum depth. Lake level is almost always higher than the dam, over which water passes without obstacle.

Tributary valley lakes also occur along the Choctawhatchee River at Pinelog Creek, Holmes Creek, Wrights Creek, and Sandy Creek (Vernon 1942a). All have dying vegetation which speaks for their recency of formation. The lower ends of these lakes are 5-10 feet deeper than the Choctawhatchee River, and its floodplain is up to 15 feet higher than the surface of the lakes. All have distributaries similar to the Chipola Cutoff.

Back Swamps. Partially filled sloughs and other wet depressions are sometimes largely protected from annual flushing on floodplains. Such depressions are called back swamps. They may be protected by one or more levees which were stranded when the main channel migrated to the far side of the floodplain. Other origins are also possible. Any flood waters that reach a back swamp have lost their velocity and are ineffective in flushing detritus. As a result, acid peats accumulate. Swamps along intermittent creeks often have the vegetation and physical characteristics of back swamps, including low pH, peat aggradation, and nominal flooding.

Floodplain Sedimentation. The floodplains of the major alluvial rivers have been aggrading substantially, as evidenced by the formation of the tributary valley lakes. This aggradation coincides with a recent eustatic rise in sea level (Fig. 22). As sea level rises, the base level of the valleys also rises, promoting aggradation of sediments. As sea level drops, the kinetic energy of the water at a given point in the valley is proportionately greater. If sufficiently great, erosion is faster than aggradation. Previously deposited alluvium and other transportable materials are removed.

Schnable and Goodell (1968) presented evidence for the removal of materials from the Apalachicola River Valley (Fig. 33). Miocene limestone underlies late Pleistocene and recent sediments at the mouth of the river. During glacial maxima, the shoreline was near the continental shelf, which

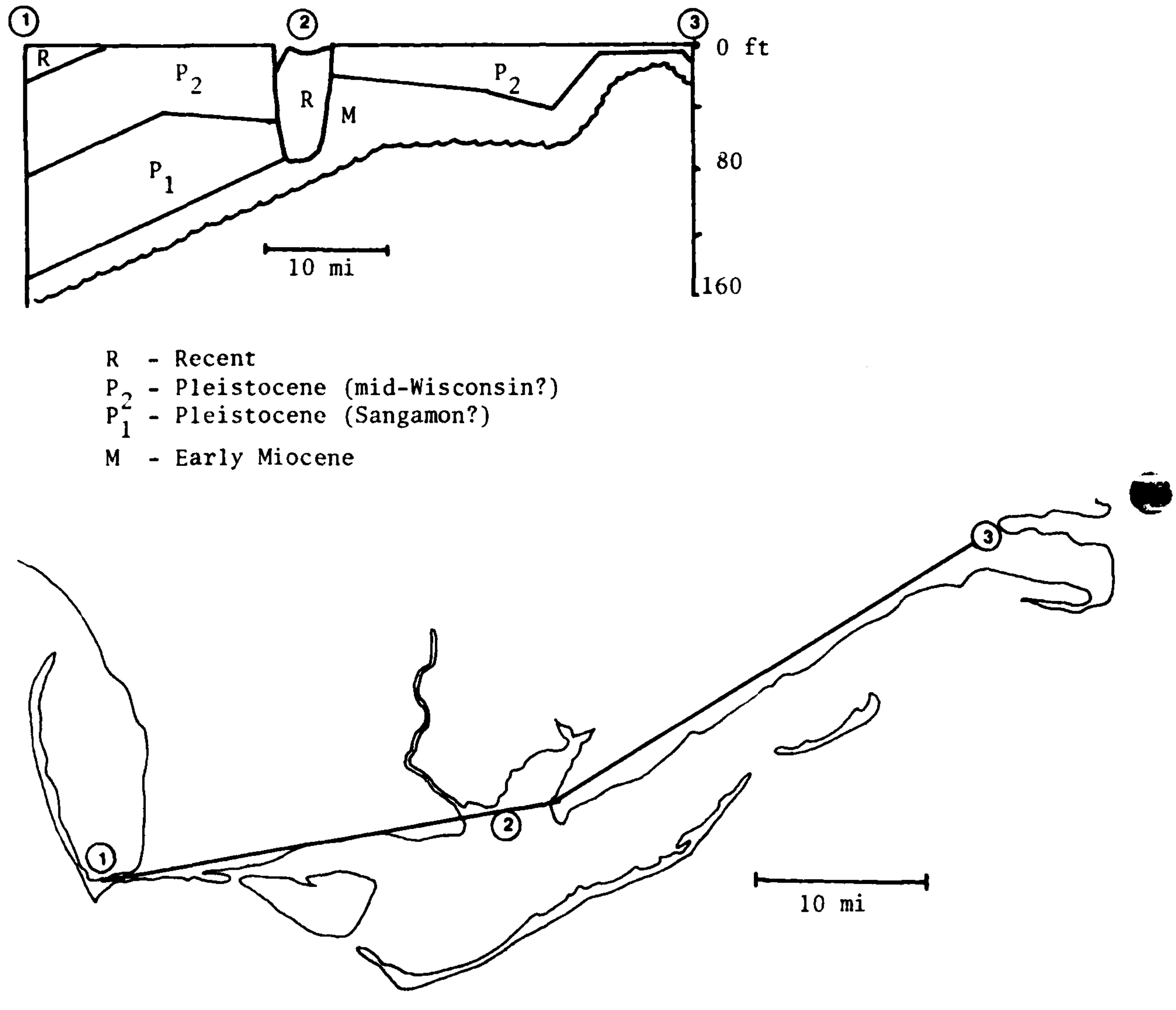


Figure 33. Cross-section, Cape San Blas to St. Teresa. Modified from Schnable and Goodell (1968).

would allow for the erosion of materials in the river valley. During these erosional cycles, any late Miocene, Pliocene, and early Pleistocene clastics were removed. With rising sea level, aggradation resumed, filling the valley to its present level. The drowned and sediment-filled valley of the Apalachicola River has been traced across St. George Island and well into the Gulf. Vernon (1942a) traced the drowned valley of the Choctawhatchee River 8 miles into the Gulf.

Regional Water Tables. The drop in sea level in glacial periods not only caused the erosion of valleys but also lowered river levels relative to the surrounding uplands. A botanically significant consequence of this lowering of river levels was a proportional depression in water tables (Vernon 1942a, Moore 1955, Martin and Webb 1974). As a result, hydric habitats became mesic, mesic habitats became xeric, and xeric habitats became semi-desserts. Evidence for this trend towards drier habitats was given by Watts (1971). He studied pollen stratigraphy in peat from lake bottoms near the Okefenokee Swamp and from peninsular Florida. He found that the lakes were dry at about the height of the Wisconsin glaciation.

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9. LAKES

Lake Origins. The lakes of the panhandle are numerous (Table 7) and may be classified according to their mode of origin. The origin of several kinds of lakes already have been described. These are sinkholes, ox-bows, prairies, and tributary valley lakes. Sinkhole lakes are generally small, circular, and deep. Many have filled with sand, forming shallow lakes with sandy bottoms. Lakes of the Lake Munson Hills are mostly sinkhole lakes (Fig. 15).

Ox-bow lakes and others formed from abandoned rivers initially assume the form of the channels from which they were derived. Subsequent deposition of sediments may be uneven. One end may fill but not the other, or the central portion may fill but not the ends. The resulting ponds are smaller and of different shapes from the original channel. Large lakes may be left stranded on abandoned valleys. Ocheesee Pond, which is three miles long and nearly half as wide, occupies an abandoned floodplain of the Apalachicola River in Jackson County. This lake is four miles west of the present river valley.

Many small lakes of the coastal lowlands occupy shallow depressions which are underlain by impermeable strata which perch the water table above the soil surface. Some of these strata are clayey Miocene clastics, such as the Jackson Bluff Formation (Fig. 23). Others are hardpans, such as sand cemented by limonite into sandstone, as commonly occurs in the Citronelle of the western panhandle (Marsh 1966).

Several lakes in the Tallahassee Hills of Leon County and perhaps elsewhere have had a more complex origin. These lakes include Lake Miccosukee (6,312 acres), Lake Jackson (4,001 acres), and Lake Iamonia

TABLE 7. Number of Named Lakes and All Unnamed Lakes of at Least 10 Acres (Hughes, 1974).

Bay	49
Calhoun	36
Dixie	76
Escambia	26
Franklin	29
Gadsden	34
Gulf	9
Hamilton	27
Holmes	62
Jackson	323
Jefferson	55
Lafayette	66
Leon	111
Liberty	30
Madison	113
Okaloosa	58
Santa Rosa	47
Taylor	96
Wakulla	44
Walton	90
Washington	279
TOTAL	1,660

(Figs. 1, 10). All are about 5-6 miles long with irregular, somewhat elongated outlines. Sellards (1910) suggested that such lakes developed in the valleys of small streams. Sinkholes formed in these valleys and enlarged them into broad basins at a time when the superficial layers of limestone were not saturated with water. Solution further lowered the floor of these basins. Water was trapped in them to form lakes.

Lake Miccosukee was thought to have developed this way in the upper St. Marks River. The river was shortened by the formation of the lake. Today, overflow from the lake eventually reaches the headwaters of the St. Marks River.

White (1958) challenged Sellard's theory. He suggested that the lake basins were formed at times of high water tables. Acidized groundwater moved laterally through the surficial clastics, dissolving the surface of the underlying limestone. Lake basins were formed wherever the limestone was more quickly soluble than elsewhere. Subsequent solution activity caused the formation of sinkholes, which were not involved in the formation of the lake basins, according to White. Instead, sinkhole formation was a secondary event which destroyed the ability of these basins to hold water without leakage.

Water Levels. An outstanding feature of virtually all natural lakes of the panhandle is that they drain or dry out completely, often after several successive years of below normal rainfall. For example, Lake Iamonia was dry in 1931, Lake Bradford in 1955, and Lake Jackson in 1957 (Hendry and Sproul 1966, Hughes 1967). Lack of rain and runoff, coupled with evaporation from the surface and transpiration of the emergent aquatic vegetation, is sufficient to dry out some lakes. Others drain into aquifers through sinkholes that are normally plugged by sediments or detritus but occasionally become open.

On the other hand, abnormally high rain can cause high water levels. Lake Jackson reached a record depth of 21 feet in 1966 after two years marked by heavy rains (Hughes 1969). Besides rainfall and runoff, some lakes receive water from the ground-water and sometimes directly from aquifers. Lake Iamonia receives water from the nearby Ochlockonee River at floodstage.

Many lakes in the panhandle are merely wet weather catch basins which dry out for at least part of each year. Some of these are prairies in the sense of Vernon (1942). Some of these are small and others extensive, including Lake Lafayette in the Tallahassee Hills of Leon County. This lake normally contains shallow water in only part of its basin. Lake Miccosukee and several other lakes normally are very shallow and seasonally dry over much of their basins, but water control structures have been built to maintain high water levels. The level of Lake Miccosukee is kept high by a low dam at the south end that retards the outflow and by an earthen dam at the north end that surrounds a sinkhole.

Reservoirs. Some lakes were created by the construction of dams across rivers. The largest of these are Lake Seminole, Lake Talquin, and Deer Point Lake (Figs. 8-10). Lake Seminole was formed by the construction of the Jim Woodruff dam across the upper end of the Apalachicola River. The Apalachicola is formed by the confluence of the Flint and Chattahochee rivers, and Lake Seminole occupies their lower valleys. The lake covers 37,500 acres in Florida, Georgia, and Alabama. The dam was completed in May, 1954, and the reservoir was filled by February, 1957. The lake was called Jim Woodruff Reservoir until 1957. Since then its water level has been controlled within a vertical range of 5 feet (USGS 1973).

Lake Talquin was created in 1930 by damming the Ochlockonee River near Jackson Bluff. The lake covers 6,850 acres of narrow, steep river valley. Its water level is kept nearly constant, except in 1957 when the dam breached and the level dropped about 20 feet. Deer Point Lake is in Bay County and was formed in 1961 by a dam across the Econfina Creek where it enters North Bay near Panama City. It covers 4,968 acres and its water level has fluctuated subsequently within about 2 feet (USGS 1973).

Lake Bradford Chain. Lake Bradford (182 acres) is a well known recreational lake on the southwest edge of Tallahassee in the Lake Munson Hills. It is up to 16 feet deep but was dry in 1957. It loses water through sinkholes on its eastern edge, but these were plugged in 1954. When nearly full it is connected to a chain of similar lakes by Bradford Brook. This chain occupies a lowland that begins at the Ochlockonee River and continues eastward through Lake Munson (Figs. 10, 13). The drainage turns south through Munson Slough, an intermittent creek that accepts overflow from Lake Munson. The lowland continues into Wakulla County, connects with MacBrides Slough, and enters the Wakulla River shortly below Wakulla Springs. Hendry and Sproul (1966) suggested that this entire lowland once was a channel of the Ochlockonee River. Stream capture rerouted the Ochlockonee to its present course and caused the former channel to be abandoned.

<u>Other Lakes</u>. Southern Washington County contains many small lakes (Fig. 8). Gages on three of them showed that lake levels have fluctuated by as much as 20 feet during the years of record (USGS 1973). These lakes and their vertical fluctuations are Porter Lake (929 acres) 20 feet, Guliy Lake (171 acres) 15 feet, and Wages Pond (100 acres) 13 feet.

There are scarcely any data available on the water quality of the lakes of the panhandle, although such data are being compiled by governmental agencies. Data by the USGS (1973) are not comparable for the few lakes being monitored. Some lakes are highly colored with tannins and other lakes are clear, suggesting wide differences in water chemistry. Basic limnological studies are unaccountably lacking for the panhandle.

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10. AQUIFERS

An aquifer is a body of water which fills the cavities and interstitial spaces in any geological stratum of rock or clastic material. The ground water aquifer is charged mainly by rain which percolates into the soil until it is interrupted by an impermeable stratum. The top of the ground water aquifer is called the water table. The water table is generally deeper on hilltops and ridges than in valleys and basins, because the ground water tends to move downhill above the impermeable stratum. The speed of this movement is regulated by the amount of rainfall, the steepness of the gradient, and the permeability of the stratum in which the water is held. Sometimes the water table rises above the soil surface in lowlands. When that happens the ground water discharges as springs or seepage on slopes or directly enters lakes, streams, swamps, or other water bodies. The height of the water table varies considerably in response primarily to rainfall and evaporation.

The ground water aquifer is unconfined, because it is not overlain by an impermeable stratum. Confined aquifers are forced beneath a less permeable stratum called a confining bed or aquiclude (Fig. 34). Water enters a confined aquifer at recharge areas. These may include sinkholes, lakes, swamps, and breaks in the confining bed which allow the entrance of ground water from an unconfined aquifer above.

The confined aquifer is under the pressure exerted by the water in the recharge areas. If a cased well were sunk into the confined aquifer, water would rise in the casing because of this pressure. The level to which the water would rise is called the potentiometric (or piezometric) surface. The potentiometric surface is not constant but fluctuates in response

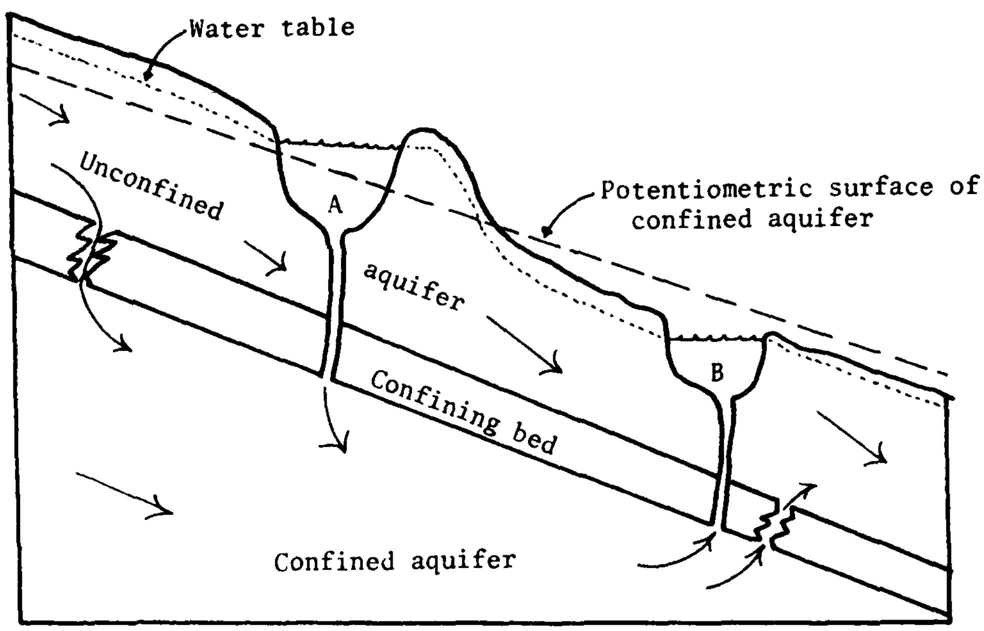

Figure 34. Aquifers. Arrows denote base flow of the ground water. Modified from Hughes (1974).

to recharge and discharge.

Discharge areas for confined aquifers, like those of unconfined aquifers, may include springs, seepage slopes, lakes, streams, and other water bodies but with an important qualification. The discharge area for a confined aquifer must be lower than the potentiometric surface (Fig. 34). In contrast, the discharge area for an unconfined aquifer is independent of the potentiometric surface of a confined aquifer beneath. The water table itself is the potentiometric surface of the ground water aquifer.

In Figure 34 Lake A is above the potentiometric surface and serves as a recharge area for the confined aquifer. Lake B is below the potentiometric surface and serves as a discharge area for the confined aquifer. Water moves between the confined and unconfined aquifers through breaks in the confining bed. Both lakes receive and release water to the unconfined aquifer as the ground water moves downhill.

If the potentiometric surface drops, Lake B will become a recharge area. This could happen regularly in dry seasons. If the potentiometric surface rises slightly, part of Lake A will be a discharge area and the other part a recharge area.

An understanding of the relationship of lakes to aquifers helps explain why some lakes fluctuate widely in water level and others very little. Lake Bradford fluctuates little but nearby Lake Cascade fills to a depth of 2-3 meters and drains in a matter of days or weeks. Both lakes are connected by Bradford Brook. The factors which cause lake levels to fluctuate are as follows:

1. Position of the potentiometric surface in relation to the surface of the lake. In general, lakes serving as recharge areas fluctuate more widely than those serving as discharge areas.
2. Ease of passage of water through sinkholes or bottom sediments between the lake and the confined aquifer.
3. Hydrological conductivity of the materials along the path of flow in the unconfined aquifer. The higher the conductivity, the greater the volume of water that enters or leaves a lake in a given time span.
4. Amount of rainfall.
5. Inflow of water from runoff after rain.
6. Size of the watershed contributing runoff.
7. The slope and permeability of the surface of the watershed. Steep slopes and impermeability augment runoff.
8. Physical restrictions, such as small channel size, that may retard the rate of overflow from a lake basin.
9. Evaporation from the surface of the lake.
10. Transpiration from emergent aquatic plants and from terrestrial vegetation near shore.
11. Season of the year. Rates of evaporation and transpiration are augmented by warm summer temperatures. Transpiration is especially reduced in winter with vegetational die-back.
12. Wind. The stronger the wind, the greater the evapotranspiration. A small lake, particularly if sunken in a depression or surrounded by trees, receives less wind than a large, open lake. As a general rule, lake levels tend to rise abruptly and fall more gradually and slowly.

The Floridan Aquifer is the name given to the confined aquifer of the panhandle. The depth to the top of this aquifer was mapped by Vernon (1973).

The springs of Florida were mapped and described by Fergueson (1947) and Rosenau and Faulkner (1975).

The loss of water from transpiration has a considerable effect on the water table, as demonstrated by Trousdell and Hoover (1955). The water table was monitored for several years in two nearly contiguous stands of loblolly pine and hardwoods in the coastal plain of North Carolina. The soil was a silt-loam with poor internal drainage. One stand had a much higher transpirational surface than the other, as indicated by the collective basal areas of the trees in each stand: 123 $feet^2$/acre in one stand and 196 $feet^2$/acre in the other. Except during the winter when transpiration was low, the water table was consistently higher in the stand with the lesser basal area (Fig. 35). Later the stand with 196 $feet^2$ was cut to a basal area of only 14 $feet^2$. Within a month the water table rose well above that of the other stand.

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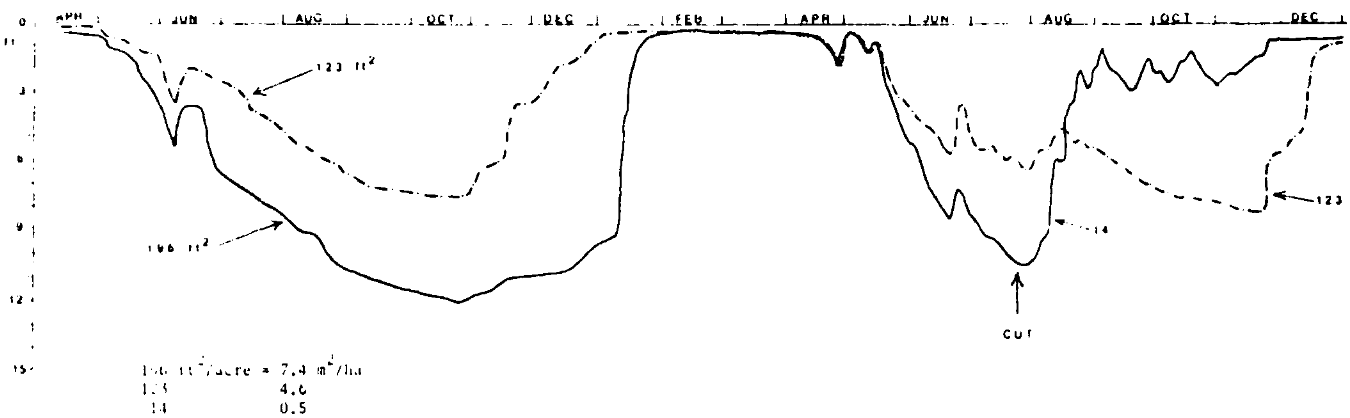


Figure 35. Effect of transpiration on the water table (modified from Trousdell and Hoover, 1955).

The water tables beneath two nearby forest stands of similar composition are shown. Each stand is identified by the total basal area of its trees. Basal area is presumed to be a function of transpirational surface area. The 196 foot-square stand was cut to 14 ft^2 as indicated.

11. SOIL

Soil is that portion of the surficial geological formation that has been modified by the combined action of weather and organisms. The soil is a dynamic biogeochemical system which provides anchorage for most vascular plants and which facilitates the exchange of water and nutrients. Most soils contain five basic components. These are mineral matter, soil atmosphere, soil water, living organisms, and dead organic matter (detritus). (Considerable information for this chapter came from Donahue, Miller, and Shickluna, 1977).

Soil Minerals. The mineral component consists of sand, silt, and clay. These separates, as they are called, are defined by their sizes (Table 2). Mineral soils derive their texture from the proportional distribution of their separates. Textural designations, such as *silty clay or sandy loam*, indicate the predominance of the different size classes. These designations are defined in the soil textural triangle (Fig. 36). A soil consisting of more than nominal amounts each of sand, silt, and clay is called a loam.

Sands of the panhandle soils are usually of quartz (SiO_2). Silt may contain various mixtures of quartz and the minerals more common to clays. Clays may contain quartz, calcium carbonate, ferromagnesians, the various "clay minerals", and other constituents. Clay minerals are complex alumino-silicates which form as the disintegration products of weathered rocks, particularly micas and feldspar.

Most clay minerals are crystalline in structure and consist of molecular layers stacked like a deck of cards. Their net charge is usually negative. As a result, cations in soil solution are attracted to their surfaces where

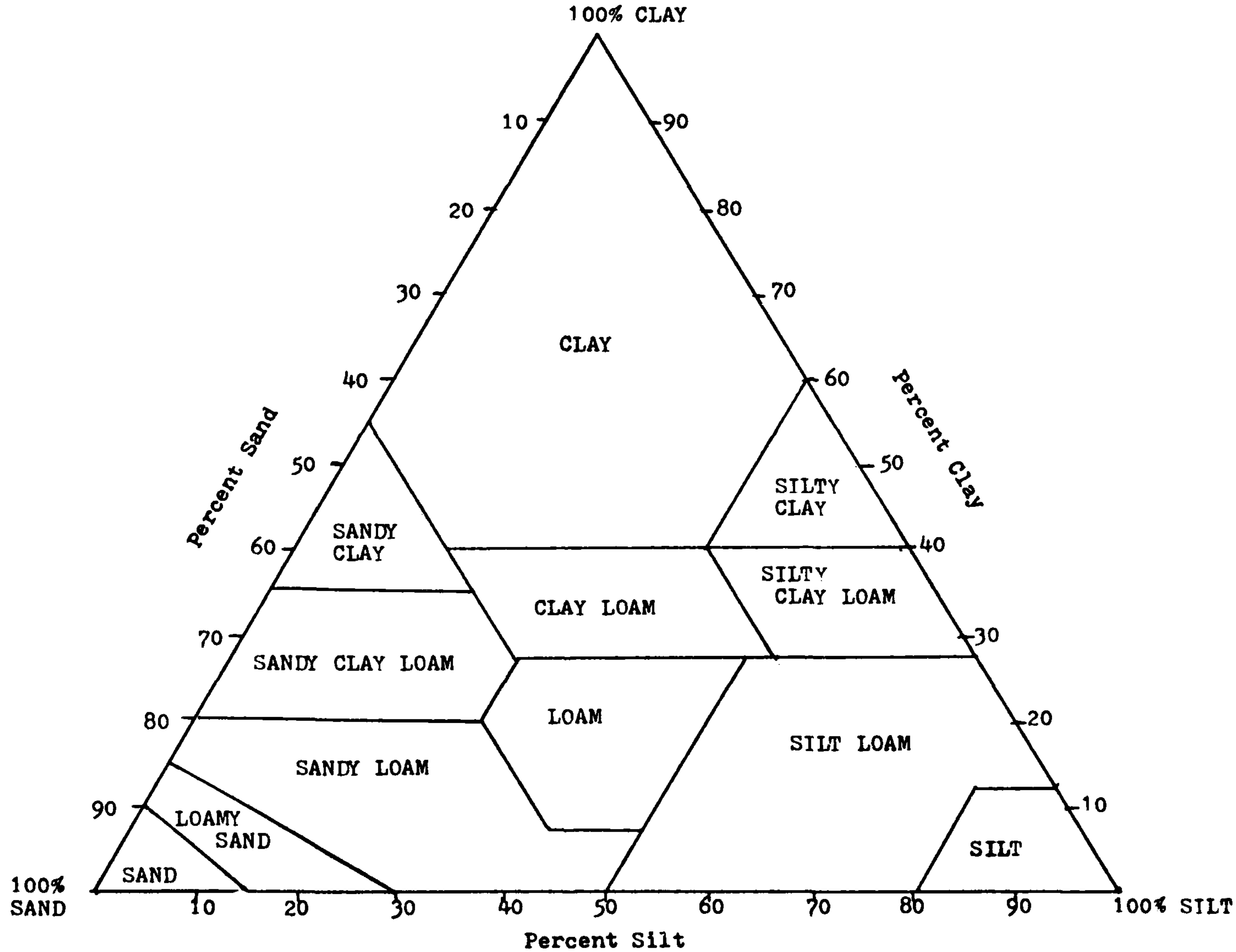


Figure 36. Soil textural triangle (redrawn from Soil Survey Staff, 1960).

they become adsorbed with varying degrees of tenacity. Hydrogen ions (H^+) are the most tightly held cations. Aluminum (Al^{+++}) is a common cation. Several cations are essential mineral nutrients for plant growth. These are calcium (Ca^{++}), magnesium (Mg^{++}), potassium (K^+), iron (Fe^{++}, Fe^{+++}), ammonium (NH_4^+), and a few minor elements.

The most common clay minerals and their most prominent elements are montmorillonite (O, Si, Al), illite (O, Si, Al, K), vermiculite (O, Si, Al, Mg), chlorite (O, Si, Al, K, Mg, Fe), kaolinite (O, Al, Si), sesquioxides (O, Fe, Al), and the amorphous (non-crystalline) clays (O, Al, Si). Kaolinite is the most common clay mineral in the southeastern United States and in the Panhandle.

Marsh (1966) described the clay lenses in the Citronelle Formation as consisting of kaolinite. Vernon (1942) reported a pure exposure of kaolinite on the face of a steephead. Hendry & Sproul (1966) reported kaolinite and montmorillonite as the dominant clay minerals in the Tallahassee Hills of Leon County.

Atmosphere. The soil atmosphere occurs in those interstitial spaces of the soil that are not filled with water. The volume of these pores may reach 60-70% in some soils. The soil atmosphere is essential for supplying oxygen to roots, to aerobic microorganisms, and to the soil fauna. Some plants of hydric habitats have other sources of oxygen, and these will be considered in a later chapter.

Water. Soil water may be divided into three categories. The first is gravitational water, which is that portion that runs off the surface as sheet flow or that percolates downwards, much of it below the zone of biological activity. The second is capillary water which is held in the capillary spaces between the soil particles, including both mineral and organic matter. The capacity of a soil to retain capillary water is generally proportional to the surface area of the particles in a given volume of soil. Surface area is least in a coarse sand and most in a clay. (The relationship between particle size and surface area is demonstrated as follows: A cuboidal sand grain 1 mm tall has a surface of 6 mm^2. If this grain were cut into 64 cubes each 0.25 mm tall, their collective surfaces would equal 24 mm^2.)

The third category is hygroscopic water which is a thin film that adheres tightly to soil particles and is removed only as vapor by heat above the boiling point. Hygroscopic water is unavailable to organisms.

Four characteristics of any given soil with regard to moisture are the maximum water-holding capacity, field capacity, moisture equivalent, and permanent wilting point. The maximum water-holding capacity is reached when a soil is saturated. The field capacity is reached after the gravitational water is removed but all capillary pores remain filled with water. The amount of soil water at field capacity is about 5% for sands and 45% for clays. Silts and loams fall between these extreme values. The percentage of soil moisture is determined by subtacting the dry weight of the soil from its wet weight, dividing this by the dry weight, and multiplying by 100.

Field capacity is essentially the same as the moisture equivalent, which is the percentage of water that an initially saturated soil retains after centrifugation for 30 - 40 minutes at 1,000 times gravity. The moisture equivalent is slightly lower than field capacity for sandy soils.

The permanent wilting point is reached when the soil moisture is insufficient for a plant to recover its turgidity at night after wilting during the day. The test plant used is often a standard crop plant like sunflower. Values for the permanent wilting point of soils will vary according to the species of the test plant. Recovery of a wilted plant at night growing in a soil approaching the permanent wilting point is possible because of reduced transpiration and sometimes because of the absorbtion of dew by leaves. Dew may play a much greater role than generally realized in supplying water to plants of xeric habitats and during droughts.

Soil moisture is more precisely defined in terms of the suction pressure needed to pull water from the soil. The unit of suction is called a bar, which equals 1.0127 atmospheres of pressure. Gravitational water is defined as that held by less than 1/3rd bar of pressure. The permanent wilting point is defined as the percent moisture held at 15 bars. The moisture held at forces of suction between 1/3rd and 15 bars is called available water and represents that held by capillarity. A few plants can remove water slowly from soils at 60 bars. All hygroscopic water is removed with 10,000 bars of pressure.

Organisms. Soil organisms include both plants and animals. The vegetational component includes bacteria, algae, fungi, and the roots and other subterranian parts of vascular plants. Bacteria are important in the decomposition and ultimate mineralization of detritus. Some bacteria are important in nitrogen-fixation and denitrification. Bluegreen algae grow on the surface of some soils and help to bind the mineral particles, thereby reducing erosion. Some bluegreen algae fix nitrogen.

Fungi break down detritus. One fungal group, the actinomycetes, are known to fix nitrogen. Many fungi form mycorrhizal connections with the roots of vascular plants. The topic of mycorrhiza was reviewed by Hacskaylo (1971) and Marks and Kozlowski (1973). Mycorrhizal connections between roots and particularly the hymenomycetes (mushrooms, bracket fungi, and their relatives) are extremely common among perennial plants, both woody and herbaceous. Annuals are also subject to mycorrhizal infections. Relatively little is known about the importance of mycorrhizae in southeastern plant communities, but their general role has been established experimentally.

Mycorrhizal fungi are unable to digest cellulose and other high molecular weight carbohydrates efficiently. Instead, their carbon source is obtained from glucose and other sugars contributed by roots. Evidence for this comes from experiments which showed that C^{14}-labeled glucose is transported from pine seedlings into the fungus (Ried and Woods 1969). Further, the growth rate of the fungus increases as seedlings to which they are connected are given increasing intensities of light.

The vascular plant, which is less efficient in absorbing nutrients from the soil than their fungal symbionts, receives nutrients directly from these fungi. Pine seedlings that were infected with mycorrhizal fungi contained higher amounts of phosphorous and potassium in their tissues than did uninfected seedlings. The respiratory rates of infected seedlings are much higher than in the uninfected seedlings.

The soil fauna is divisible into at least three categories. The burrowing animals increase the aeration of the soil with their tunnels. The more deeply burrowing forms cause the vertical mixing of the soil by bringing excavated materials to the surface. Nutrients leached below the root zone may be recovered, and developing hard pans may be perforated. Common burrowers in the panhandle are moles, mice, shrews, cotton rats, pocket gophers, gopher turtles, crayfish, ants, and earthworms.

The detrital feeders reduce larger detrital particles into smaller ones which, because of their smaller size, can be decomposed more efficiently by microorganisms. Common detrital feeders are mites, millipeds, springtails, bristletails, ants, snails, slugs, sow bugs, earthworms, and nematodes. The soil predators control the populations of detrital feeders and include moles, spiders, centipeds, mites, ants, nematodes, and many others.

Most soil organisms are adversely affected by a reduction in the soil atmosphere or by a reduction in the exchange of oxygen and CO_2 between the soil atmosphere and the ambient atmosphere. Flooding, especially during the growing season, may kill trees and greatly reduce the abundance of mycorrhizal fungi. Nitrogen-fixing organisms are aerobic, and their efficiency is dependent on adequate aeration. Aeration, though, is reduced by compaction by the trampling of cattle and by the weight of vehicles.

Organic Matter. The dead organic matter (OM) in the soil is derived in large part from decomposing leaves and roots. Other sources of detritus are from wood, bark, flowers, and fruits, and from the corpses and feces of animals. Organic matter which has decomposed to the point that its source is no longer recognizable is called humus. Fallen leaves that are still recognizable to species constitute the litter. Leaf mold that has decomposed beyond recognition to species is called duff. Soils that consist largely or entirely of organic matter are called peats if the consistency is fibrous or mucks if it is non-fibrous. The percentage of organic matter in a soil is estimated by comparing the weight of a dry sample before and after its placement in a furnace at low temperatures. All organic carbon is volatilized as carbon dioxide in the furnace.

Acidity. Soil acidity has little direct effect on vegetation except in extreme instances. Many species, including most dominate ones, tolerate a wide range of pH values. To a large extent the pH is a result of the action of the vegetation on soil rather than a factor that closely regulates plant distribution. Carbonic acid is formed continually as CO_2 is released into the soil water by roots and other organisms. The organic acids released during decomposition add further acidity. The decomposition products of oak and particularly pine leaves are especially acid.

Very high acidity may be detrimental. Aluminum becomes more soluble with increasing acidity and may reach toxic levels for most plants. High acidity also causes phosphorous to form insoluble complexes with iron and aluminum, thereby reducing fertility. High acidity may also adversely affect microorganisms which in turn affect vascular plants.

The ability of roots to absorb water is diminished in highly acid soils. Plants of acid habitats are often structurally adapted to conserve water, as are plants from xeric habitats. Thick, coriaceous, evergreen leaves are one such manifestation. Such plants of acid habitats are called physiological xerophytes.

Soils along the coast that receive tidal inundation or salt spray tend to be alkaline. These soils are usually sands or peats with little native nutrients except those contributed by sea water and any nitrogen that is fixed. The nutrients carried by sea water are available only to a few species of halophytes which tolerate the high salinities. No other alkaline soils are known from the panhandle.

Soil Fertility. To a large extent, fertility is a function of the abundance of available mineral nutrients. The total nutrient content includes both the available nutrients in the soil solution and the extractable nutrients that are adsorbed on soil colloids. The determination of nutrients in the soil is not necessarily an accurate measure of fertility, because at any given time most of the nutrients may be incorporated in the protoplasm of living organisms. Further, the multitude of chemical tests (Chapman 1966) for determining available soil nutrients only give approximations. An accurate analysis of fertility must include quantitative determinations of nutrients both in plant tissues and in the soil.

Such an analysis gives an idea of the nutrients present at a particular time. It does not measure the rate of loss of nutrients by leaching below the root zone or by erosion. It does not account for the increase of nutrients as parent materials are weathered or as eroded materials from elsewhere accumulate or even as nutrient-rich salt spray from the surf is deposited inland by the wind.

A useful criterion for judging fertility of soils is the cation exchange capacity (c.e.c.). The c.e.c. is defined by the quantity of exchangeable cations that can be adsorbed on the clay minerals, humus, and other negatively charged surfaces of a soil, including the surfaces of roots. The c.e.c. is expressed as milliequivalents (m.e.) per 100 grams of soil, which actually denotes the number of sites at which a cation can be adsorbed. Usually, the higher the c.e.c., the higher the soil fertility.

The normal range of c.e.c. for soils of different textures is as follows:

Sand	1-5
Fine sandy loam	5-10
Loam and silt loam	5-15
Clay loam	15-30
Clay	30+

There is considerable variation in the c.e.c. for the common soil colloids:

Humus	100-300
Vermiculite	80-150
Montmorillonite	60-100
Illite	25-40
Kaolinite	3-15
Sesquioxides	0-3

The exchange of cations between the soil solution and colloidal surfaces is driven largely by metabolism in roots and soil organisms. During metabolism CO_2 is released into the soil solution and forms carbonic acid. Hydrogen ions (H^+) become more plentiful . They are more strongly attracted to negatively charged exchange sites than are the nutrient cations. The hydrogen ions "bump" the nutrient cations from the surfaces to which they had been adsorbed and exchange places with them. Upon going into the soil solution, the nutrient cations are absorbed readily by roots and microorganisms. This mechanism holds nutrient cations and makes them available upon biological demand. If these nutrients remained in solution continuously, they would be subject to leaching below the root zone by percolating rain water. Such leaching is minimized because of cation exchange.

Soil fertility with regard to nutrient cations is not only a function of the c.e.c. but also the quantity of cations held by adsorbtion at the exchange sites. Base saturation is a measure of this quantity and is defined as the percentage of exchange sites held by nutrient cations, as opposed to those of H^+ and Al^{+++}. The higher the percentage, the higher the soil fertility. Taken together, the c.e.c. and the percentage of base saturation allow a good estimation of fertility.

Klawitter, Young, and Case (in Carlisle and Pritchett 1971) estimated the level of fertility in seasonally wet Florida pinelands with reference to pine growth:

Level	m.e./100g soil	% Base Saturation
Low	under 5.5	0-33
Medium	5.6-15.2	34-66
High	over 15.2	67-100

Soil fertility is also a function of the nutrient anions, particularly nitrate (NO_3^-), phosphate ($H_2PO_4^-$ and HPO_4^{--}), and sulfate (SO_4^{--}). The anions are made available gradually as the humus decomposes. Like the nutrient cations, these anions are readily absorbed by roots and microorganisms when released into the soil solution. They are also subject to leaching below the root zone with percolating water.

Phosphorus is the element in least supply in the panhandle, at least in those soils classified as sands. As mentioned previously, phosphorous tends to become bound in a form unavailable to plants in highly acid soils, which are common in the panhandle. Nitrogen is usually the next most deficient nutrient in the sandy soils and is perhaps the most deficient nutrient in finer textured soils.

The most fertile soils of the panhandle may be those of the floodplains of the major alluvial rivers, particularly the Apalachicola. The clayey alluvium has a high c.e.c., suggesting that clay minerals with higher cation exchange capacities than the predominate kaolinites are being imported from the continental interior. The flood waters also carry nutrients of all types in solution which may be absorbed directly by roots without the expenditure of metabolic energy to drive the cation exchange mechanism. Late winter and early spring floods carry these nutrients onto the floodplains at the initiation of each new growing season.

The high diversity of plants growing where limestone is near the surface suggests that the soil is enriched by nutrients made available from the solution of limestone. Southern red cedar and cabbage palm are often indicators of surficial limestone. Maidenhairfern is one of several herbaceous species seen primarily or exclusively with limestone outcrops.

Other relatively fertile soils are those loams that developed from calcareous and phosphatic deposits, including the Hawthorn and the Miccosukee formations of the Tallahassee Hills. These soils are not as rich, though, as those soils of prime agricultural lands of the Great Plains. The abundance of kaolinite suggests that these soils have been subjected to leaching in a warm, moist climate for many thousands of years. This extensive weathering of the clay minerals resulted in the development of kaolinite and rendered the soil less fertile.

Soil Development. Soil development or pedogenesis is a gradual process that involves the leaching of certain materials as rain water percolates through the soil. The nature of the materials leached depends on the mineral composition, the humus, and the effects of organisms on soil chemistry. The leachates mostly consist of dissolved substances and colloidal-sized particles, both mineral and detrital.

The original parent material from which the soil is formed is transformed into distinct layers or horizons. These are mainly divisible into an upper eluvial (or "A") horizon from which materials are leached, and a lower illuvial (or "B") horizon in which the leachates accumulate. The A horizon is commonly called topsoil and the B horizon the subsoil. The horizons of a typical, well developed soil are diagrammed in Figure 37. Collectively, the horizons constitute the soil profile.

The depth of the profile is a function of the depth to which materials are leached. Leaching continues to the point where percolating water is

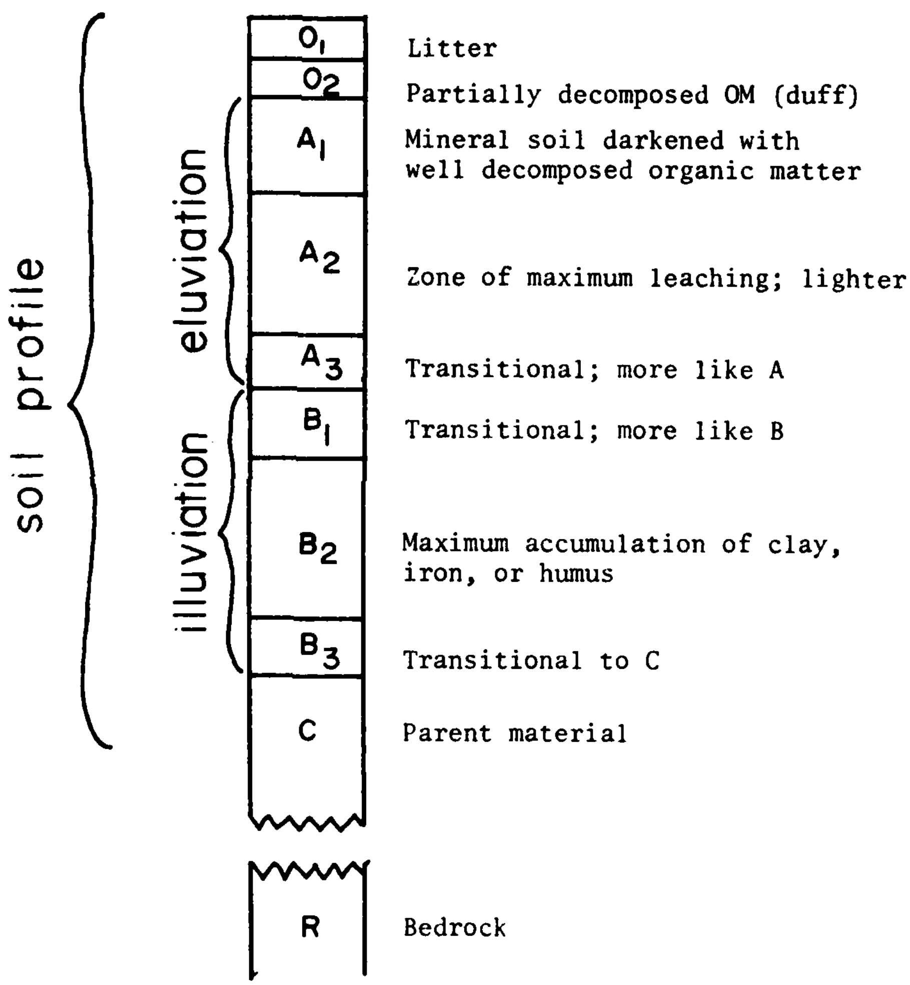


Figure 37. Soil horizons.

arrested by capillarity or until it reaches an impermeable layer or the water table. The water table is near the soil surface in many regions of the panhandle, particularly during the wet season when leaching is most prevalent. As a result, the lower horizon indicates the position of the normal upper limit of the water table in many soils.

The term sequum refers to an eluvial horizon and its illuvial horizon. Many soil profiles in the panhandle, though, are bisequums, which contain more deeply buried horizons. Bisequums may form by the deposition of new parent material over an existing soil. A dune, for example, may migrate over a flat with an existing sequum, and the dune eventually develops its own profile. A bisequum may also arise if there is a change in the average depth of the water table. If the B horizon developed on top of the water table but then the water table rises to a new, average level, a second B horizon may develop just above the new water table. The resultant soil profile will contain two distinct B horizons.

There are two kinds of illuvial horizons that are distinctive in the panhandle. An argillic horizon is one consisting primarily of silicate clay. Argillic horizons are particularly distinctive in soil profiles that are otherwise sandy. The other is a spodic horizon, which consists of very fine humus which is cemented somewhat by iron and/or aluminum compounds that are leached with the humus. Spodic horizons are particularly common where the leachates accumulate just above a shallow water table.

Argillic and spodic horizons may serve as hardpans which are rather impermeable to the percolation of water and to the penetration of roots. The horizons are often able to perch a water table above them after heavy or prolonged rains. Drainage is inhibited, thereby affecting soil moisture and aeration. Root penetration may not be inhibited mechanically but rather by the lack of sufficient oxygen for continued downward growth.

Permanently waterlogged argillic horizons are denied oxygen from the soil atmosphere. Iron compounds are reduced to the ferrous condition, causing the horizon to become gray or bluish and sticky. Such a horizon is called gleyed. Roots and burrowing animals sometimes penetrate gleyed horizons. Later these channels are filled with materials that sift into them from upper, oxygenated horizons. The oxygenated materials are yellowish or reddish from their iron oxides and contrast strikingly in color with the gleyed materials. The outline of former burrows and root cavities are marked indefinitely by their color.

Another distinctive feature of the B horizon of some soils are plinthite layers. These are iron-rich, humus-poor mixtures of clay, usually with some quartz or other diluents, which commonly occur as dark red mottles or reticulate patterns in a brownish matrix. Plinthite layers are soft unless exposed to repeated wetting and drying, in which case the plinthite hardens irreversibly into what is called ironstone.

Soil Taxonomy. The classification of soils, like that of plants, is an essential but at times frustrating undertaking. The soil series is the basic unit of classification and is comparable to the rank of species in biological classification. As with species, many soil series tend to grade into one another, making the classification difficult, if not arbitrary. The identification of soils is made complex in distinguishing between related series and requires expert judgement. Classification of southeastern soils has undergone recent changes, and series that were recognized a decade ago are now allied with other series or are separated into two or more series. Furthermore, only the soils associated with agricultural lands and commercial forests have been studied in depth. Those of coastal regions, swamps, floodplains, and bluffs are poorly known.

The U.S. Soils Classification System (Soil Survey Staff 1960, 1975) groups the many soil series into ten orders. Each order is subdivided into lesser categories of suborder, great group, and several finer divisions until the rank of series is reached. The soils of Florida were described by Carlisle and Pritchett (1971) and were mapped county by county by Kolb et al. (1974). From these two works and a few others cited later the soil series of the panhandle are listed below, each ranked according to order and great group. This list will grow as non-agricultural soils become better known. It will also be subject to change as soils taxonomists refine their system of classification.

Six of the ten orders of soils are known from the panhandle. These are Entisols, Inceptisols, Spodosols, Alfisols, Ultisols, and Histosols. Figure 38 gives a generalized distribution of the more widespread great groups in the panhandle.

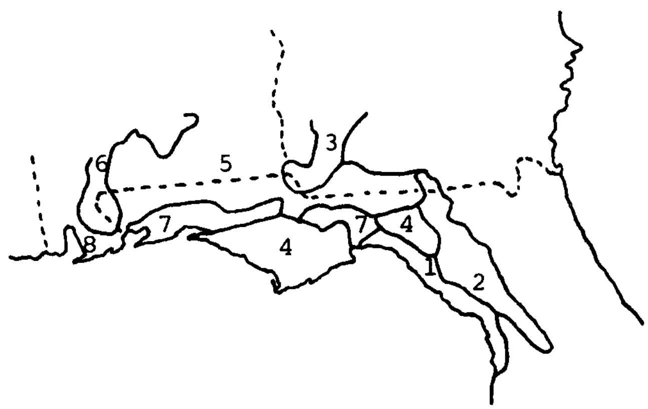
ENTISOLS. Soils lacking a profile or with only a weakly developed A_1 horizon.

Haplaquents (seasonally) wet, fine textured, gleyed or mottled.

Bibb

Psammaquents (seasonally) wet, coarse textured, gleyed or mottled.

Osier
Scranton



1. Ochraqualfs, Psammaquents
2. Quartzipsamments, Paleudults
3. Quartzipsamments, Umbraquults
4. Haplaquods, Quartzipsamments
5. Paleudults
6. Paleudults, Ochrquults, Fragiaquults
7. Paleudults, Quartzipsamments
8. Haplaquepts, Ochraquults, Paleudults, Hapludults

Figure 38. Predominant soil great groups. Redrawn from U.S. Forest Service (1969).

Quartzipsamments Quartz sands

Alaga
Chipley
Kershaw
Lakeland
Paola
St. Lucie

INCEPTISOLS. Moist or waterlogged soils with weak profiles which includes a dark, thick A_1 horizon and/or a weakly developed B_2 horizon.

Humaquepts Thick, acid dark surface horizon; gleyed or mottled subsoil; poorly drained.

Rutledge

Haplumbrepts Acid, brownish, freely drained, and rich in organic matter.

Fort Meade

SPODOSOLS. Strongly acid soils of low base supply with a well leached A_2 horizon and a B_2 horizon containing considerable accumulations of organic matter and/or iron and aluminum compounds.

Haplaquods Seasonally wet with little free iron oxides in subsoil

Leon
Lynn Haven
Mascotte
Olustee

Haplohumods Freely drained with a large accumulation of OM relative to iron in the spodic horizon

Rimini

ALFISOLS. Usually moist soils with gray to brown surface horizons, a medium to high base supply, and a subsurface accumulation of clay.

Albaqualfs Seasonally wet gleyed or mottled soils with a light colored top soil

Meggett

Hapludalfs Seasonally moist with thin or brownish subsoil

Oktibbeha

Paleudalfs Seasonally moist with thick, reddish subsoil

Susquehanna

ULTISOLS. Usually moist, strongly acid, highly weathered soils with a low base supply, and a thick B_2 horizon of clay accumulation

Ochraquults Seasonally wet, gleyed or mottled, either with a light-colored or a thin black surface horizon

Alapaha
Bladen
Coxville
Dunbar
Grady
Leaf
Lumbee
Lynchburg
Myatt
Pelham
Plummer
Rains

Umbraquults Seasonally wet, gleyed or mottled with a thick black surface horizon

Bayboro
Portsmouth

Fragiaquults Seasonally wet, gleyed or mottled with a dense brittle horizon of the subsoil

Pansey
Pantego

Paleaquults Seasonally wet, thick mottled gray subsoil

Surrency

Hapludults Freely drained, low in surface OM, with a thin clayey subsoil

Cahaba
Kalmia

Fragiudults Freely drained, low in surface OM, with a dense brittle horizon or the subsoil

Irvington
Savannah

Paleudults Freely drained, low in surface OM, with a thick clayey B horizon without appreciable weatherable minerals

Albany
Angie
Ardilla
Bonifay
Bowie
Carnegie
Cowarts
Dothan
Duplin
Esto
Eustis
Faceville
Fuquay
Goldsboro
Greenville
Leefield
Lucy
Magnolia
Marlboro
Norfolk
Orangeburg
Red Bay
Ruston
Sawyer
Stilson
Shubuta
Tifton
Troup
Wagram

HISTOSOLS. Organic soils, including peat and muck.

Medifibrists Fibers not destroyed by rubbing; botanic origin recognizable

Brighton

Medihemists Plant materials as much as 2/3rds decomposed and most fibers destroyed by rubbing

Dorovan

Medisaprists Predominantly decomposed plant materials

Pamlico
Ponzer

There has been no concerted effort to equate soil series with specific vegetation types; however, the descriptions of many soils series contain enough data on habitats and associated plant species to allow the following concordance:

Well drained Longleaf Pine Woods

ENTISOLS

Quartzipsamments

Chipley
Kershaw
Lakeland

ULTISOLS

Paleudults

Albany
Bonifay
Bowie
Eustis
Goldsboro
Lucy
Stilson
Tifton
Troup

Hapludults

Kalmia

Well drained Longleaf Pine Woods and Pine-Oak-Hickory Woods

ULTISOLS

Fragiudults

Savannah

Paleudults

Carnegie
Cowarts
Dothan
Norfolk
Orangeburg
Red Bay
Ruston

Pine-Oak-Hickory Woods

ALFISOLS

Hapludalfs

Oktibbeha

ULTISOLS

Paleudults

Faceville
Magnolia
Greenville
Sawyer

Longleaf Pine Flatwoods

INCEPTISOLS

Haplumbrepts

Fort Mead

SPODOSOLS

Haplaquods

Leon
Mascotte
Olustee

ALFISOLS

Albaqualfs

Meggett

ULTISOLS

Ochraquults

Alapaha
Coxville
Dunbar
Lynchburg
Pelham

Paleudults

Ardilla
Duplin
Esto
Leefield

Fragiudults

Irvington
Pansey

Savannahs and Bogs, including Boggy Pine Flatwoods

ULTISOLS

Ochraquults

Bladen (bogs with argillic subsoils, also known from acid swamps)
Plummer (bogs with sandy subsoils)

Acid Swamps (see Coultas and Calhoun (1975) and Coultas (1976))

ENTISOLS

Psammaquents

Ozier

INCEPTISOLS

Haplaquepts

Humaquepts

Rutledge (also in wet pine flatwoods)

UTISOLS

Ochraquults

Grady
Lumbee
Rains

Umbraquults

Bayboro
Portsmouth

Fragiaquults

Pantego

Paleaquults

Surrency

HISTOSOLS

Medisaprists

Ponzer

SPODOSOLS

Haplaquods

Sand Pine-Scrub

ENTISOLS

Quartzipsamments

Paola

Floodplain Swamps

ENTISOLS

Haplaquents

Bibb.

ALFISOLS

Paleudalfs

Susquehanna

Ponds

HISTOSOLS

Medifibrists

Brighton

Medihemists

Dorovan

Coastal Dunes and Beaches

ENTISOLS

Quartzipsamments

St. Lucie

SPODOSOLS

Haplohumods

Rimini

Salt Marshes (from Coultas 1969, 1970, and Coultas and Gross 1975, and Coultas, personal communication, 1978, the series not identified)

Juncus roemerianus Zone

ENTISOLS

Sulfaquents

Psammaquents

Hydraquent

SPODOSOLS

Haplaquods

Spartina alterniflora Zone

SPODOSOLS

Haplaquods

ALFISOLS

Natraqualfs

Distichlis spicata Zone

SPODOSOLS

Haplaquods

ALFISOLS

Ochraqualfs

Soil and Vegetation Type. The preceding concordance shows some correlations between soil and vegetation. It appears that the driest woods, represented by longleaf pine-turkey oak or by sand pine-scrub, are associated with Quartzipsamments and that the more important mesic longleaf pine and pine-oak-hickory woods are associated with Paleudults. Secondary pine-oak woods that occupy former agricultural lands in the Northern Highlands and Marianna Lowlands (Fig. 15) are also associated mainly with Paleudults. Another obvious correlation is between bog and savannah vegetation and Ochraquults.

More striking, though, are the dissimilarities between soil and vegetation. Longleaf pinelands are not confined to one or few series but are associated with five orders: Entisols, Inceptisols, Spodosols, Alfisols, and Ultisols. The longleaf pinelands are much more influenced by the frequency of fire than by edaphic (soils) factors. Acid swamps include the shallower titi and bay zones and the deeper cypress and blackgum zones. The Rutlege series is common to all of these zones as well as to the adjacent pine flatwoods. On the other hand, the other series associated with acid swamps belong to four orders: Entisols, Inceptisols, Histosols, and four great groups of Ultisols. Position of the water table and to a lesser extent, fire seem more important to the distribution of plants in acid swamps than do edaphic factors.

The lack of correlation between plant zonation in salt marshes and soil taxon is due to the fact that the salinity regimen is the overriding factor in vegetational zonation, followed by soil moisture. Salinity is under tidal control, and particular regimens of soil moisture are not specific to single soil series.

As the plant communities are described in later chapters it will become apparent that factors other than soils are most important in determining vegetational distribution. The frequency and intensity of fire is the most important factor and even influences the vegetation of hydric habitats. The seasonal position of the water table is also paramount. Since the water table is often near the surface in the panhandle, slight changes in topographic relief cause considerable changes in soil moisture. The vegetation responds to these moisture differences in terms of distinct and abrupt vertical zonations in nearly level topography. Salinity becomes an important determinant for coastal vegetation.

Edaphic factors play secondary roles in shaping the vegetation . The level of soil fertility, for example, may determine the growth rates and productivity but has little influence on determining species composition. The extremely low pH in some habitats may limit species composition, but the acidity was contributed by the plants and their detrital remains after the vegetation became established. The correlations that do exist between soil type and vegetation seem to be more the result of parallel development of both soil and vegetation under the control of fire and other forces, rather than the result of soil acting on the vegetation.

Soil Maps. Because of the lack of correlation between soils and vegetation and because of the distinctive vertical zonation of vegetation over nominal horizontal distances, it is nearly impossible to construct a map that shows both vegetation and soils. Maps by Kolb *et al.* (1974) and others consist of mapping units that include several, often diverse soil series. To add vegetation to such maps leads to confusion at best or simplification beyond utility at worst. This point is emphasized, because environmental planners have the propensity to combine soils and vegetation on a single map, and such a practice must be discouraged.

A generalized soil map of Florida was prepared by the Florida Agricultural Experiment Station (1962). More detailed soil maps are available for the following counties: Escambia (Walker et al. 1968), Washington (Huckle and Weeks 1965), Holmes (Sullivan et al. 1975), Gulf (Leighty et al. 1968), Gadsden (Thomas et al. 1959), Leon (Wilder et al. 1906), and Jefferson (Jones et al. 1907). Adjacent Grady and Thomas counties, Georgia, were mapped by Bennett (1900) and Benett and Mann (1909), respectively. The soils of the Osceola National Forest, which lies just east of our area, were mapped and described by Avers and Bracy (1975). Forest soils of the coastal plain were discussed by Pritchett and Crowe (1975).

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12. FIRE

Introduction. Nearly all plant communities in the panhandle are affected by fire, at least occasionally. The character of the vegetation at most sites tends to be shaped more by the frequency and intensity of fire than by any other environmental factor or combination thereof. An appreciation of the effects of fire on plants is prerequisite to the understanding of the regional vegetation.

In 1528 the Spanish explorer, Cabeza de Vaca, visited the panhandle and wrote (in Hodge and Lewis 1907), "Many of the standing trees were riven from top to bottom by bolts of lightning which fall in that country of frequent storms and tempests." It seems more perceptive than coincidental that this first written account of our region should comment on lightning---the source of ignition of natural fires. Baker (1973) tallied the incidence of lightning-struck trees at the Tall Timbers Research Station, which lies in Leon County between Lake Iamonia and the state line. His data conservatively suggest that one tree is struck per hectare every 18 years. Komarek (1966) demonstrated the relationship between thunderstorms spawned by cold fronts and lightning-set fires in the panhandle and elsewhere on the continent. He concluded that the number of thunderstorm days per year and thus the number of lightning-set fires are predictable, just as are other meteorological phenomena, such as temperature and precipitation.

Ignition and Spread. Ignition may occur at the moment a bolt strikes, or it may cause the punky core of a lightning-struck tree to smoulder for hours or days. Stoddard (1931) wrote, "We have personally witnessed the start of one 'flatwoods' fire that was set by lightning. In this case the punky top of a huge cypress growing on the edge of a lime 'sink' was ignited and burned throughout the accompanying shower and until the wiregrass below had dried out sufficiently in the ensuing sunshine to catch fire, when a typical 'grass fire' was started." Once ignited, fire can spread indefinitely in the flat to rolling topography, as long as there is fuel to burn. The fuel consists of vegetation, leaf litter, and other detritus. In dry, windy weather fires can burn through swamps, jump creeks, and continue burning unobstructed.

Man has restricted the area over which fires might spread by building roads and cultivating fields. On the other hand, intentional fires are ignited to keep the woods open and grassy for grazing by cattle, to promote the growth of pine trees, to maintain habitat for wildlife, and for other reasons. In recent decades most intentional fires have been set in the winter, rather than in the summer thunderstorm season. Since about the turn of the century the game plantations of northern Leon County have been burned annually after the hunting season in late February and March. Elsewhere in the panhandle the vast pine flatwoods and sandhills were ignited whenever the fuel was dry enough to burn, regardless of season. Cattlemen, who used these lands as open range, depended on the tender shoots of grasses that sprouted after fire as a prime source of forage for livestock. This practice of burning at all seasons dated to Indian times. After the fence law was passed in the 1940's, land managers switched to winter burning on nearly all lands.

Kinds of Fire. Fires are classified by various criteria. Those that consume the litter and undergrowth are called surface fires. Those that burn the overstory of a forest are called crown fires. Those that smoulder in dry peats are called _ground fires_. Wind-driven fires are called _head fires_. Fires that are ignited along a road, stream, or other break in the fuel and which burn into the wind are called _back fires_. Intentional fires for purposes of habitat management are called _prescribed fires_ by the U. S. Forest Service and _controlled fires_ locally by wildlife specialists on game plantations. Other fires are called _wild fires_ (Mobley _et al_ 1973).

Most prescribed fires are surface fires which are ignited so as to burn as head fires. The flames of head fires often leap erratically, sometimes singeing the crowns of smaller trees. The speed with which head fires move usually prevents sustained heat from damaging any but the most superficial plant tissues. Sometimes embers in the leeward shadow of a tree trunk linger, damaging the bark and causing a fire scar to form at the base of the tree.

Younger trees may be more severely damaged or killed. The most susceptible trees are those with thin, tight bark which conducts heat rapidly to the cambium. Once the cambium (innermost layer of bark) is heat-killed all the way around the trunk, the tree is effectively girdled and dies within a few weeks or months. Some pines are among the most fire-resistant trees in the panhandle. Their thick bark consists of many thin flakes between which are trapped layers of air. These layers serve to forestall heat transfer, just as dead air spaces do in commercial insulations.

Heat rises and thus temperatures are scarcely increased in the soil. Most shrubs and trees that are consumed by fire in winter will resprout from their root crowns, a process called _coppicing_. Perennial herbs likewise resprout from their rootstocks. The seeds of some herbs are known to be heat-scarified by fire, facilitating their germination, including annual species of Cassia (Martin et al. 1975). The seeds of most pines require mineral soil for successful germination. Mineral soil is often exposed when fire consumes the leaf litter.

Summer fires tend to kill many coppicing hardwoods that would survive annual winter burns indefinitely (Lotti 1956). Food reserves in winter are stored in the roots of these plants, but in summer the reserves are used in the actively growing shoots. Presumable several successive summer burns reduce the reserves to the point that sprouting is no longer possible and the roots die.

Back fires creep slowly against the wind. In contrast to head fires, the flames are low but high temperatures may persist longer at any given location. A back fire may be more damaging than a head fire because of the prolonged heat at one place. On the other hand, if the amount of fuel is low and its moisture content high, a back fire may be cool enough to spare saplings slash pines only a meter tall.

Crown fires may begin in at least two ways. First, they may ignite on sites containing massive accumulations of fuel. Frequent prescribed fires are usually intended to prevent such accumulations. Second, crown fires may occur when two separate head fires converge, causing severe turbulence which carries flames high into the canopy of a forest.

Crown fires burn into swamps after successive drought years. Stoddard (1969) said that during the droughts of the early 1930's that, "...many of the cypress and gum swamps burned through." Severe droughts occurred in 1892, 1910, 1918, 1927, 1934, 1941, and 1955 (Fig. 35) or about every 12 years. During these dry years the fire hazard was great in all habitats. The desiccated peats in swamps and dry lake bottoms have been known to ignite and smoulder for weeks.

Wildfires may be widespread and burn through swamps during brief but severe droughts. In July, 1977, a 2,400-acre fire burned uncontrolled in San Pedro Bay near Madison. Other wildfires occurred in Dixie and Taylor counties and in the western Apalachicola National Forest. An early summer drought was responsible, as is evidenced from monthly rainfall records logged by the weather bureau in Tallahassee:

	1977 Rainfall	Average Rainfall
January	6.4 inches	4.0
February	3.1	4.7
March	6.1	5.0
April	2.7	3.9
May	3.4	4.1
June	2.1	6.6
July	3.2	8.0

Interactions between fire and vegetation. The effect of fire on a plant community depends on many factors, including wind speed and direction, ambient temperature and humidity, moisture content of the fuel, the combustibility of the fuel, and the changes in temperature, moisture, and wind as a fire progresses. As a result, no two fires behave exactly alike. Even the most intense fires will not necessarily burn evenly, and small islands of vegetation may be spared.

The unpredictability of the effect of fire was illustrated in a magnolia-beech hammock in Georgia just above the Leon County line (Blaisdell *et al*. 1973). Magnolia-beech hammocks seldom burn, and when they do the loss of trees may be substantial. A wildfire ignited after a long spring drought and was pushed by a strong wind. Conditions were seemingly ideal for a destructive fire. The fire swept through the undergrowth so quickly that the heat was not sustained long enough to kill any of the larger trees, and only a few were fire-scarred.

Foresters agree that grasses, particularly wiregrass (Aristida stricta) with a "needledrape" of pine straw, carries a sustained, evenly burning fire better than any other kind of fuel. Wiregrass may even burn in a light rain. Grasses in general burn best following a wet growing season that promotes copious growth. Sparser growth in dry years may cause uneven or poorly spreading fires. The foliage and litter of most broad-leaved hardwoods, such as oaks, ignite with difficulty and burn poorly, except when very dry on a hot, windy day with low humidity. Some woody species, such as wax-myrtle, are highly combustible, because of their high content of wax or essential oils.

Low nitrogen levels in sandy soils cause plants to produce an excess of fibrous (sclerenchymatous) tissues at the expense of green (chlorenchymatous) tissues because of a high C:N ratio in the meristems. This effect can be appreciated by observing the small crowns of tall pines growing on sterile soils. It can also be noted by observing microscopically a cross section of a leaf of wiregrass. Relatively few cells contain chlorophyll and most cells are fibrous (Wells and Shunk 1931). It is the fibrous tissues that are especially flamable. As a result, the likelihood of fire is enhanced in habitats with sterile soils.

These sterile soils also prevent the establishment of many relatively inflamable shrubs and trees and retard to growth of others. If the soils were more fertile, these woody plants would grow rapidly and would replace the more flammable grasses, particularly during any particluarly prolonged fire-free periods. Once the grasses were eliminated, the flammability of the habitat would be reduced and concommitently the frequency of fire as well.

In habitats which commonly experience surface fires there is a verdent flush of new growth following each fire. This copious growth occurs after annual fires as well as periodic fires. The rapid greening of the habitat begins within a few days after the next rain, at least during warm weather. It is generally assumed that the ash from the fire becomes a soluble fertilizer upon being leached into the soil, stimulating growth. Much of the new growth is from herbaceous perennials which appear in dense profusion and bloom vigorously for a year or two following fire.

If fire is infrequent, the coarser grasses, including wiregrass, may suppress many of these herbs. Coppicing shrubs and trees may also suppress the grasses in time. If the growth of woody plants continues, most herbs and grasses survive indefinitely as dormant rootstocks. Only a few scattered individuals produce aerial shoots during any given year. After the next fire the cycle starts anew with another copious flush of herbaceous growth. This growth is from rootstocks rather than from seedlings, except for the very few species of annuals in these habitats.

Dormant plants of many herbaceous species may be released by soil disturbance as well as by fire. The herbaceous vegetation of a recently tilled site may mimic that of a burned site, as long as soil moisture is sufficient to allow the surviving plants to reestablish their root systems. This observation suggests that light, rather than increased nutrient levels from ash, stimulates herbaceous growth. It would seem logical to assume that the ash would increase the growth rate of herbaceous plants released from competition by fires.

Fire and Soil. The effect of burning on properties of the soil has been researched and debated extensively. Ralston and Hatchell (1971) reviewed this subject and cautioned that most any position could be documented by the reports of reputable researchers. They emphasized that valid evaluations must include measurements of all soils factors. They cited Australian studies that showed that temperatures of 200°C for 16 hours had no effects on the organic matter of soils. Further, the properties of the clay minerals were unaffected until temperatures reached 550°C.

Ralston and Hatchell (1971) cited studies in southeastern pinelands that showed that temperatures of surface fires are much lower. One investigation showed that few fires in longleaf pinelands generated temperatures above 52°C for more than 15 minutes at a depth of 3-6 mm. A maximum of 66°C was recorded at a depth of 25 mm.

A number of studies in the southeastern coastal plain suggest that fire has a net beneficial effect on soil fertility. Heyward and Barnette (1934) studied 18 longleaf pinelands from South Carolina to Louisiana. They reported that total nitrogen, organic matter, replaceable calcium, and pH were significantly higher in soils after fire than in adjacent sites which had not been burned for at least ten years.

Greene (1935) compared annually burned plots with plots that were unburned for 7-9 years in longleaf pinelands in southern Mississippi on relatively fertile soils of the Orangeburg, Norfolk, Ruston, and Kalmia series. Soils in annually burned plots had about as much as, or up to 1.6 times more organic matter than in unburned plots. The nitrogen content of the soil was consistently higher in the burned plots in January but was higher in some of the unburned plots in April. The crude protein and ash contents of grasses were both higher in burned plots than in unburned plots. The biomass of grasses and the density of legumes in burned plots was more than double that in unburned plots. Soil bacteria counts were higher in the burned plots, and soil moisture was about the same in burned and unburned plots.

Jorgensen and Hodges (1971) made counts of bacteria, fungi, and actinomycetes in burned and unburned plots in South Carolina. There were no significant differences between unburned plots and those plots burned at various frequencies, including annually, in the top 2.5 cm of the soil or deeper. Bacteria and actinomycetes were reduced significantly only in the annually burned plot in the duff layer. Their populations recovered rapidly in response to ash after fire.

Wells (1971) reported 20 years of observations on the effect of burning on a poorly drained, fine sandy loam soil in a loblolly pine forest on the coastal plain of South Carolina. Treatment plots were: no burn, periodic winter burn, periodic summer burn, annual winter burn, and annual summer burn. Periodic burns were at 5 year intervals. The results were as follows.

Charred leaves and branches remained on the soil surface after fire, regardless of treatment. About half as much duff and litter remained on annual summer-burned plots as on annual winter-burned plots. A 30% increase in organic matter was recorded in the burned plots over the unburned plots in the upper 5 cm of soil. Most of this accumulation occurred during the first 10 years.

Nitrogen content was correlated with organic matter content. Nitrogen decreased after fire in the duff but increased in the upper 5 cm of the mineral soil as the organic matter accumulated after fires. In plots subjected to periodic winter-burns the nitrogen loss in the duff equaled the nitrogen gain in the upper mineral soil. In an annually burned plot the nitrogen content of the soil increased by 900 lbs/acre during the second ten year period. Especially high soil moisture in this plot may have stimulated nitrogen-fixation by anaerobes.

The amount of phosphorus in the upper 10 cm of the soil was slightly but significantly higher in the annually winter-burned plots than in other plots. Otherwise, phosphorous levels were unaffected by the various treatments. Calcium and magnesium increased significantly in the burned plots in the upper 5 cm of soil, but potassium was unaffected. The pH increased slightly in burned plots because of the alkaline nature of the ash and the combustion of the acid-forming duff.

Wells (1971) also reported the results of experiments, in which loblolly pine seedlings were grown in pots containing soil from the various treatment plots. After a half year the dry weights and nutrient contents of the seedlings were determined. The dry weights were not significantly different regardless of whether or not the soils came from burned or unburned plots. Tissue analysis, though, revealed some differences in nutrient content.

The pines took up 16-40% less nitrogen in soil from the annually summer-burned plots than from unburned and periodically winter-burned plots. Wells suggested that the nitrogen in the upper 5 cm of annually summer-burned soils is relatively unavailable for absorbtion by roots. Some pots were covered with forest litter and others with glass wool. Those covered with litter had much better growth.

Phosphorus and potassium uptake was higher in soils from burned plots than from unburned plots. This result was obtained only when the soil was taken from the plot and placed in the pot as an undisturbed core, rather than being mixed. The uptake of nitrogen was positively correlated with the uptake of phosphorus. The uptake of calcium, magnesium, zinc, and manganese was the same, regardless of the plot from which the soil came.

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13. SOME BASIC VEGETATION TYPES

The next four chapters, which discuss succession and climax, paleoecology, and primeval vegetation, require some familiarity with the more important plant communities of the panhandle. This chapter gives resumes of six vegetation types.

Community Delimitation. The delimitation of plant communities in the panhandle is challenging, given the diverse vegetational panorama and the subtle distinctions between habitats. Some plant communities are distinct from each other in some habitats but linked by transitional vegetation in others. Certain general vegetation types regularly consist of a mosaic of well defined zones, such as those surrounding lakes or comprising tidal marshes. Should these zones be classified as distinct plant communities, or should they be considered merely as subdivisions of a polytypic plant community?

Several alternative systems of classification could be proposed, each with justification. As stated in the introduction, this report contains a conservative classification to emphasize vegetational similarities.

Regardless of the system of classification selected, it is possible to define the plant communities or their major subdivisions by physiognomy, reproductive strategy for community perpetuation, and the strategy for the procurement of mineral nutrients. These criteria are largely a function of two or three additional criteria: the moisture regime, and in coastal habitats the salinity regime. Lesser categories could be proposed strictly on the basis of floristic composition.

The six vegetation types described below demonstrate to a large extent the gamut of expression of each of these criteria as seen in the vegetation of the panhandle. These descriptions also emphasize that the modes of expression of certain criteria are vital in the characterization of some communities but inconsequential in others.

Reproductive strategy involves the concept of succession. Succession is defined as community development through species replacement or changes in species abundance, assuming constant physical conditions of climate, hydrology, fire, etc., except for those physical conditions directly modified by the vegetation.

Some aspects of the following descriptions are based on inference for lack of hard data. The extent and quality of the evidence will be discussed in the detailed community descriptions given in subsequent chapters. An index to common and scientific names is given on pages ix-xii.

Mesic Hardwood Hammock. This community is characterized by several or many species of trees, mostly deciduous hardwoods. The undergrowth consists of tree saplings. Shrubs and herbs are relatively unimportant. Soils are moist but rarely saturated. Fire is rare and potentially destructive. Nutrients are cycled by the decomposition of organic matter by organisms of decay. The reproductive strategy is often microsuccessional. Individual trees die from lightning or other causes, creating gaps in the canopy. Light reaches the forest floor in an opening, stimulating the growth of many seedlings and saplings of the various tree species. Competition reduces these to a few individuals after a few decades and later to a single tree which replaces the one that originally occupied that site. The mature forest is not even-aged but rather a mosaic of microsuccessional units of various ages, a process termed gap-phase succession.

PREDOMINANT CHARACTERISTICS. Community perpetuation by succession as it is traditionally defined, often in microsuccessional units.

Bottomland Hardwood Forest. This forest occurs on floodplains. It is similar to the mesic hardwood forest, except that the soil is seasonally flooded. Leaf litter is swept away before it decomposes. Nutrients are imported as alluvial deposition of organic and mineral matter or as solutes in river water.

PREDOMINANT CHARACTERISTICS: Community perpetuation by succession as it is traditionally defined, and the import of nutrients.

Longleaf Pinelands. This community complex is characterized by a dense, prairie-like turf of many flammable herbs and low shrubs. In mature stands the pines are scattered and ecologically less important than the undergrowth. In the ecologically and floristically related bogs and savannahs the pines and other trees are sparse or absent, thereby accentuating the importance and independence of the undergrowth. The soil is wet to dry but never saturated for prolonged periods. Surface fires occur nearly annually. Nutrient cycling is accomplished primarily by the reduction of the undergrowth to ash by fire. Nearly all species are perennials that resprout after fire from their undamaged rootstocks. There are no mechanisms in the natural environment that kill these perennials, at least in substantial numbers. Seedlings of other species either succumb to the competition of these well established perennials or to fire. The longleaf pine is an exception and is the only tree of the panhandle capable of surviving fire as a seedling. The reproductive strategy of the community is the indefinite persistence of each plant of the undergrowth by vegetative means. Plants comprising the undergrowth presumably germinated from seeds centuries or millenia ago, following a major change in environmental conditions that opened the habitat for large-scale colonization.

PREDOMINANT CHARACTERISTICS: Frequent surface fires and community perpetuation based on the indefinite persistence of colonizing plants.

Scrub. The scrub communities consist of dense growths of shrubs and small trees which mostly have broad, persistent, leathery leaves. Collectively this woody growth is called scrub. Sand pine or slash pine may form an overstory, or taller trees may be absent. Herbaceous plants are virtually absent, owing to the density and competition of the scrub. The soil is generally dry or at least well drained. Fire is irregular and occurs every few decades under exceptionally favorable conditions for its ignition and spread. Otherwise the scrub is difficult to ignite and carries a fire poorly. The plants of the scrub coppice immediately after fire, reestablishing the community without intermediate successional stages. Nutrient cycling is from ash after fire, from the decomposition of organic matter by organisms of decay at other times, and from the impaction of salt spray in coastal habitats. The reproductive strategy of the scrub is the indefinite persistence of each plant by vegetative means, as in the longleaf pinelands. Sand pine and slash pine, if present, seed-in after fire. Scrubs occupy coastal uplands primarily. Acid swamps of bay or titi are the ecological equivalents of scrub in poorly drained sites, both coastal and inland. The main difference is that acid peats accumulate in these swamps.

PREDOMINANT CHARACTERISTICS: Infrequent crown fires and community perpetuation based on the indefinite persistence of colonizing plants.

Palustrine Marsh. The predominant plants are emergent, largely perennial herbs, sometimes with shrubs intermixed. These marshes are flooded with shallow water in wet seasons but may become completely dry at other times. Fire may be frequent or absent but has little effect on the plants which resprout rapidly from their often massive rootstocks after fire. Nutrients are obtained as solutes in the water, as ash after fire, or through mineral cycling by organisms of decay. Tree saplings that invade a marsh are killed either by desiccation during dry periods or by fire or by prolonged flooding. Sites where water level fluctuation is less severe often contain trees of pond-cypress interspersed in the marsh. (Sites with even less fluctuation contain swamps of pond-cypress and/or blackgum.) The emergent marsh plants survive drought and other inclemencies either as rootstocks or as seeds, assuring the perpetuation of the community.

PREDOMINANT CHARACTERISTIC: Fluctuating water levels.

Needlerush Salt Marsh. Needlerush is a rhizomatous herb that grows in very dense and often pure stands on coastal flats. It germinates on sand but forms its own peat as its older roots and rhizomes are sloughed off. Needlerush is shallowly inundated several times a month by particularly high tides. The tidal flow tends to slide over the peat rather than to penetrate it, keeping the soil moist but aerated. Fire may be frequent or absent. Needlerush resprouts immediately after fire from its rhizomes, restoring the stand. Salinity is kept relatively constant by the frequent tidal inundations. High salinities common to some tidal marsh zones are not attained. Nutrients are obtained as solutes from sea water, as salt spray that is impacted on the plant, as ash after fire, and from the decay of organic matter by organisms of decay. Once estab-

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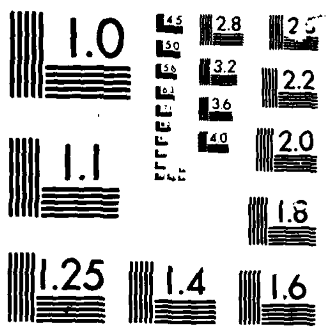

MICROCOPY CHART

lished, needlerush persists indefinitely by vegetative propagation.

PREDOMINANT CHARACTERISTICS: Moderate salinity, moist but aerated soil, and community perpetuation based on the indefinite persistence of colonizing plants.

14. SUCCESSION AND CLIMAX

Succession. Theories of succession and climax were the philosophical focal points of most ecological investigations during the first half of this century (McCormick 1968, Drury and Nisbet 1973). Succession begins with the invasion of colonizing or pioneering species on a disturbed or open site. Succession is termed primary if it begins on a site virtually devoid of organic matter, especially living plants, seeds, spores, and other propagules. Such sites include land that has just emerged from the sea, recent alluvial and aeolian deposits, and newly formed lakes and other water bodies. Succession is termed secondary if living vegetation, propagules, or even a soil microflora is present.

Colonizing plants generally are able to survive the rigors of open habitats, such as widely variable diurnal temperatures and moisture regimes, full exposure to sun and wind, and poorly differentiated soils. As a class, they are often described as being competition-intolerant, small in size, short-lived, and capable of producing seeds or other propagules in abundance. (This description has many exceptions.) As these plants cast shade and contribute humus, the extreme habitat conditions are ameliorated to the point that plants of other species are able to germinate successfully and survive. These plants are generally more competitive and soon replace the initial colonizers. This second group of plants further reacts with the environment to the point that other, even more competitive species become established. The process continues until a climax community develops, whose component plants are able to reproduce under their own cover and maintain relatively stable species-populations indefinitely.

The driving force behind succession is often considered to be the reaction of the plant on the environment, causing the habitat to be modified to the point that previously excluded plants of other species are able to invade. The concept is called the reaction theory.

For terrestrial habitats succession is often described as beginning with annual herbs which are replaced by perennial herbs, often grasses. These are replaced by shrubs, then trees of open areas and finally trees of deep forest conditions. The entire process from the initial invasion by colonizers until the attainment of the climax community is called a sere. In the panhandle it takes at least 100 years for a sere to develop on fallow agricultural land to the point that a climax species (magnolia, beech) begin to assume dominance (Kurz 1944). Since the life-span of forest dominants is one or several centuries, and since it may take two or several generations of dominants before ultimate climax stability is reached, a sere may require several centuries or even a millenium for its final development. Authors generally talk of a forest as climax, though, once a tall overstory of dense trees is attained. It is assumed that further development will result in minor shifts in dominance but not in floristic composition or physiognomy. Such an assumption strains the climax concept but may be justified for utilitarian needs, such as land planning.

Succession is presented in many biology textbooks as a series of community replacements until the climax community is developed. Egler (1954) called this process of community replacement relay floristics (Fig. 39A). Other authors described succession as a largely non-synchronous invasion and development of individual species-populations (Fig. 39B)

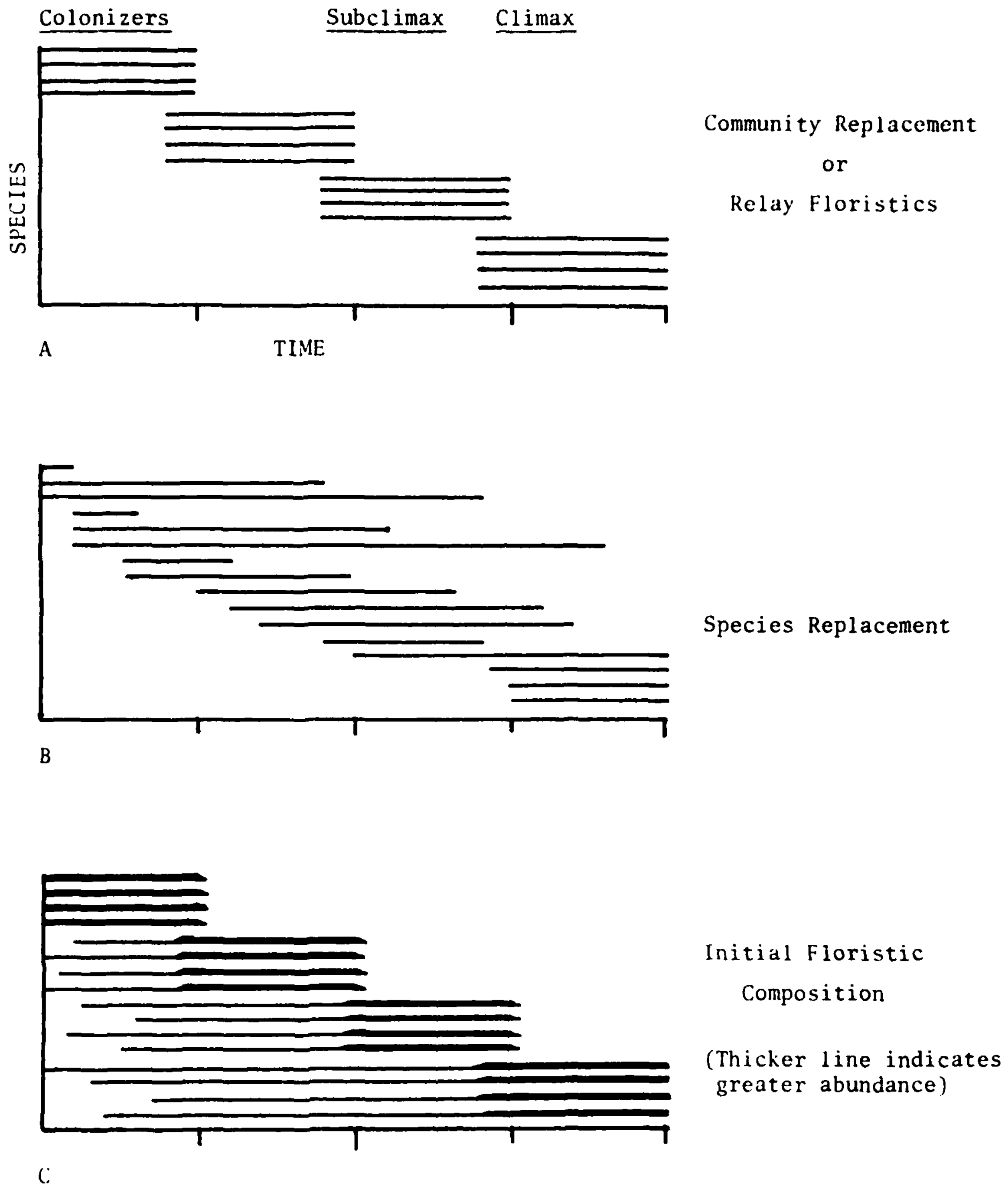

Figure 39. Models of succession and climax, assuming a stable physical environment.

Climax. Early climax theorists proposed that any given region of uniform climate, as defined by regimes of precipitation and temperature, could support only a single mesic climax community. This monoclimax concept assumes that all other communities are seral. They will eventually converge towards the monoclimax through the reaction process and through physiographic processes such as erosion and deposition. Potentially all sites are capable of supporting the monoclimax vegetation, even though relatively stable subclimax communities persist because of edaphic (soils) differences, fire, or other non-climatic and non-physiographic reasons.

Seres which begin with dry, xeric habitats and end in the mesic monoclimax community are called xeroseres. The habitat becomes increasingly mesophytic as the vegetation contributes increasing amounts of shade and moisture-retaining organic matter. Seres that begin as aquatic communities in lakes and end in the mesic monoclimax community are called hydroseres. The lakes gradually fill with sediments. The submerged aquatic plant community is replaced by an emergent marsh community. With further sedimentation the marsh yields to a swamp. Continued development leads to the mesic monoclimax community.

The monoclimax theory severely strains certain realities. For example, in the time it takes for a sere to develop to the climax stage, the climate will have changed. Further, the monoclimax theory ignores edaphic, hydrological, and pyric (fire) factors, which may help perpetuate highly stable communities. In spite of these shortcomings, the monoclimax theory is incorporated in many biology textbooks today, at least implicitly.

Nonetheless, many ecologists adhere to a polyclimax theory, which allows for different climax communities within the same climatic region, depending on edaphic, hydrologic, and other differences. The climax concept was extended by the continuum theory, which allows for gradual shifts in dominance and species composition from one region to another in response to gradual changes in climate between regions.

Initial Floristic Composition. Egler (1954) proposed a theory of initial floristic composition, which was a radical departure from traditional concepts of succession and climax. He observed that the initial colonizing species in fallow agricultural fields persist at least in part into later seral stages and sometimes into the climax (Fig. 39C). Egler felt that any sere was governed jointly by two vegetational processes, initial floristic composition and relay floristics. The relative importance of these two processes varies with local circumstances.

Egler's theory may explain the variation between mature stands of vegetation which occur in similar habitats within the same climatic region. The initial colonizing species may vary considerably from place to place within a region because of local variations in seed source. As a result, seral development and the composition of the climax community may vary between neighboring stands. Even if none of the colonizing species survives until the climax is reached, they may influence the ultimate composition of the climax by their competitive interactions with other species.

Egler's paper on "initial floristic composition" was not widely noted, undoubtedly because it contradicted 50 years of acceptance of the "initial philosophical tradition" of relay floristics. Further, the paper was published at a time when most ecologists were losing interest in climax theory and were directing their attention to such topics as ecosystem dynamics and population ecology.

Descriptive community ecology and concomitant climax theorizing has been largely abandonded by academic ecologists and is now claimed by the environmental specialists. Descriptive studies are to be found in environmental impact statements and in planning documents. The traditional notions of succession and climax are expressed or implied in these reports. If traditional concepts are not applicable, and if more radical proposals such as initial floristic composition are more appropriate for interpreting vegetational processes, then the predictions of environmental impacts with regard to proposed land uses or resource management may be in error.

Climax Vegetation in the Panhandle. Harper (1914), who was an early proponent of the polyclimax theory, applied that theory in classifying the vegetation of the panhandle. Many subsequent authors (Gano 1917, Kurz 1944, Hubbell et al. 1956, Quarterman and Keever 1962, Kuchler 1964, Monk 1968, Veno 1976, Delcourt and Delcourt 1977) were impressed by the tendency of hardwoods to invade pinelands following fire suppression. They also observed that pines represented a seral stage in the development of a hardwood climax on former agricultural fields that were lain fallow. These authors adhered to the notion that a mixed hardwood forest either represented the monoclimax community for our region or was of central importance in a polyclimax conceptualization. They considered fire to be either a disturbance or a retarding influence on seral development. Fire-regulated communities were considered to be subclimax.

The only argument among these authors was whether or not the climax hardwood community consisted of magnolia-beech (-holly) or consisted of 5-9 dominant species at any given site. Those supporting the latter, mixed hardwood concept claimed that the dominant species varied geographically according to climatic or other environmental gradients. This view superimposes a continuum concept on a generalized climax community of mesophytic hardwoods.

The agreement on some form of a hardwood climax for the southeastern coastal plain is so universal that Quarterman and Keever (1962) said, "No serious ecologist entertains the concept of a pine climax in the Coastal Plain." Nonetheless, Chapman (1932) had raised the possibility that the longleaf pinelands constituted a climax community. If climax is based on climate, and lightning is considered a climatic feature then lightning-set fires should be considered equaly with precipitation and temperature in defining climate and climax. Lightning can be quantified by such measures as the number of thunderstorm days per year, just as temperature is quantified by degrees and precipitation by inches of rainfall.

Not only is the longleaf pine community stable, but also it once covered at least two-thirds of the panhandle (Williams 1827). On the other hand, hardwood communities are confined to a very small portion of the panhandle, mainly the bluffs and ravines associated with the larger rivers, to some of the Gulf hammock lands, and to sites where fire has been restricted by man. It seems incongruous that the climax community occupies such a small portion of the natural vegetation. If the longleaf pinelands are considered as a climax community, then other stable, fire-regulated communities should also be deemed as climaxes. By including other stable communities that are shaped by particular hydrological conditions or by salinity regimes along the coast, we return to a polyclimax concent of Harper (1914) which allows any stable vegetation to be considered a climax community.

In recent years it has become customary to equate the climax community with steady-state community, where community production equals community respiration. Seral communities generally have excessive production. It is difficult to determine whether or not a forest represents a steady-state. If physiognomic stability and floristic continuity are accepted as indicators of a steady-state, then it can be argued that many communities of the panhandle, including longleaf pinelands, are in a steady-state condition. If this argument is accepted, then a polyclimax classification as espoused by Harper (1914) is a compatible concept.

Potential Natural Vegetation. The proponents of the mesophytic hardwood climax in the panhandle often express or imply a climax of potential natural vegetation, rather than primeval vegetation. Kuchler (1964) defined the potential vegetation as,

> "...the vegetation that would exist today if man were removed from the scene and if the resulting plant succession were telescoped into a single moment. The latter point eliminates the effects of future climatic fluctuations while the effects of man's earlier activities are permitted to stand."

The potential natural climax avoids the need of determining the primeval vegetation. In spite of the lament by Quarterman and Keever (1962) to the contrary, it is quite possible to determine the primeval vegetation from early records and from the study of near-virgin stands.

The concept of potential vegetation raises the difficult problem of predicting a climax that has yet to develop fully. Mature vegetation that bears the impact of selective cutting, grazing, or the introduction of exotic species may seem like it is in the climax state but may undergo considerable change if the overstory trees are allowed to develop for another generation or two. The description of primeval vegetation may be easier to determine than the prediction of a climax stemming from seral vegetation modified by man. If the first mature stage of near-climax vegetation is all that is required, then the potential vegetation is easily predictable. Such a requirement may satisfy the needs of land managers in most instances. For more accurate or more theoretical considerations, the determination of potential vegetation becomes suppositional and subjected to "if---then" thinking.

A well known example of "if---then" thinking is the successional diagram proposed by Monk (1968: 444). If certain communities are "released from fire" or if others somehow attain "improved drainage", then they will resume their previously arrested seral development to a climax of mixed hardwoods. The arrest of seral development involves natural conditions which can be changed only with man's intervention. It would be just as logical to extend Monk's diagram with, "if man flooded the mixed hardwood forest, then it would develop into a swamp." Monk's diagram is instructive for purposes of planning habitat manipulation, but it obscures the realities of natural vegetational processes.

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15. PALEOECOLOGY

Climax considerations for the southeastern coastal plain are dependent upon a knowledge of past floras and environments. Fortunately, paleoecological data have accumulated to the point that some important trends are becoming apparent.

Evidences. Evidences for paleoecology include microfossils (pollen and spores), macrofossils (larger plant remains), C^{14} dating, stratigraphic position of fossils, climatic assumptions (based on tropical vs. northern taxa in fossil deposits), and habitat assumptions (based on properties of the geological formations bearing fossils). Pollen and spores contain thick walls that resist decay, often for millenia, especially in anaerobic environments. They are usually identifiable to family, often to genus, and occasionally to species by their size, shape, and external ornamentation. It is nearly impossible to differentiate the species of such important genera as *Quercus* (oaks) and *Pinus* (pines) from pollen alone, but fossilized wood and leaves may allow species determinations. Grasses are difficult to identify beyond the level of family. The study of fossil pollen is called palynology.

The radiocarbon dating method has several inherent sources of inaccuracy, and any C^{14} dates must be considered as approximations. The margin of error increases in older deposits, and the method cannot be used on materials more than 30 - 35,000 years old. Nonetheless, C^{14} dating is a powerful method, particularly when used in conjunction with other evidences.

Stratigraphic position is also important, particularly where fossils are deposited with peat or mineral sediments, such as bogs or lake bottoms. The deeper the deposit, the older the fossils in a stratigraphic sequence. Habitat assumptions can be made in some detail. A peat deposit connotes a wet environment where erosion from waves or currents was minimal. Fragments of peat are often identifiable to genus or species. As a result, the habitat in which a fibrous peat was formed can be identified as tidal marsh, fresh water marsh, or swamp. Animal remains, including microscopic fossils, are often sufficient to distinguish a marine deposit from a fresh water deposit. Former dunes of aeolian origin can be distinguished from water-deposited features by mechanical analysis and by the degree of abrasion of the sand grains.

A pitfall of paleoecological analysis is determining with accuracy whether or not a fossil was deposited in situ or was transported. Preserved or fossilized wood may represent trees that floated great distances down rivers into estuaries. Wind-borne pollen may have carried hundreds of miles to the point of deposition. Another pitfall is the bias caused by the probability that plants of hydric habitats are more likely to be fossilized than those of xeric habitats. As a result, the only fossilized remains of a semi-desert environment might be those hydric plants preserved in the sediments of widely scattered ponds. Another bias is introduced by the fact that pollen that is wind-dispersed is proportionately better represented in profiles than pollen that is animal-dispersed. These pitfalls can be avoided by the synthesis of several kinds of evidences that are obtained for a given deposit.

Tertiary Floras. The panhandle had not begun to emerge from the sea until the Miocene roughly 25 million years ago, but the present flora of the southeastern coastal plain was already represented in Eocene deposits that were twice that old. Such important genera as Quercus, Fagus, Carya, Ulmus, Tilia, and Alnus were known from the Arcto-Tertiary Geoflora of Alabama. These elements were thought to have developed into the Eastern Deciduous Forest Formation essentially as it is presently constituted in the Southeast during the Miocene. The early Teritary climates were warmer than at present. Tropical coastal strand vegetation, known as the Wilcox flora, was well preserved in the Gulf states in the Eocene. Tropical genera such as Coccoloba, Ficus, and Canna, were mixed with warm-temperate genera such as Magnolia, Nyssa, and Liquidambar (Graham 1964).

Quaternary Floras. The Tertiary ended with the Pliocene epoch, at which time the climate was becoming cooler. The Quaternary began with the Pleistocene epoch and its great fluctuations in climate, sea level, and water table. There is evidence of plant and animal migrations and extinctions in response to these relatively rapidly changing conditions. Some of the manifestations of these changes are expressed in the present vegetation in terms of species with tropical affinities growing intermixed with those of northern affinity, of narrowly endemic species which presumably were once much wider ranging, and of other species with unusual distributions.

Mitchell (1963) described the flora of the Marianna Lowlands and said,

"Northern visitors are understandably surprised when a walk along a boulder-studded nature trail reveals columbine, needle palms,

> spicebush, bloodroot, southern Magnolia, false rue anemone, Spanish moss wood nettles, atamasco lilies, and May apples occurring together as if latitudinal zones were nonexistent."

He also said, "...both northern and southern disjuncts occur within an area of less than 1,200 acres."

Pleistocene fossils of spruce and sometimes other typically boreal trees were discovered in deposits in east-central Texas (Graham and Heimsch, 1960, and papers cited therein by Potzger and Tharp), Louisiana (Brown 1938, P. Delcourt and Delcourt 1977), and from southern Georgia to mid-Peninsular Florida (Watts 1969, 1971). These species presently grow in the northern Great Lakes region and New England and extend southwards at increasingly higher elevations in the Appalachians.

Kurz (1928) listed 23 species which reached their southern limits of distribution near Tallahassee in the Tallahassee Hills. Kurz (1933) listed several species of widespread distribution farther north that were disjunct in the Tallahassee Hills, the Apalachicola River Bluffs, and the Marianna Lowlands. Thorne (1949) showed that many northern species extended from the interior uplands into southwest Georgia (and the panhandle) along the Chattahoochee River Valley. Mitchell (1963) said that several species previously thought to be northern disjuncts in the panhandle had continuous distributions into the mountains along the Chattahoochee-Apalachicola river system. Delcourt and Delcourt (1975) described a similar distribution along the Mississippi River into the Tunica Hills of Louisiana.

Some species have disjunct distributions within the coastal plain. Their present distributions may represent the remnants of continuous and widespread distributions in the past. An example is Nolina atopocarpa which grows in the lower Apalachicola River region and along the east coast of peninsular Florida. Other examples are Linum westii and Rhododendron chapmanii, both of which grow near the Apalachicola River and in northeastern peninsular Florida (Clewell 1977).

Other species are narrowly endemic within the panhandle or some of them extending a short distance into adjacent Alabama and Georgia. Nine are endemic within portions of the Apalachicola River watershed. Torreya taxifolia and Taxus floridana are essentially limited to the bluffs of the Apalachicola River. Croomia pauciflora occurs on these bluffs and in similar habitats in southern Georgia and Alabama. Several species are endemic to the savannahs, bogs, and cypress strands of the lower Apalachicola River region, including Harperocallis flava (a monotypic genus discovered by McDaniel 1968), Macbridea alba, Cuphea aspera, Euphorbia telephoides, Scutellaria floridana, Oxypolis greenmanii, and Verbesina chapmanii. The habitats of these endemics commonly occur throughout much of the panhandle and beyond. The restriction of these species to a single locality is remarkable. Further comments on endemics were written by Gray (1875), Chapman (1885), Harper (1919, 1949), Kurz (1927, 1933), Neill (1957), James (1961), and Clewell (1971).

Neill (1957) noted how the ranges of various species of both plants and animals stop abruptly at particular rivers, even though the habitats continue on both sides of a river. An outstanding example is the Atlantic white-cedar (Chamaecyparis thyoides), which is a dominant species in the western panhandle but has yet to be discovered in the panhandle east of the Ochlockonee River. This species is also abundant in the pine barrens of New Jersey, suggesting that it is not restricted by narrow, environmental tolerances.* It reproduces in abundance by seed, and there seems to be no reason for its absence in the eastern panhandle. Many other species could be cited which show similarly restricted distributions.

Neill (1957) suggested that these distributions were related to the fact that several river systems were once marine embayments, among them the Escambia-Blackwater-Yellow river system, the Choctawhatchee-Alaqua system, and the Apalachicola River and its tributaries. Neill said,

> "I suggest that the barrier is not the present river but the broad saltwater channel that occupied its position during long periods of the Pleistocene."

Recent geological data on sea levels might require that these channels be dated into the Pliocene.

Palynological Studies. The most significant information on late Quaternary vegetation in our general region was obtained by Watts. He examined the pollen in the several strata of peats which were deposited as bottom sediments in three lakes. The younger strata were C^{14} - dated. The lakes were Mud Lake, which is in the Big Scrub region near Ocala, Marion County, north-central peninsular Florida (Watts 1969); Lake Louise in Lowndes County, Georgia, which is near Valdosta and the western edge of the Okefenokee Swamp (70 miles e.n.e. of Tallahassee); and Scott Lake near Lakeland, Polk County, central-peninsular Florida east of Tampa (Watts 1971). Table 8 summarizes the results.

*White-cedars from the panhandle are recognized by some authors as *C. henryae*, a closely related species.

TABLE 8. Late Quaternary Vegetation as Derived from Pollen Profiles in Peat Deposits from Three Lakes between Lakeland and Valdosta by Watts (1969, 1971).

ZONE	YEARS BP	VEGETATION AND INTERPRETATION
M1	0-5,000	Pinelands predominating as they do today: longleaf pinelands near Lake Louise and Lake Scott; sand pine-scrub near Mud Lake. Cypress ponds, bay swamps, and hardwood hammocks with beech (Fagus) were also present.
M2	5,000-8,500	Oaks predominating; pines secondary. Perhaps widespread scrub with patches of bluestem prairie. Pollen of Artemisia and Ambrosia suggest very dry, open terrain early in the deposition of this zone.
Sedimentational Hiatus		Zone of clastic sediments lacking peat and pollen. Interpreted as a time when the lakes were dry during the full Wisconsin glaciation. Water tables were low, corresponding to a eustatic depression in sea level.
M3	before 35,000	Oaks predominating. Probably a sand pine-scrub at Mud Lake and either scrub or some other kind of oak-pine vegetation at Lake Louise and Lake Scott. Cypress ponds, bay swamps, and hardwood hammocks present. Early Wisconsin.
M4, M5		Pine, oak, hickory, and sweetgum all common. Some beech, basswood, sugar maple, and ironwood. Pines a little more common in M4 than in M5. Sangamon interglacial.
M6		Pines predominating. Also present were spruce (Picea), beech, basswood, sugar maple and ironwood. Sangamon or perhaps Illinoian.

Watts' studies show rapid changes in the environment and in the vegetation during the post-Wisconsin period (Fig. 22, p. 80). All three lakes were dry during the full Wisconsin glaciation, as was evidenced from the sedimentational hiatus of Table 8. Studies cited elsewhere in this chapter also suggest cooler temperatures. The prairie-like vegetation in zone M2 is further evidence of xeric conditions. Watts (1971) commented,

"Sea level seems to have risen rapidly from about 14,000 to 7,000 years ago (Milliman and Emery 1968), with a continuing slow steady rise up to the present in Florida (Scholl, Craighead, and Stuvier 1969). In this case, the water table must have been at least 12 m below that of today. With the predominantly coarse sandy soils of the region, rainfall may have been lost very rapidly by sinking through sandy soils to a deep-lying water table....*It may have been combined with a slightly* lower average annual precipitation than at present."

This rapid rise in sea level corresponds nicely with the conclusions of Broecker et al.(1960), who found several evidences for an abrupt and world-wide warming trend about 11,000 BP. Surface temperatures of the Atlantic Ocean rose several degrees Centigrade. Glaciers melting in response to higher temperatures would account for the rapid rise in sea level.

In response to the rapidly changing environmental conditions, the vegetation changed radically. Watts (1971) said,

"Pollen studies show how apparently very elaborate ecosystems may be assembled or disintegrate in relatively short periods of time."

The shift from oak-dominated scrub to longleaf pineland took place suddenly about 5,000 years ago. This change appears to have been widespread, because it occurred both at Valdosta and at Lakeland. The time span for this vegetational conversion has yet to be documented but appears to have taken about a millenium or less. Charcoal throughout the M1 zone suggests the frequent fires which are necessary for maintaining longleaf pinelands.

Another instance of rapid vegetational change was seen in the aquatic vegetation at Lake Louise. With rising sea level one would expect a concomitant rise in the water table and a gradual filling of the lake basin. Emergent marsh species would be expected first, followed by deep water species such as water lilies (Nymphaea). Evidence from the pollen profile suggests that Nymphaea occurred first, then emergents, and finally a fringe of bay swamp. This sequence suggests a very rapid rise in the water table. Emergent marshes likely developed on the fringes of the lake after water levels stabilized near their present stage. Swamps of bay and cypress developed later, also in response to high and relatively stable water levels. The appearance of pollen of beech and other mesic hardwoods also is correlated with the time that the water table was relatively high.

The possibility of a prairie-like vegetation during or shortly after the full Wisconsin glaciation is supported by prairie patches which have persisted since post-Wisconsin times elsewhere in the eastern United States. Braun (1955) summarized the literature on these priaries, which include the "Prairie Peninsula" in Ohio, the "Knobs" region of Kentucky, and the "Black Belt" of Alabama. Neill (1957) spoke of prairies in Florida during a climatic optimum, a period of high temperatures and relatively low rainfall that he dated at 5,000 - 7,500 BP. He cited zoological evidences for prairie conditions.

Watts (1971) said that the pollen profiles suggest that environmental conditions were not as extreme during the Sangamon Interglacial stage as they were in the post-Wisconsin period.

Full-Glacial Vegetation. Watts (1970) studied pollen of the full-glacial period (20,100 and 22,900 BP) from two ponds in northwestern Georgia. Pine was dominant, and Pinus banksiana was identified from fossil needles. Small amounts of pollen were identifiable as spruce (Picea), oak (Quercus), hop-hornbeam type (Ostrya) and herbaceous species. He said,

> "If one considers the list of species identified from the Pinus-Picea zone, the total assemblage can be found in New England, and the great majority of the components, but not all, in the Great Lakes region.... A displacement southward of some 700 miles would be required to bring the same species assemblage back to Georgia."

Species of such typically southern genera as Liquidambar and Nyssa were absent during the full-glacial period and returned later.

Watts' study in northwest Georgia shows that the vegetational displacement southward during the Wisconsin glaciation was not as severe as Deevey (1949) and others suggested. Otherwise, a boreal forest of spruce-fir would have predominated. Deevey's contention that the Eastern Deciduous Forest Formation was pushed into southern peninsular Florida and Mexico was based in part on reports of spruce pollen from bogs in Texas. Graham and Heimsch (1960) reexamined the evidence and made additional studies. They found no basis for,

> "postulating the presence of large stands of spruce and fir in the area or...(for) a relatively recent migration of these boreal elements into Texas."

They suggested that spruce may have occurred in isolated relic stands dating to an even colder period than the Wisconsin. These stands persisted near the Texas bogs until about 12,500 BP.

The position that temperate vegetation was not displaced greatly during the Wisconsin glaciation was supported by Martin and Harrell (1957). They found no evidence of temperate biota which would have persisted in northern Mexico, assuming a Mexican glacial refugium. Braun (1955) also argued against the possibility of a Mexican refugium.

Some authors argued for a mixing of north-temperate and sub-tropical floras in the Gulf states during the full Wisconsin glaciation. Mitchell's above-quoted statement supports this contention. Much of the impetus for this theory came from a study by Brown (1938), who discovered Wisconsin-age fossils of northern and southern forms intermixed in Louisiana. P. Delcourt and Delcourt (1977) restudied the site and discovered two strata rather than one. The lower was Sangamon in age and contained only warm-temperate species. The other was late glacial and Holocene (12,740-3,457 BP) and contained white spruce, tamarack, and other trees of cool-temperate mesophytic forests. The late glacial-Holocene fossils were embedded in a terrace of the Mississippi River which lies 15-30 meters above the maximum historic flood stage. As a result, these fossils must have been deposited in situ and were not "rafted in" from northern regions.

The abundance of boreal vegetation in Louisiana seemingly conflicts with the evidence of Watts (1970) and Graham and Heimsch (1960), who demonstrated temperate conditions for the full-glacial period. This inconsistency was explained by Delcourt and Delcourt (1975):

"The cold, meltwater-fed Mississippi River and a dense, cold air mass funneling down the alluvial valley would have provided a localized cooling influence upon adjacent uplands. Contact of the cold river water and associated cold air mass with relatively warmer, moist Gulf air, would have given rise to persistent advection fogs along the Blufflands. Frequent fogs supplied moisture, increased cloud cover (and thus decreased evapotranspiration) and provided a cooler, more humid microclimate (cooler summers?) to the Blufflands adjacent to the major waterway of the Mississippi....This hypothesis is sufficient to explain all occurrences of vascular plant disjunction (of those associated with mesic deciduous woodlands) known for the southern Atlantic and Gulf coastal plains."

Stratigraphy at Bradwell Bay. Cameron and Mory (1976) studied the stratigraphy of Bradwell Bay and contributed information on the development of the large, acid swamp that now occupies the site. Bradwell Bay lies in Wakulla County near the Ochlockonee River north of Sopchoppy (Fig. 12). It is underlain by limestone of the St. Marks Formation (early Miocene) and in its western half by the marls of the Jackson Bluff Formation (late Miocene). The northern edge is limited by a low sand ridge, which represents the remnants of the Wicomico Shoreline (Fig. 15). Bradwell Bay is limited on the east and west sides by an ancient beach ridge complex which presumably formed when sea level was nearly as high as the Wicomico Shoreline. At that time Bradwell Bay was a marine lagoon.

The stratigraphy of Bradwell Bay is shown in Figure 40. Zone B consists of clastic sediments which were transported into the near-shore marine environment by rivers. Wood fragments are common in Zone B and

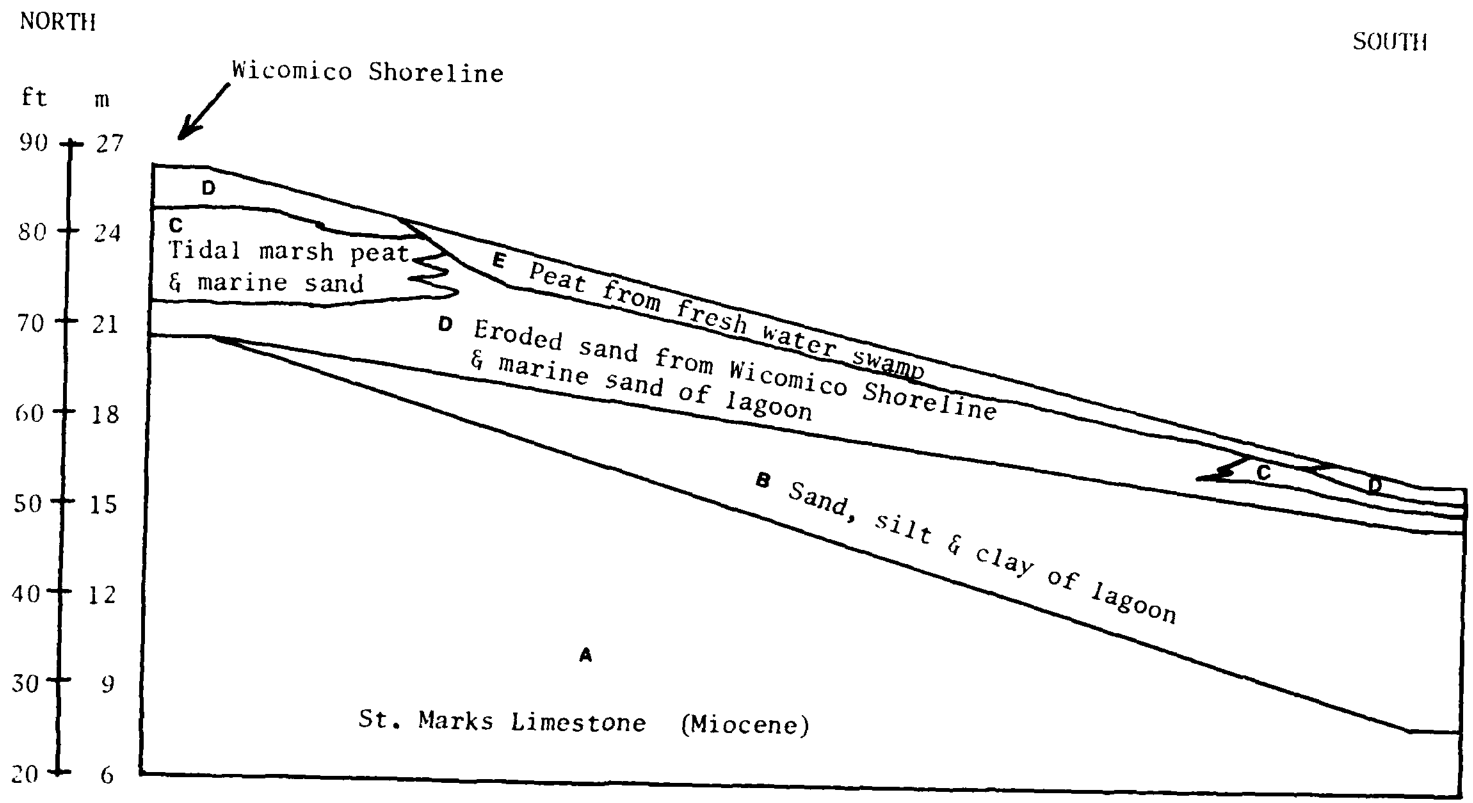

Figure 40. Bradwell Bay stratigraphy. After Cameron and Morey (1976).

are thought to represent trees that washed into the lagoon.

Zone D is wind-blown sand which eroded from the Wicomico Shoreline and became intermixed with marine sands of the lagoon. Zone C consists of tidal marsh peats in some places and marine sands in others. The tidal marshes were discontinuous, just as they are today around lagoons. Some of the peats were covered subsequently by eroded materials from the Wicomico Shoreline.

Eventually sea level became lower, creating a poorly drained, fresh water environment. Titi, Sphagnum (peat moss), and other plants of acid swamps occupied the site and created a bed of peat, Zone E. Bradwell Bay is mostly covered with titi swamp today, with some deeper swamps of sweetbay, blackgum, and pond-cypress scattered primarily in the western half. Charcoal in Zone E suggests that much peat was consumed by past fires.

The deepest sediments (about 8 m) of Zone B correspond in elevation with the highest sea levels attained during the Pleistocene interglacial stages. Part, and perhaps all of Zone B is Pleistocene, although some could date into the Pliocene. All late Miocene and early Pliocene deposits must have been eroded during later periods of high sea level. Zone D is apparently younger than Zone B. Further study of these sediments might yield more precise information on the extent of intrusion of Pleistocene seas.

If Zone D is largely from wind-blown sand, the vegetation cover must have been negligible. Otherwise the vegetation would bind the sand as it does today. The prairie conditions at the time of the Wisconsin glaciation may have allowed the aeolian transport of sand. Buried cypress [illegible] discovered by C. L. Coultas (personal communication 1978) nearby [illegible] appears to be caused by wind-blown sands. Again, further study [illegible] this area promises important clues [illegible] environments.

Okefenokee Swamp Development. Additional information on the development of acid swamps was contributed by Cohen from studies on the Okefenokee Swamp. This region is characterized by several vegetation types, including cypress and bay swamps, wet open marshes called prairies locally, and lakes. Peat deposits reach a maximum depth of about 14 feet. Radiocarbon dates of the deepest peats from three large prairies were 6,235, 6,490, and 6,585 years BP (Cohen 1973). These dates conform rather nicely with the beginning of Watts' M1 Zone (Table 8), when swamps became important regionally.

Cohen determined that the peats of these prairies were strictly derived from marsh plants, rather than from trees. They began as water basins in topographically low areas. Cohen (1974) said,

> "The paleoecological reconstructions show that the water table in these areas has risen at approximately the same rate as the rate of peat accumulation."

Cohen (1974) noted lenses and streaks of charcoal-rich peat in all cores that he sampled. He recorded several instances of cypress peat, then charcoal, and finally peat from water-lilies (*Nymphaea*). This sequence suggests a severe fire which destroyed a cypress swamp and burned deeply into the peat, creating a lake. He also discovered charcoal lenses which were especially rich in spicules from sponges. Spicules do not burn. If peat burns, the spicules contained in it would become concentrated and would serve as evidence for past fire.

The observations of Cohen suggest the following scenario. Marshes and swamps developed and produced an increasingly thick deposit of peat as water tables rose. During prolonged droughts (or perhaps during minor eustatic depression in sea level) the upper peat layers became desiccated and ignited. All vegetation was killed by fire, because the roots were burned, preventing coppicing. After the drought a lake formed. Aquatic plants invaded, and their peat eventually accumulated until they were replaced by emergent marsh plants and these later by cypress and other swamp trees. This hydrosere might be repeated after a subsequent peat fire.

Cypert (1961) elaborated on this possibility in his study of the effects of fires in the drought years of 1954-5 in the Okefenokee Swamp. Approximately 80% of the swamp suffered fires, most of it only moderately or lightly burned. The drought lowered water levels 3.5 to 3.9 feet below their average levels for the 12 pervious years. In all but the most severely burned areas some trees survived. Regrowth was essentially of the same species that occurred there before the fire, and coppicing was noted (Table 9).

Cypert said that there were historical records of fires accompanying droughts in 1844, 1860, 1910, and 1932. He quoted O. K. Mizell who, in 1844, wrote,

> "In 1844 there was a terrible drought and the Okefenokee caught fire and holes were buned out which were the cause of the majority of the lakes there."

Cypert said at least 40 lakes were formed by peat fires, the larger being Gannett Lake (28 acres), Cowared Lake (22 acres) and Double Lakes (36 and 18 acres). He said,

TABLE 9. Survival of Trees on Typical Burns (Hot Burns Excluded) in the Okefenokee Swamp after the Fires of 1954-5 (Cypert 1961).

	Basal Area per Acre of All Trees (Alive and Fire-Killed)	Percent of the Basal Area That Represents Live Trees
Nyssa biflora	126	94
Magnolia virginiana	40	81
Persea borbonia	10	61
Taxodium ascendens	8	99
Acer rubrum	7	61
Gordonia lasianthus	6	53
Ilex cassine	4	92
Cyrilla racemiflora	4	43

"In no case was there an indication of a relationship between the presence of the lake and the topography of the underlying sand floor. In other words, the lakes are holes in the peat, rather than holes in the underlying sand, which gives credence to the belief that the lakes were fire caused."

Cypert (1961) said,

"It was only where pockets of peat were burned out that the larger cypresses and blackgums were killed....Pockets of peat burned.... to a depth of two or three feet. Usually all trees were killed where peat burned to this depth. These pockets were usually less than 1/10th acre. Over most of the area the burns were surface fires which generally killed most of the reproduction and underbrush but rarely burned severely enough to kill the larger trees. In many places the fire swept over lightly, burning the surface duff and killing only the smaller underbrush. Some places were missed entirely. At no place was the fire intense enough to cause a complete kill of woody cover over as much as one acre. The most severe burns occurred in places where timber operations had been conducted in past years.... where low brushy growth was most dense.... Virgin cypress forest burned lightly,....and virgin....blackgum and bay....burned lightly except....small pockets."

Cypert continued,

"The Okefenokee prairies were caused by extreme hot fires which killed all plants, root systems included, and burned away the peat to a low enough level to prevent the re-establishment of woody vegetation. Charred stumps, embedded in the peat throughout the prairies, are evidence of extensive forests which were killed by fire."

This statement suggests an alternative origin of prairies from that of Cohen (1974), who proposed that the largest prairies were never forested.

The studies on Bradwell Bay and on the Okefenokee Swamp support the contention of Watts for the rapid demise of well established vegetation following major environmental change and for the persistence of a given vegetation type throughout periods of lesser environmental fluctuations. Superimposed on this generalized vegetational response is the hydrosere, as traditionally defined, initiated by intense peat fires. The importance of this hydrosere has yet to be determined outside of the Okefenokee Swamp, but it may account for the mixed stands of blackgum (a more hydric species) with sweetbay (a less hydric species) in some acid swamps. The bays may represent a recent invasion into blackgum swamps that are aggrading with peat.

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16. THE DISPLACEMENT MODEL

The paleoecological record, at least since the Sangamon interglacial stage, suggests two major trends in the development of the present vegetation. The first trend might be termed traditional succession and climax, involving relay floristics and/or non-synchronous species replacement. The effect of initial floristic composition may also be influential in part (Fig. 39). One or some combination of these models seems to fit the mesic hardwood forests of river bluffs and associated ravines, the hydric forests of floodplains, and probably the Gulf hammock lands, although the latter have been scarcely studied.

In contrast to other habitats, the severity of environmental changes since the Pleistocene has been moderated in the larger valleys by the special microclimate described by Delcourt and Delcourt (1975) and probably by the seepage of ground-water along the slopes. Because of the moderated conditions, the various hardwood forests seem to have persisted with only gradual changes in dominance or composition over many millenia. There may have been minor vertical adjustments on the slopes as water tables changed and aluvium was eroded or deposited in response to fluctuating sea levels (Fig. 33).

The second trend is one of the persistence of colonizing species in stable communities until such time as a major environmental change forces substantial vegetational displacement. This displacement model is protrayed in Figure 41 and fits the aforementioned data of Watts (Table 8, also the Lake Louise hydrosere). Vegetation that seems to fit this displacement model includes longleaf pinelands, slash pinelands,

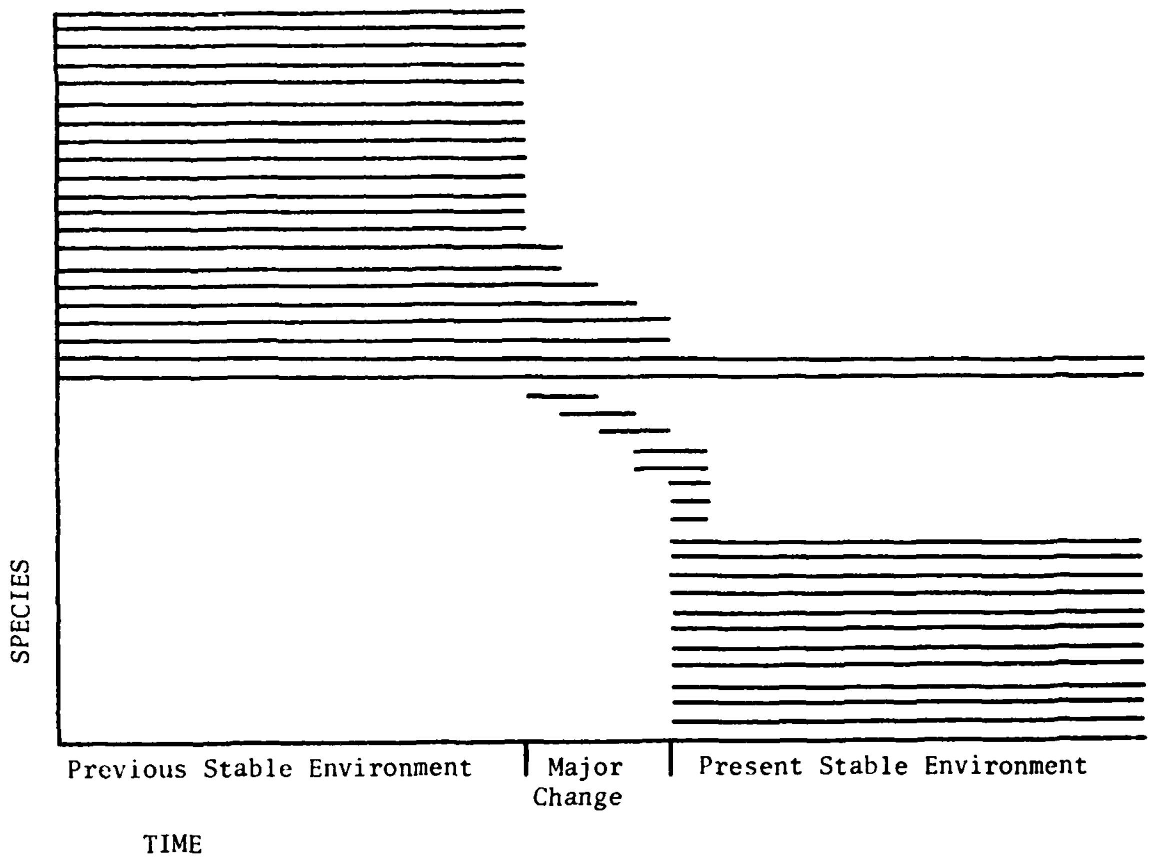

Figure 41. The displacement model. Persistence of colonizing species and vegetational replacement following major environmental change.

savannahs, bogs, acid swamps of titi, bay, pond-pine, and blackgum, scrubs, at least some fresh water marshes, tidal marshes, seagrass beds, and the aquatic vegetation of spring-runs.

The major environmental changes are those associated with the changing position of the water table as sea level fluctuates. Climatic changes, particularly in reference to precipitation and evaporation, may also have been instrumental in effecting vegetational displacement. The moisture regime, as influenced by the position of the water table or by climate, affects not only the moisture balance within plants but also the flammability of habitats. For example, increasingly hydric conditions may eventually kill the flammable grasses, thereby reducing the frequency of fire and allowing the colonization of fire-intolerant shrubs and trees.

The stability of colonizing species is attained only through some physical property of a habitat that favors a particular community at the expense of all other kinds of vegetation. This property may be fire, a fluctuating water table in lake basins, swiftly flowing water in spring-runs, or the salinity regime near the coast. The effects of these physical determinants may be reinforced by secondary factors. High acidity may restrict the number of potential invading species. Infertile soils may retard the early growth of invaders, prolonging the time during which they are most susceptible to elimination from competition or from physical stress.

Most authors consider vegetation that is stabilized by fire, salinity, and similar factors, as representing an arrested seral stage. If these so-called disturbance factors disappear, succession would proceed to the climax. This contention is another example of "if... then" reasoning without basis in the realities of coastal plain vegetation. The disturbance factors disappear only at a time of major environmental change. Therefore, a new sere towards an entirely different climax could be the only predictable vegetational development. Previous authors, though, have accepted the position that the climax vegetation of the southeastern coastal plain consists of a hardwood forest and that all other vegetation is seral.

"Succession" usually connotes seral development assuming stable environmental conditions. "Succession" loses its conceptual usefulness when applied indiscriminately to all vegetational changes. Cowles (1911) considered the vegetational change caused by widespread climatic change in a region as succession, but he distinguished it as a special category, apart from succession driven by competition or by topographic changes (erosion and deposition).

The concept of the persistence of colonizing species has already been suggested but not for the vegetation of the panhandle. Drury and Nisbet (1973) wrote,

> "...succession on a single site usually involves a sequence of species...because no one species can dominate the vegetation throughout the period of growth. In other words the basic cause of the phenomenon of succession is the known correlation between stress tolerance, rapid growth, small size, short life, and wide dispersal of seed. The few exceptions to this general correlation -- mangroves, redwoods, coconut palms, douglas firs -- are also exceptions to the generalization of succession: they are both 'early successional' and 'climax' species."

The practice of considering an "early successional" vegetation as "climax" is also an indiscriminate use of terms. "Climax" connotes vegetation that has resulted following a series of community or species replacements. Etymologically, how can something represent a climax without previous action leading up to it?

The concepts of succession and climax do not conform to most of the vegetation types in the coastal plain and should not be applied to them. These terms become applicable when fire or other stabilizing factors of the natural environment are modified or eliminated by man's activities. Only in the absence of any effective stabilizing determinant is seral development possible. Then a potential climax comprised at least in part of mixed hardwoods is usually predictable.

Supporting evidence for the displacement model will be given in detail in later chapters describing the individual plant communities. Indirect evidences from extant vegetation support the displacement model and are summarized below. None of these evidences are conclusive, but neither are those that have been advanced in support of a mono-climax of hardwoods.

1. There is no evidence of succession or change in most communities that fit the displacement model. Nearly all plants have effective mechanisms for vegetative propagation, including many species of larger trees which coppice from their roots after crown fires. Pines are an obvious exception, but they are adapted to seeding-in after fire.

2. Wiregrass, turkey oak, saw-palmetto, and other dominant species of the mesic and xeric habitats rarely reproduce sexually. Seedlings

are absent in some of those communities that fit the displacement model. Neither are there agencies in the habitats of these communities that kill plants. In other communities, particularly hydric ones, plants may be killed but are replaced sexually by others of the same species without intervening seral stages.

3. A general lack of transition zones (ecotones) between many pairs of communities or zones within generalized communities seems to indicate a threshold phenomenon. The often subtle environmental changes along a gradient reach a point where key species of one community are no longer able to survive, and another community begins. These gradients are associated with the stabilizing determinants, such as fire, the moisture regime, and salinity.

4. Certain of the more hydric communities appear to be mere assemblages of plants lacking any apparant interactions or regularized distributions.

Endemism and the Displacement Model. The preceding discussion allows the proposal of a new hypothesis to explain endemism for species that occur in vegetation that fits the displacement model. It was stated previously that many endemic species are confined to particular localities, even though the habitats to which they belong are continuous over wide areas. These species include *Harperocallis flava* and the others of the lower Apalachicola River watershed. The hypothesis is based on two premises that are compatible with the displacement model. First, that most habitats contain stable, vegetatively propagating and indefinitely persisting stands of colonizing species.

Second, that these habitats are closed, i.e., filled with vegetation and lack space that additional plants could occupy.

Many such habitats were available for colonization about 5,000 years ago (Table 8). The plants that invaded were those for which seeds or other propagules were available. Thereafter, there was no opportunity for a species to increase its range. The narrowly endemic species are those whose seeds were limited to a particular location at the time that colonization was possible. Subsequently, propagation was mainly vegetative, with only here and there a small opening being available for colonization by seedlings. The endemics have persisted very well by vegetative means, just as the more widely ranging species have persisted, also mainly by vegetative means.

This hypothesis for endemism also can be broadened to help explain the distribution of more widely ranging species that seem unable to spread into contiguous regions with identical habitats.

The reasons why the seeds or propagules of some species were widespread and others restricted at the time of colonization are not addressed by this hypothesis. Neill's (1957) observation on marine embayments might be involved. Other evidences may be masked beneath the Gulf of Mexico following the rise of post-Wisconsin seas. Answers will likely require detailed paleoecological studies.

At the risk of using circular reasoning, this hypothesis on endemism reinforces the displacement model.

Land Management and the Displacement Model. The plant communities that fit the displacement model depend upon their stability through the continued operation of factors, such as fire. If these stabilizing determinants are ineffective, the displacement model ceases to fit, and a sere begins. The later reestablishment of the original vegetation may be possible but requires that the stabilizing determinants be incorporated into the management plan. This reestablishment may not be sufficient, though, in communities where sexual reproduction of the dominant species is depressed and unpredictable. In general, it is less difficult to reconstitute a hydric community but virtually impossible to replace a longleaf pineland or other wiregrass habitat.

If a natural stand of upland vegetation that fits the displacement model is to be preserved, it must be managed with great care. Soil disturbance causes irreparable damage. Reduction in the burning regime causes irreversible changes. The wiregrass-covered pinelands that once covered the great majority of the panhandle have been reduced by site preparation for commercial forestry and by other disturbance. At the present rate of destruction, these pinelands may soon become a rare sight in Florida.

Lands that are covered by NEPA and other lands that are proposed for developments of regional impact should not be touched without the preparation of an impact statement that addresses the consequences of further reduction of wiregrass lands. Federal lands should be set aside in the National Wilderness Preservation System to preserve sizeable examples of what little remains. The wilderness areas must be managed with frequent fires. Pine timber on other public lands should be managed without disturbing the soil.

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17. PRIMEVAL AND OTHER VEGETATION

Definitions. The terms, primeval, original, virgin, primary, and natural, when applied to vegetation, are used rather loosely and mean different things to different people. Semantic difficulties with these terms interfer with the rational communication between various groups or individuals concerned with preservation, conservation, resource management, and development. This chapter defines these terms as used in this report.

Original and Primary are terms that denote vegetation that has not been disturbed or exploited, such as a stand of timber that has never been cut. They are the converse of secondary or second-growth vegetation which replaces the original stand. These terms are not always easy to apply. Second-growth stands of longleaf pine, for example, often grow in the original, undisturbed undergrowth consisting of several dozen species.

The terms primeval and virgin are often used synonymously with original and primary, and they all denote vegetation that has not been disturbed by man. Two questions arise. What constitutes an alteration and what is man? Man certainly includes peoples of other continents who immigrated to North America, beginning with the Spanish in the 1500's. Some authors consider Indians as part of the "natural" biota and distinct from "modern man". This viewpoint assumes that Indians lived in harmony with nature and that all of their alterations of the vegetation were "natural". If this contention is accepted, then in what year did the ancestors modern man leap from the depths of primitiveness into the modern era? Unless that question can be answered, how can any member of the genus _Homo_ be considered separate from "modern man"?

The futility of invoking a dual concept of man in defining primeval vegetation is seen from the following scenario: Mastodons consumed great quantities of vegetation. Indians hunted them, leading to the eventual extinction of mastodons. The vegetation changed dramatically in the absence of mastodons. Is the new vegetation primeval? Of course it is, if one assumes that all Indians lived in harmony with nature. Of course it isn't, if one argues that Indians were using their developing elements of civilization in exterminating mastodons. We may never know if mastodons had such control over the vegetation or even if primitive man was responsible for their demise, but the possibility demonstrates how arbitrary any definition is that attempts to separate modern man from other hominoids.

We possess historical records that show unequivocally that the Indians encountered by the first explorers and settlers from Europe were burning and tilling the land in our region. The question arises, did these activities alter the vegetation? If so, substantially or permanently? Evidences presented in later chapters point to an affirmative answer in some instances. The applicability of the terms, primeval, original, and virgin for our vegetation suddenly becomes nebulous.

Nonetheless there remains an obvious distinction between that vegetation which appears to be original and that which is entirely ruderal. _Ruderal_ describes any vegetation that develops in response to disturbance of habitats by man's activities. The vegetation of roadsides and weedy fields is ruderal. Other vegetation falls variously between the extremes of original and ruderal.

Since there is a continuum between original and ruderal vegetation, the question of what constitutes an alteration of original vegetation becomes important. If one Indian trampled a blade of grass, was the vegetation altered forever from its primeval state? If a forest was cut down and the site planted to cotton, later left fallow, and allowed to revert back to an identical forest, can such a forest be called primeval? Absolute answers to these questions are impossible without invoking value judgements.

The entire situation is complicated by considerations of climax. Is primeval vegetation necessarily in the stable climax state or at least in a steady state? Such a connotation is usually implicit with conceptions of what constitutes primeval vegetation. Is the highly unstable vegetation resulting from natural environmental perturbations to be deemed primeval, even if it resembles ruderal vegetation? Example of such natural but ruderal-like vegetation occur on river banks, beach strand dunes, and along the margins of ponds with widely fluctuating water levels. Change in nature is axiomatic. Only the rate of gradual change or the degree of abrupt change is in question. If we could preserve a tract of primeval vegetation in perpetuity as if it were photographed, how could we know whether or not it would have changed naturally without our intervention?

Pragmatic Considerations. Even though the concept of primeval-ness defies definition, it must be addressed. There is a definite need to preserve vegetation which has the attributes commonly perceived as primeval. These needs are spiritual, aesthetic, recreational, educational, scientific, and even technological. Vast amounts of energy and funds have been invested to preserve primeval sites. Legislation has been enacted and agencies created to protect these sites.

The perception of what attributes constitute that which is primeval differs according to ones experience. A friend once mentioned to me that urbanites who came to the wilds of the panhandle to hunt thought that a tree farm of row-planted slash pines was comparable to the scenery in a Tarzan movie, and that these hunters would have felt more comfortable if a public telephone were attached to each tree.

The resolution of the problem of what constitutes primeval, original, or virgin habitat is found in the Preamble of the Wilderness Act of 1964 (Wilderness Society 1970). This Act attempts to preserve those sites which resemble America when the first European settlers and explorers arrived. This definition, based on presettlement vegetation, avoids the argument of whether or not Indians are equivalent to modern man and all considerations of climax vegetation.

It raises two questions, though. First, how much disturbance is tolerable, assuming that most any site with primeval qualities will contain at least minor evidences of disturbance? The answer is professional judgement based on experience in other primeval areas and guided by reasonable criteria. These criteria should address such questions as, will the scars of disturbance heal within a reasonable time?

The other question is, how do we determine whether or not a site looks like it did several centuries ago? That question is more easily answered than many would believe. A search of historical and legal documents may yield important clues and even vegetational descriptions in diaries and letters. Past land use can be assessed by anthropologists with only a few artifactual fragments. Stands of vegetation for which there is good evidence for little or no disturbance can be compared to those for which disturbances are known. A botanist uses such knowledge to detect botanical clues that would indicate primeval conditions or past disturbance in other stands.

Witness Tree Studies. Perhaps the most useful sources of information, though, are the diaries of the surveyors who made the initial land surveys as the frontiers of the United States were being settled. Surveyors marked witness trees or bearing trees at regular intervals to show the positions of survey lines and corners. Since these trees were mapped and identified, their density and frequency can be determined. Since larger trees were selected as witness trees, the quantitative estimates derived from surveyors' diaries represent the dominant forest species of presettlement vegetation. Methods have been developed for detecting biases that a surveyor might have had in selecting witness trees.

These methods were used by Plummer (1975) in Georgia. Witness tree data confirmed a presettlement forest of longleaf pine in the coastal plain and a pine-oak-hickory forest for parts of the Piedmont.

Longleaf pine was present in these Piedmont stands, and post oak was important. Dogwood and hickory were recorded commonly. The forest became more diversified near the Flint River. This vegetation appears to be similar to that described by Watts (1970) from post-Wisconsin pollen profiles.

These methods were also used by Delcourt and Delcourt (1974), who described presettlement forests of magnolia, holly, and beech from the Tunica Hills adjoining the Mississippi River in Louisiana. Delcourt (1976) described a mixed longleaf pine-oak forest in northern Louisiana. Delcourt and Delcourt (1977) used the method to describe a mesic forest dominated by magnolia and beech in the Apalachicola River Bluffs.

The witness tree method is powerful but subject to misinterpretation without a first-hand knowledge of the habitats in the field. The Apalachicola River Bluffs are steep and the ravines of the tributary creeks very narrow. The distance between witness trees is relatively great. The quantitative data by Delcourt and Delcourt (1977) suggested dominance by magnolia and beech, but near-virgin forests at Torreya State Park clearly reveal that magnolia and beech are restricted to the lower slopes. An oak forest dominates the upper slopes. The spacing between witness trees was too great to detect this obvious zonation. A reconnaissance in the field suggests that the pines, which the Delcourts thought to have been the source of surveyors' bias in tributary creeks, were probably longleaf pines of the contiguous but entirely different pine-oak uplands. The dominant oak of these uplands is Quercus laevis, not the rare Q. marilandica, as was presumed by the Delcourts from the common name of blackjack oak, used by the surveyors.

An alternative method of using surveyors' field notes would be to deduce the plant community from the witness trees or other vegetation listed for a given site. Some surveyors made copious botanical descriptions with each change in the vegetation along a survey line. A vegetation map based on these descriptions is easily prepared without resorting to quantitative methods. The accuracy of this qualitative method depends on the researcher's familiarity with the region and its mature vegetation.

The decision of which method should be used involves two fundamental questions of descriptive ecology: First, can the quantitative approach be made sensitive enough to detect the important vegetational nuances? Second, is the qualitative description of an observer sufficiently free of bias to assure reasonable accuracy? The answers to these questions are never entirely satisfactory. Perhaps the quantitative methodology of the witness-tree surveys should be applied individually to the mapping units derived from qualitative determinations of communities.

Wilderness Management. Once a site has been secured as a wilderness representing primeval or near-primeval vegetation, it must be managed to preserve its wilderness qualities. The Wilderness Act of 1964 calls for such management. The methods of management must be as natural as possible. The results of management should be the preservation of primeval habitat or the enhancement of slightly disturbed habitat. The purpose of such management should not be directed at preserving or increasing in abundance particular species but at preserving the habitat.

The preserved site does not have to be sheltered from change. If a plant community ordinarily undergoes cyclic or progressive changes, nothing in the management plan should interfere with these changes. A few forest types burn to the ground at lengthy but regular intervals. Such fires should not be prevented and perhaps should be intentionally set. Surrounding lands should be managed so that such a fire is unlikely to escape and damage neighboring property.

Several plant communities are maintained only by near-annual surface fires. Roads, firelanes, fields, and other artifices serve as fire breaks to the spread of lightning-set fires, and such fires are often extinguished by firemen before they spread far. As a result, many preserves must be burned by prescription (Wright, 1974).

The removal of feral hogs may be important in management. Exotic plants and row-planted pines must also be removed. Unneeded trails and other open sites might be prepared or even planted for their revegetation by native species. Dense stands of second-growth pines or other timber should be thinned to speed the maturation of a forest. Water control structures may have to be installed to restore the moisture regime of a modified watershed. Trapping or hunting may be required, but only if animal populations are augmented beyond the carrying capacity of the habitat because of immigrations from surrounding regions.

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18. PLANT RESPONSE TO HYDRIC CONDITIONS*

Dissolved Oxygen and Carbon Dioxide. Tomatoes and other mesophytes are grown hydroponically with their roots immersed continually in water. Such plants are vigorous with rapid growth, but only if air is bubbled into the water, saturating it with oxygen. Excessive water in itself is not harmful to plants, but oxygen depletion is not tolerable.

Dissolved air generally contains relatively more oxygen and much more CO_2 than does atmospheric air; however, the total volume of air held in solution is small. The amount of oxygen dissolved in a given volume of water is often less than 5% of that present in an equivalent volume of the atmosphere. The rate of diffusion of dissolved oxygen is several thousand times slower in water than in air. Roots and the soil biota remove oxygen continuously and replace it with CO_2. This process is intensified in warm seasons. Not only does metabolic activity increase with higher temperatures, but also the capacity of water to hold dissolved gasses decreases accordingly (Arber 1920, Kramer 1951).

Oxygen in motionless water is depleted rapidly by organisms but is replenished quickly by rain, even by small showers. Agitation of the water's surface accelerates gas exchange with the atmosphere, even in a calmly flowing river. Photosynthetic activity of aquatic plants contributes dissolved oxygen to the water (Sculthorpe 1967).

The CO_2 concentration is pH dependent but is generally abundant in saturated soils. Respiration from roots and other soil biota continually produce CO_2 which is not evolved rapidly into the atmosphere

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*This chapter is based on an unpublished manuscript by H. Leitman.

because of slow rates of diffusion through water. It is generally thought that while oxygen concentrations are often low enough to be inhibitory, CO_2 concentrations are rarely high enough to cause injury (Kramer 1969, Meyer et al. 1973). Sweetgum and water tupelo have been tested for tolerance to high CO_2 levels (partial pressures of 10% or more of CO_2). Sweetgum was very intolerant but the more hydric water tupelo was tolerant of these levels (Hook and Brown 1973).

Anaerobic Respiration. The proper functioning of the aerial parts of a plant are determined largely by the limited supply of CO_2 needed for photosynthesis and of water vapor needed to preclude excessive transpiration. In a water medium this relationship is reversed. Water and CO_2 are abundant and oxygen is in short supply. The ability of a plant to survive in hydric environments may depend upon its ability to tolerate anaerobic conditions.

The energy output from anaerobic respiration is much lower than that of aerobic respiration and is usually inadequate for normal maintenance of cellular processes. In addition, metabolic by-products of anaerobic respiration quickly accumulate to toxic levels. These substances may include ethanol and various organic acids. When soils become saturated or flooded, the rate of anaerobic respiration accelerates in the roots of most plants. Flood-tolerant hydrophytes are often exceptional, in that they maintain enzymatic control of this metabolic reaction. This control mechanism prevents excessive rates of anaerobic respiration, thereby limiting the production of toxins. Steward et al. (1936) found that cells developed in water will absorb salts and respire normally at lower oxygen concentrations than cells developed in well aerated media. Kramer (1951) suggested that roots which developed underwater contain a different respiratory enzyme system than do those produced in well aerated media. Anatomical features of hydrophytes promote the leakage of toxic substances of anaerobic respiration into the substrate (Hook 1974), as will be discussed in subsequent paragraphs.

Internal Transport of Oxygen. Hydrophytes often contain cortical or other largely parenchymatous tissues in which the intercellular spaces (lacunae) are much enlarged in comparison to mesophytes. Such tissue is called aerenchyma. The lacunae form a continuous, though tortuous system of passageways between cells which extends from the aerial or uppermost portions of the plant all the way into the developing root tips. These air spaces make the plant spongy, as in the petiole of a water-lily. It is assumed that this system provides an internal atmosphere that allows submersed organs to obtain oxygen which enters the stomates or which is generated from photosynthesis. Evidence for this contention is a gradient of oxygen within aerenchymatous plants, which is greatest in the leaves and progressively lower towards the roots. The rates of photosynthesis (oxygen release) and foliar respiration (oxygen consumption) affect the internal oxygen gradient. The steepness of this gradient and the internal resistance of the plant to diffusion determine the rate of downward oxygen transport (Sculthorpe 1967).

Hydrophytic trees often contain an abundance of lenticels, supposedly facilitating the entrance of oxygen into the aerenchymatous passages of the stems. Inundation causes lenticels to increase in size, number, and permeability, and causes the intercellular spaces to enlarge, thereby facilitating gas exchange in the stem. The phloem and cortex have the most pronounced intercellular spaces. Volatile substances, such as ethanol produced by anaerobic respiration in the roots, may escape through the lenticels and stomates by way of the aerenchymatous passages (Hook 1974).

The cambium and the parenchymatous rays in the xylem generally receive oxygen from the stream of water passing through the vessels and tracheids. In the more flood-tolerant trees small perforations interrupt the ray initials of the cambium. Oxygen may diffuse laterally from the aerenchymatous cortex or phloem through the perforations of the cambium and into the rays of the xylem. Perforated ray initials are not characteristic of mesophytes. In mesophytes any anaerobic by-products are released by the cambium into the transpirational flow. These substances may reach toxic levels which harm the aerial portions of a tree. In hydrophytes some of these toxins are transferred into the aerenchyma, thereby reducing their concentrations to levels not inhibitory to normal metabolism.

Oxidation of the Rhizosphere. Deep and prolonged flooding may result in highly reduced soil conditions with high concentrations of reduced iron and manganese as well as hydrogen sulfide, CO_2, and other gasses. One or more of these compounds may be present in sufficient concentration to be toxic to normal roots. If the root is protected by an oxygen shield, it not only survives but may also grow and function normally (Hook 1974). This shield is the rhizosphere, which is that soil that immediately surrounds the roots and in which root-soil interactions occur.

In several flood-tolerant trees, new roots grown in flooded conditions readily oxidize their rhizosphere, as long as aerial portions of the tree are exposed to the atmosphere. The rhizosphere does not become oxidized if the lenticles of aerial stems are covered (Hook et al. 1970). Roots developing in aerated soil lack the capability of oxidizing their rhizosphere. Oxidation appears to be dependent on the efficiency of the internal gas transport system. Armstrong (1967) proposed that oxidation may occur enzymatically in bog plants.

Root Growth. Lack of oxygen interferes with the translocation of substances in the phloem. Flooding creates a physiological girdle at the water line which inhibits downward translocation. Foods and growth substances accumulate at the water line and stimulate vegetative growth at that point. This growth may take the form of adventitious roots, callus tissue, aerenchymatous tissue, and buttresses, depending on the kind of plant (Kramer 1969).

Various types of adventitious roots develop in herbaceous hydrophytes in response to flooded conditions. Some emergent hydrophytes form air roots, permitting greater transport of oxygen to the submerged organs than would be possible by diffusion from the aerial shoots alone. These roots are inflated with aerenchyma and grow erect, sometimes protruding above the water's surface (Sculthorpe 1967). Rice plants contain such roots. Flooded plants which produce adventitious roots the most rapidly suffer the least injury and show the greatest degree of recovery (Kramer 1951). Adventitious root development is not always necessary for plants to survive flooding. Floodplain trees show various combinations of root adaptations with and without adventitious root development.

In most hydrophytic trees, secondary roots deteriorate when flooded and are replaced by new, more succulent and less branched roots which arise from the original root system. In addition, adventitious roots may develop from the submerged portion of the trunk in some species. In less flood-tolerant species the secondary roots die but are not replaced by new roots nor by adventitious roots from the trunk. In contrast to herbaceous hydrophytes, the roots of woody, flood-tolerant species lack aerenchyma. Instead the epidermis is poorly if at all suberized. The endodermis is poorly differentiated, and the Casparian strip is absent (Hook 1974).

Table 10 summarizes the adaptations of several trees of floodplains with regard to their survival during flood stage. This table was prepared from information in Broadfoot (1967), Broadfoot and Williston (1973), Dickson and Broyer (1972), Dickson et al. (1965), Hook (1974), Hook and Brown (1973), Hook, Brown and Wetmore (1972), Hook, Langdon, Stubbs and Brown (1970), Hosner (1960), Hosner and Boyce (1962), McDermott (1954), Parker (1950), Wagner and Kurz (1954), and Yelenosky (1963).

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TABLE 10. Root and Stem Adaptations of Floodplain Trees.

Species in approximate order from most to least tolerant	Adventitious root development	Non-adventitious roots	Roots oxidize rhizo-sphere	Sizeable intercellular spaces among cambial ray initials
Bald-cypress *Taxodium distichum*	many	1^o and 2^o roots die; replacement by adventitious roots.		
Water tupelo *Nyssa aquatica*	none	2^o roots die and new 2^o roots develop	yes	yes
Green ash *Fraxinus pennsylvanica*	few to many	some mortality of 2^o roots, new 2^o roots develop	yes	yes
Black willow *Salix nigra*	many	tips of some 2^o roots die, new root system develops		
Eastern cottonwood *Populus deltiodes*	many	all roots except 1^o die		
Silver maple *Acer saccharinum*	many	dormant during flooding, recovery afterwards with little mortality		
Red maple *Acer rubrum*	many	dormant during flooding, rapid recovery afterwards		
Hackberry *Celtis laevigata*	none	all roots except 1^o die		
Sycamore *Platanus occidentalis*	many	new 2^o roots form near surface, all 2^o and lower 1^o roots die	no	no
Sweetgum *Liquidambar styraciflua*	none	some 2^o roots die, upper laterals grew to surface	no	no
American elm *Ulmus americana*	few to many	2^o roots die		
Willow oak *Quercus phellos*	none	some mortality of 2^o roots		

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19. LONGLEAF PINE

Distribution. Longleaf pine (*Pinus palustris* Mill.) is native on the coastal plain from southeastern Virginia south through most of peninsular Florida and westward through Alabama, southern Mississippi, parts of Louisiana, and into eastern Texas. It is also native to parts of northern Georgia and Alabama (Little 1971). It had been virtually replaced by loblolly pine in Virginia nearly a century ago (Mohr 1897). The original stands of longleaf pine generally contained no other trees except on sandhills where an understory of oaks occurred, mainly turkey oaks. Occasionally slash pine mixed with longleaf pine in the wetter parts of pine flatwoods. In loamy hill country, longleaf pines sometimes formed open woods with mockernut hickory, post oak, and Spanish oak.

Virtually all original-growth stands have been logged or otherwise disturbed, which has resulted in a general reduction in the abundance of the species.

Growth. The longleaf pine is said to be in the cotyledon stage during the first half year following germination. For the next five or six years (rarely 2 and sometimes 8 or more) it is in the grass stage, during which time it develops an extensive root system. The terminal bud remains at ground-level and produces a dense rosette of needles resembling a clump of wiregrass. Rapid aerial growth marks the growing stage which ends in two or three years upon reaching a height of 4.5 feet. The trunk generally remains unbranched throughout the growing stage and into the sapling stage.

Saplings and young trees are subject to intense competition from each other and from older trees. Individuals that are no longer able to compete will bend noticably, as if their trunks were etiolated and unable to support their branches. Such trees quickly succumb to surface fires. Original-growth longleaf pines invariably have very narrow annual rings, the result of severe competition. Mature trees may reach 120 feet tall, 35 inches in dbh, and become 300-400 years old. Their principal branches are well spaced. Lightning is the usual cause of death. The probability is low of a longleaf pine surviving past about 250 years without being lightning-killed.

Original-growth longleaf pines are easily identified by the flattened or beveled appearance of the top of their crowns. The ultimate growth of the trunk is zigzagged, rather than straight, and the branches arising from this terminal portion produce the flattened aspect to the crown. Nearly all second-growth longleaf pines have straight trunks and rounded crowns. Some second-growth trees appear as if they are beginning to flatten out. These trees are restricted to severe habitats such as sandhills and particularly coastal sites where the trees are notably shorter than elsewhere.

Fire and Competition. The longleaf pine is the most fire-resistant tree in eastern North America. It survives surface fires regularly in the grass and growing stages. A dense growth of moist needles protects the terminal bud and young stem from fire. The bud is also protected by a covering of silvery scales. No other native tree survives fire as a seedling or young sapling. During the grass stage, the tap root becomes about 2-3 cm in diameter with a well developed bark just below the terminal bud. Upon entering the growing stage, the developing stem is already as thick as this root. The stem is protected from the heat of surface fires by the bark which is thick and flakey just beneath the portion bearing needles. The unusually thick stem may serve to prevent intense heat on one side from being transmitted across the stem to the other side.

The bark of a mature longleaf pine is thick and laminated. A student at Florida State University once removed a slab of bark from a mature tree, placed the bulb of a thermometer on one side, and exposed the other side to an acetylene torch for one minute. The temperature rose only 3^{o} F, explaining why surface fires do not girdle the trunks with heat.

If flames should leap into the crown of a tree, igniting the lower branches, the long distances between branches reduces the chances of the upper part of the crown from igniting. The extreme intolerance of competition assures wide spacing between trees. This spacing eliminates the possibility of a crown fire spreading through the canopy of a longleaf pine stand.

Wide spacing also allows considerable light to reach the undergrowth. Wiregrass and other flammable components of the ground cover thrive in this light. They constitute the fuel that carries surface fires over wide areas at intervals frequent enough to kill the seedlings of all other tree species. Competition-intolerance, in effect, is essential to promote the fires necessary to exclude trees of competitive species.

Fire not only kills seedlings of more competition-tolerant tree species, but it also exposes mineral soil on which longleaf pine seeds must fall for successful germination. Otherwise, the persistent wings of these seeds become suspended in the grasses. With moist conditions the seeds germinate and die without being able to reach the soil.

Harper (1943) stated that the eminent British geologist and colleague of Darwin, Sir Charles Lyell, was the first to recognize that longleaf pine forests owed their existence to fire. Lyell made this observation on a visit to Alabama in 1847. Harper (1911) added substance to Lyell's contention. He visited stands of longleaf pine in 200 southeastern counties and found evidence of fires in each of them. He estimated that the average lightning-set fire spread over several miles.

An additional benefit of fire is that it controls brown spot disease of longleaf pine needles. The causative agent is a fungus which spends part of its life in leaf litter which, of course, is able to accumulate only in the absence of fire (Chapman 1932). Fires do not reduce growth unless they cause needle-scorch, which delays growth until a new flush of needles appears (Wahlenberg 1946).

Original-growth Stands. There are various descriptions of the original longleaf pine stands. For example, Loughridge (1884) described the longleaf pinelands of southern and eastern Georgia as covering a vast plain on which the trees were spaced at 50-75 per acre, "with only here and there some undergrowth." Many photographs of such stands were published by Schwarz (1907), along with age-size relationships. Trees 60 years old were as little as 4 inches in dbh, demonstrating the extraordinary competition that well spaced trees provide each other. Trees 200 years old were only 18-32 inches in diameter. Penfound and Watkins (1937) described several virgin stands in Louisiana. On the average there were 114 trees per acre which provided 30% cover. The individual trees averaged 107 feet tall, 21.4 inches in dbh, and were 190-215 years old. Wahlenberg (1946) said that longleaf pine growing on a favorable site in Alabama were 12 inches in dbh at age 85, 15 inches at age 108, and 20 inches at age 150.

Second growth stands grow about twice as fast as the trees in virgin stands. A stand of second growth longleaf pine in Mississippi grew more wood in 80 years than was produced by a virgin stand about 200 years old (Fowells 1965). The quality of the second growth timber is lower, but the density of sound trees is higher in the second growth stands.

Wahlenberg (1946) noted that sapling longleaf pines in virgin stands grew rapidly following the logging. The larger the tree though, the less spectacular its growth upon release from competition. Many stands of second growth longleaf pines contain a few scattered flat-topped individuals which were not quite of merchantable size when the virgin growth was logged. These trees are often surpassed in both height and girth by those of the second growth, despite their greater age.

Root System. The longleaf pine produces a large tap root from which radiate several elongated lateral roots. Secondary tap roots or "sinkers" develop along these laterals. The fine "feeder" roots also arise from the laterals and proliferate just beneath the soil surface. Heyward (1933) studied the roots of longleaf pines in the arid sandhills of Calhoun County. He described one tree with a tap root 14 feet long and a lateral root 75 feet long. Saplings up to 30 inches tall had tap roots 3-9 feet long, their depth limited by the water table. This elaborate root system helps explain why longleaf pines often resist hurricane-force winds.

Wahlenberg (1946) said that the extension of the lateral roots caused root competition to be effective within a radius of about 30 feet on the average from a mature tree. In other words, two trees less than 60 feet apart would receive the effects of each other's competition. Chapman (1926) elaborated,

> "In every case where two or more trees stood close together, the seed production for trees of identical size and crown capacity dropped so far that a single isolated tree of this size would yield practically as much seed as the two together."

Hough et al. (1965) introduced a radioactive tracer (I-131) into a sandhill soil in a longleaf pine-turkey oak stand. The trees were monitored for gamma radiations, which would indicate whether or not their roots extended to the spot where I-131 was introduced. The results showed that longleaf pine roots extended as far as 55 feet and oak roots 48 feet from individual trees. They wrote,

> "Data from our study indicates that all pine trees between plot center and 17 feet had a connection with the source area. All oaks 15 feet of the point of application showed uptake. We also found that 50 percent of the

longleaf pine approximately 30 feet from plot center would be expected to be in contact with this spot, as would half of the turkey oaks about 23 feet away. Thus a seedling growing at plot center would be competing for water and nutrients with a very large number of trees."

Hodgkins and Nichols (1977) exposed lateral roots in longleaf pines on a loamy soil in Alabama. The average depth of the laterals was about 2-27 cm. Their lengths ranged from about 1-21 m. Isolated trees had longer laterals than those trees growing close together. The spread of individual laterals from the base of the tree was up to about 14 m. They observed that,

"Often, lateral roots were literally 'bent around' the main stems of neighboring trees."

They also observed that every square meter of soil contained the roots of several longleaf pines.

Hodgkins and Nichols (1977) noted that the laterals of trees 115-125 years old were only 40-50 years old. They suggested that there might be a cyclic renewal of the main laterals as has been demonstrated in certain fruit trees.

Seeds and Seedlings. Good seed crops are produced irregularly on the average of every 5-7 years. Bumper crops are needed to insure regeneration because wildlife consumes at least 99% of the seed (Wahlenberg 1946). The seeds fall from late September through December depending on latitude and generally germinate within one week (Fowells 1965). Gemmer et al. (1940) sowed seeds at a depth of one-half inch in different substrates and tallied germination. All seedlings died in both pine straw (needles) and oak leaves and only 4% survived on dry broomsedge. Survival was high on humus or ash derived from pine straw, oak leaves, or broomsedge. These results accentuate the need for fire to prepare the seedbed if germination is to be successful in natural stands.

In the western Florida sandhills, regeneration is made difficult owing to dry soils. Successful germination is accomplished if a wet year accompanies pollination and fertilization, a dry year follows that promotes seed formation, and a subsequent wet year allows germination and growth (Wahlenberg 1946).

In wet, sultry weather the seeds germinate before leaving the cone, thus destroying the entire crop (Mohr 1897). On clayey sites the root of the seedling may be too weak to penetrate the soil, thereby limiting the species to sandier soils (Wahlenberg 1946).

The cotyledon stage seedling is killed by fire. Since successful germination generally is preceded by fire that removes the ground cover, the chances are minimal that sufficient fuel could accumulate to carry fire when the seedlings were still in the cotyledon stage. Fire must be frequent, but not annual for effective regeneration. Grass stage longleaf pines can survive repeated annual fires, but annual burning inhibits them from entering the growing stage. On the other hand, complete fire suppression allows enough growth of other plants of the ground cover to inhibit the initiation of the growing stage. Competition-suppressed pines in the grass stage may survive for 20 years or more but eventually succumb (Chapman 1926, 1932, Garren 1943, Fowells 1965).

Pines in the grass stage are more sensitive to flooding than at later stages. Livestock can cause severe damage at the grass stage. A single hog in one day can eradicate the grass stage pines on an acre of land. Horses and cattle also damage one-year-old plants (Wahlenberg 1946).

Growth stage pines are also in some danger of fire. At a height of 18 inches they receive the hottest temperatures of the flames of a surface fire (Heyward 1939). If the terminal bud is heat-killed, the pine dies.

Wahlenberg (1946) noted that multi-aged stands of longleaf pine consist of patches of even-aged trees. Such patches suggest that successful germination occurred simultaneously, perhaps following a tornado or a multiple lightning strike of those pines that previously occupied the site. Clusters of lightning-killed pines are fairly commonly seen today.

Details of the anatomy, auxin physiology, and genetics of longleaf pine seedlings were given by Brown (1964).

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20. OTHER PINE SPECIES

Six additional pines are native to the panhandle besides longleaf pine. They often occur as dominant species in natural communities. These pines are:

Slash Pine	_Pinus elliottii_ Engelm.
Pond Pine	_Pinus serotina_ Michx.
Loblolly Pine	_Pinus taeda_ L.
Spruce Pine	_Pinus glabra_ Walt.
Sand Pine	_Pinus clausa_ (Chapm.) Vasey

None of these pines has a grass stage, rather, aerial growth of the stem begins within the first growing season after germination. The stem and bark of the young saplings are thin, allowing rapid heat transmission during fires. Unlike the smaller saplings of longleaf pine, those of the other pines tend to be branched, and their needles do not form a dense protective covering around the terminal buds and young stem. As a result, seedlings and saplings are unable to survive relatively cool surface fires until they are at least 1-2 m tall. Even though some saplings survive fire at that height, mortality and weakening from fire damage is relatively high.

In contrast to longleaf pine, the larger trees are moderately competition-tolerant and may grow in dense stands, often mixed with trees of other species. Their crowns are also more densely branched.

The bark of mature slash pine, pond pine, loblolly pine, and shortleaf pine is thick and flakey. This bark protects the larger trees of these species from the heat of fire just as in longleaf pine. The smaller trees and saplings, though, are less heat resistant than longleaf pines of comparable size. The bark of spruce pine and sand pine is thinner and tighter, making them much less fire tolerant than the others.

Slash Pine. The slash pine (called Cuban pine by some early authors) is native only on the coastal plain and ranges from southern South Carolina south into the Florida Keys and west through southern Alabama and Mississippi into southeastern Louisiana (Little 1971). Trees in southern peninsular Florida are segregated as *Pinus elliottii* var. *densa* Little & Dorman.

The native habitats of slash pine are obscured by its widespread invasion into disturbed habitats and into places where the natural fire frequency has been reduced by man's activities. Its invasion into cut-over longleaf pine flatwoods and into old fields will be documented in later chapters. It is the most commonly planted pine in commercial forests, even on xeric sandhills.

The early literature shows that slash pine formerly was restricted to moist habitats. Elliott (1824) wrote,

> "Along the marshes near the mouths of freshwater rivers, (at least in Georgia) this pine is very common....Grows in damp soils and those that are partially mingled with other forest trees."

Mohr (1897) wrote,

> "Groves of the Cuban Pine skirt the low shores of the numerous inlets and estuaries of these coasts, and cover the outlying islands. More or less associated

> with the Loblolly and Longleaf Pine, it forms a part of the timber growth of the open pine forests which grow in unbroken monotony over the flats for long distances. It is only in the lower part of Florida, where the tree extends from the Atlantic across to the Gulf of Mexico, south of Cape Canaveral and Biscayne Bay, that, as the only pine there, the Cuban Pine forms forests by itself. Toward the interior it occurs scattered among the varied growth of broad-leafed evergreens and cone-bearing trees which cover the swamps along streams."

He mentioned that slash pine never grows in alluvial bottoms. Roth (in Mohr 1897) said that between the Suwannee and Apalachicola rivers the slash pine comprises about 15% of the trees in flatwoods which otherwise consists essentially of longleaf pine. He said that slash pine forms a fringe along the Gulf coast of a few to several hundred yards in width.

These comments as well as personal observations suggest that slash pine is native to three general habitats in the panhandle. The first is the coastal pine flatwoods, including both scrubs and grassy areas on flats and in swales, both on barrier islands and bordering tidal marshes on the mainland. The second is the acid swamp environment, including the bay swamps and non-alluvial floodplains of streams. The third is the wetter portion of pine flatwoods and associated open seepage bogs, expecially near bay swamps and cypress strands. Wet or boggy flatwoods are particularly characteristic of the Tates Hell region of Franklin

County (Figure 15).

All three of these general habitat types are subjected to fire, but at less frequent intervals than in the pure longleaf pinelands. The small size of barrier islands and the irregularities of coastal topography (dunes, inlets, etc.) prevent lightning-set fires from spreading over wide areas, thereby reducing the fire frequency at any given site. Bay swamps experience crown fires at long intervals, usually killing all but the largest slash pines. Seeds from these evidently restock the site, as the hardwoods slowly coppice from their undamaged rootcrowns. The wet or boggy flatwoods are less likely to burn as evenly, as intensely, or even as frequently as do continuous but better drained flatwoods.

Sapling slash pines seem to tolerate fire better than those of all other pines except longleaf pine. I have seen slash pines about one meter tall that survived cool backfires with scarcely any needle-scorch.

Mature slash pines resemble longleaf pines in height, girth, and crown size. In flatwoods, growth is as slow as it is in longleaf pines. In bay swamps, growth is accelerated in spite of heavy competition and sterile acid, water-logged soils. Hebb and Clewell (1976) reported slash pines in a bay swamp in Wakulla County that were at least 38 cm in dbh and 30 m tall, but only about 85 years old. The largest were 64 cm in dbh, 37 m tall and undoubtedly older than 85 years.

Seeds fall in October and germinate in about two weeks. Seed production is heavy about every third year (Fowells 1965) at least in managed stands. My observations in natural stands suggest that seeding may be less frequent or at least irregular. Pessin (1938) showed that the survival and dry weights of slash pine seedlings were lower than those of longleaf pine in dry soil (5% soil moisture). In wet soil (35% soil moisture) the slash pine seedlings had double the weight of longleaf pine seedlings, and the survival was high for both species.

The root-spread of sapling slash pines is considerable. Pritchett and Robertson (1960) reported that the roots of two year old pines had a radius of up to about 19 feet and five year old saplings to about 32 feet. Sinker roots from the main laterals are commonly formed.

Fowells (1965) said that young seedlings and saplings suffer greatly from the competition of neighboring plants, both from older pines and from other vegetation. The degree of competition can be appreciated by the results of interplanting on a series of former agricultural fields in Georgia (Bennett 1954, Jones 1975). Slash pine seedlings were planted in rows 12-15 feet apart. The next year other rows were interplanted between the original rows. Eight years after interplanting, the initially planted pines averaged 5 inches in dbh and 28 feet tall. The interplanted pines were only 2.7 inches in dbh and 20 feet tall. They also suffered 9% mortality. After 25 years, the initially planted trees averaged 9 inches in dbh while the interplanted ones were only 5 inches in dbh.

The body of literature concerning slash pine in managed or commercial forests is enormous and will be reviewed in part in a later chapter on pine plantations. In great contrast, the published information on slash pine in natural communities is scanty.

Pond Pine. The pond pine ranges from southern New Jersey south to mid-peninsular Florida and westward into southeastern Alabama and throughout the Florida panhandle. Outlier populations are known from the

Piedmont of North Carolina and central Alabama (Little 1971). It grows in acid flats (pocosins) and in depressions where the soil is too poorly drained to support longleaf pine. The undergrowth is typically shrubby, often including titi (Cyrilla spp., Cliftonia monophylla), fetterbush (Lyonia lucida), large gallberry (Ilex coriacea), and wax myrtle (Myrica cerifera). Switch-cane (Arundinaria) may be common. Pond pine does not penetrate into the deeper portions of acid swamps where slash pine, sweetbay, or loblolly bay are dominant in the overstory. Instead, pond pine grows along the edges of such bay and slash pine swamps where fire is more common, the soil is not as peaty, and where drainage is slightly better.

Wendel et al. (1962) described pocosins containing pond pine from North Carolina with particular attention to the biomass of the undergrowth's flammability. Pond pine habitats burn at intervals of roughly 10-20 years. The nearly annual fires of contiguous longleaf pinelands are unable to spread into pond pine habitats, because the undergrowth ignites with difficulty and carries a fire poorly except under particularly favorable conditions for burning. These conditions include dry, windy, warm weather and at least several years' accumulation of fuel consisting of dense undergrowth and litter.

Once ignited under these conditions, a hot crown fire consumes the undergrowth, kills the shoots of any sapling pond pines, and often kills all but the largest branches of the more mature pond pines. After fire, the sapling pond pines coppice freely from the collar of their undamaged root systems. Dormant buds beneath the bark on the trunks of larger pines sprout after fire. Tufts of needles develop from these buds and sometimes cover much of the trunk. These needles assume an important photosynthetic role until new branches replace those that were fire-killed in the crown.

Pond pines produce an abundance of serotinous cones, i.e., cones that remain closed indefinitely until stimulated by heat to open and release their seeds. Edmisten (1965) heated 8-year-old cones at 130-140^{o}F. The cones opened in 15 minutes, releasing seeds with 75% viability. Edmisten cited the observation by Coker that viable seeds were recovered from cones twelve years old.

Fire is the source of heat in natural habitats. The seeds withstand considerable heat and remain viable even if their cones were badly charred (Fowells 1965). Germination is most successful after an intense fire that provides a clean seed bed.

Subsequent growth is best on mineral soil, particularly if it contains some silt or clay. Growth is inferior on peaty soils (Woodwell 1958). Wet soils impede growth. Shoot growth begins in the spring after the water table drops (Fowells 1965). Three months of continuous flooding permanently injures the roots (Hunt 1951). These observations explain why pond pine is restricted to the exterior edges of acid swamps. Interior portions are too peaty and wet for its site requirements.

Woodwell (1958) measured nutrient levels in pond pine habitats. His data suggest that ammonium produced by fungi was the primary source of nitrogen. He argued that the acidity was too high to support N-fixing bacteria. He also showed that levels of P, K, Ca, and Mg were much lower than in soils of nearby river swamps. He noted that P forms insoluble compounds with Fe and Al in highly acid soils such as those of pond pine habitats. He gave convincing, though indirect evidence that draining pond pine swamps removes the source of P, which otherwise maintains an equilibrium between an available form and an insoluble form.

Pond pines may attain a height of about 100 feet. They are often much smaller, reflecting poor site conditions and the interruptions in growth following fire.

Loblolly Pine. The loblolly pine grows from southern New Jersey through the coastal plain and Piedmont to mid-peninsular Florida and westward through nearly all of Georgia and Alabama, most of Mississippi and Louisiana, and parts of adjacent Tennesses, Arkansas, and eastern Texas (Little 1971). It occurs in many habitats from river bottoms to sandhills. It is so common on uplands today that one would expect that it is primarily an upland species. The older literature, though, shows that it was largely confined to bottomlands under original conditions.

Williams (1827) said that it grew in valleys. Mohr (1897) said that it grew "...scattered along the swamps bordering water courses." Forbes (1930) said,

> "Pure forests of virgin loblolly pine were never common, and are now found only in southeastern Texas and southeastern Arkansas on flatlands just above the overflow of the main streams."

Forbes said that loblolly pine was invading cut-over longleaf pine uplands. It also aggressively invades fallow agricultural fields throughout the coastal plain and adjacent interior provinces, more so on loams than sands.

Its primary natural habitats were the better drained sites on alluvial floodplains and in the bottomlands along the larger non-alluvial streams. In these sites, it generally grows with deciduous hardwoods, such as sweetgum and water oak. It may have been an incidental component of other natural plant communities, such as magnolia-beech hammocks and pine-oak-hickory woods, perhaps because of its propensity of colonize natural openings. Growth is rapid. Trees may attain a height of 120 feet in only 50 years. The largest individuals are about 63 inches in diameter and 151 feet tall.

Loblolly pine rarely grows intermixed with slash pine in natural habitats, even though both are important species in swamps dominated largely by hardwoods. Slash pine is restricted to the ponded acid swamps, and loblolly pine is restricted to the woods along more permanently flowing streams and rivers. Slash pine sometimes replaces loblolly pine in the intertidal river swamps. I have observed both pines growing together along the Blackwater and the Suwannee rivers, where the distinction between acid and alluvial habitat is unclear. Wherever they grow together near streams, loblolly pine generally occupies the sligntly lower sites where flooding is more frequent.

Seed production is variable from year to year (Fowells 1965), but cones are produced more regularly by loblolly pine than by longleaf pines and slash pines, at least in the panhandle. Seedfall occurs mostly from October through December, and germination follows shortly thereafter. The effective dispersal range is estimated to be 200-400 feet from the parent trees, and an instance was reported of dispersal of 2.5 miles (Chapman 1942, Bormann 1953, Fowells 1965).

Germination and survival are best on mineral soil in the absence of competition. Seedlings on upland sites are often summer-killed by drought. Cattle grazing has been known to remove the insulation afforded by grasses in open woods, exposing seedlings of loblolly pine to lethal summer temperatures (Chapman 1942). Presumably such hazzards would rarely occur in the native bottomland habitats of this species.

Saplings that become established under large hardwoods may persist for some years but eventually succumb to competition. Several authors have demonstrated that loblolly pine requires high light intensity and high soil moisture if it is to maintain any competitive advantage with hardwoods, e.g., Kozlowski (1949), Oosting and Kramer (1952), and Korstian and Bilan (1957). Kozlowski showed that oaks had higher rates of photosynthesis than did loblolly pines at all light intensities. Oaks grew larger root systems than did loblolly pines and were therefore more effective in obtaining water in droughts. Chapman (1942) further noted that the shallow roots of loblolly pines made them more susceptible to droughts than the more deeply rooted oaks.

In spite of its disadvantages, loblolly pine is still competitive with hardwoods. Oosting and Livingston (1964) reported that a stand of 35-year-old loblolly pines on a former agricultural field in North Carolina was destroyed by a crown fire. Coppicing hardwoods from the original understory threatened to overtake the loblolly pines that seeded-in following the fire. After 29 fire-free years, though, loblolly pine was dominant in the overstory. Six species of hardwoods and shortleaf pine also shared the overstory but all in low densities.

Chapman (1942) observed that the original longleaf pine stands in Louisiana lacked loblolly pines except occasionally along streams where the brush was less flammable. As usual, the longleaf pines were always found growing in practically pure stands. He noted that loblolly pines invaded the longleaf pine stands with fire exclusion and were able to survive subsequent fires once they were 8-10 years old, creating for the first time a mixed stand. Obviously the intervals between fires in the pure stands of longleaf pine must have been consistently less than 8 years to have excluded loblolly pine.

Chapman (1942) gave an example of the aggressiveness of loblolly pine over longleaf pine. A former longleaf pine woods had been logged and subsequently invaded both by loblolly pines and the usual complement of hardwoods. This young stand was fire-killed when the pines were 11 years old. The hardwoods coppiced, and seeds of three pine species (loblolly, longleaf, and shortleaf) germinated after the fire. When these were upwards to eight years old, the trees of all species were counted in a quadrat. Nine years later they were recounted. The percentages of survival during this nine-year span were as follows: longleaf pine 0%, loblolly pine 53%, shortleaf pine 75%, sweetgum 88%, and six additional hardwood species 93%.

Shortleaf Pine. The shortleaf pine ranges from Long Island to eastern Oklahoma and south to northern Florida and eastern Texas (Little 1971). In Florida it is essentially restricted to the Northern Highlands of the panhandle (Figure 15) on well drained loam soils. Shortleaf pine grows rather rapidly and may attain heights of 130 feet and diameters of 36 inches or more. It grows best in full sunlight and is moderately intolerant of competition. In dense stands it survives competition from other pines and hardwoods as long as the crown receives full sunlight.

Seedfall is mostly from late October through November. Most trees contain a prolific growth of cones every year, and excellent seed crops are attained regularly every 3-6 years. The average dispersal distance downwind from a parent tree is 250 feet and the maximum distance is one-quarter mile. Germination is delayed until early spring (Fowells 1965). Germination is best on mineral soil but may occur on litter. Grano (1949) noted the following numbers of seedlings of shortleaf and loblolly pines in Arkansas on milacre plots: 13.3 on pine litter, 2.9 on hardwood litter, and 3.2 in heavy grass. The litter averaged 1.3 inches deep on a site that had not been burned for at least 15 years.

Shortleaf pines tolerate surface fires, even as saplings. Young trees readily coppice from their root crowns if their tops are fire-killed. These pines retain this capacity to coppice until their twelth year (Chapman 1942) or until they reach 6-8 inches in diameter (Fowells 1965).

Shortleaf and loblolly pines often invade cut-over longleaf pine uplands and fallow agricultural fields. Sweetgum, various oaks, and other hardwoods invariably accompany these pines and form the undergrowth. Chapman (1942) said that shortleaf pine is more drought resistant than loblolly pine and is more abundant on drier sites. Shortleaf pine grows more slowly but in greater density than loblolly pine. These observations also apply to mixed stands of these pines at the Tall Timbers Research Station in Leon County. Chapman noted that young shortleaf pines survive fire by coppicing, while young loblolly pines escape fire by their more rapid height growth.

Schopmeyer (1939) conducted transpriation studies on these pines and concluded,

> "With soil moisture at the wilting coefficient, shortleaf pine had a higher transpiration rate, more total water, and a lower osmotic pressure than loblolly pine... Shortleaf pine absorbed more water from the soil and at the same time maintained a higher total water content in its leaves even when soil moisture was limited."

Spruce Pine. The spruce pine ranges from southern South Carolina into northern Florida and westward through southern Georgia, Alabama, Mississippi, and eastern Louisiana (Little 1971). It grows almost exclusively in dense mesic forests, often in association with magnolia. It uncommonly invades moist fallow fields, but only if seed trees are nearby. It is common on river bluffs and will invade into fire-suppressed longleaf pine sandhills bordering such bluffs. Trees growing on sandhill sites generally appear stressed.

The spruce pine is most unusual among pines because it is a component and sometimes a dominant in "climax" hammocks of southern mixed hardwoods. Unlike most pines, it seems to be entirely fire-intolerant and relatively competition-tolerant. Since the species has low economic value, little is known about it. The largest individuals reach about 125 feet tall. Cone production is usually prolific. Examinations of stumps and increment borings usually reveal extraordinarily wide growth rings, indicating rapid growth. Saplings survive under a dense canopy.

Perhaps the species is opportunistic, in that saplings survive in shade and then grow rapidly when an overstory tree falls, allowing light to penetrate the canopy. The extraordinarily dark green foliage suggests that spruce pine may be highly efficient at absorbing any available light for photosynthesis. Dial et al. (1976) noted that the survival of seedlings required mycorrhizal infection.

Sand Pine. The sand pine is native only to the central two-thirds of peninsular Florida and to the coastal strip (Figure 15) of the panhandle, including adjacent Baldwin County, Alabama (Little 1971). It occurs in dry sandy scrubs dominated by such undergrowth as sand-live oak (Quercus geminata), myrtle oak (Q. myrtifolia), and rosemary (Ceratiola ericoides). It also invades the longleaf pine-turkey oak sandhills if fire is excluded.

In peninsular Florida the cones are serotinous and their cones remain closed indefinitely until opened from the heat of fire. Seed viability decreases gradually with age. Cooper (1951) found 18% viability among seeds in cones 5 years old. Sand pine cones are not serotinous in the panhandle. The peninsular Florida variety with serotinous cones is called Ocala sand pine. The panhandle variety is called Choctawhatchee sand pine.

Germination may take place at any season. Seedling survival is assured only during the winter when soil temperatures are not excessive. Growth is quite rapid, and individuals may increase two feet in height annually if competition is minimal. The largest trees seldom exceed 75 feet tall and 26 inches in dbh. The trees are often short and scrubby with dense branches at ground level. Sand pines are relatively short-lived.

Fowells (1965) said that the, "stands tend to break up considerably after they reach 50 to 60 years old." Laessle (1958) mentioned a report of one sand pine 105 years old.

By that time, though, the stand, at least under natural conditions, would have been consumed by fire. Sand pines are very intolerant of fire. A hot surface fire which causes needle scorch is sufficient to kill them. The fuel in sand pine habitats is generally sparse and difficult to ignite. Fires are very infrequent. Once ignited, the sand pine is quite susceptible to damage because of its thin tight bark and its low branches that transmit flames into the upper branches.

Sand pine and spruce pine are nearly identical and scarcely distinguishable except by their strongly contrasting habitats. These habitats are very seldom contiguous and generally remote from each other, allowing the identification of these pines by habitat alone.

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21. SOME OAKS

Live Oak. The live oak, Quercus virginiana Mill., grows mostly on the coastal plain from Maryland to the Florida Keys westward through central Texas. It is also known from a few localities in Cuba, Oklahoma and northeastern Mexico (Little 1971). The closely related sand-live oak is usually treated as a variety, Q. virginiana var. maritima (Michx.) Sarg. It is treated here, though, as a separate species, Q. geminata.

Large live oaks are only about 40-50 feet tall but are immense in girth (6-7 feet in dbh) and crown spread (150 feet). Although the larger specimens appear as if they must be enormously old, it is doubtful that many such trees exceed 100-150 years. One tree 54 inches in diameter was only 67 years old (Fowells 1965).

Live oaks are not strictly evergreen as their vernacular name implies. The last season's leaves fall about 1-3 weeks before the new ones appear in early March.

Epiphytes are common in live oaks, especially Spanish moss (Tillandsia usneoides) and resurrection fern (Polypodium polypodioides). Factors favoring epiphytes likely include the exceptionally rough bark. Seeds become lodged in the furrows rather than sliding off. Needed moisture is retained after rains by this bark, and the umbrella-like canopy traps humidity nearly year-around. The horizontal branches allow considerable surface for colonization without crowding.

Live oaks are fire-killed when young, but the older saplings and young trees coppice profusely when damaged either by fire or mechanically. Once established, live oaks are exceptionally difficult to destroy. The shadows cast by the densely leafy and wide-spreading crowns of larger trees preclude grasses or other undergrowth that could carry fires beneath the tree. Live oak, then, has two defenses against fire: coppicing when young and eliminating flammable undergrowth by its shade.

Live oaks occur on moderately to well drained soils and are intolerant of flooded conditions.

Wharton (1977) reviewed an unpublished manuscript written by H. L. Stoddard, Sr., in 1955. Stoddard said that many magnificent live oaks bordering lakes in northern Florida were destroyed by several feet of water which was held for over a year following 27 inches of rain in the spring of 1948.

Live oaks occur in many habitats and in association with many plant communities. It has been my observation, though, that there are only three basic environments in which it likely occurred under original conditions. First, it forms a ring bordering lakes, ponds, sinkholes, wet prairies, and other depressions. This border separates the upland vegetation (often longleaf pine-turkey oak) from the wetland vegetation. This ring of live oaks lies above the highest water level expected during a year with average rainfall.

Second, live oaks are common in coastal hammocks of slash pine, southern red cedar, cabbage palm, and sometimes magnolia, diamond-leaf oak, and other hardwoods. These hammocks typically form a narrow border along the interior edges of salt marshes or along protected shores and sloughs.

Third, live oaks occur occasionally on high levees on floodplains and near the upper edge of river bluffs and slopes.

All three of these environments represent ecotones between contrasting plant communities. They also occur at a point where there is a change in elevation. Presumably live oaks could be components in other relatively fire-free habitats with moderately drained soils, particularly hammocks of southern mixed hardwoods. Wherever live oak occurs in such hammocks, there are often evidences of disturbance. An example is the hammock along the east side of the Wakulla River at the bridge of SR 365. Records from the Florida Division of Archives, History, and Records Management indicate evidences of a settlement there, probably dating to Territorial days.

The spread of live oak in the wake of man's activities has been well documented. Heyward (1939) spoke of its invasion into longleaf pinelands after fire exclusion. Laessle and Monk (1961) demonstrated its invasion into scrubs. In all eight stands that they examined in northeastern Florida, all were protected from frequent fires by roads, fields, parks, or bodies of water. Live oaks are commonly seen on former agricultural fields, along old fence rows and at former home sites. Many of these oaks serve as shade trees in yards after subdivisions are built in formerly rural areas.

Scrub Oaks. There are seven species of oaks in the panhandle that are loosely called "scrub oaks". They are:

Quercus geminata Small --- Sand-live oak (abundant in coastal scrubs on dunes and beach ridges; rare inland).

Quercus myrtifolia Willd. --- Myrtle oak (abundant in coastal scrubs on dunes and beach ridges).

Quercus chapmanii Sarg. --- Chapman oak (uncommon in coastal scrubs)

Quercus marilandica Muenchn. --- Blackjack oak (Pine-oak-hickory woods on dry ridges with clayey subsoils; rare in Florida).

Quercus laevis Walt. --- Turkey oak, also locally called blackjack oak in Florida (abundant on sandhills in association with longleaf pine).

Quercus incana Bartr. --- Bluejack oak (rather common on sandhills in association with longleaf pine).

Quercus margaretta Ashe --- Sand-post oak (occasional on sandhills and in dry pine-oak-hickory woods).

All of the scrub oaks grow in xeric habitats. All are shrubs or small trees. Individuals exceeding eight inches in diameter or 30 feet tall are exceptionally large. Turkey oaks are known to exceed 60 feet, but such specimens are very rare.

The term "scrub oak" refers only to the habit of the plant and does not infer that the plant is necessarily a component of "scrub" vegetation, such as the sand pine scrub community.

Garren (1943) said that scrub oaks are seldom fire-killed. They show a remarkable ability to continue sprouting when the tops are burned back by repeated fires.

Sand-live oak is distinguished from live oak by its smaller stature, its strongly revolute leaves, and its paired acorns (live oak has acorns borne singly on the peduncle). There is some morphological overlap between these species, making identification difficult. This overlap may be the result of hybridization, or perhaps these species have never been entirely separated from each other in an evolutionary sense. Difficulties in distinguishing them have led most authors to consider them as varieties of the same species. I am recognizing them as separate species for their different habitat preferences which complement their morphological differences. Any taxonomic decision with regard to these oaks is necessarily arbitrary.[1]

Sand-live oak sometimes grows side-by-side with live oaks, for example, where the scrubs of low dune fields grade into coastal hammocks near the leeward shore of barrier islands. Sand-live oaks (or intergrades between sand-live oak and live oak) occur uncommonly in the Woodville Karst Plain (Figure 15) encircling sandhill ponds. Other sand-live oaks occur as scattered populations in the coastal lowlands. At least some of these populations are associated with the Pamlico shoreline (Figure 22) and may be relics that have persisted since Sangamon times.

Kurz (1939, 1942) noted that sand-live oaks have the ability to proliferate by adventitious growth if drifting sands accumulate beneath them. Kurz (1942) wrote,

> "If the burial is slow and begins early in the life of the oak when the branches are still small, the oak will send out subterranean running stems which emerge vertically as new shoots. These shoots by indefinite branching and production of roots may, in reaction to sand covering, spread and grow indefinitely and form a large complexity of partly buried, partly exposed shurb or thicket. Detachment of any surviving part makes a new plant."

[1]There are many other instances of such taxonomic value judgements in the delimitation of the species in our flora, more than are generally realized. The taxonomist cannot recognize too many entities as separate species, lest identification becomes inordinately difficult. On the other hand, lumping these biologically distinct entities into a single species masks important biological differences, including ecological responses. For these reasons, most any system of classification represents from necessity an uncomfortable balance between biology and utility.

The adventitious roots, borne from stems, insures that the root system is within the well oxygenated portion of the soil.

Turkey oak is by far the most abundant of the scrub oaks of sandhills. The others, bluejack oak and sand-post oak, are unable to tolerate the drier sandhill sites (Wells and Shunk 1931). Sand-post oak is fairly common on sandhills near river bluffs, where the water table is not especially deep.

Leaf litter is sparse on sandhills, probably from the combined effects of slowly growing vegetation, low biomass and the rapid removal of litter by fire or decomposition. As a result, the white sandy surface of the mineral soil is often exposed. The reflection of sunlight from this surface adds to the light that directly strikes the leaves. It is assumed that this excessive light increases the transpirational loss of water and perhaps causes other physiological stress. Turkey oak minimizes exposure both to sunlight and reflected light by holding its leaves more or less vertically. The effectiveness of this orientation was demonstrated by Wells and Shunk (1931), who wired some leaves in a horizontal position. These leaves became chlorotic, an indication of physiological stress.

In spite of the excessively drained soils of sandhills, the roots of turkey oaks grow largely within a few inches of the surface. Woods (1957) suggested several reasons. He said that rain of up to 0.4 inches only penetrated the upper three inches of the soil, leaving the subsoil relatively dry. He noted that winter soil temperatures were up to 10° F warmer near the surface than at greater depths. He said that the higher temperatures favored root growth, which is considerable during the winter. He also demonstrated higher levels of nutrients (Ca and N) in superficial soils. These nutrients were held just below the surface by a shallow layer of humus derived largely from the decomposed roots of wiregrass.

Many sandhills are covered by essentially pure stands of turkey oak. The earlier literature makes clear that such sites once contained an open overstory of longleaf pines. Once logged, the pines were unable to become reestablished, mainly for lack of an adequate seed source. With the removal of the pines, the turkey oaks increased in density (Stoddard 1931, Pessin 1933, Bozeman 1971). This increase in density suggests that longleaf pine, in spite of its intolerance to competition, maintained a competitive advantage over turkey oaks in the original-growth stands. Turkey oaks also occur occasionally in sand pine scrubs. Webber (1945) observed that turkey oaks were not characteristic of the original growth, but entered following disturbance by man.

Runner Oaks. There are two stoloniferous oaks in the panhandle, *Quercus pumila* Walt. (running oak), and *Q. minima* (Sarg.) Small (dwarf-live oak). Both are common in the undergrowth of pine-palmetto flatwoods. They may attain a height of about 6-8 feet if kept fire-free, but they are typically 1-3 feet tall. Both grow from thick, elongated, branching stolons that lie just beneath the surface of the mineral soil. Aerial shoots arise from these stolons at frequent intervals, forming dense patches. These shoots are fire-killed, but new ones readily coppice after each fire. An individual plant of runner oak enlarges not so much in height and diameter but rather by the proliferation of its stolons.

Laurel Oak and Diamond-leaf Oak. Authors traditionally have recognized *Quercus laurifolia* Michx. as an overstory tree of floodplains and bluffs. It is commonly called laurel oak (Fowells 1965, Little 1971). Those laurel oaks on bluffs usually occur only on the best drained sites and are separated ecologically from the laurel oaks on the floodplain below. Those on the bluff have small acorns and narrow, mostly mucro-tipped leaves. The floodplain trees have larger acorns and broader leaves that mostly lack mucro-tips.

The oaks on the bluffs have been recognized by some authors as a separate species, *Q. hemisphaerica* Bartr. If two species are recognized, *Q. hemisphaerica* is called laurel oak, and the bottomland species, *Q. laurifolia*, is called diamond-leaf oak (Kurz and Godfrey 1962). I am recognizing both species for much the same reasons that I recognize sand-live oak as being distinct from live oak.

Diamond-leaf oak is restricted to bottomlands where the soil is occasionally flooded but never for extended periods. Laurel oak is a tree of well drained soils. It was probably restricted largely to high bluffs in the original forests, but it has spread aggressively following disturbance by man into many upland sites that are essentially fire-free. It has also invaded mesic to xeric stands of longleaf pine from which fire has been excluded for many years.

Stool Sprouts. Merz and Boyce (1956) noted that many oaks in southern Ohio appeared to be seedlings but were actually much older. They removed 100 oaks upwards to 4.5 feet tall and counted annual rings in the shoots and roots. Only 12 oaks were true seedlings or young saplings. The rest had older roots than shoots. One six-year-old shoot had 37-year-old roots. The site had no history of fire, so that coppicing following fire was not involved. Instead, the shoots died back every few years. New sprouts arose from the root collar and are called stool sprouts.

Stool sprouts in oaks or other genera have not been reported in Florida but could be expected in hardwoods forests on bluffs and other fire-protected sites. Potentially, stool-sprouting could be an important mechanism in the gradual increase of one species over another in "climax" forests. This mechanism may work in the following manner.

It is assumed that light intensities beneath a closed canopy are so low that a spindly sapling a few feet tall receives about as much light as a seedling. The sapling requires much of its photosynthate for the maintenance of its shoot, and little is available for the roots. As a result, root growth is slow and the storage of carbohydrate in the roots is minimal.

A sapling that periodically dies back to its root collar and subsequently stool-sprouts can utilize a greater proportion of its photosynthate in enlarging its roots and perhaps even storing carbohydrates in them. When an overstory tree falls, allowing light to reach the forest floor, the stool sprout will grow faster than the sapling because of its larger root system and carbohydrate reserve. It will overtake the sapling and any seedlings that may have just sprouted. Eventually it will reach the overstory, replacing the tree that fell. If the tree that fell was of a species incapable of stool-sprouting, that species' importance in the forest can be expected to wane in relation to those species which have stool-sprouting capacities.

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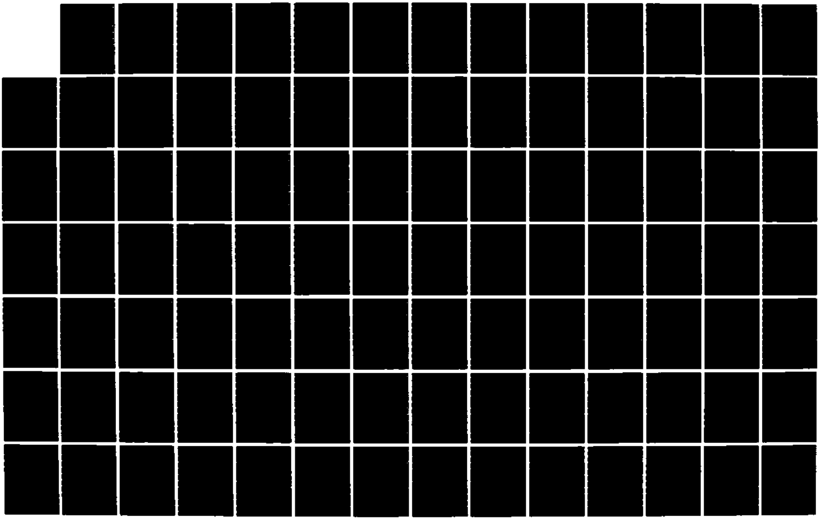

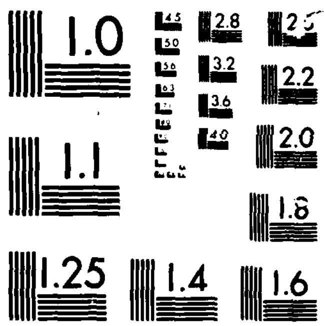

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22. THE MAGNOLIAS

There are six species of the genus, Magnolia, native to the panhandle (Little 1971, 1977). The southern magnolia and sweetbay are evergreen and are of major importance ecologically. The other four are deciduous species which grow in mesic hardwood forests on bluffs and ravines from the Ochlockonee River westward. They are M. ashei Weatherby, M. cordata Michx., M. pyramidata Bartr., and M. tripetala L. These deciduous species are of little consequence ecologically and will not be considered further.

Southern Magnolia. The southern magnolia or bull-bay, M. grandiflora L., is often called simply "magnolia", as is the practice in this manuscript. It ranges on the coastal plain from North Carolina south to mid-peninsular Florida and westward into eastern Texas. The larger trees are at least 60-80 feet tall, 2-3 feet in girth, and 80-120 years old (Fowells 1965). Age is difficult to determine because of the occurrence of false annual rings (Flanders 1950).

Magnolias grow in all habitats wherever fire is light or absent and moisture conditions are within a broadly mesic range. In most undisturbed sites of this description, the magnolia is the most abundant tree of the overstory. It is probably the most important dominant in the southern mixed hardwood community of the panhandle. It is not necessarily a dominant species in every stand belonging to this forest community. Nonetheless, magnolia is usually abundant in virgin stands, suggesting that in time, it may increase in abundance at the expense of other tree species.

Magnolia has tight, thin bark which likely explains its sensitivity to fire. Saplings coppice from their roots after the shoots are destroyed by fire, and Blaisdell et al. (1973) reported an instance where saplings 12-15 years old survived fire entirely. Coppicing magnolias are absent from sites that are frequently or annually burned. Unlike many oaks and other hardwoods, magnolia evidently is unable to coppice repeatedly after frequent fires.

Large trees, though, are able to tolerate light annual surface fires indefinitely, as was demonstrated at the Greenwood Plantation in Thomas County, Georgia. An open pine-oak-hickory woods evidently was kept fire-free long enough for the invasion of magnolia and beech. About the time these trees entered the overstory, annual burning was introduced in this stand. After 19 years of annual burning, these trees were vigorous but conspicuously fire-scarred at the base, beech more so than magnolia.

Larger trees of magnolia often produce a sprout at the point where the trunk emerges from the soil. In a few years these sprouts may attain the size of large saplings with a girth of several cm while attached to the parent tree. Presumably these sprouts develop their own root systems. When the parent tree dies, the sprout becomes independent. Its size gives it considerable advantage over any other seedlings or saplings in replacing the parent magnolia in the overstory. The soil next to medium-sized magnolias sometimes bears a faint ring of organic matter, indicating the position of the parent tree from which the present magnolia was formed vegetatively. This medium-sized magnolia may soon form its own basal sprout, thereby initiating a second vegetative generation. This process could continue indefinitely in an undisturbed forest. The seed which initiated this sequence may have germinated many centuries previously. Basal sprouts, though, are usually seen on a minority of the larger magnolias in any given stand, suggesting that sexual reproduction is of greater importance in perpetuating the stand.

The showy flowers of magnolia each produce a large, woody, cone-like aggregate of follicles. Each follicle dehisces upon maturity, exposing a large seed with a bright red, pulpy seed coat. The seed is retained only by a short, thread-like connection to the follicle. Birds consume these seeds in quantity, passing the indurated portion containing the embryo through their digestive tracts unharmed (Blaisdell et al. 1973). Evans (1933) reported that seeds retaining their pulpy seed coats were often destroyed by fungi. This observation suggests that the removal of the seed coat by digestion by animals may be obligatory for germination. The cones fall and slowly decompose through the sequential colonization by fungi, arthropods, and other organisms that collectively comprise a miniature heterotrophic sere.

Successful germination only occurs in the shade on a soil containing leaf litter. Magnolia seedlings usually do not appear on fallow fields until after a canopy of young pines has already developed. Sweetgum, oaks, and other hardwoods typically have already formed an understory in such stands by the time the magnolia seedlings appear. Magnolia is absent from open, annually burned pine woods. At the Tall Timbers Research Station, plots were established in such pinelands, and fire was excluded thereafter. Magnolia seedlings began to appear in these plots about 12 years later. These plots contained a dense tall thicket of oaks and other hardwoods which had survived by coppicing previous to the period of fire-exclusion. That magnolia seedlings are able to compete in these thickets is testimony for the extraordinary competitive ability of the species. The fact that magnolia seeds germinate only in decomposing leaf litter suggests that the seedlings may depend on a mycorrhizal association for their survival, but such a possibility has not been researched.

Even though seeds are produced in abundance and are widely dispersed by birds, germination is erratic (Fowells 1965). Kurz (1944) noted that magnolia seedlings never occur beneath mature magnolia trees. Little else grows beneath magnolia, although Kurz noted that seedlings of beech (Fagus grandifolia Ehrh.) were an exception. Kurz suggested that the deep shade beneath magnolia trees was a factor which precluded plant growth, and that the litter of the large coriaceous magnolia leaves mechanically interferred with germination. Preliminary investigations by students engaged in term projects suggested the possibility of a strong inhibitor being leached from magnolia leaves. Blaisdell et al. (1973) noted that magnolia seedlings did not appear after the selective cutting of a magnolia hammock until 20 years later, suggesting that it took that long for an allelopathic substance produced by magnolia trees to become leached or detoxified. The evidence for the production of an allelopathic substance is indirect and needs verification.

The inability of magnolia to reproduce by seed under its own cover appears to be overcome by its ability to sprout vegetatively and to germinate and grow in competition with overstory trees of other species. The seedlings of magnolia and beech seem to be able to withstand the competition of overstory trees better than those of any other tree species.

Kurz (1944) and Blaisdell et al. (1973) suggested that these two species are therefore the most important in the mesic hardwood forests of the panhandle. From my own experience, this possibility seems likely in the ravines of the Northern Highlands but may not hold for steep river bluffs or for hammocks in the coastal lowlands. The resolution of this question may come with the discovery and analysis of more undisturbed stands containing these species.

Kurz (1942) reported that magnolia is the most important dominant of coastal hammocks, which he considered to represent a climax community. He demonstrated that magnolias responded to partial burial from moving dunes by the production of adventitious roots along the buried trunks and branches and by the production of stoloniferous shoots from buried branches. This response is similar to that of sand-live oak, reported in the previous chapter, and to several other trees of coastal hammocks as noted by Kurz (1942).

Sweetbay. The sweetbay, Magnolia virginiana L., generally occurs from Long Island south nearly to the Florida Keys and west into Texas with extensions or outlying populations into the interior portions of the southeastern states and some isolated pockets as far north as Connecticut (Little 1971). The trees may grow to about 80 feet tall and 3 feet in girth.

Sweetbay is often a dominant species in an array of hydric habitats that rarely experience fire. In this regard, sweetbay is the ecological equivalent of southern magnolia in habitats too wet for the latter. At least the younger trees are able to coppice following a crown fire and probably the older as well. The larger trees sometimes produce basal sprouts comparable to those formed by southern magnolia.

The sweetbay reaches its greatest abundance in acid, peaty, poorly drained swamps. It is also common in hydric depressions of southern mixed hardwood forests and in backswamps on floodplains.

In titi swamps, bogs, and other habitats where fire is somewhat frequent, sweetbay survives by coppicing, but shoot growth is generally slower than that of other associated woody species. Trees in such habitats are essentially stunted by reoccurring fires.

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23. WIREGRASS

Range and Common Names. Wiregrass, *Aristida stricta* Michx., ranges on the coastal plain from southeastern North Carolina south to the Everglades in Florida and westward through the panhandle and adjacent southern Georgia and southern Alabama to coastal Mississippi. Two other grasses are called wiregrass, *Sporobolus junceus* (Michx.) Kunth and *Muhlenbergia capillaris* (Lam.) Trin. (The latter includes plants identifiable as *M. expansa*.) These grasses grow in the same habitats as *Aristida stricta* but are nearly always much less common, at least in the panhandle. *Aristida stricta* is often designated by the awkward common name, pineland three-awn, which does not apply to the other wiregrasses. In this manuscript the name, wiregrass, applies only to *A. stricta*.

Habit. Wiregrass is a cespitose perennial or bunch grass which arises from a clump that is up to about 15 cm across at the base. The narrow blades are strongly involuted so that they appear round, rather than flat (thus the name, wiregrass). Hundreds of leaves may arise from a single plant (clump). The leaves may attain a length of 5 dm, but they arch, making the plant only about half that tall. The leaves are highly sclerenchymatous (Wells and Shunk 1931). Parrott (1967) reported that 85% of the leaves die within 12 months of their formation. The leaf dies back progressively from the apex. Dead leaves are not shed for at least a year or two, but persist in place within the clump. The sclerenchymatous nature of the leaves, their abundance, and the persistence of dead leaves makes the plant highly flammable. These features also make the plant rather impalatable to grazing animals, except during the first six weeks or so of new growth following a fire, while the leaves are still tender and all alive.

The roots are wiry and often very dense. Parrott (1967) said that they may reach a depth of 18 inches but that 55-60% of the root biomass lies within the upper 2 inches of the soil.

A small clump of wiregrass consists of a solid growth of tillers (shoots). As the clump expands in diameter, the central portion dies, making the clump doughnut-shaped. The soil of the central portion is peaty from the dead remains of roots and tillers. With continued expansion to a diameter of about 15 cm, the "doughnut" begins to fragment. Each isolated fragment is now a small clump which has the potential to expand and form its own "doughnut". Such growth probably takes years and represents a very slow mode of vegetative propagation. No other method of asexual reproduction is known for wiregrass.

Woods et al. (1959) studied wiregrass in the sandhills of the Chipola Experimental Forest in Calhoun County. They reported that carbohydrate reserves in the roots were highest in February and lowest in mid-July. Nitrogen reserves in the roots dropped sharply in September and gradually accumulated thereafter.

Populations and Competition. A remarkable feature of wiregrass is that wherever it grows without disturbance, it is always uniformly dense. Quadrat studies in the Apalachicola National Forest (Research Summary 11) showed a consistent density of 5 plants ("doughnuts") per square meter, regardless of the degree of tree cover or soil moisture. This density is maintained right up to the very edge of its geographic limit of distribution. It reaches this limit in the longleaf pinelands of northwestern Escambia

County, where other grasses abruptly replace wiregrass beneath these pines. Up to that edge, though, wiregrass retains its usual high density.

This density assures that the roots of neighboring clumps of wiregrass are intermingled. It also guarantees that the mature leaves of any given clump overlap with those of its neighboring clumps, facilitating the even spread of surface fires.

Observations in a virgin stand of longleaf pine at Greenwood Plantation, Thomas County, Georgia, revealed that hardwood seedlings or coppicing sprouts were absent from the undisturbed turf of wiregrass. One or more sprouts, though, were common wherever a clump of wiregrass had been killed or removed. One would assume that the removal of one clump of wiregrass would not reduce the effectiveness of fire in killing the seedlings of invading hardwoods. Therefore, it is possible that the competition afforded by the overlapping roots of wiregrass plants may contribute to the exclusion of hardwoods.

Wells and Shunk (1931) also suggested that wiregrass roots effected strong competition with other species. They wrote,

> "Anywhere in sandhills where weed vegetation has invaded old fields bordering wiregrass with bare areas between tussocks, no weeds appear, even during rainy seasons during which thousands of weeds sprout a few feet away on the old field."

They suggested that there was competition for nutrients in that instance, but they also speculated that the comp tition might be for water in xeric sites. During droughts, the superficial root system of wiregrass would absorb the water from infrequent showers without allowing water to percolate deeper, where the roots of most other plants are located. The lower soil horizons are drier than the upper horizon (Woods 1957).

Woods (1958) also showed that wiregrass, rather than turkey oak, was responsible for the removal of water by transpiration from droughty sandhill soils at the Chipola Experimental Forest. He noted that it took 15 rainless days for the soil moisture to drop from 8% (slightly above field capacity) to the wilting point (1.5 - 1.9%) in natural stands of longleaf pine-turkey oak-wiregrass. In a plot where the turkey oaks were deadened by herbicides, the same reduction in soil moisture also took 15 days, demonstrating that turkey oaks were inconsequential in removing water by transpiration. But on plots where at least half of the wiregrass had been removed by plowing furrows, it took 23 days for the soil moisture to reach the wilting point. This result shows that wiregrass effectively removes water from the soil by transpiration. Woods (1958) estimated that it would take 30 days for the soil to reach the wilting point if wiregrass were entirely eliminated. He continued,

> "On denuded areas. soil moisture in the first foot remained well above the wilting range even during the most extended droughts. This was true despite the fact that the moisture-retention capacity of the undisturbed plots was greater than that of the denuded plots, apparently because of the higher organic matter content."

One wonders how wiregrass is able to survive on dry sandhills during prolonged droughts. One possibility that lacks verification is that the copious blades are constructed for the efficient collection of dew. Some dew is probably absorbed directly by the leaves. Other droplets are encouraged to flow down the [illegible]ing leaves to the base of the clump where the superficial roots [illegible]rb this moisture.

Wiregrass is native not only to sandhills but also to pine flatwoods, open bogs, and savannahs. The great majority of the panhandle was once covered by these vegetation types. It is probable that wiregrass has a greater coverage than any other species in the panhandle. Because of the abundance of flammable wiregrass, these habitats were subjected to nearly annual surface fires.

Fire suppression in recent years, though, has weakened or eliminated wiregrass from some sites. Beckwith (1967) reported no wiregrass in a longleaf pine woods at Chinsegut Hill, Hernando County, Florida from which fire had been excluded for 34 years. The relatively clayey soil promoted the rapid growth of understory hardwoods which presumably eliminated wiregrass. It can only be surmised that wiregrass occurred there from its presence elsewhere in the longleaf pinelands in that vicinity.

Hardwoods were unable to invade a pine flatwoods at the Olustee Experimental Forest, Columbia County, Florida after 25 years of fire exclusion because of the sterile, sandy soil. Nonetheless, foreman John Perry (personal communication) said that wiregrass was not evident beneath the rough of saw palmetto and gallberry. A few weeks after fire, though, wiregrass, sprouting from previously dormant tussocks, covered the site.

Wiregrass was suppressed in a stand of longleaf pine five miles north of Monticello, Jefferson County (Research Summary 10). Fire had been excluded for 17-20 years, and hardwood undergrowth was fairly dense on the relatively fertile sandy loam soil. In the deepest shade, a few wiregrass tussocks contained one or few living blades. A fire in such a stand theoretically could eliminate wiregrass. The intense heat from the unusual accumulation of fuel would heat the superficial layer of soil which contains the wiregrass roots. Embers might ignite the peaty centers of the "doughnuts", allowing a smouldering fire to come into direct contact with the already weakened roots.

Soil Moisture. At the Caloosa Experimental Range in southern Florida, Parrott (1967) observed wiregrass along transects which went from moist to wet soils. He noted over a two year period that wiregrass grew in soils in which the water table was continuously within two inches of the soil surface for up to 114 days. He transplanted wiregrass clumps into a sloping tank with the lower end immersed in water. Where the water table remained within two inches of the soil surface, all plants died within 200 days. Where it remained 2-5 inches below the surface, some plants survived. Where the water table was deeper, all plants survived.

Parrott (1967) noted that wiregrass plants were elevated on tussocks about 4 inches tall in wet sites. I have seen similar tussocks and observed that they were formed from earthworm castings which are deposited and accumulate in the centers of clumps of wiregrass (Clewell 1971). Wiregrass roots developing in these tussocks would be aerated. If there were a gradual rise in the water table, wiregrass would be able to survive at lower elevations than would be expected through this mechanism.

The elevation at which wiregrass is limited by excessive soil moisture is sharp and distinctive. The contiguous vegetation on the wetter sites is usually of titi or other acid swamp species. Fires burn through the wiregrass to the edge of these swamps but are unable to carry into the poorly burning titi, except under unusually favorable conditions. Titi and associated species are unable to invade into the wiregrass lands because of the frequent fires. As a result of fire limiting the titi and the soil moisture limiting the wiregrass, the distinction between wiregrass lands and acid swamps is usually sharp, essentially without an ecotone.

Sexual Reproduction. Parrott (1967) noted that inflorescences were produced only following fire, defoliation, or minor soil disturbance. Defoliation could be effected by grazing, but the probability is low that a grazing animal would defoliate a fibrous plant of wiregrass with its many dead leaves. Grazing is common only after fire, which in itself is a method of defoliation that would have already stimulated floral induction. There is no natural mechanism for soil disturbance in wiregrass lands with the possible exception of the burrowing of gopher turtles.

Anthesis occurs 5-9 months following burning, defoliation or disturbance, but the flowers are rarely perfect and almost never produce seeds. Parrott (1967) performed a number of experiments involving floral induction with conflicting results. His data suggest, though, that the temperature and photoperiod must be satisfactory if perfect flowers and seeds are to be produced. The details are complicated by the unequal responses of plants from different geographic areas, suggesting genetic differences. He never observed perfect flowers at the Caloosa range, except once following a fire in July and again following defoliation in September. No seeds were produced, though.

The lack of seed production is emphasized in floristic manuals. Small (1933) did not describe the seeds of wiregrass. Radford et al. (1968) examined specimens from 39 counties in the Carolinas but said that the grain was not seen. The species is represented by specimens from 13 Florida counties in the Herbarium of Florida State University. None have seeds. Fifty specimens of wiregrass in the Herbarium of the Missouri Botanical Garden all lack seeds.

To my knowledge, the only occurrences of seeds are as follows. In 1955 Q. Kyle (Clewell 1971) observed wiregrass in the Apalachicola National Forest with the inflorescences bent over, presumably from the weight of seeds. Doves were numerous and were presumably feeding on these seeds. The inflorescences were produced following an early summer fire. Parrott (1967) found seeds in several populations in North Carolina. Floral induction was stimulated by fires in several months, both summer and winter. In 1975 Bruce Means discovered seeds in Bay County, Florida on a site that had been summer burned. I germinated some of these seeds on moist filter paper. In 1977 seeds were collected by personnel at the St. Marks National Wildlife Refuge, again following a summer fire. This site is under observation for seedlings (Joe White, personal communication). Finally, I collected fruiting specimens at Torreya State Park in November, 1977, which had developed subsequent to a summer fire. All of the seeds had been destroyed by a fungus whose black spores filled all space within the seed coat.

No seedlings have ever been reported in the field.* Woods (1959) said that wiregrass normally propagates vegetatively, but will increase in abundance after seeds are produced following fire. All evidence suggests that this was merely unfounded speculation. Since 1962 I have asked many individuals if they have ever seen wiregrass reproducing in the field. None gave affirmative replies, and these individuals included

*After this chapter was written, seedlings were reported at the St. Marks Refuge site, mentioned above. See pages 646-648 for details.

botanists, ecologists, range specialists, wildlife specialists, foresters, SCS personnel, surveyors, anthropologists, and overseers of game plantations.

Parrott (1967) ran several germination experiments. He found that germination was effected both in the light and in the dark. At least 75% of the seeds germinated that were placed in dry sand and exposed to a temperature of 248°F for 800 minutes. Seeds placed in wet sand likewise germinated after exposure to 212°F for 10 minutes, but the percentage of germination dropped sharply if either the temperature or the time were increased. It took 127 days for 3-month-old seeds to germinate on moist filter paper, and the germination percentage ranged from 2-33%, depending on the population from which the seeds were obtained. One-year-old seeds germinated in 15 days with the germination percentage at 60-97%, depending on the population.

From the preceeding discussion, it seems probable that sexual reproduction in wiregrass is dependent upon sequential criteria, all of which must be met. They are: 1) Summer fire (at least in Florida) which stimulates the production of inflorescences with perfect flowers. 2) An unknown event that allows perfect flowers to develop viable seeds, perhaps a weather-dependent pollination mechanism. 3) After-ripening of the seeds for most or all of a year. It is possible that after-ripening may be speeded by the heat of a fire, as suggested by Parrott's findings on the heat tolerance of the seeds. 4) Mid-summer temperatures at the time of germination.

This sequence of events would only occur in its entirety at irregular intervals. Even then the seeds may be consumed by herbivores. Once a site becomes colonized by seedlings and these mature into larger plants, there is no agency in the natural environment that could cause their demise. There would be no need for additional seedlings in the future, even centuries or millenia. The "fragmentation of the doughnut" hypothesis would allow for the eventual filling of gaps until the usual density of five plants per meter square was attained.

It seems likely that the development of present-day wiregrass stands occurred at the end of the M2 period of Watts (1971, c.f. page 194), about 5,000 years BP. It was at this time that regional water tables rose in response to the rise in post-glacial seas, creating the present soil moisture regime. The predominance of pine during the past 5,000 years presupposes the establishment of a wiregrass turf that would be capable of carrying the frequent fires necessary for the maintenance of pure stands of longleaf pine. The possibility that other grasses initially assumed that role cannot be ruled out. Nonetheless, it seems reasonable to say that some of the existing clumps of wiregrass may have persisted vegetatively following seed germination 5,000 years ago.

Population Reductions. The shallow root system makes wiregrass susceptible to being uprooted, particularly since the habitats in which it grows contain relatively loose, sandy soils. If uprooted, a plant may become reestablished if the roots are in contact with moist soil. Nonetheless, nearly any kind of soil disturbance will destroy at least some wiregrass plants. Traditional logging practices such as the skidding of logs caused the thinning of wiregrass in the game plantation region between Tallahassee and Thomasville, Georgia.

Once destroyed, wiregrass does not become reestablished because of its nearly nonexistant reproductive potential. Its inability to become reestablished was noted long ago. Loughridge (1884) observed in southern Georgia that wiregrass,

> "...once destroyed, either by cultivation or otherwise, does not return."

Bennett and Mann (1909) noted the absence of wiregrass in cultivated fields in Thomas County, Georgia. Wells and Shunk (1931) wrote the following about wiregrass in the sandhills of North Carolina,

> "One of the most peculiar facts to be noted in the response of vegetation to habitat changes is that related to the flora coming in following the abandonment of cultivated areas. Outstanding is the observation that the wiregrass does not return. Areas abandoned as much as 15 years ago show no wiregrass; the transition from the weed flora to the adjacent native wiregrass cover is as sharp as the plow furrow which broke the original wiregrass sod. Consistent search for an abandoned field or orchard in the extensive sandhill area in which there was evidence of the return of Aristida failed to disclose any."

Wells (1932) elaborated,

> "Once it is plowed up, as it has been over thousands of acres, it will not return when the field is abandoned. Cotton patches and peach orchards abandoned over ten to twenty years ago show no trace of its coming back; yet it will be thick in the adjoining woodland right up to the old field

edge. Here is a botanical "believe it or not" which needs investigation."

Hebb (1957), studying the sandhills of the western panhandle, wrote, "A field remains clear of oaks and wiregrass for years after it is abandoned."

The late H. L. Stoddard, Sr., became interested in wiregrass and transplanted some clumps to a plot in a woods he owned in Grady County, Georgia. He mentioned that he had established this plot in the late 1930's to his colleagues, Ed and Roy Komarek. In 1974 the Komareks and I rediscovered this plot. The site had once been a longleaf pine woods from which fire had been excluded long enough for the development of a mixed pine-oak-hickory stand. Evidently the competition had been sufficient to destroy all but a few widely scattered clumps of wiregrass. The plot was one by two meters in size and consisted of two straight rows of densely planted wiregrass. Two additional clumps grew within 2 meters of the plot, but they obviously were not part of it. Whether they were there when Stoddard established the plot nearly 40 years before, or whether they represent reproduction will likely never be known for sure. If they do represent reproduction, the reproductive rate is environmentally inconsequential.

Other isolated clumps of wiregrass are seen occasionally in old barrow pits and in former fields of sharecroppers. These also could represent very modest examples of reproduction. On the other hand, the clumps in barrow pits may have washed in from the edges during heavy rains, and the ones in sharecroppers' fields may have always been there, owing to the inefficiencies of non-mechanized agriculture.

Modern practices of commercial forestry nearly always include chopping, disking, or other modes of soil disturbance during site preparation. Such practices are designed to eliminate wiregrass and other native vegetation that compete with planted pines. Woods (1959), Grelen (1962) and Hebb (1971) reported that double chopping on the sandhills of the Chipola Experimental Forest practically eliminates all wiregrass. Grelen said,

> "A few clumps of Aristida stricta were missed by the chopper; they increased in size but no seedlings were recorded."

Hebb (1971) said that wiregrass decreased from a natural density of 14.8 plants per 1/4 milacre to less than 0.1 after chopping. Wiregrass is also adversely affected by site preparation in pine flatwoods. Shultz and Wilhite (1974) reported that wiregrass was reduced by disking in Baker County, Florida. Harris et al. (1974) said that wiregrass declined with increasing intensities of site preparation in Hamilton County. White et al. (1975), working in Hamilton County, compared plant biomass in flatwoods that were site prepared with and without soil disturbance. They discovered that the biomass of wiregrass in the sites that suffered soil disturbance was reduced by 73-89% below the biomass produce on undisturbed soil.

Hilty (Research Summary 11) surveyed 30 pairs of natural and neighboring site prepared stands of wiregrass in the Apalachicola National Forest. The sites were equally divided (10 each) between dry sandhills, mesic flatwoods, and wet bogs and savannahs. Site preparation always involved some form of soil disturbance. Wiregrass density was reduced by 75% on the average in the wet sites, 85% in the flatwoods, and 91%

in the sandhills. These results indicate that wiregrass has a better chance of recovering in wet soils than in dry soils.

Wiregrass is being destroyed on thousands of acres each year in the panhandle by intensive site preparation for commercial forestry. Additional wiregrass is destroyed as lands are cleared for agriculture, urban development, and other purposes. At the present rate of destruction, wiregrass, which was once the most abundant plant in the panhandle, could become rare in a few decades. It is not even safe on public lands, such as the national forests. Mechanical site preparation on the wiregrass lands at the St. Marks National Wildlife Refuge stirred a major controversy recently. Since the destruction of wiregrass on federal lands constitutes an irreversible and irretrievable impact, the National Environmental Policy Act requires that an environmental impact statement be prepared to assess the consequences of this action and to recommend alternative management or mitigating procedures. The U.S. Forest Service knew about this adverse impact at least seven years ago (Clewell 1971), but no such impact statement has been attempted.

It could be argued that wiregrass could potentially reproduce. It certainly must have reproduced previously, or it would not have become so abundant and widespread. The evidence presented earlier in this chapter, though, suggests that reproduction, at least in Florida, requires a summer burn. Resource managers are very reluctant to attempt summer burning, at least as a general practice on a wide scale. Summer fires are sometimes difficult to ignite and will burn slowly in the rainy season, requiring costly supervision. If a summer fire gets out of control, though, it can be nearly impossible to contain. The possibility of loss of life, property and timber is too great.

It is unfortunate that summer burning is impractical and will become more so as public lands are increasingly boxed in by improvements on adjacent properties. Summer fires would reestablish the patterns of natural fires originally caused by lightning during the summer thunderstorm season. Encroaching hardwoods, which easily coppice after winter burns, would be more likely to succumb to summer fires, because their carbohydrate reserves, which are located in the shoots during the growing season, would be lost. Two to four annual summer fires are sufficient to kill sprouting hardwoods (Lotti 1956).

Associated Species. There should be concern over the destruction of wiregrass because it was formerly so abundant, and because it is the best fuel for carrying the frequent fires that are necessary to maintain longleaf pinelands and associated bogs and savannahs. Another reason for concern is that some of the associated species of wiregrass also seem to have a low reproductive potential and seldom become reestablished, at least in significant numbers, on a formerly disturbed site. Among these species are several of the more important species in the undergrowth in wiregrass lands.

Wells and Shunk (1931) were the first to suggest that other species in wiregrass associations did not reproduce, including *Dasystoma* (=*Aureolaria*) *pedicularia*, *Galactia* sp., *Gaylussacia dumosa*, *Lacinaria* (=*Liatris*) *punctata*, and *Stillingia sylvatica*. *Gaylussacia dumosa*, a low growing huckleberry, is a dominant in pine flatwoods and is also a wildlife food plant.

Some other candidates for the list of plant species from wiregrass lands that reproduce poorly if at all are turkey oak, bluejack oak, sand-post oak, both runner oaks, *Vaccinium myrsinites* (a blueberry), and saw-palmetto. All are dominant species in at least some habitats, and all are major winter food plants for wildlife (Murray and Frye 1964, Harlow and Jones 1965, Powell 1965, Hebb 1971). Other additions to the list are *Kuhnia eupatorioides* and *Tephrosia virginiana*. Many other species could probably be identified as growings primarily or entirely on relatively undisturbed wiregrass lands.

On the other hand, certain species are favored by the disturbance of wiregrass lands, including *Andropogon virginicus* (broomsedge), *Eupatorium compositifolium* (dog-fennel), *Rubus cuneifolius* (blackberry), *Pityopsis adenolepis* (golden-aster), and species of *Dichanthelium* (the low-growing panic grasses). It is easy to spot a site that was disturbed years ago, because its vegetational composition is distinctive.

A striking example occurs in the Apalachicola National Forest in Leon County near Dog Lake. Some fields were cleared within wire-grass lands, row cropped, and later abandoned in the early 1940's. Site conditions were seemingly conducive to colonization by the plants of the adjacent undisturbed habitats, but this colonization never occurred. When slash pines were planted in these former fields, the soil was not mechanically disturbed during the minimal site preparation, according to the district forester. Former fence rows between these fields stand out today as narrow, well defined strips of scrub oaks, bracken, and wiregrass. These plants have yet to spread vegetatively into the adjacent, formerly cultivated lands (Research Summary 62).

If a wiregrass site is disturbed by chopping, disking, or other mechanical site preparation and then planted to pines, many of the native plants are not killed and often persist, at least in low numbers. Some may spread vigorously until suppressed by the developing canopy of planted pines. Chopping often cuts the stems of the scrub oaks into short segments, each of which may sprout, if buried, and form a new tree. Sandhill plantations often contain dense undergrowths of turkey oaks for this reason.

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24. SAW-PALMETTO, GALLBERRY, AND TITI

Saw-Palmetto. The saw-palmetto, *Serenoa repens* (Bartr.) Small, ranges from southernmost South Carolina on the coastal plain south throughout Florida and westward near the coast into eastern Louisiana (Little 1977). It is most abundant and widespread in longleaf pine flatwoods. It also grows at low densities on the lower elevations of sandhills, where it sometimes mingles with turkey oaks. It is common in the various scrub associations and on the leeward side of coastal foredunes.

Although the saw-palmetto grows within a very broadly mesic range of site conditions, it is excluded from wet habitats. When grown in saturated soils, the root development of seedlings was half that of those grown in soil at field capacity. Greenhouse-grown seedlings died within a year after being transplanted to a fresh water marsh and to a seasonally flooded prairie in south Florida. Only 20% of the seedlings survived that were transplanted into a bayhead, as compared to 60% survival in native habitats of the species (Hilmon 1969).

Saw-palmetto tolerates repeated burning and regains 80% of its crown cover within a year following a winter fire. Hough (1965) found that palmetto regained 55% of its original dry weight a year following a fire on a 15-year rough near Waycross, Georgia. Flower production a year after fire does not necessarily lead to seed production. Flowering increases substantially after five years of fire suppression and fruiting after six to nine years of suppression (Hilmon 1969).

Seed germination is delayed several months because the endocarp and seed coat exclude oxygen. Hilmon (1969) noted that a few seeds, though, that passed with the feces of a raccoon,germinated immediately. The oxygen blockage presumably was overcome by digestive processes. Since deer, turkey, and other animals consume large quantities of palmetto fruits, it is quite possible that those that pass undamaged with the feces would germinate without delay.

Seedlings are uncommonly seen in native habitats. Hilmon (1969) reported studying a field that had lain fallow for 40 years, which contained few palmettos. The field previously had been a pine-palmetto flatwoods and was still bordered by such vegetation. Asexual reproduction is important and consists of the proliferation of the branching rhizomes. Fire stimulates the growth of sprouts from the rhizomes.

Palmettos accumulate calcium. Those growing in marly sand contained twice the calcium content of palmettos growing in silicious sand. Palmettos also grow vigorously in response to rock phosphate (Hilmon 1969).

Foresters often try to reduce the abundance of palmetto. Hilmon (1969) said,

> "With increased emphasis on pine management and fire control in the 1940's and 1950's, the less shade tolerant herbs declined. Saw palmetto coverage increased rapidly and the species became an obstacle to pine management, if not a competitor."

Hilmon was not as convined as some foresters, though, that palmetto was a serious competitor to planted pines. He said,

> "Slash pine growth was similar on chopped and unchopped plots where palmetto cover varied from 2 to 40% over a five-year period. The suggestion by some authors that pine seedlings and saw palmetto compete was not substantiated by the results of this study."

Hough (1968) said that heavy kills of palmetto may never be accomplished by fire alone. Cross chopping following a burn reduces the cover significantly, probably because 89% of the roots lie within the upper foot of the soil. Five years after chopping the cover was only 3%, while an adjacent untreated control plot had a 21% cover of palmetto (Hilmon 1969). Schultz and Wilhite (1974) compared the vegetation on a disked and bedded flatwoods site in Baker County, Florida, with the natural growth that occurred on the site previous to site preparation. They said,

> "The most striking change in vegetation was the virtual elimination of saw-palmetto on all but the disk-harrowed plots between strips."

Herbicidal control of palmetto is feasible, particularly in the early autumn of the year following a winter burn. At that time the carbohydrate reserves are lowest in the rhizome (Hough 1968).

Saw-palmetto is one of the most important honey plants in Florida. The fruits are the second most important source of food for deer in Florida during the autumn, according to sources cited by Hilmon (1969). Cattle will graze the fronds of palmetto within four months of the last fire. Heavy grazing does not adversely affect palmetto.

Gallberry. The gallberry, *Ilex glabra* (L.) Gray, is an abundant shrub in pine flatwoods. It is very similar to *Ilex coriacea* (Pursh) Champm. (large gallberry), which is fairly common in acid swamps where it is associated with titi. Both gallberries are generally restricted to the coastal plain. The following discussion pertains only to *Ilex glabra*.

Gallberry spreads aggressively from rootstalks. It burns readily and increases the intensity of fire when it is abundant. Following fire new shoots are soon produced by coppicing. Hough (1965) determined that gallberry regained 70% of its dry weight within the growing season following a fire in a flatwoods that had not been burned for 15 years.

Houghes and Knox (1964) burned flatwoods plots annually for three years to determine whether or not gallberry growth could be reduced by frequent fires. They reported a downward trend in height growth only in those plots that were burned each year in August or in October. August falls within the summer thunderstorm season, when lightning-set fires occurred under natural conditions. It seems likely that gallberry is more prolific today than previously because of the present practice of winter burning and because of the general reduction in the frequency of prescribed fires in flatwoods.

Houghes and Knox (1964) determined that the seasonal patterns of carbohydrate distribution in the plant were unaffected by the season of burning. The carbohydrate content returned to normal levels within one year after fire, regardless of the burning regime. They concluded that,

> "Growth of gallberry may be checked temporarily by annual burning, particularly by late summer burning, but measures other than fire are needed to give permanent control."

Hough (1964) noted that reproduction by seeding is rare, even though gallberry produces seeds prolifically. Germination is best at 60 F. In Georgia flatwoods, the seeds germinate in March and April when soil and air temperatures average close to 60 F.

Gallberry generally survives mechanical site preparation in pine plantations and regains its normal density within about four years (Schultz and Wilhite 1974). Gallberry shows a wide range of responses to different fertilizer treatments in young pine plantations (White 1977). The application of herbicides reduces the abundance of gallberry but is not particularly effective in eliminating entire populations (Burton and Hughes 1961). Eradication is considered desirable, because dense growths interfere with forestry operations and increase the fire hazzard.

Titi. Three species of the family, Cyrillaceae, are all known as titi. They are, *Cliftonia monophylla* (Lam.) Britt. (black titi or buckwheat tree, so named for its 3-winged fruit that resembles buckwheat); *Cyrilla racemiflora* L. (swamp cyrilla), and *Cyrilla parvifolia* Raf. (little-leaf cyrilla). Most authors do not recognize *C. parvifolia* as being distinct from *C. racemiflora*, but differences in the size and shape of the leaves and fruits and the length of the inflorescence are sufficient to distinguish them (Kurz and Godfrey 1962). All are large shrubs or small trees.

Black titi ranges on the coastal plain from Georgia into the Florida panhandle and extends westward to eastern Louisiana. Swamp cyrilla ranges on the coastal plain from Virginia to northern Florida and west to Louisiana with scattered populations in eastern Texas, the West Indies, and the Caribbean coast of Central America (Little 1977). Little-leaf titi ranges near the Gulf coast from Taylor County, Florida, to Louisiana (Small 1933, Kurz and Godfrey 1962).

All three titis occur in the same habitats, sometimes individually but often together. They are abundant in the more elevated portions of acid swamps bordering pine flatwoods. They also grow in creek swamps, back swamps, cypress sloughs, and boggy flatwoods. Little-leaf cyrilla is the least common of the titis and seems to be more closely associated with the swamps and sloughs bordering boggy flatwoods and savannahs than with other habitats.

All of the titis occur in habitats subjected to irregular fires which usually crown and destroy the aerial portions. The titis readily coppice after fire. They almost invariably have multiple trunks, probably attributable to coppicing after fire.

A peculiar trait of the titis is that they do not segregate according to subtle gradients in the habitat, as is often the case with related species. Their distribution is seemingly random. It seems as if once a titi plant, regardless of species, by chance became established at a given location in a newly created swamp, it persists indefinitely surviving fire by coppicing.

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25. WHITE-CEDAR

The white-cedar (or Atlantic white-cedar), *Chamaecyparis thyoides* BSP., occurs near the coast from Maine to North Carolina and from just west of the Ochlockonee River in the Florida panhandle to Mississippi. Isolated populations occur in South Carolina, Georgia, and northern peninsular Florida (Fowells 1965). The peninsular Florida populations are in Putman and Marion counties and were discussed by Ward (1963). Li (1962) segregated the white-cedars from the Florida panhandle to Mississippi into a separate species, *C. henryae*, but subsequent authors have yet to accept this interpretation.* In the panhandle, white-cedars grow in creek swamps, bayheads with braided stream channels, boggy flatwoods, and in shallow cypress sloughs through savannahs.

Fowells (1965) summarized the previous literature on site conditions and reproductive biology for white-cedar, drawing heavily on papers by Korstian and Brush (1931) and Little (1950). Fowells said that white-cedars mostly grow on peaty soils underlain by sand. I have seen white-cedars growing on clayey sands and loams in the panhandle. Fowells said that the pH of these soils is generally between 3.5 and 5.5. Collins *et al* (1964) recorded a pH value of 7.5 in peninsular Florida.

Korstian (1924) said that cones are produced on saplings only four years old and that good seed crops are produced annually. Seedfall occurs in the winter. Seed dispersal is both by wind and water.

Fowells (1965) said that the root system of the seedlings is shallow. As a result, the seedlings require wet soil for survival. On the other hand, they are unable to tolerate standing water. The seeds may germinate

*E.g., Little, E. L., Jr. 197[illegible]. Checklist of United States trees (native and naturalized). USDA, Forest Service, Agric. Hdbk. No. 541, p. 87.

successfully on peat, sphagnum, sand or even rotten wood, but not in deep hardwood leaf litter or pine straw. Saplings need light and generally do not survive for long beneath a closed canopy. Wells (1942) said that even low brushy growth of such species as *Smilax laurifolia* will suppress young white-cedars. If the seedlings of white-cedars are densely stocked, though, they crowd out their brushy competitors and grow into a dense, tall stand. White-cedars are unable to reproduce beneath their own cover. Unless fire or another agency opens up the stand, the white-cedars gradually will be replaced by hardwoods, such as sweetbay, redbay, and swamp cyrilla (Wells 1942).

Under favorable conditions, growth is rapid. The younger trees may grow 1-1.5 feet in height annually (Fowells 1965). Eleuterius and Jones (1972) measured white-cedars in Mississippi that were up to 100 feet tall and 28 inches in girth. The older trees are usually up to 200 years old, although older specimens have been reported (Fowells 1965). The larger trees are susceptible to wind-throw because of their shallow root systems and the infirm soil in which they grow.

White-cedars are also susceptible to fire at all ages (Korstian 1924). The larger trees can survive a surface fire, but any fire in a white-cedar stand is likely to crown and kill the trees of all sizes. If a fire occurs at a time when the peaty soil is flooded, the seeds of white-cedar in this peat are protected and will regenerate the stand (Korstian 1924, Wells 1942). If the peat is burned, the seeds in it are killed. Unless there are white-cedars in the vicinity to supply seeds, the stand will likely be replaced by trees of other species.

Slash pines are known to succeed white-cedars after fire in the northeastern Gulf region. Sometimes the roots of hardwoods that had been growing with white-cedars will have survived a light peat fire. These hardwoods persumably regain their former importance by coppicing. Deeper peat fires favor the stocking of hardwoods only by seed. If the peat was burned deeply enough, only hydric hardwoods, such as blackgum, would be able to occupy the site (Fowells 1965). Subsequent aggradation of peat might make the site available for recolonization by white-cedar, assuming a seed source, proper soil moisture, and a fire that opens up the forest.

In summary, white-cedar has exacting requirements for successful germination and is relatively intolerant of both fire and competition. In spite of these limitations, it is often a dominant species in several habitats within its unusual geographic range. Its continued dominance on a given site is not at all certain because of the vagaries of fire.

Collins et al. (1964) described three stands in Putnam County, Florida. These stands grew on coarse sands and gravel that were usually overlain by up to [illegible] inches of peat. Charcoal was common in the peat, indicating past fires. Sweetbay and redbay were dominants along with white-cedar. Other trees included loblolly pine, dahoon, cabbage palm, red maple, [illegible], sweetgum, and tulip poplar. They wrote,

> "Some old [illegible] twelve feet of the boles. Perhaps past fires [illegible] impede hardwood invasion.

Eleuterius and Jones (1972) said,

"No evidence of fire was noted in the Mississippi stand and this may explain the presence of many hardwoods and shrubs."

Some of the more common species with white-cedar in Mississippi were slash pine, blackgum, bald-cypress, American holly, and red maple. Others were southern magnolia, sweetbay, tulip-poplar, sweetgum, swamp cyrilla, and black titi.

I have examined white-cedar forests along the Blackwater River (Santa Rosa County). White-cedar is the dominant overstory tree along most of the length of this river. American holly is dominant in the understory. Other species include live oak, southern magnolia, redbay, loblolly pine, swamp cyrilla, horse-sugar, wild olive, water oak, blueberry (Vaccinium elliottii), and locally slash pine and mountain-laurel.

Along Sweetwater Creek at S.R. 4 in Santa Rosa County, white-cedar grows with swamp cyrilla, black titi, water oak, diamond-leaf oak, southern magnolia, sweetbay, loblolly pine, red maple, American holly, redbay, blackgum, and tulip-poplar. It also occurs in bayheads that drain into the Escambia River. Associated species include slash pine, black titi, sweetbay, and tulip-popular. Boggy longleaf pine flatwoods nearby include patches of white-cedar in the undergrowth. Similar boggy flatwoods are common in the Tates Hell region of Franklin County.

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26. CYPRESS

Classification. The genus, *Taxodium*, is represented in the Southeast by bald-cypress, *T. distichum* (L.) Rich., and pond-cypress. Pond-cypress is considered by some authors as a variety of the bald-cypress, *T. distichum* var. *nutans* (Ait.) Sweet, and by others as a distinct species, *T. ascendens* Brongn. The latter interpretation is followed in this manuscript.

The leaves of bald-cypress are linear-oblong and spreading. It grows on floodplains of alluvial rivers where the pH generally is above 5.5. The leaves of pond-cypress are linear-acuminate and appressed to the twig. It grows in peaty depressions and ponds where the pH is lower and where fires are sometimes common. Gunderson (1976) demonstrated that the seedlings of bald-cypress and pond-cypress, when grown together under uniform conditions, retained their specific characteristics. Morphological differences, therefore, are probably genetic, rather than phenological responses to different habitats.

Bald-cypress ranges from Delaware southward on the coastal plain throughout Florida and westward to central Texas, also northward up the Mississippi Valley and adjacent regions to southern Indiana. Pond-cypress ranges from southeastern Virginia southward on the coastal plain throughout Florida and westward into eastern Louisiana (Fowells 1965).

These two cypresses are sometimes difficult to distinguish. Shaded branches of pond-cypress often have the spreading leaves characteristic of bald-cypress. The cypress trees in the swamps bordering the larger black water rivers are mostly identifiable as pond-cypress, but they lack the thick red bark characteristic of that species (R. K. Godfrey, personal communication).

Reproduction. Cones are produced on cypress trees nearly annually, and the seed crop is heavy about every third year. Seedfall occurs in the winter (Fowells 1965). Dispersal is by water. The seeds may germinate immediately; however, they are known to remain dormant and viable for 30 months when stored in water. Germination requires wet soil, and the soil must remain wet but not flooded for at least 1-3 months thereafter. A seedling survives flooding only if its cotyledons are partially exposed. Seedlings less than two years old (i.e., up to about 16-20 inches tall) succumb to complete inundation within about 10 days in the summer (Demaree 1932). Presumably, they would tolerate somewhat longer periods of inundation when temperatures are lower during the late winter and spring, which are the primary flood seasons along southeastern rivers.

Browder et al. (1974) reported that cypress seedlings attained their greatest growth in terms of biomass where they received 80% of full sunlight. Seedlings are sometimes abundant in the deep shade of swamps, but these seedlings generally do not survive for long. The seedlings of water tupelo (*Nyssa aquatica*) are much more shade tolerant (Demaree 1932).

It has been established that cypress is able to reproduce only in relatively open habitats where the soil is wet but not subjected to prolonged flooding. Harper (1912) made an observation on the distribution of cypress that is at least somewhat consistent with these requirements. He said that cypress was absent from the banks of rivers having an average seasonal fluctuation of more than 10-12 feet. Cypress was limited largely to the margins of oxbow lakes on the floodplains of such rivers. Oxbow lakes, which are formed when a meander loop of the main channel is cut off, are protected from the extremes in river stage experienced along the main channel. Harper suggested that the age of an oxbow lake could be determined by counting the annual rings of cypress trees along its margin. Harper's contention is upheld for the Apalachicola River. Cypress trees are rare along the river banks but abundant in the interior oxbows. The smaller rivers of the panhandle commonly have cypress lining their banks.

Cypress trees are common in habitats where prolonged flooding is normal. The question arises as to how the seedlings survived that grew into these trees. A possible explanation is that not all years have normal rainfall. Flood surges are less extreme and less prolonged. Runoff from rainfall does not accumulate to the usual depths in oxbow lakes or in ponds on the upland. Evaporation is extreme, because thunderheads are not present to shield the midday sun. If such conditions persist for two or more years, cypress seedlings could grow sufficiently to survive upon the subsequent return of normal water levels. The seedlings of most potentially competing hardwoods, though, would not survive after the normal hydric conditions were reestablished.

Growth. Virgin cypress trees grow slowly and attain heights of 100-120 feet (maximum 150). These trees are mostly 36-60 inches in dbh (maximum 96) and 400-600 years of age (maximum 1,300). When the maximum height of a tree is attained, the crown flattens out on top, much as in the longleaf pine. Diametric growth continues, though. The determination of age is made difficult by the production of false annual rings, which in one study averaged 1.6 per year (Fowells 1965).

Many enormous virgin cypress trees line the rivers of the panhandle. Most are hollow and show crown damage from wind or perhaps lightning. These trees were probably spared from logging because of their inferior value for lumber. Old trees often are infected by a fungus that rots out small pockets of wood. Lumber from such trees is called pecky cypress.

Second-growth trees usually grow rapidly. Fowells (1965) cited one study in which century-old second growth trees were about 100 feet tall.

After logging, vigorous sprouts often arise from the living stumps and replenish the stand. It is not uncommon to find overstory cypress trees that are growing from such stumps. The abruptly smaller trunk of these trees distinguishes them from the larger stumps from which they have arisen.

It was common practice to girdle virgin cypress trees 6-12 months prior to logging. Girdling killed the roots, thereby reducing water transport to the trunk. Felled trees would not float unless they had been girdled. Stumps of girdled trees did not produce sprouts (Fowells 1965).

Buttresses. Buttresses are a common and conspicuous feature of most cypress trunks. Wagner and Kurz (1954) showed that buttresses are the result of wider annual rings than elsewhere on the trunk, and not of additional annual rings. Buttresses are scarcely if at all present on cypresses growing on savannahs and other sites that are rarely if ever flooded. Kurz and Demaree (1934) and Wagner and Kurz (1954) presented observational evidences that buttress formation was related directly to the regime of water level fluctuation at any given site.

They identified four basic forms of buttresses. The first and most common is the columnar buttress which tapers gradually upwards from a broad base. This kind of buttress develops in habitats where the water level fluctuates regularly. The longer that a given portion of trunk is under water during the year, the broader the buttress at that point. Since the base of the tree is under water the longest, the buttress is broadest there.

The bottle buttress, shaped like a Coca-cola bottle, developes in lakes with widely fluctuating water levels, such as at Lake Cascade in Leon County. The water level is usually either very low or very high. The buttress is swollen near the base and near the summit but is constricted in between at heights where water levels are not maintained for long.

The platform buttress consists of a low flange at the base of the trunk, which may be wide enough to walk on. It develops on trees that are more-or-less permanently exposed to very shallow inundation.

The hanging buttress is an abrupt, bell-shaped protuberance on an otherwise columnar trunk. It develops only after cypress trees have been subjected to deep and permanent flooding, as might be expected following the filling of a new reservoir. The buttress forms just below the normal water line and does not extend more than a foot or two down the trunk.

The mechanism that causes cypress trees to form buttresses has yet to be elucidated, but the hypothesis of physiological girdling seems to fit well (c.f. page 231). This hypothesis states that the downward translocation of foods and growth substance in the phloem is dependent on oxygen that enters through the bark. The limited oxygen supply in water is insufficient for maintaining rapid phloem transport. As a result, the foods and growth substances accumulate just below the water line, stimulating exaggerated growth which is manifested as a buttress.

<u>Knees</u>. Cypress knees are outgrowths from the superficial lateral roots. They often attain the height of the average water level during the wet season. This relationship between height and water level suggests that growth may be stimulated by some mechanism similar to that responsible for the formation of buttresses. Wagner and Kurz (1954) noted that knees did not grow in permanently and deeply flooded habitats, suggesting that aeration is involved in their development. They also noted that knees did not attain the height of the average high water level in Cascade Lake, where water levels fluctuated very widely.

The older literature generally stated that knees serve as organs of aeration for the roots. Kramer <u>et al.</u> (1952) were unable to confirm that contention from experiments on gas exchange. Wagner and Kurz (1954) observed that some knees contained chlorophyll at their apices and suggested that some of the oxygen produced by photosynthesis could be transported into the roots. They also noted that the chlorenchymatous tissue of knees was often shielded from light by the bark. Any important physiological function that knees may have has yet to be demonstrated.

<u>Roots</u>. Kurz and Wagner (1954) said that tap roots were not characteristic of larger trees. They wrote,

> "Except in three cases, where the trees were on well drained slopes, the writers have not seen a live taproot persisting in a mature cypress tree."

Superficial lateral roots are responsible for anchorage. Where soils are relative well aerated, these laterals become very elongated. They measured one that extended 110 feet from the base of a tree growing in the floodplain of the St. Marks River south of Tallahassee. They said that the lateral roots were consistently thicker distal to that portion where the knees arose. These thicker portions gave rise to smaller roots that were effective in anchoring the lateral roots well away from the trunk of the tree. This anchorage gave added protection against the possibility of the tree being wind-thrown.

Adventitious roots from the buttresses are abundant in habitats where flooding is prolonged. Evidently such roots are of vital importance in the oxygenation of submerged portions of the tree. Kurz and Wagner (1954) measured one adventitious root 12 feet long which was freely suspended in the water. The larger adventitious roots survive desiccation when water levels are low. Fine roots sprout from them upon subsequent flooding. Tufts of fine roots also grow upwards from the superficial lateral roots and extend like brushes above the soil and into the water.

Permanent Flooding. In spite of the fact that cypress is unable to reproduce in a permanently inundated habitat, several places are known where mature cypress forests exist on such sites. Permanent flooding must have come about after these forests became established. Demaree (1932) spoke of the slumping of the land beneath cypress swamps during the New Madrid earthquake of 1811-12. Previously, these swamps were seasonally flooded. One was along the St. Francis River in Arkansas, the other along the Mississippi River in Tennessee. The latter site is now known as Reelfoot Lake. The land slumped as much as 6 meters to create this lake, and the water rushed in.

Most of the trees were killed by the sudden and prolonged flooding. The wood of cypress resists decay almost indefinitely. Demaree was able to examine this submerged forest of mostly dead but still standing trees.

Surviving trees grew in no more than 9.3 feet of water. Kurz and Demaree (1934) described the hanging buttresses on these trees at Reelfoot Lake. These buttresses developed subsequent to the formation of the lake.

The tributary valley lakes of the Florida panhandle also contain cypress that is permanently flooded. Wagner and Kurz (1954) described the forest of mostly dead cypress trees at Dead Lake (c.f. pages 113-115). Their original crowns were lost, and their present, scanty branches arose adventitiously from the trunks. Adventitious roots are abundant along the submerged portions of the trunks. Surviving trees grow in up to 16 feet of water. Wagner and Kurz (1954) suggested that cypress trees tolerated this depth (as opposed to 9.3 feet in Reelfoot Lake) because of somewhat fluctuating water levels.

Davis (1943) observed permanently flooded cypress trees in southern Florida and said,

> "Since some cypress trees now grow in deep water, as deep as 5 feet during normal dry seasons, even these deep water areas must have at some time in the recent past had no surface water for a long enough period to allow the seedlings to start growth.... Their presence and conditions serve as clues to past as well as present surface conditions, and these conditions may be significant in the interpretation of the geologic development."

Vernon (1947) suggested that submergence was largely the result of rising water tables in response to a rise in mean sea level. He also hypothesized that some cypress stands could have been lowered by the solution of carbonate formations beneath them.

Pond-Cypress Habitats. Pond-cypress grows in strands and depressions. Strands are low areas over which shallow water slowly flows during wet seasons. There is no defined channel, but rather the water is essentially a sheet flow. Such strands or stringers are common in the lower Apalachicola River region, including Tates Hell. Cypress forests in these strands are usually open with a turf of sedges beneath. Some of the cypress trees extend into adjacent savannahs and boggy flatwoods of slash pine and even longleaf pine. The bark of such trees is dark from the charring by frequent fires. Cypress trees in some strands are stunted. One tree in Liberty County was 8 inches in dbh and contained nearly 300 rings. A stand in Tates Hell consists of flat-topped cypress only 6-8 feet tall with growth rings too small to count without a strong lens.

The forests of pond-cypress that grow in pond-like depressions assume various forms, depending on the water level. In deeper lakes the cypress may constitute a ring around the edge. Vernon (1947) termed such forests as cypress doughnuts. Shallower depressions contain a continuous growth of cypress. Almost invariably such stands contain the tallest trees in the center with the other trees being progressively shorter towards the periphery. These stands are called cypress domes or cypress heads. In the shallowest depressions pond-cypress shares the overstory with sweetbay, swampbay, loblolly bay, blackgum, and sometimes slash pine. These various pond-cypress swamps often serve as headwaters for streams. Pond-cypress and the various bays, blackgum, and slash pines often extend along such streams as creek swamps.

The water feeding into cypress ponds and domes is usually from surface runoff rather than from an aquifer (Vernon 1947). Monk and Brown (1965) discovered clay pans or lenes beneath 19 cypress heads in northern peninsular

Florida. Ewel (1976) said that these clay layers prevented cypress swamps from serving as recharge areas for the Floridan aquifer. She also said that not all cypress swamps in peninsular Florida were underlain by a clay pan. Odum (1976) said that the evaporation for the surface of a pond shaded by pond-cypress was only 70% as much as that evaporating from an open pond.

Ewel (1976) said that vegetational diversity in cypress domes was inversely proportional to the degree of fluctuation of the water level. Open domes with low biomass tend to occur where the water level fluctuates considerably, which is also where the nutrients are in shortest supply. Monk and Brown (1965) gave general ranges for nutrient values in cypress heads. They were: Ca 20-28 ppm, Mg 5-20 ppm, K 5-30 ppm, P 1-5 ppm. They also noted pH values of 4.1-4.6 and organic matter at 2-17%. Clay, organic matter, and K increased significantly from edge to center. Calcium and Mg increased slightly from edge to center. Phosphorus and pH decreased slightly from edge to center. Additional nutrient values were presented by Coultas and Calhoun (1975) from northern peninsular Florida.

Spangler et al. (1976) determined that the peat in cypress domes was about 2-4 feet thick near the center and progressively thinner towards the edges. Brown and Monk (1965) suggested that aggrading peat would continue until sweetbay and other hardwoods would be able to invade.

Various suggestions as to why a cypress forest assumes a dome shape have been advanced. Harper (1927) wrote,

> "The little trees at the edges have probably had just as much time to grow as the large ones in the middle, but they must be dwarfed by some unfavorable soil condition."

Kurz (1933) wrote in response to Harper's statement,

> "The present writer has made a study of the growth rings and finds that the largest trees in the center are actually the oldest and those nearer the edge are successively smaller and younger."

Kurz observed that seedling mortality near the edge was greater than near the center of cypress domes. He suggested that the trees near the edges are continually dying and being replaced. Kurz pondered, though, over the fact that growing conditions were better in the shallower water near the edges than in the center.

Vernon (1947) suggested that a regional rise in the water table was making the deep, central portions of domes too deep for reproduction. The established trees in the center grew taller, while reproduction was limited to the exterior, thereby forming the dome.

Duever et al. (1976) studied cypress at Corkscrew Swamp in southern Florida and suggested that fire was partially responsible for dome formation. They said,

> "The point where the 1974 minimum water level intersected the peat profile is where the age and DBH of the trees increase abruptly.... We theorize that severe widespread fires entering from adjacent uplands have not penetrated beyond (that point) during the past 200 years because of generally higher moisture levels in the vicinity of the deep peat soils. The slow outward dispersal of new cypress trees from the old tree seed source, interacting with the effects of occasional fires pushing the cypress back, has resulted in the present size distribution of cypress outward from (that point)."

They also gave observational evidence for deep peat fires that had destroyed cypress stands. Widely isolated old cypress trees that evidently survived the fire and buried stumps in a sawgrass marsh are the primary evidence. They suggested that sufficient peat accumulated since the fire to allow the establishment of a sawgrass marsh, which is now frequently burned. In one area of the marsh where fire has been excluded in recent years, willows invaded, followed by cypress seedlings.

Browder et al. (1974) suggested that cypress is a "climax pioneer", one of the first components of the climax community that invades, following the initial colonizers. The observations of Duever et al. (1976) sustain this supposition. Cypress swamps therefore fit the displacement model presented in Chapter 16 (p. 209).

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27. THE GENUS, *NYSSA*

Classification. Four species of *Nyssa* occur in the panhandle, all trees, three of major importance. They are:

Nyssa aquatica L., water tupelo, an important dominant of the more hydric sites on alluvial floodplains, often growing with bald-cypress. Water tupelos range from southeastern Virginia on the coastal plain to Georgia (excluding the Okefenokee region) and the Florida panhandle (at the Ochlockonee River) westward into eastern Texas, also up the Mississippi Valley to Illinois and interior regions locally in Georgia, Alabama, Tennessee and Kentucky.

Nyssa ogeche Bartr., ogeechee tupelo or ogeechee lime, an important tree of river banks and slough margins along black water and alluvial rivers. It ranges on the coastal plain from the southernmost tip of South Carolina across southeastern Georgia (including the Okefenokee region) and into northern Florida as far west as Walton County.

Nyssa sylvatica Marsh., sourgum, an occasional tree of pine-oak-hickory woods, usually growing on virgin soils. A wide ranging species in the eastern United States with disjunct populations in southeastern Mexico.

Nyssa biflora Walt., blackgum, an important tree of peaty acid swamps such as in pineland depressions, along creeks, and in the back swamps of alluvial floodplains. It often grows with pond-cypress. Many authors prefer to treat blackgum as a variety of sourgum, *N. sylvatica* var. *biflora* (Walt.) Sarg. Blackgum ranges on the coastal plain from Delaware to Florida and westward into eastern Texas. A small, bushy form occurs in the boggy flatwoods and savannas of the lower Apalachicola River region.

It was segregated as N. ursina Small, but it appears to represent typical blackgum which is made bushy by coppicing after frequent fires.

Water Tupelo. The water tupelo grows to a height of about 110 feet with diameters up to 3-4 feet. On a favorable site, water tupelos grow 70 feet in 50 years and may attain diameters of 20-26 inches in 50-75 years. The trunk is straight and typically unbranched for most of its length. Water tupelo is classed as intolerant of shade and competition. It is thought to be restricted to exceptionally wet sites because of its inability to compete with trees of most other species (Fowells 1965).

Seedfall is heavy nearly every autumn. Dispersal is by water and by small animals. Germination occurs the following summer after flood-waters recede (Fowells 1965). Like bald-cypress, its seeds are unable to germinate successfully in a site that is constantly flooded (Shunk 1939).

Dickson et al. (1965) grew seedlings in pots for 84 days under various regimes of soil moisture. They discovered that water tupelo grew best in terms of height and biomass in continuously saturated soils. The biomass was reduced by 61% when grown in soil held at the moisture equivalent. Kennedy (1970) noted that growth in height was retarded but survival was unaffected by increasing the depth of the water that flooded the soil in which young water tupelos were growing. Harms (1973) showed that the growth of two-year-old water tupelos was much better in moving water than in stagnant water.

Ogeechee Tupelo. Fowells (1965) summarized what little is known about this narrowly ranging species. Permanently wet alluvial soils are required for growth and regeneration. It tolerates prolonged flooding but usually on sites where the water is flowing at least slightly. The trees generally grow best at an elevation just above the average water level and rarely grow more than two feet above that elevation. Seedfall is generally heavy every year and takes place mainly in the late summer. Seedlings may grow 2-3 feet annually during the first three years. Mature trees tend to be much branched from near the base or even shrubby. Most are only 25-35 feet tall, some reaching 50 feet. The maximum height is 65 feet.

Ogeechee tupelos are common along some rivers of the eastern panhandle but nearly absent along others. They are abundant on the banks of the upper Suwannee River but uncommon along its tributary, the Withlacoochee River. They are common at least locally along the Ochlockonee and Apalachicola rivers. When they grow on floodplains away from the main river channel, they line the sloughs and oxbows, including those which have become essentially filled with sediments. Such trees may have persisted since the time that the sites on which they are growing were once river banks.

An extraordinary example of what probably constitutes a relic population along a filled river channel occurs at the head of Monkey Creek in the Bradwell Bay Wilderness in Wakulla County. The site is a large virgin blackgum swamp which probably contains standing water throughout those years with average rainfall. The former river channel of Monkey Creek is outlined by two winding rows of ogeechee tupelos, marking the former river banks. The filled channel is only slightly deeper than the surrounding terrain and contains no trees. It is evident from the size of the ogeechee tupelos that all trees are old. The meager evidence at hand suggests that ogeechee tupelo seeds germinate successfully only along the banks of flowing rivers. Watts (c.f. p. 194) demonstrated that present water tables have been maintained for the past 5,000 years. Monkey Creek was likely flowing in a defined channel just prior to that time, when regional water tables were lower. This possibility is consistent with the observations of Cameron and Mory (c.f. pages 199-202). The logical conclusion is that the ogeechee tupelos that now stand on the former banks of Monkey Creek are more than 5,000 years old.

This possibility is not as remote as it might seem, because ogeechee tupelos may be constructed in such a way that they could persist indefinitely. The trunk of the tree is usually barrel-shaped and hollow, about 1-3 meters tall and often a meter or more in diameter. The bark and sapwood form a thin shell, often only 3-5 cm thick around the central cavity. The top and bottom of this "barrel" are often open. From its rim arise many tall, arching branches which form the crown of the tree. When these branches are only about 10-15 cm in diameter near the base, they are already hollow. Eventually a branch becomes too heavy to be supported by its weakened basal portion, and it snaps off at or just above the rim of the barrel-shaped trunk. New branches are continually forming on the rim, replacing those that fall. The branches and undoubtedly the roots are being replaced continually. Only the barrel-shaped trunk might reveal the true age of the tree. Unfortunately, only the most recent annual rings are available to be counted. Palaeoecological work is needed in Bradwell Bay to test the Monkey Creek hypothesis. Autecological work is needed on ogeechee tupelo to determine the conditions necessary for reproduction and to establish the limitations, if any, of its longevity.

Another autecological aspect also needs investigation. At flood stage the open, barrel-shaped trunks could catch leaves and other detritus carried by the river. This detritus later would be subject to microbial decomposition. Roots grow from the callus lining the inner wall of the trunk. These may absorb the nutrients released by decomposition. The barrel-shaped trunk, then, essentially attracts its private compost heap. Janzen (1976) suggested that the feces from animals occupying hollow trees would contribute to the nutrition of such trees. Fisher (1976) related an example of roots produced from callus within a hollow basswood that penetrated detritus. I have also seen such roots within a hollow sweetgum on the floodplain of the Apalachicola River. It is even possible that roots from the callus would enter the soil (the base of the barrel-shaped trunk) and extend outward as new lateral roots. The convoluted base of larger ogeechee tupelos suggests a complex origin of the lateral roots.

Blackgum. Blackgum resembles water tupelo in that it usually produces a single straight trunk which is branched above the middle and which is buttressed when growing in deep swamps. The largest specimens are 120 feet tall and about 4 feet in diameter (Fowells 1965). Most trees are not quite so large. Hall and Penfound (1939) described a virgin stand in Louisiana that more closely resembles the older growth in the panhandle. These trees were 200 years old, averaged 83 feet tall, 15.5 inches in diameter above the buttress, and 25.7 inches in dbh. The stand was flooded from January to June. The water table was never more than a foot beneath the soil surface during the dry season. Once during a 15 year period flood, waters were 12 feet deep.

DeBell and Hook (1969) trapped seeds over a 4-year period and obtained 0 to 833,000 seeds per acre per year, most of them falling in November. The seeds are disseminated by gravity and birds, particularly robins. Germination percentages were 45-63%.

Hook et al. (1971) obtained information that helps explain why blackgums survive well during prolonged flooding. Seedlings that developed in flooded soils were able to oxidize their rhizosphere from air that entered the lenticels and diffused to the roots through the cortex or phloem and into the soil. The roots of hydroponically grown seedlings were able to tolerate flowing water with a 10% concentration of CO_2 without adverse effects. Growth and metabolism were diminished when the concentration was increased to 31%, but the seedlings survived. They also discovered that the roots are capable of accelerating the rate of anaerobic respiration in the absence of oxygen.

Fowells (1965) said that sprouts will develop from young tree stumps of blackgum.

Blackgums and water tupelos do not occupy the same habitat, although both grow on floodplains. Harms (1973) began to elucidate the differences in ecological response by growing two-year-old plants of both species under controlled conditions. For the substrate he used soil from a water tupelo swamp and soil from a blackgum swamp. He grew plants of each species in these soils and subjected the plants to three moisture regimes: deep (20 cm) stagnant water, deep moving water, and moving water at the soil surface. Blackgums showed no particular difference in growth, regardless of treatment. Water tupelos did much better on their own soil than on the less fertile soil from the blackgum swamp.

Blackgum and pond-cypress sometimes grow together in acid swamps and ponds, but often they form distinct zones in such habitats. Blackgum occupies the deeper sites where flooding is more prolonged and continuous. Pond-cypress occupies the peripheral higher terrain where the water level fluctuates more frequently above and below the soil surface.

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28. SEA OATS AND BLUESTEMS

Sea Oats. Sea oats, *Unicola paniculata* L., grow on coastal dunes and ridges from southeastern Virginia south throughout Florida and along the Gulf coast to Tabasco, Mexico, also Cuba and the Bahamas. This grass is the primary sand-binding herb on exposed sites throughout its range (Woodhouse *et al.* 1968).

Seeds mature in the fall and remain inside the spikelet. The spikelet is the dispersal unit and contains on the average of 2.2 seeds. The spikelets are dispersed by the wind and sometimes by waves during storms (Wagner 1964). Germination is delayed until spring at least in northern populations by an inhibitor in the endosperm (Westra and Loomis 1966). The effects of the inhibitor are overcome by cold treatment (Seneca 1972). Seeds from Alligator Point in Franklin County showed weak inhibition. The germination percentage rose from 80% to 97% after seeds were stored for 30 days at 40°F.

The spikelets must be buried at least 2 inches beneath gradually accumulating sand if germination is to occur. The seedlings are unable to reach the soil surface, though, if the spikelets are more than 6 inches deep (Wagner 1964). Seedling survival is negligible if the sand is drifting too fast (Seneca, cited by van der Valk 1974a).

Most seedlings germinate on upper beaches (Woodhouse *et al.* 1968). Often such seedlings are growing in organic drift which is shallowly buried by sand (Wagner 1964, Oertel and Larsen 1976). The abundance of seedlings in drift lines might be due to the fact that many spikelets are washed by waves into these lines along with other detritus. It could also be that germination and survival are enhanced by the moisture or nutrients supplied by the detritus.

The seeds have a low salt tolerance (Seneca 1969), but they have been known to germinate in water which is up to 30-45% sea strength. Seedlings that are watered with sea water are stunted and do not survive for long (Wagner 1964, Woodhouse et al. 1968). Mature plants are also adversely affected when watered daily with sea water (Oosting and Billings 1942).

The roots of seedlings are shallow but extend for considerable distances from the base of the plant. Extensive tillering begins in the second year. Leaves and inflorescences develop from the tillers. These aerial portions of the plant act as baffles to trap drifting sand. Rhizomes are produced beneath this accumulation of sand. New tillers arise from the nodes of these rhizomes, forming new clumps of sea oats which trap more sand. The rhizomes do not grow downwards but rather either laterally or obliquely upwards, keeping the nodes which produce new tillers near the surface. Eventually the internodes of the older rhizomes decay, fragmenting the colony into a number of independent plants (Wagner 1964).

The sand is stabilized by the extensive latticework of rhizomes and tillers. This process continues indefinitely for years, as long as sand continues to accumulate. The end result is the formation of a dune or dune ridge on what had been merely a sloping upper beach. This dune may be 10 meters or more in height, if there is sufficient sand and strong enough winds to carry the sand to the top. There is general agreement that this process is responsible for building the foredunes along the Atlantic coast.

The growth and vigor of sea oats is proportional to the accumulation of sand. When the sand supply is cut off, growth ceases and the plants begin to die. Growth is resumed, though, by the application of fertilizer. Woodhouse et al. (1968) reported a five-fold increase in biomass after a stunted stand was given two applications of 100 lbs. of 30-10-0. Sea oats respond well to most any fertilizer application, especially to N and P.

These observations raise the questions of how sea oats obtain nutrients in sterile beach sand and why they remain healthy only when sand accumulates. Boyce (1954) showed that sea oats trap not only sand but also the salt spray that is carried by the wind. Oosting (1945) showed that sea oats are highly tolerant of salt water sprayed on leaves. The inrolled, heavily cutinized leaves are unable to absorb the nutrients in this salt spray through the leaves. Neither are the toxic chlorides of the salt spray able to enter the leaf. Rain dissolves the salt crystals on the shoots and carries them in solution to the root zone where the mineral nutrients are absorbed. The chlorides are diluted by rain water below toxic levels.

Sand ceases to accumulate if the speed of the wind is reduced. Low wind speeds are also unable to carry the salt spray which is essential for mineral nutrition in sea oats. Thus the accumulation of sand is not prerequisite to the vigor of sea oats but rather the salt spray that accompanies the sand (van der Valk 1977).

Boyce (1954) fertilized sea oats in a natural population with sodium nitrate. These plants grew much taller than the unfertilized controls. Shortly after these observations were made, this population of sea oats was subjected to a period of intense salt spray. All of the plants treated with sodium nitrate were killed or exhibited severe symptoms of chloride damage.

To determine the cause of injury, two sets of experiments were run. One set showed that the injury was not attributable to an intercellular effect caused by the nitrate. The other set showed that the leaves of nitrate-treated plants developed small lesions in the epidermis, after flapping in the wind. These mechanical injuries likely occurred because of the increased pliability and the thinner cuticle of the leaf. Unfertilized controls did not suffer lesions. The lesions allowed the entrance of chlorides from salt spray into the leaf.

Van der Valk (1977) elaborated on Boyce's results and wrote,

> "However, it is also essential for the survival of these grasses in coastal habitats that nutrient levels around the plants never build up to optimal levels for growth. Although optimal levels of nutrients would greatly increase the growth of individuals of (sea oats), it would also make them susceptible to salt spray injury because of increased mechanical injury to the leaves (Boyce 1954). This would greatly reduce their chances for survival on coastal dunes. Such a buildup of nutrients around the plants is prevented by the rapid leaching of nutrients by rainfall from dune soils (Boyce 1954; van der Valk 1974b). Because of the presence of salt spray in the coastal dune environment, coastal dune grasses are in a rather unusual situation first pointed out by Boyce (1954). Suboptimal nutrient levels are required for their survival in their normal habitat. Because of the

peculiarities of the coastal dune environment, the foliar uptake of nutrients, then, would not benefit dune grasses."

Asexual reproduction is possible in natural populations, because segments of severed rhizomes will take root. The rhizomes are not easily fragmented (Wagner 1964), and Woodhouse and Hanes (1966) determined that propagation is primarily by seed. Seneca (cited by van der Valk 1975) reported that the seedlings of sea oats and several other coastal herbs were severed and killed by wind-blown sand. This decapitation would help explain why plants do not colonize the seaward faces of dunes and other sites exposed to especially strong winds.

Natural populations of sea oats are often rather sparse. Sand accumulates beneath individual plants, and other sand is wind-eroded between them, making a hummocky dune field. Van der Valk (1975) said that artificial dunes constructed in North Carolina were planted to sea oats which never established dense populations. The inability of their rhizomes to grow downwards into the sand impairs their effectiveness in stabilizing a preexisting dune.

Bluestems. At least 17 species of the bluestem grasses are native to the panhandle. These are all considered by some authors to belong to the genus, *Andropogon*. Other authors prefer to segregate one group of the bluestems into the genus, *Schizachyrium*. This manuscript opts for the recognition of two genera and follows the practice of Correll and Johnston (1970) of referring to the species of *Andropogon* as the "bluestems" and those of *Schizachyrium* as the "little bluestems".

The little bluestems generally behave as integral components of the natural vegetation of longleaf pinelands, bogs, savannahs, and coastal dunes. In general, they are not weedy. Schizachyrium maritimum is often a dominant in sea oats zones on coastal dunes. Schizachyrium tenerum, S. scoparium, and S. stoloniferum grow in wiregrass lands and replace wiregrass as dominants in a few places in the northwestern panhandle.

The bluestems are mostly weedy species with a few exceptions like Andropogon gerardii. These non-weedy species are uncommon in the panhandle. The most abundant bluestem is Andropogon virginicus, which is usually called broomsedge. It is exceedingly abundant in fallow agricultural fields and many other disturbed sites, including recently site prepared pine plantations. Its presence as a vigorous plant is almost always an indication of soil disturbance. Certain coastal varieties and the closely related A. glomeratus are not necessarily weedy where they occur on the brackish margins of salt marshes and on overwash prairies. Broomsedge is common and sometimes dense in undisturbed wiregrass lands. The plants, though, are always stunted and rarely if ever produce an inflorescence. These plants never grow as a large clump as is typical of broomsedge in disturbed habitats. Andropogon ternarius is much less abundant than broomsedge but often is mixed with it on disturbed sites.

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29. SEAGRASSES

Classification. None of the seagrasses are true grasses. All are aquatic monocots which are completely submerged except during unusually low tides. There are six seagrasses along the coast of the panhandle. Five are strictly salt water species which reach their northernmost limits of distribution in the northern Gulf of Mexico. The sixth species, widgeongrass, is more common in brackish rivers but extends into estuaries. It ranges from Canada to Mexico. The six species are:

Turtlegrass, Thalassia testudinum Koenig.

Manateegrass, Syringodium filiforme Kutz. Synonyms are Cymodocea manatorum Asch. and C. filiformis (Kutz.) Correll.

Shoalgrass, Halodule wrightii Asch. A synonym is Diplanthera wrightii. den Hartog (1970) segregated plants of this species from the Gulf of Mexico into a separate species, H. beaudettei, based on the number of apical teeth on the leaves. Plants from the Caribbean were retained in H. wrightii. Phillips et al. (1974) showed that the number of apical teeth was variable and that the reproductive structures were indistinguishable between plants of Gulf and Caribbean populations. They did not recognize H. beaudettei as a valid species.

Halophila engelmannii Asch. There is no common name for this species.

Halophila baillonis Asch. This species is known from waters at least six meters deep in the open Gulf southeast of Alligator Point, at similar depths off Pensacola, and in deep water in Apalachicola Bay (Humm 1956, 1973). This tropical species may be limited to deeper water where winter temperatures are not as extreme as they are nearer shore. It will not be considered further.

Widgeongrass, *Ruppia maritima* L.

Turtlegrass. The turtlegrass grows in dense beds wherever the water is clear and the surf is not heavy. With respect to other seagrasses, its leaves are of intermediate length and stiffness (Strawn 1961). It usually grows at a minimum depth of about 0.5 meters. It rarely grows more than 11-12 meters deep in the Gulf (Moore 1963), but it was recorded at 23 meters in the Virgin Islands (Humm 1973). It prefers a substrate of sandy muck or marl. Its normal salinity range off Taylor County is 17-36 o/oo and averages 20-25 o/oo. Its optimum range is 25-38.5 o/oo and has been recorded in water as high as 48 o/oo. It is absent from waters that are consistently below 20 o/oo or above 45 o/oo. It was recorded in water in Crystal Bay which was 10 o/oo and near Econfina River at 6 o/oo, both readings being unusually low for these locations because of heavy rains (Phillips 1960, Moore 1963, Zimmerman and Livingston 1976).

Turtlegrass leaves become flaccid at 30° C. These leaves eventually break off after exposure to this temperature, and they float in the Gulf in great rafts. Leaves are also killed in water less than 15° C, although the rhizomes tolerate temperatures at least as low as 9° C. Leaf-kill was reported in winter at Tampa upon exposure to air at low tide (Phillips 1960).

The biomass of turtlegrass off Taylor County constituted 79% of all seagrasses and reached a maximum in June of 1,789 g/m^2. It occurred in 71% of 472 quadrats 0.09 m^2, more than any other seagrass, off St. Marks lighthouse (Gidden, unpubl.).

Manateegrass. The leaves of manateegrass are relatively long and stiff. At Cedar Key and off Taylor and Wakulla counties it grows at a minimum depth of 0.4-0.6 meters. In the Tampa area it is rarely seen with its leaf tips exposed at low tide. It has been recorded at a maximum depth of 25 meters but usually occurs within about 12 meters of the surface.

Manateegrass tolerates somewhat longer periods of low salinity, lower temperatures, and more turbid water than turtlegrass. Off Taylor County its normal range of salinity is 17-36 o/oo and averages 20-25 o/oo. It grows most abundantly at less than 25 o/oo, because it does not have as much competition from turtlegrass at lower salinities. It has been recorded at 38.5 o/oo. It grows on sandy muck and has been reported from hard packed sand at Cedar Key. It suffers extensive leaf-kills during colder winters at Tampa.

Manateegrass constituted 17% of all the seagrasses off Taylor County and was recorded as having a maximum biomass of 643 g/m^2. It occurred in 42% of 472 quadrats 0.09 m^2 near St. Marks lighthouse.

Shoalgrass. The shoalgrass grows in shallower water than all other seagrasses and forms dense, pure stands in water 0.24 meters deep at Cedar Key. Similar stands have been reported from shallows along beaches and barrier islands throughout our area. At greater depths it is uncommon and often very patchy. It may be interspersed with turtlegrass but not where turtlegrass forms a continuous bed. When turtlegrass is removed, shoalgrass will invade and become dominant temporarily until turtlegrass returns. The evidence suggests that shoalgrass tolerates extremes in environmental conditions but not competition from other species.

Shoalgrass has been reported from 30 meters deep. McMillan (1974) claimed that it had the greatest tolerance to salinity of any of the seagrasses in the Gulf. It does well at salinities of 6 o/oo, but tolerates brief periods of fresh water. It also tolerates hypersaline water of up to 60 o/oo but these plants are dwarfed (McMillan and Moseley 1967). It prefers muck bottoms and withstands high turbidity and color. It tolerates higher temperatures (39.4°C) and longer exposure to air than all other seagrasses in the Gulf. Nonetheless, it suffers leaf-kill at Tampa in winter, even when submerged.

In Taylor County, shoalgrass constituted 2% of all the seagrasses and had a maximum biomass of 133 g/m^2. Near St. Marks lighthouse it occurred in 63% of 472 quadrats 0.09 m^2, but its biomass was much lower than that of turtlegrass and manateegrass. It occurs in tidal creeks within salt marshes near St. Marks lighthouse.

Halophila engelmanii. Plants of this species stand only about 10 cm tall. It is the least abundant of the seagrasses and is patchy in its distribution. It usually grows with turtlegrass and manateegrass but is relatively common only where these are not dense. It is probably shade-tolerant because it tends to be hidden beneath turtlegrass. Zimmerman and Livingston (1976) found it near river mouths where conditions were too variable to support dense growths of turtlegrass and manateegrass. It withstood high turbidity and color, winter temperatures as low as 9°C, and salinities of 11 o/oo. On the contrary, Humm (1973) and Eleuterius and Miller (1976) found *Halophila engelmannii* to be less tolerant, especially of low salinity, than manateegrass and turtlegrass. It tends to grow offshore at St. Marks lighthouse where salinities are higher, rather than near the mouth of the St. Marks River. It grows at depths of at least 73 meters, at temperatures up to 31.6°C., and in salinities up to 35 o/oo. It prefers muck substrates.

Its biomass off Taylor County constituted less than 1% of the seagrasses and was never higher than 64 g/m^2 dry weight. It was also the least abundant of the seagrasses near St. Marks lighthouse in terms of biomass. It occurred there in 14% of 472, 0.09 m^2 quadrats.

Widgeongrass. The widgeongrass grows in the more saline portions of brackish rivers and extends beyond the river mouths into the turtlegrass beds. It prefers substrates containing much silt or muck. It grows well at depths of about 0.4 to 2 meters, probably being limited to shallow depths by the high turbidity of river mouths.

Its seeds germinate at 15-20°C in the late winter, and new sprouts arise from the rhizomes of persisting plants at these same temperatures. Vegetative growth continues at temperatures of about 20-25°C. Flowering and fruiting take place at 18-35°C. Widgeongrass was once recorded growing in water 39.4°C but a leaf-kill soon followed (Phillips 1960). In our region, widgeongrass becomes increasingly abundant until late autumn when it is largely consumed by overwintering waterfowl.

Widgeongrass tolerates virtually fresh water indefinitely. It flourishes in fresh water impoundments at the St. Marks National Wildlife Refuge in Wakulla County. Salt water is introduced into these pools only once every few years. It was absent from the lighthouse pool, an impoundment that had been kept fresh for at least 25 years. In 1972 hurricane Agnes pushed salt water into this pool, and widgeongrass grew there 2 years later. Widgeongrass has been recorded in water with a salinity as high as 33 o/oo, but it rarely sets seed if the salinity exceeds 28 o/oo. It was seen in abundance near Tampa in water of more than 20 o/oo on a site where shoalgrass had been winter-killed. Widgeongrass declined in abundance as shoalgrass slowly returned the next year.

Widgeongrass comprised up to 338 g/m^2 in dry weight in November off Taylor County, but it was usually much less abundant. It was recorded at 11 g/m^2 at the mouth of the St. Marks River in July, 144 g/m^2 8 miles up stream in late summer, and 52 g/m^2 12 miles upstream also in late summer (Thompson 1977). It grew no farther up stream, and the salinities at that point averaged 1 o/oo but once reached 12 o/oo.

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30. SAWGRASS, NEEDLERUSH, AND CORDGRASS

Classification. Sedges, rushes, and grasses constitute important components of intertidal marshes. Among the more abundant plants of these families are those belonging to the following species.

Cladium jamaicense Crantz --- sawgrass (=Mariscus jamaicensis (Crantz) Britt.). Sawgrass ranges mostly near the coast in brackish and fresh-water marshes from Virginia to Florida and westward into Texas, also the Caribbean region. A variety is native to China and Japan. Sawgrass is the predominant plant of the Florida Everglades. It is abundant in the panhandle in the intertidal marshes along rivers.

Juncus roemerianus Scheele --- needlerush or black rush. Needlerush occurs along the coast from Maryland to Florida and westward into Texas. It is the predominant species in Gulf coastal salt marshes and occupies most sites that are inundated by tidal sheet flow less than daily. It is also common in brackish marshes along rivers.

Spartina alterniflora Loisel. --- smooth cordgrass. The smooth cord-grass ranges along the coast from eastern Canada to South America. It is the predominant salt marsh species in areas flooded daily at high tide.

Spartina spp. --- cordgrasses. The cordgrasses grow primarily in coastal habitats in the Americas, Europe, and Africa. Besides S. alterniflora, four others are native in the panhandle. Little is known about them autecologically, and they will not be treated individually. They are, Spartina patens (Ait.) Muhl., which is known as saltmeadow cordgrass or as couchgrass. It occurs along the Atlantic, Gulf, and

Pacific coasts, the Great Lakes region, and West Indes, and in Europe. It grows in low-chlorinity soils and tolerates higher chlorinities only if the soil is moist (Kurz and Wagner 1957). Spartina spartinae (Trin.) Merr., the Gulf cordgrass, ranges along the shores of the Gulf of Mexico, the Caribbean region, Mexico, and elsewhere in Latin America. It occupies relatively well drained marsh sites and beaches that are not particularly saline. Spartina cynosuroides (L.) Roth, is also called salt reedgrass and big cordgrass. It ranges from Massachusetts to Texas, grows to about 2 m tall, and occurs mainly along river banks where salinities are slightly brackish. Spartina bakeri Merr., is a densely cespitose species of Georgia and Florida that occurs in brackish, relatively well drained marshes and aggressively invades disturbed salt marshes, such as those which become less saline by the restriction of tidal flow.

Sawgrass. Not too much is known about sawgrass, other than it grows mostly in brackish to fresh marshes near the coast and carries fires exceedingly well. Penfound and Hathaway (1938) recorded a maximum soil chlorinity beneath sawgrass of 0.2%. Chabreck (1972) obtained readings of 4 $\pm$ 3 o/oo in the water of a sawgrass marsh. Sea strength is about 36 o/oo or approximately 3.5% chlorinity (Adams 1963).

Recent studies in the Everglades by Steward (1974) and Steward and Ornes (1975) revealed some additional information, based primarily on nutrient levels in sawgrass tissues and in the soil. They discovered that sawgrass has low nutrient requirements, particularly in contrast to the higher nutrient requirements of several fresh water marsh species as reported by others in the literature. Sawgrass is especially capable of withstanding low levels of available P and Cu, both of which are very low in Everglades soils. These soils are also low in K and N.

They established that the dominance of sawgrass in the Everglades is attributable to its ability to prosper in spite of low nutrient levels that would inhibit the growth of other species. Sawgrass is further favored by its ability to resprout from its rhizomes following fire. The habit, stand density, and fibrous nature of its shoots all favor its ignition and its ability to carry fire over large areas.

Needlerush. The anatomy and reproductive biology of needlerush were studied in detail by Foster (1968), Seibert (1969), Eleuterius and McDaniel (1974), and Eleuterius (1974, 1975, 1976). Needlerush is a rhizomatous perennial. The shoots grow year around, usually in very dense stands. Prairies of needlerush are often a meter or more tall and have a characteristic brownish gray-green cast. Needlerush grows within about the same salinity range as the smooth cordgrass but on soils that are better aerated. Chabreck (1972) recorded salinities of water in needlerush marshes of 14 $\pm$ 8 o/oo. Cooper and Waits (1973) recorded salinities from nearly zero to about 20 o/oo. Kurz and Wagner (1957) measured soil chlorinities from 0 to 3% with a median reading of 1.4%. Needlerush is unable to tolerate the higher chlorinities of salt flats. It may grow in near-coastal marshes where the salinity is barely perceptible.

Kurz and Wagner (1954) showed that plant height is influenced by soil chlorinity. Needlerush shoots averaged 37 cm tall in soils at 1.0% chlorinity and 181 cm tall at 0.1% chlorinity. Plant height is also influenced by the soil moisture. Kurz and Wagner noted that in a site with a soil chlorinity of 0.8% that the shoots averaged 60 cm tall when the soil moisture was 18% and 104 cm tall when the soil moisture was 33%.

Needlerush seeds germinate only on open sand (Eleuterius 1975). Germination requires both light and wet site conditions. Germination is most successful in fresh water, but the seedlings tolerate low salinities (Seibert 1969). The mature plants of needlerush characteristically grow on beds of fibrous peat. The root mat in these peat beds is 10-20 cm thick, but 50-75% of these roots are dead, though well preserved (Coultas and Gross 1975). It seems apparent that once a needlerush colony becomes established on bare sand, the older roots and rhizomes die and form an ever-deepening layer of peat.

The water table may lie 3-12 cm below the soil surface under needlerush, even when the marsh is inundated at high tide. The sheet flow slides over the rather impermeable peat, temporarily trapping a soil atmosphere which contains oxygen (Kurz and Wagner 1957). The pH of these peats may drop as low as 3.5, and H_2S is generated in the peat. Needlerush grows in soils with the pH upwards to 7.1, suggesting that pH is not a limiting factor. The lower pH values are the result of acids of decomposition in the peat.

The gray hue of needlerush marsh is attributable to the dead stalks which persist for weeks before falling over. Upon disarticulation from the rhizome they are sometimes transported in giant eddies across the marsh, presumably during exceptionally high tides. They are deposited in a swirled pattern over an area about the size of a house, where they weight down the living needlerush. Such areas are called "cow licks" locally.

As this detritus decomposes an N-fixing bacterium often occupies the stem cavities. Eventually the stalks fall apart and the pieces are converted into detrital aggregates by benthic algae. These aggregates or their decomposition products are transported to the Gulf where they enter the estuarine food webs (Ribelin 1978). Needlerush marsh is inundated a few times a month and the upper marsh a few times a year. As a result, detrital transport to the estuary likely is a pulsating phenomenon, which must be considered in evaluating the role of needlerush in estuarine productivity.

Needlerush often occurs between the salt flats and the flatwoods. This zone may be extensive if the gradient is low, or it may be abbreviated or absent if the gradient is steep. Soils of the upper needlerush marsh are often sandier and contain less peat than in the lower needlerush marsh. They retain less water in droughts and are less frequently replenished by water from sheet flow. The needlerush of the upper marsh is shorter than in the lower marsh (Kruczynski _et al_. 1978).

Smooth Cordgrass. The smooth cordgrass grows along tidal creeks and on protected beaches where it receives tidal inundation almost daily. A stunted form also grows on flats in the interior of salt marshes where tidal inundation is less frequent and salinities are often higher. Smooth cordgrass grows where the soil is wet or saturated most of the time.

Kurz and Wagner (1957) determined that the median value of soil chlorinity in smooth cordgrass marsh was 1.4% (the same median value as in needlerush marsh soils). The range in values was nearly zero to 4.0%, greater than in needlerush marsh. Chabreck (1972) found that the salinity of the water in smooth cordgrass marsh was 15 ± 8 o/oo. These salinities approximate those of the tidal creeks and estuaries which flood the Spartina marshes at most high tides. ("Spartina" as used in recent literature, normally refers to S. alterniflora , the smooth cordgrass.)

Kurz and Wagner (1957) noted that the lower elevational limit of Spartina on the seaward side of protected beaches was nearly identical to mean sea level throughout the panhandle. Rhizomes extend to lower elevations, but the shoots arising from them are stunted and often die back.

The upper limit of Spartina on these beaches corresponds closely to the highest predicted tide (Kurz and Wagner 1957). The exact limit is variable, depending on soil and slope. Water retention is greater in mucky or silty soils rather than sandy soils, therefore, the upper limit of Spartina will be at a higher elevation on a mucky soil than on a sandy soil. If a hardpan is present, percolation of water will be retarded, thereby retaining soil moisture longer at low tide. A low gradient drains more slowly than a steeper one, again promoting longer periods of soil saturation. The upper limit of the Spartina zone also may be limited by drift lines of organic matter which are stranded near the high tide mark. This detritus (variously called tidal hay, flotsam, or rack) consists mainly of leaves of seagrasses which decompose, smoothering the plants of Spartina beneath. Adams (1963) ran nutrient solution experiments and showed that Spartina became chlorotic with decreasing concentrations of Fe. (Needlerush was not so affected). He found that soluable iron concentrations were higher as elevation decreased in the marsh, perhaps because the iron becomes available through the action of anaerobic iron-reducing bacteria.

Kurz and Wagner (1954) showed that soil chlorinity affected plant height. Plants growing in soil with 0.8% chlorinity averaged 92 cm tall, while plants growing in soil with 1.3% chlorinity were only 17 cm tall.

Odum and Fanning (1973) said,

"It has recently been shown that Spartina grasses belong to the C_4 class of photosynthetic types that grow well under conditions of high temperature, high light intensity and low water availability..."

The C_4 plants have higher transpiration efficiency (require less water per gram of dry matter produced) and exhibit little photorespiration at high light intensities. Odum and Fanning (1973) wrote,

"It is concluded that vigorous daily tidal irrigation provides an 'energy subsidy' which, coupled with the adaptive advantages of the C_4 photosynthetic pathway, counteracts the physical stresses of the high salinity tidal marsh environment; thus *S. alterniflora* is able to equal or exceed in productivity the related species *S. cynosuroides*, which does not have to expend as much energy in osmoregulation, but, in turn, does not have the benefit of as much water flow energy."

The "tidal irrigation" brings nutrient-rich waters and sediments which can be exploited by *Spartina*.

Parrondo *et al.* (1978) said that tidal inundation created an anaerobic root environment that precludes the survival of nearly all halophytes from the zone occupied by *Spartina*. Teal and Kanwisher (1966) demonstrated a decreasing oxygen gradient from the culms to the roots, suggesting that oxygen produced in the shoots was diffusing internally to the roots.

Parrondo et al. (1978) found that the dry weights of Spartina plants were inversely correlated to NaCl concentrations above 8 grams per liter of soil. They also showed, though, that root growth was unaffected until the NaCl concentration reached 32 g/l. They further determined that the dry weight of the plants was lower if growing in drained, rather than in saturated soil. They concluded that chlorinity was less important than soil saturation in the distribution of Spartina in salt marshes.

The tall form of Spartina is as much as 2-3 m tall, but the dwarf form reaches about 10-40 cm tall. Transplantation experiments by Stalter and Batson (1969) and Stalter (1973) were suggestive of ecotypic (i.e., genetic) differentiation between these forms, but their misfortune in growing the controls made their data inconclusive. Mooring et al. (1971) showed that seedlings grown under uniform conditions segregated into height classes, strengthening the evidence for dwarf and tall ecotypes.

Shea et al. (1975) were unable to substantiate these findings, though, with transplantation and electrophoretic studies. Valiela et al. (1978) increased the nutrient supply to the short-form plants of Spartina and induced them to grow into tall forms. They wrote,

> "If sedimentation leads to elevated marsh surfaces, as it usually does, competition by the extant plants reproducing vegetatively eventually results in short plants. This succession may be reversed by an increase in nutrient supply."

It is evident that the controversy remains with regard to a genetic basis for the height forms of Spartina.

Mooring et al. (1971) reported that seeds germinated in an alternating diurnal thermoperiod of 18-35 C (65-95 F) after being stored eight months in sea water at 6°C. Seeds that were stored dry for eight months did not germinate.

Broome et al. (1972) said that most previously published information suggested that Spartina produces few viable seeds and that rhizomes are more important in the reproduction of the species. They found, though, that seedlings are the primary means of natural colonization in North Carolina marshes. Germination takes place in March and occurs to a large extent in drift lines at the high tide mark. It also occurs at lower elevations in protected intertidal areas. A seedling may grow into a mature plant which produces seeds within its first growing season. Broome et al. (1972) said that the seeds were ready for harvest in September. They noted that the quantity of seeds produced and the percentage of germination varied between stands. The quantity and germination percentage were highest in young stands of the tall form near tidal creeks. Reproduction by seed in the populations of the stunted form was far inferior to that of the tall form. Freezing was detrimental to germination. Germination was best if the seeds were stored in estuarine water for five months at 2-3°C. Those stored over a year did not germinate. Those stored five months at 2-3°C in distilled water, or dry but suspended over water, also germinated well. An after-ripening process was detected. Seeds allowed to germinate upon their harvest in September failed to reach 50% germination until after 24 days. Those allowed to germinate in February reached the 50% point in only four days. They wrote,

> "The elevation range over which seedlings can be expected to survive is limited to about the upper 20-50% of the elevation range of naturally occurring stands in a given area."

This range was determined by storms and wave action. They also noted that drifting sand smoothered seedlings.

Kruczynski *et al.* (1978) observed that the shoots die back in the winter and are produced in the spring. New shoots are not produced continuously as in needlerush.

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31. VEGETATIONAL SYSTEMS

A two-ranked system of classification is proposed to emphasize the relationships between ecologically similar communities. The various communities comprise the lower rank. These communities are grouped into 10 systems, which comprise the upper rank. Nine of these systems are for natural communities, and a tenth system is one of convenience for all ruderal communities. The upper and lower ranks correspond more or less to Levels II and III, respectively, in several mapping and classification systems in current use by planning and regulatory agencies (Anderson et al., 1976; Florida Division of State Planning, 1976; Kuyper et al., 1979). The ten systems are described in the following chapters. The characteristics shared by all communities of a system are presented at the beginning of each chapter. The communities are described thereafter, with an emphasis on the details which distinguish the communities from one another.

The following criteria are discussed for each system: community organization, species richness, physiognomy, physical parameters with regard to soil, salinity, fire, and moisture, mineral nutrients, community maintenance, responses to disturbance, mode of origin, and ecotones.

Community organization concerns the degree of integration of the species populations that comprise each of the communities of the system. In some systems, there is considerable indication of intergration, i.e., interspecific interactions or interdependencies. Other communities do not display obvious interactions, and their species seemingly occur together only because of similar autecological requirements. These non-integrated communities are often zones of one or few species along a moisture or salinity gradient.

Species Richness is the approximate number of species that could be expected in a stand. Data on species richness are scarce, and estimates must be considered as tentative. The term "low", in system descriptions signifies perhaps up to 15 species. "Moderate" signifies about 10-40 species and "high" about 40-100+ species.

Physiognomy is described for forested systems in terms of overstory (canopy trees), understory (smaller trees, saplings, and larger shrubs), and ground cover (all other vegetation). "Undergrowth" designates vegetation lacking distinct strata below the canopy.

With regard to moisture, emphasis is given to the moisture regime, i.e., the seasonal changes in moisture. Of particular importance in the moisture regime is the duration of the hydroperiod, i.e., the time that the soil is flooded or that the surface layer saturated.

Mineral nutrients are described according to their probable source (if imported) or their mode of being recycled. Nutrient input might be the result of alluvial, colluvial, or atmospheric transport. Mineral cycling may be facilitated by microbial decomposition or by the formation of soluble ash by fire. Mineral cycling might be retarded when nutrients are incorporated in accumulations of peat or are made chemically unavailable. Comments on mineral cycling are nearly all speculative for lack of data and are presented as hypotheses with hopes of stimulating research in this field of study.

Maintenance of the communities is described in terms of factors that promote continuity or permanence, as opposed to permitting changes in physiognomy, dominance, and species composition. Responses to disturbance are described with regard to repair mechanisms in the system after suffering disturbances that are not irreversible. The principle mode of origin is proposed as being by initial floristic composition (displacement model) or by succession (climax theory). Ecotones are described for the more important instances of intergradation between communities belonging to different systems.

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32. FIRELANDS SYSTEM

The firelands system includes longleaf pine-xeric oak woods, pine flatwoods, grass-sedge bogs, and several variations of these vegetation types. All vegetation containing longleaf pine belongs to this system. Slash pine may also be present. The pinelands of this system were called the pine barrens by settlers and early naturalists. As was mentioned on page 30, approximately two-thirds of the panhandle was covered originally by pine barrens. Smith (1884) wrote:

> "One who has never traveled through the pine barrens can have little idea of the impression of utter desolation on which they leave upon the mind. Nothing is to be seen in any direction but the tall, straight columns of the pine, with here and there a pond or lakelet."

The "barrens", though, are actually very rich botanically and pose many fascinating problems for the ecologist. Unfortunately, this once vast resource has been reduced severely by agriculture, modern forestry, urbanization, and careless husbandry of the land. It is becoming increasingly difficult to find a relatively unblemished stand which resembles the barrens alluded to by Smith.

Community Organization. The communities of this system are structurally and floristically complex, yet they display a predictable consistency between stands in similar habitats. These communities seem to be constructed in such a way as if to invite frequent burning. These features strongly indicate that firelands communities are well integrated ecologically and are not haphazard assemblages of miscellaneous species.

Species Richness. The number of species is moderate in drier sites and high in wetter sites. There are probably more species per unit area in grass-sedge bogs than in any other community in the panhandle. Large numbers of species are easily observed in firelands within a year of burning, preferably if visited at two seasons at times when the soil is moist from recent rains. Plants of the less common herbaceous species become increasingly difficult to locate in subsequent years after fire, as shrubs and tussocks of wiregrass grow and conceal the smaller herbs.

Physiognomy. The most characteristic structural feature of firelands is the dense ground cover consisting of grasses, forbs, and generally rather low-growing shrubs. Wiregrass or other densely cespitose or coarsely fibrous grasses or sedges are typically abundant. These and other herbaceous species become less abundant in relation to shrubs with time since the last fire (Green 1935, Lewis and Hart 1972). Plants of many herbaceous species evidently become dormant with increasing competition from shrubs and survive as rootstocks until released by fire. After about eight fire-free years, the ground cover reaches an equalibrium and does not change much until the next fire (Lemon 1949).

An open overstory of pines is often present, except in some bogs where the overstory is either absent or is composed of scattered hardwoods and pond-cypress. The drier sites typically have an understory of oaks. Otherwise, an understory is absent in firelands.

Soils. Fireland communities occur on sands and sandy loams representing a wide spectrum of soil series. Longleaf pinelands are known to grow on soils representing five orders (see p. 156). Litter and duff do not accumulate because of the frequent fires. The "A" horizon is often dark from the decomposing roots of wiregrass and the many other superficially rooted species, also from the contribution of fine charred organic particles which are spared from total combustion in fires. The dark topsoil is usually several centimeters thick in xeric and mesic sites, but is often much thicker in bogs. The decomposition products of pine and oak tissues, among others, produces a rather acid soil reaction.

Moisture. The drier sites are excessively well drained and droughty. The water table is always one or few meters below the surface, even in wet seasons. It is likely that some of the sandhills that are occupied by firelands represent the most xeric habitats in the panhandle. Woods (1957) described sandhills in which the water table was 12-15 m or more deep. In wetter sites, the water table may remain near the surface for much of the year, often perched there by a spodic horizon. The water table will drop to a depth of a meter or more only during droughts. The soils are rarely flooded, and then only shallowly so for a few days following heavy rains. The first few centimeters of soil are rarely saturated for more than several days at a time, except in bogs where the hydroperiod may be several weeks or months in duration.

Fire. Surface fires are frequent (see p. 239). Chapman (1932a) suggested a natural frequency of lightning-set fires of 3-4 years prior to human occupancy in longleaf pinelands. He compared this to a possible 10 year frequency in slash pinelands. Heyward (1939) said that until recently, longleaf pinelands burned once every 3-4 years. Wahlenberg (1946) suggested a pre-Indian frequency of fire at every 2-3 years in longleaf pinelands. Xeric sites burn slightly less frequently than mesic sites. Droughty conditions increase the length of time between fires for the establishment of a sufficiently dense ground cover to serve as fuel. In mesic sites and bogs annual burning is not only possible, but is sometimes practiced as a land management technique.

Mineral Nutrients. A general characteristic of the vegetation of fireland systems is the low proportion of green, chlorophyllous tissue to woody and other fibrous tissue. This observation is likely the direct result of the infertility of the soil. Since there is no obvious source of minerals being imported into the system, and since the system is exceptionally stable, it seems reasonable to assume that nutrient cycling is very efficient. This assumption contrasts with that of Woodwell (1979) who argued that the pine barrens of New Jersey represented a "leaky" system. Direct data are unavailable, and a study of nutrient cycling in fireland communities is needed.

Much organic matter is reduced by fire to soluble nutrients in the form of ash. The ash percolates into the soil with the first rain where it is likely absorbed by roots which form a very dense, continuous mat just beneath the surface. Some of these nutrients are certainly absorbed by mycorrhizal fungi and by N-fixing microorganisms. Some ash might be lost (or imported) through the atmosphere before it is wetted. Not all organic matter is consumed by fire, and some nutrients are released through microbial decomposition.

Maintenance. Fireland communities are maintained by frequent surface fires. If species from other systems should invade, their seedlings would be unable to survive these fires. The fires are facilitated in several ways. First, breezes which help fires to spread are not interrupted by dense growths of trees and large shrubs. Second, this lack of taller woody plants allows abundant light to flood the habitat, thereby promoting the growth of the dense ground cover which serves as the fuel for fires. Third, the available nutrients are in short supply, stimulating the production of fibrous tissues which enhance flammability. Nutrient deficiencies may also place at a competetive disadvantage any invading plants from other systems. Hydroperiods are not prolonged to a point that becomes intolerable for grasses and other highly flammable plants. Nearly all plants of the ground cover are long-lived perennials which sprout readily from their undamaged rootstocks following fire. This vegetative propagation helps maintain stability in species composition and species abundance. As a corollary, it seems reasonable that metabolic energies can be directed at other competetive interactions which maintain stability rather than at sexual reproduction.

Response to Disturbance. Common disturbances in firelands include timber harvesting, fire suppression, soil disturbance, and grazing.

Virtually all of the original-growth pines have been harvested, usually by clear cutting. The overstory in most flatwoods has been reestablished either from undamaged seedlings and saplings that were present at the time of harvest or from seeds that were dispersed from adjacent uncut pine stands. The density of second-growth pines is often greater than that in original-growth stands, and mortality among the competing trees is high,suggesting an eventual return to normal stocking. In some flatwoods, the natural reestablishment has resulted in low densities of pines, particularly in boggy flatwoods where prolonged hydroperiods evidently have interferred with the survival of pine seedlings.

In xeric pinelands, natural reestablishment has been relatively unsuccessful. Pines have not regenerated in many large areas of sandhills, or only a few widely scattered original-growth pines that were spared from harvest now serve as seed sources for limited regeneration. In lieu of pines, the understory oaks have increased in density (but not in height), forming thickets or semi-closed woodlands.

The ground cover shows no significant deleterious effects from the removal of the overstory, except where prolonged fire suppression or moderate soil disturbance accompanied timber harvest. There has been a general reduction in the biomass of the ground cover in xeric sites where oaks have proliferated. Otherwise, in comparison to second-growth pinelands, sites that have lacked an overstory for several decades show little or no change in floristic composition, species dominance, physiognomy, or the ability to carry frequent fires.

Fire suppression, rather than fire itself, is a form of disturbance. The initial response to fire suppression has been a proliferation of the growth of shrubs of the ground cover. The proportion of shrubs to herbs has changed in favor of shrubs, and the total biomass has increased per unit area. When suppression continued for about two decades (on moist or fertile sites) or three decades (on dry or infertile sites), young trees indigenous to other fireland systems became conspicuous in the undergrowth. Once these trees formed a canopy, the plants in the ground cover succumbed from competition, generally beginning with the herbs.

Soil disturbance can be minor or severe with regard to the ground cover. If the soil is scrapped with a bulldozer blade or turned with a plow or chopper, the disturbance is severe and causes irretrievable changes in the ground cover. If the soil is disked, the disturbance is moderate, but will cause some lasting changes in floristic composition or species abundance.

When the ground cover is used as unimproved rangeland for cattle, the effects of grazing are similar to those of light or moderate soil disturbance. Preferred grasses and legumes become scarce or at least inconspicuous but apparently recover after cattle are removed. Trampling may cause localized disturbances of a more severe nature. The rooting of feral hogs may also result in localized disturbances, although no studies have verified the permanence of the damage. Feral hogs forage on pine seedlings and have been identified as a major cause of understocking of second-growth pines in flatwoods.

The topic of disturbance in firelands is complex, particularly with regard to fire suppression and soil disturbance. These topics are explored in greater detail in the discussion at the end of this chapter.

Mode or Origin. Present evidence strongly suggests that all fireland communities developed through the process of initial floristic composition rather than by relay floristics or other seral elaboration. The development of firelands vegetation serves as the primary example in support of the displacement model (Chapter 16). Plant succession in its traditional sense is initiated in firelands only by human disturbances and leads ultimately to a potential natural vegetation of southern mixed hardwoods.

Ecotones. The frequent fires limit the possibilities of natural transition zones between firelands communities and those of other systems. The firelands communities usually stop abruptly, at least where natural fire frequencies have been maintained in recent decades. In the Northern Highlands and in similar physiographic regions of Georgia and Alabama, some intergradation occurs between longleaf pinelands and pine-oak-hickory woods. Wahlenberg (1946, p. 57) wrote with reference to the spatial relationship of these two communities in the interior uplands:

> "Inland the longleaf forest followed the multiple ramnifications of minor ridges, leaving the lower sites--those too moist to burn over often--to hardwoods trees."

The extent of this intergradation has not been documented, and the opportunity to do so has passed because of a century of disturbances associated with land use. The lack of documentation by early naturalists between these vegetation types suggests that the ecotone between these communities were not extensive or pronounced.

Other ecotones occur between longleaf pinelands and hardwood hammocks on the rims of river bluffs, between flatwoods and titi swamps, and between grass-sedge bogs and shrub-bogs. These ecotones largely are the result of fire suppression and are discussed later in this chapter under the heading of disturbance through fire suppression.

Communities. A number of firelands communities have been recognized by naturalists, botanists, foresters, ecologists, range specialists, planners, and others. Some communities have been narrowly defined and others broadly defined, causing overlaps between community concepts. No consensus has been reached with regard to the names applied to each community. Some communities were likely not part of the original vegetation but were derived through modifications caused by logging.

Table 11 attempts to account for the multiplicity of names and to organize the vegetational concepts they represent. The natural communities fall within two broad categories, pine barrens and bogs. The pine barrens are divisible into the high pinelands and the flatwoods. Six communities are recognized within these broader categories: longleaf pine-xeric oak woods, longleaf pine savannahs, pine flatwoods, boggy flatwoods, grass-sedge seepage bogs, and grass-sedge savannahs. Each community is defined by distinctive elements in its vegetation in terms of physiognomy and/or species composition. Each community exhibits its own habitat preference in terms of soil moisture and soil texture. For the most part, the communities are easily distinguishable in the field. Intergradations occasionally occur, particularly along protracted environmental gradients or wherever unusual combinations of habitat factors occur.

The longleaf pine-coastal scrub oak woods is a variant of the longleaf pine-xeric oak woods in which sand-live oaks and sometimes myrtle oaks are present, often as dominants in the understory. Several variants occur within natural flatwoods communities: longleaf pine flatwoods, slash pine flatwoods, and pond pine flats. These variants merely indicate the principal tree species, which is usually of minor consequence in

TABLE 11. Conspectus of Firelands Communities.

Communities (Numbered)	Soil Moisture in Summer Wet Season	Usual Soil Texture	Vegetation
PINE BARRENS (pinelands)	Dry to moist, not remaining saturated long after rains		Open, pine-dominated overstory
High Pinelands			Ground cover conspicuously herbaceous
1. Longleaf Pine-Xeric Oak Woods (longleaf pine-turkey oak woods, longleaf pine-scrub oak woods, sandhills, sand ridges)	Rapid percolation of rain water	Sandy	Understory of scrub oaks with turkey oak or sometimes bluejack oak dominant
1a. Longleaf Pine - Coastal Scrub Oak Woods			Understory with *Quercus geminata* common.
1b. Xeric Oak Woods			Lacking pine overstory for failure of natural pine regeneration following clear cutting
2. Longleaf Pine Savannahs	Moderate percolation of rain water	Loamy	No understory
Flatwoods			Ground cover conspicuously shrubby; saw-palmetto common
3. Pine Flatwoods (pine-palmetto flatwoods, dry pineland)	Moderate or slow percolation of rain water	Sandy	Pines only in the overstory
3a. Longleaf Pine Flatwoods			Longleaf pine overstory
3b. Slash Pine Flatwoods			Slash pine overstory; occurred originally along the Gulf coast and later inland as slash pines invaded clear cut longleaf pine flatwoods.

TABLE 11, continued.

Communities (Numbered)	Soil Moisture in Summer Wet Season	Usual Soil Texture	Vegetation
3c. Longleaf Pine-Slash Pine Flatwoods			Longleaf and slash pines in overstory, the consequence of partial invasion of slash pines into former longleaf pine flatwoods after clear cutting
3d. Palmetto Prairies			Lacking pine overstory for failure of natural pine regeneration following clear cutting
4. Boggy Flatwoods (moist pine barren)	Surface soils saturated for days at a time after rains	Sandy-peaty	Longleaf and/or slash pine overstory (less commonly pond pine) and sometimes pond-cypress, blackgum, sweetbay white cedar, etc.
4a. Pond Pine Flats			Overstory of pond pines
BOGS	Soil surface remaining saturated for weeks at a time		Trees absent or nearly so
Grass-Sedge Bogs (pitcher-plant bogs)			Ground cover conspicuously herbaceous
5. Grass-Sedge Seepage Bogs (marginal bogs, strands)	Water table seeping from soil surface	Sandy-peaty	Scattered shrubs or small trees often present; natural or sometimes derived following clear cutting boggy flatwoods and a resultant prolongation of the hydroperiod from a reduction in transpiration
6. Grass-Sedge Savannahs	Water table perched	Clayey	Shrubs and trees essentially absent except St. John's-wort

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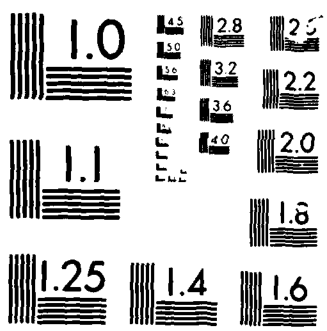

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firelands vegetation. Three other variants are recognized that were derived as a result of logging operations. The xeric oak woods and the palmetto prairies came into existance following the failure of pine reproduction after clear cutting. The longleaf pine-slash pine variant developed as trees of both species invaded former longleaf pine flatwoods following clear cutting. The slash pine flatwoods variant is often derived when slash pines were the only trees that naturally restocked a former longleaf pine flatwoods after clear cutting. The slash pine flatwoods variant also occurred naturally in the original-growth pinelands but was largely restricted to sites just inland from tidal marshes and other coastal environments. Some grass-sedge seepage bogs were also derived after the clear cutting of boggy flatwoods.

1. Longleaf Pine-Xeric Oak Woods

The overstory consists of scattered longleaf pines with a canopy closure of approximately 10-40 percent. Rarely a few trees of other species may be present, such as Spanish oak, live oak, and black gum. Such trees may have become established because of fire suppression or minor soil disturbance. If hardwoods occur, they often grow only where the subsoils are loamy or where site conditions are relatively favorable.

The understory consists of scrub oaks, with turkey oak often being the most important species and usually the only oak on drier sites. Blue-jack oak is usually present and occasionally locally dominant. It is the next most tolerant understory species to xeric conditions. Sand-post oak is the least common of the typical understory oaks and attains abundance only along the edges of bluffs or sinks where moisture is relatively plentiful. Sand-live oak is sometimes present, often accompanied by myrtle oak. Such stands are usually small and isolated and are most easily interpreted as relics of scrub vegetation on old beach ridges that have been isolated inland since times of higher mean sea level.

Other occasional large shrubs and small trees of the understory include tree sparkleberry (*Vaccinium arboreum*), Florida blueberry (*V. stamineum*), persimmon (*Diospyros virginianum*), dogwood (*Cornus florida*), chinquapins (*Castanea alnifolia*, *C. pumila*), and blackjack oak (*Quercus marilandica*). Blackjack oak is rare and limited to sand ridges in the Northern Highlands where the subsoils are clayey. Chinquapins are also largely restricted to the Northern Highlands. Little is known about the character of the understory in original-growth stands. From old photographs and scanty descriptions in the older literature, it seems likely that the trees were less dense and sometimes taller than in second-growth stands. Canopy closure in the understory varies widely and is very approximately inversely proportional to the closure of the overstory.

The ground cover is conspicuously herbaceous, but low shrubs and woody vines are always present. Wiregrass is almost universally present in its usual density of about 5 plants (large clumps) per meter-square. Several other grasses are always present, but not necessarily the same species in every stand. Some of the more common ones are Gymnopogon brevifolius, Muhlenbergia capillaris, Dichanthelium ovale, Sorghastrum secundum, and Sporobolus junceus. Other herbs that are often common or abundant are bracken (Pteridium aquilinum), partridge peas (Cassia fasciculata), rattlebox (Crotalaria rotundifolia), beggar's ticks (Desmodium spp.), sensitive-brier (Schrankia microphylla), goat's rue (Tephrosia virginiana), green eyes (Berlandiera pumila), golden-asters (Pityopsis graminifolia, Chrysopsis mariana), blazing-star (Liatris tenuifolia), rose-rush (Lygodesmia aphylla), blackroot (Pterocaulon pycnostachyum), butterfly-weed (Asclepias tuberosa), nettle (Cnidoscolus stimilosus), croton (Croton argyranthemus), Dyschoriste oblongifolia, Petalostemum albidum, P. caroliniense, Phlox floridana, jointweed (Polygonella gracilis), and Tragia urens.

Some of the more common shrubs in the ground cover are pawpaw (Asimina longifolia), New Jersey tea (Ceanothus microphyllus), dwarf-huckleberry (Gaylussacia dumosa), gopher-apple (Licania michauxii), poison-oak (Rhus toxicodendron), and blueberry (Vaccinium myrsinites). Woody vines are sometimes common trailing over the ground or climbing in the understory trees. They include yellow-jessamine (Gelsemium sempervirens) and muscadine (*Vitis rotundifolia*).

The vegetation of the ground cover has a total cover of about 50% a few months following fire and nearly 100% a year or two later. On the driest sites complete cover is infrequently observed even years following the last fire.

The soil is generally sandy, although loamy or clayey subsoils are common in the Northern Highlands. The surface generally is white with a veneer of quartz sand. The shallow root zone is sandy and darkened with organic matter. Below about 5 cm deep the sand is white or only slightly discolored. Internal drainage is rapid and not inhibited by pans or high water tables. Broadfoot (1973) noted that a rise in the water table caused by the formation of Lake Seminole caused the deaths of those turkey oaks near the lake.

Fire is frequent, although probably less frequent than in other firelands vegetation because of the slow growth of flammable plants in the ground cover. A natural frequency of once every 3-6 years may be surmised.

This community is common and widespread, particularly in the Gulf Coastal Lowlands in karst plains and in the sandhill country bordering New Hope Ridge and the Western Highlands. Research Summaries 1 and 2 describe stands of this community.

2. Longleaf Pine Savannahs

The overstory consists of longleaf pines with an approximate canopy closure of approximately 20-40 percent, or greater in young second-growth stands. Other tree species, if present, are uncommon and likely became established with fire suppression or minor soil disturbance. Longleaf pines attain their maximum height and girth in this community. An understory is absent.

The ground cover is dense and generally more conspicuously herbaceous than woody. Wiregrass is almost universally present and abundant. Saw-palmetto is sometimes present but not dense, at least over wide areas. Some of the more common low shrubs of the ground cover are huckleberries (*Gaylussacia dumosa*, *G. frondosa*), runner oaks (*Quercus pumila*, *Q. minima*), and blueberry (*Vaccinium myrsinites*, *V. darrowi*). Bracken is atypically abundant. Grasses are common. There are places in the Western Highlands (e.g., n.w. Escambia Co., n.w. Okaloosa Co.) where wiregrass is absent. These areas represent the eastern edge of the "bluestem range", which is the term designating the longleaf pinelands of the northern Gulf coast from Alabama to eastern Texas. Wiregrass is replaced by a mixture of grasses, including beardgrass (*Andropogon elliottii*), broomsedge (*Andropogon virginicus*), threeawn (*Aristida virgata*), panic-grass (*Dichanthelium aciculare*), switchgrass (*Panicum virgatum*), little bluestem (*Schizachyrium scoparium*), and slender bluestem (*S. tenerum*) (Penfound and Watkins 1937, Pessin 1938, Wahlenberg *et al*. 1939). Slender bluestem and *Muhlenbergia capillaris* are important where wiregrass is absent in the panhandle. Wiregrass is curiously absent from longleaf pine savannahs in the Tallahassee Hills of northern Leon County. The bluestem range grasses may have occurred there initially, or intensive land used, starting with Indian agriculture and extending through the cotton era, may have eliminated the species.

Other herbs in the ground cover include partridge-peas (Cassia fasciculata, C. nictitans), butterfly-pea (Centrocema virginianum), beggar's-ticks (Desmodium spp.), milk pea (Galactia macreei), bush-clover (Lespedeza repens), pencil flower (Stylosanthes biflora), asters (Aster adnatus, A. dumosus, A. tortifolius), elephant's-foot (Elephantopus elatus), thoroughworts (Eupatorium spp.), sunflower (Helianthus radula), golden-asters (Pityopsis graminifolia), blazing star (Liatris chapmanii, L. gracilis), goldenrod (Solidago odora), milkweed (Asclepias michauxii), meadow-beauty (Rhexia alifanua).

The soil is usually loamy, at least in the subsoil. Internal drainage is fairly rapid and not interrupted by pans. Soil moisture is not as dry as longleaf pine-xeric oak woods, but often drier than pine flatwoods. The natural frequency of surface fires is about once every 2-4 years.

This community is largely restricted to slopes in the Northern Highlands. Much land that originally supported longleaf pine savannahs is now in agricultural use. Some well kept original-growth stands are in the plantation lands in Grady and Thomas counties, Georgia, just above the state line. Other stands occur in the Western Highlands. On sandier slopes, this community is more of a transitional zone between longleaf pine-xeric oak woods on ridges and longleaf pine flatwoods lower on the same slopes. The unimportance of saw-palmetto is curious and may be related to an intolerance of that species to loams and clays. The flatwoods adjoining grass-sedge savannahs are clayey and also lack an abundance of saw-palmetto. Floristically the longleaf pine savannahs are very similar to pine flatwoods. Two less common species, Lespedeza capitata and Nolina atopocarpa, may be restricted to longleaf pine savannahs and the flatwoods near grass-sedge savannahs. Research Summaries 3 and 4 describe examples of longleaf pine savannahs.

3. *Pine Flatwoods*

The overstory consists of longleaf pine (in longleaf pine flatwoods) or of slash pine (in slash pine flatwoods). Both pines may be present (in longleaf pine-slash pine flatwoods), but mixed stands are restricted to second-growth, as noted in Table 11. An understory is absent.

The ground cover is characterized by dense growths of saw-palmetto. The shrubby species are more conspicuous than the herbaceous species, except during the first few months following a fire. Shrubs that are almost universally present and dominant are gallberry (Ilex glabra), runner oaks (Quercus pumila and/or Q. minima), dwarf huckleberry (Gaylussacia dumosa and sometimes G. frondosa), blueberries (Vaccinium myrsinites and/or V. darrowi), wax-myrtle (Myrica cerifera), in more moist areas fetterbush (Lyonia lucida), and at least one species of St. John's-wort (e.g., Hypericum hypericoides, H. microsepalum, H. stans). Staggerbush (Lyonia ferruginea) may be locally abundant, sometimes in close priximity to longleaf pine-coastal scrub oak woods (Clewell, 1971).

Herbs include the species already listed for the longleaf pine savannah community. To these may be added yellow-eyed grass (Xyris caroliniana), Tephrosia spicata, deer's-tongue (Carphephorus odoratissimus), milkworts (Polygala grandiflora, P. lutea), queen's-root (Stillingia sylvatica), and many others.

The soil is generally sandy or sometimes loamy, often well darkened with organic matter in the upper few centimeters. Internal drainage is often impeded by a spodic horizon which perches a water table during wet seasons. Fire frequency is high.

This community is abundant and widespread throughout the panhandle. It is particularly common in the Coastal Lowlands. Research Summaries 5 and 6 describe stands of this community. The stands from Research Summary 6 adjoin grass-sedge savannahs and are transitional to the longleaf pine savannah community.

4. *Boggy Flatwoods*

The overstory consists mainly or entirely of pines, although non-pine species may be present and even dominant in patches. The pines are generally longleaf pine and/or slash pine. Pond pine may be present in low numbers or rarely as the dominant species, forming a pond pine flat. The non-pine species, if present, are typically those of acid swamps, including pond-cypress, blackgum, white-cedar, sweetbay, titi, and myrtle-leaf holly. Deciduous hardwoods are rare. The canopy is open if pines predominate. Non-pine species may occur in small groves with a locally closed canopy, or they may occur as scattered individuals like the pines. An understory is generally absent or may consist of irregular shrubby patches of shrubs and saplings. If the site has not been burned with the usual frequency (as is the case for much of the extensive boggy flatwoods in Tate's Hell Swamp), then an understory develops, dominated by species common to acid swamps. In time a shrub bog replaces the boggy flatwoods.

The ground cover is conspicuous for its woody element. Saw-palmetto and many other species common to the pine flatwoods community are present, often in abundance. Other woody species may include large gallberry (Ilex coriacea), odorless wax-myrtle (Myrica inodora), Hypericum tetrapetalum, and coppicing plants of the overstory. Cinnamon fern (Osmunda cinnamomea), Virginia chain-fern (Woodwardia virginica), cane (Arundinaria gigantea), and pitcher-plants (Sarracenia flava) are often conspicuous. In the wettest areas bordering acid swamps wiregrass may be replaced entirely by Florida dropseed (Sporobolus floridanus).

The soil is similar to that of pine flatwoods except the hydroperiod is longer. Fires are not quite as cleanly burning as in flatwoods because of the increased moisture and also probably because of the deflection of air currents by the wall of vegetation of adjacent acid swamps and shrub bogs.

The boggy flatwoods community characteristically forms a narrow zone separating pine flatwoods from acid swamps and shrub bogs. Near the coast, boggy flatwoods are common in expansive seepage areas, such as Tate's Hell Swamp. Most boggy flatwoods occur in the Coastal Lowlands, but some stands occur elsewhere, particularly in conjunction with seepage slopes. Research Summary 8 describes a stand of this community. Eleuterius and Jones (1969) described a stand from southern Mississippi.

5. *Grass-Sedge Seepage Bogs*

Seepage bogs have no distinct overstory or understory, rather the relatively few trees or large shrubs grow as widely scattered individuals or small thickets. The woody species present are essentially the same as those in boggy flatwoods, including slash pine (but not longleaf pine), uncommonly pond pine, pond-cypress, blackgum, white-cedar, sweetbay, swamp bay, titi, large gallberry, and myrtle-leaf holly.

The ground cover is the only prominent vegetational stratum and contains many of the same species as in boggy flatwoods. Saw-palmetto is uncommon. Wiregrass is usually the dominant grass, but in wetter sites it is absent and replaced by similar coarse graminaceous plants, often species of Rhynchospora. Insectivorous plants (species of Sarracenia, Drosera, Utricularia, Pinguicula) are common. Herbs, particularly monocots, are more conspicuous than shrubs. The species composition is quite variable from place to place. Rush-featherling (Pleea tenuifolia) and Barbara's-buttons (Marshallia graminifolia) are indicators of this community and are rare or absent from the floristically similar grass-sedge savannahs.

The upper soil horizon is a deep peaty sand. This horizon is saturated or nearly so during wet seasons. Fires are frequent and prevent the encroachment of trees.

Seepage bogs are common in the western half of the panhandle near the coast and towards the base of slopes. A common position for them is between a bay swamp along a creek or river and a pine flatwoods at mid-slope. Seepage bogs occur elsewhere, including along the Cody Scarp and other escarpments where ground-water seeps to the surface. Fire suppression has turned some seepage bogs into dense pine-hardwood forests which have no resemblance to bogs. Many bogs in the hills of the western panhandle were once very extensive but have been converted into pine plantations. This community has suffered a considerable reduction in area in the last two or three decades. Research Summary 8 describes the physical environment for a seepage bog.

C. *Grass-Sedge Savannahs*

Trees and shrubs are absent or are much more widely scattered than in seepage bogs. If occasional isolated mature pines occur, they almost invariably grow on sandy knolls with improved soil aeration. Such sites are minute pine flatwoods and contain species distinctive of flatwoods. If slash pines are established in the savannahs proper, (which is usually only by intentional planting) they remain stunted saplings with a dimunitive crown. Such trees resemble old fashion hat racks. An occasional isolated pond-cypress or blackgum may grow near shrub bogs or cypress stringers. Coppicing sweetbays and titi bushes may also occur in these wetter areas. St. John's-wort (Hypericum fasciculatum) is the only shrub of significance. It seeds-in the year after fire in abundance and begins to overtop the ground cover in three years. After about eight fire-free years, it will form a diminutive mature "tree" about 1-1.5 meters tall with a single trunk. These plants form a closed canopy, but their acicular leaves allow an abundance of light to reach the herbaceous plants beneath. It is entirely fire-killed and rarely survives to coppice.

The ground cover is a low turf about 3-6 decimeters tall of dense wiregrass, sedges (mainly *Rhynchospora* spp.), and other herbs, particularly monocots. Woody species are essentially absent, with the exception of St. John's-wort and a few scattered trees and shrubs that invade from adjacent swamps and that persist by coppicing. Other than sundews (*Drosera capillaris*) and bladderworts (*Utricularia juncea*), virtually all of the many herbaceous species are rooted within the tussocks of wiregrass. Earthworms deposit castings within these tussocks, and new tillers are produced within this new soil. This process continues until the wiregrass is growing on a pedestal several centimeters above the original level of the soil. This increased height allows wiregrass and other plants rooted with wiregrass the advantage of improved soil aeration and perhaps increased nutrient availability.

Some of the more abundant species in the ground cover are *Rhynchospora chapmanii*, *R. plumosa*, and *Dichanthelium acuminatum*. Limited observations indicated that additional species of *Rhynchospora* are also abundant, each one maturing at a slightly different time of year. Many spectacular wild flowers characterize these savannahs, including colic-root (*Aletris lutea*), grass-pink (*Calopogon pulchellus*), coreopsis (*Coreopsis gladiata*, *C. nudata*), white-tops (*Dichromena colorata*), leopard lily (*Lilium catesbaei*), snowy orchid (*Plantanthera nivea*), rose pogonia (*Pogonia ophioglossoides*), several milkworts (*Polygala cruciata*, *P. cymosa*, *P. ramosa*), meadow-beauty (*Rhexia alifanus*), cone-flower (*Rudbeckia graminifolia*, *R. mohrii*), marsh pink (*Sabatia bartramii*, *S. stellaris*), pitcher-plants (especially *Sarracenia psittacina*), yellow-eyed grass (*Xyris ambigua*, *X. stricta*), and crow poison (*Zigadenus densus*, *Z. glaberrimus*). The narrow endemic, *Verbesina chapmanii*, is limited to this community and is common there.

The soils are loamy or clayey. Sometimes the clays are overlain by shallow sands. In one savannah the clay stratum exceeded 2.7 meters in depth (Clewell 1971). Fissures develop in these clays during droughts, but in most seasons the soil is wet and very poorly aerated. Water stands between the tussocks of wiregrass for several days following heavy rains. The flat terrain prevents appreciable surface runoff, and the clays prohibit internal percolation. The root zone is exceedingly shallow for lack of aeration in the gleyed soils. Pritchett (1969) showed that the growth of slash pines were inhibited both by poor aeration of the soil and by the unavailability of phosphorous. High levels of aluminum were detected, suggesting the possibility of toxicity to trees. Frequent fires are another hazard to trees, especially since retarded growth prevents them from quickly attaining a size large enough to escape severe fire damage.

The grass-sedge savannahs have a limited distribution in the Apalachicola River basin in Liberty, Calhoun, and Franklin counties. Evidently the clay soils in Liberty County represent alluvial deposits at a time when the Apalachicola River valley was further eastward of its present location. The extent of this community in the western panhandle has not been determined, and it may be that the community is restricted largely or entirely to the lower Apalachicola River watershed. Two examples of grass-sedge savannahs are described in Research Summary 9.

Discussion

Flora. One of the most characteristic features of firelands vegetation is the large number of species in the ground cover. Most authors overlook this important point, a notable exception being Ripley et al. (1962). The Research Summaries include lengthy species lists. None of these lists represent the total flora, because some stands were visited only in one season, and the inventory of most stands was limited to small areas of usually less than two hectares. The ground cover in each of five longleaf pine stands was sampled in quadrats totalling 30 m^2 (Research Summaries 1, 3, 4, 6). The number of species occurring in the quadrats in each stand ranged from 59 to 67. These represent from about half to two-thirds of the species in the ground cover seen at each stand, suggesting that many species are common and evenly distributed.

The high number of common species is suggested strongly by their frequencies in meter-square quadrats (Table 12). The cumulative means for nine stands showed that 5.8 species occurred in at least half of the quadrats, that 12.0 species occurred in 30 percent of the quadrats, and that 29.2 species occurred in at least 10 percent of the quadrats.

Table 13 gives additional floristic information from eight stands of fireland vegetation. The total number of species ranged from 66 (longleaf pine-xeric oak woods) to 133 (longleaf pine flatwoods adjoining grass-sedge savannahs). The total number of species was higher in wetter habitats. The percentage of herbaceous species ranged from 68.1% (longleaf pine flatwoods) to 80.5% (grass-sedge savannah). The combined species in the overstory and understory was from 0 to 4 in seven stands and 20 in one stand which had been fire-suppressed for many years.

TABLE 12. Number of Ground Cover Species per Frequency Class in 9 Fireland Stands.

Frequency Class	Number of Species	
	Mean	Cumulative Mean
.90-1.00	1.2	1.2
.80-.89	1.0	2.2
.70-.79	0.8	3.0
.60-.69	1.4	4.4
.50-.59	1.4	5.8
.40-.49	2.2	8.0
.30-.39	4.0	12.0
.20-.29	6.3	18.3
.10-.19	10.9	29.2
.01-.09	22.3	51.5

Species frequencies were determined in at least 30, meter-square quadrats in 2 longleaf pine-xeric oak woods, 2 longleaf pine savannahs, 3 longleaf pine flatwoods, and 2 grass-sedge savannahs (Research Summaries 1-6, 9).

TABLE 13. Number of Species in 8 Firelands Stands.

Location	Number of Species					Percent Herbaceous Species
	Trees		Ground Cover			
	Over-story	Under-story	Other Woody	Herbs	Total	
LONGLEAF PINE-XERIC OAK WOODS						
Thompson's Woods	1	5*	23	61	89	68.5
Spring Hill	1	4	11	50	66	75.8
LONGLEAF PINE SAVANNAHS						
Big Woods	1	0	23	74	98	75.5
Wade	1	0	28	64	93	68.8
LONGLEAF PINE FLATWOODS						
Buckhorn	1	2*	21	49	72	68.1
Liberty 4 & 17	1	0	30	102	133	76.7
BOGGY FLATWOODS						
Tate's Hell	3	17*	12	82	111	73.9
GRASS-SEDGE SAVANNAH						
Liberty 4 & 17	0	0	25	103	128	80.5

*Includes trees of the overstory species.

Data from Research Summaries 1-7, 9. The high number of understory trees in the stand at Tate's Hell reflects fire suppression, not typical conditions. "Other woody species" include shrubs, woody vines, and coppicing (or seedling) trees of species not represented in the overstory and understory.

Grass-sedge savannahs contained many species (128), but the number of species occurring in quadrats was lower than in pinelands: 33 species in 30 m^2 and 38 species in 60 m^2. Evidently there are many relatively rare species in grass-sedge savannahs.

Table 14 treats the herbaceous vegetation of these same eight stands with regard to taxonomic groupings. Monocots generally are unimportant in drier habitats (15-16% in longleaf pine-xeric oak woods) but are more nearly equal to dicots in wetter habitats (52% in boggy flatwoods). An increase in sedges (Cyperaceae) accounts for part of that increase, and much of the rest comes from miscellaneous monocot families (e.g., Liliaceae, Xyridaceae, Eriocaulaceae). Grasses (Gramineae or Poaceae) are fairly constant components of the flora in all habitats (5-18%). Composites (Compositae or Asteraceae) are also constant and numerous, regardless of habitat (17-38%). Legumes (Leguminosae or Fabaceae) are common in pinelands (19-37%) but are entirely absent in boggy flatwoods and grass-sedge savannahs. This absence of legumes in bogs might be related to the inability of N-fixing symbionts to tolerate prolonged hydroperiods. Wells and Shunk (1928) found no legumes in a savannah in North Carolina.

The species lists in the Research Summaries allow a comparison of floristic composition between communities. Only 18 percent of the species in longleaf pine flatwoods were shared in common with the species in adjacent grass-sedge savannahs (Table 15). Quadrat data for Research Summaries 6 and 9, from which this percentage was calculated, showed that only one species, wiregrass, was comparable in abundance in both communities. The grass-sedge savannahs were more closely related floristically to a boggy flatwoods. They shared 29% of their species.

TABLE 14. Percentage Composition of Selected Taxa of Firelands Herbs.

Location	Number of Herbaceous Species	Percentages								
		Grasses	Sedges	Other Monocots	Composites	Legumes	Other Dicots	Ferns	All Monocots	All Dicots
LONGLEAF PINE-XERIC OAK WOODS										
Thompson's Woods	61	13	2	0	28	18	37	2	15	83
Spring Hill	50	14	2	0	22	26	34	2	16	82
LONGLEAF PINE SAVANNAH										
Big Woods	74	14	4	0	27	27	27	1	18	81
Wade	64	17	2	0	31	29	19	2	19	79
LONGLEAF PINE FLATWOODS										
Buckhorn	49	8	4	14	29	14	27	4	26	70
Liberty 4, 17	102	5	3	8	38	15	30	1	16	83
BOGGY FLATWOODS										
Tate's Hell	82	11	16	25	17	0	27	4	52	44
GRASS-SEDGE SAVANNAH										
Liberty 4, 17	103	10	11	20	23	0	32	4	41	55

Data from Research Summaries 1-7, 9.

TABLE 15. Percentages of Shared Species between a Longleaf Pine Flatwoods, a Boggy Flatwoods, and a Grass-Sedge Savannah.

Community Comparisons	Number of Species Not in Common	Number of Species in Common	Total Number of Species	Percentage of Shared Species
Longleaf Pine Flatwoods	111	17	217	8
Boggy Flatwoods	89			
Longleaf Pine Flatwoods	90	38	215	18
Grass-Sedge Savannah	87			
Boggy Flatwoods	54	53	180	29
Grass-Sedge Savannah	73			

Data were from Research Summaries 6-7, 9. Taxa identified only to the generic level were not included in the tabulations.

This boggy flatwoods only shared 8% of its species with the longleaf pine flatwoods.

The species lists in the Research Summaries also point to the preponderance of perennial species in firelands. Among the very few annuals on these lists are the partridge-peas (Cassia fasciculata, C. nictitans) whose seeds are stimulated to germinate by fire (see p. 164). Other annuals are parasitic or hemiparasitic (species of Cuscuta, Agalinis, Seymeria; see Fitzgerald et al. (1975) for comments on Seymeria). Blue-curls (Trichostema dichotomum), an annual mint, persists in low numbers. Some bog plants may grow as annuals in wetter habitats and as perennials in drier ones (e.g., Drosera capillaris, Utricularia juncea), but no observations have been made to substantiate this prospect.

Soils. Pritchett and Smith (1968) succinctly described the soils of pine flatwoods, and their description is quoted below, except for references to the literature and figures:

> "The Ground-Water Podzols (Haplaquods) predominate in the coastal lowlands. These soils, such as Leon and Immokolee sands, generally have a gray to dark gray surface 3 to 20 cm thick overlying light gray sands. The presence of a prominent spodic horizon, usually beginning at 35 to 106 cm depths, is a distinguishing feature of many of the soils of this great soil group. The spodic horizon consists primarily of sands more or less cemented by organic matter commonly referred to as an "organic pan". In the virgin state, pH of the sands varies from 3.8 to 5.6. These

forest soils frequently nitrify poorly because they have existed for a long time at a low pH, with low nutrient content, and occasionally poorly aerated. These conditions result in an inefficient or small population of nitrifiers. Fortunately, nitrate is not a good N source for absorbtion by mycorrhizal roots of forest species. Pines almost always grow in acid soils where ammonification is probably the dominant and terminal conversion of available N materials.

Organic-matter content of the surface horizon usually varies between 2 and 4 percent, and cation exchange capacity varies from 4 to 8 me/100 g soil. Organic matter contributes most of the limited cation exchange capacity for the retention of plant nutrients, as one percent of organic matter adds about 2 me of exchange capacity per 100 g of soil.

Total P of unfertilized surface soil will generally average from 70 to 120 ppm, largely in the organic fraction, while neutral NH_4OAc extractable P varies from 0.1 to 10 ppm. Exchangeable K, Ca, and Mg vary from 15 to 50 ppm, 100 to 500 ppm, and 25 to 125 ppm, respectively."

Effects of Clear Cutting. Several authors have commented on the failure of longleaf pine to become reestablished after the clear cutting of the original growth. Forbes (1930) said,

"It is estimated that of approximately 42,100,000 acres [in the Southeast] of cutover longleaf and slash pine

land, 22,400,000 acres have not restocked, either because
of fires, absence of seed trees, or both."

With regard to the formation of xeric oak woods from the longleaf pine-xeric oak woods, Harper (1921) wrote that scrub oaks, "...seem to increase in abundance after logging operations, perhaps chiefly because the removal of the pines allows the soil to become drier..." Pessin (1933) attributed a lack of seed source for the reason longleaf pines did not recover, allowing turkey oaks to take over. Bozeman (1971) said that the scrub oaks took over following the harvest of pines and a subsequent reduction in fire in Georgia, and Faust (1976) briefly described such a stand there.

Previous authors commented on the former restriction of slash pine flatwoods to coastal areas and the subsequent invasion of slash pines into longleaf pine flatwoods after clear cutting. Forbes (1930) wrote:

"Extensive pure stands of virgin slash pine were rare except in the lower peninsula and Gulf coast of Florida. From South Carolina to eastern Louisiana, individuals or small groups of slash pines, like loblolly, were present in the virgin forest along small streams and in swamps throughout the flatwoods of the coastal plain, and these have provided the seed for great acreages of beautiful second growth on adjacent cut-over longleaf land, and on occasional old fields. Abundant seed production, very vigorous early growth, and ability to adapt itselt to a wide range of soils are characteristic of this species. It is, however, sensitive to fire for the first few years. With the spread of fire protection in the South, slash

> pine will undoubtedly be greatly benefited in its competition with longleaf for the moist flatlands, and it shows some evidences of taking possession of the moderate slopes as well."

Elderedge (1935) said that there had been considerable fire protection on large holdings during the past 6-8 years, and that as a result, slash pine, "... marches almost at once out of the swamps to the drier lands to fill the gaps among the longleaf pines". Penfound and Watkins (1937) wrote,

> "With the increase of fire protection, slash pine undoubtedly will be greatly benefited in its competition with longleaf..."

Wahlenberg et al. (1939) wrote of the "well recognized tendency" of slash pines to migrate slowly from the swamps to the better drained soils under fire protection. Garren (1943) cited several other references to the invasion of slash pine in cut-over longleaf pine flatwoods. Chapman (1932b) went so far as to venture,

> "...If complete fire protection must be enforced on the vast areas of longleaf pine lands of the South, and is successful, the longleaf pine will disappear as a species."

Clewell (1971) cited the observations of a retired forester from Wakulla County who stated that longleaf pine was the exclusive tree of the flatwoods until the suppression of fire began in the 1930's. Both pond pine and slash pine, which previously had been restricted to bay swamps, invaded the pine flatwoods, as did some of the "brush" species of bays.

Boggy flatwoods that are cut-over have been known to undergo a modest transformation until they resemble grass-sedge seepage bogs. The removal of the original-growth pines reduced transpiration, thus prolonging the hydroperiod to the point that longleaf pine regeneration was prevented. Fires prevented the invasion of trees of other species. Pitcher-plants and other bog species were favored and increased in abundance. Documentation of this mode of origin for some bogs was given by Wells and Shunk (1931, p. 485), Pessin (1933), Pessin and Smith (1938), Garren (1943), Wahlenberg (1946), Clewell (1971), and Dohrewend and Hollis (1977). The term, secondary bog, is proposed for use when it is desirable to differentiate natural seepage bogs from those formed by the removal of pines from boggy flatwoods.

B. W. Wells (in Wells and Whitford 1976) said that he personally observed the creation of a grass-sedge bog from a North Carolina swamp by the use of intentional annual fires. Later he witnessed the reestablishment of the swamp after fire was suppressed. The entire process took 60 years. Annual burning was initiated in a swamp containing blackgum, sweetgum, and red maple. The first consequence was the formation of a pocosin of sweetbay, red bay (Persea), Leucothoe, and Smilax. With continued annual burning, a grass-sedge bog resulted. This same process could be happening with changes in fire frequency in the panhandle. A boggy flatwoods could become a grass-sedge bog in response to an increased frequency of fire and perhaps also to logging. The same boggy flatwoods could become a shrub bog in response to fire suppression. The grass-sedge savannahs are not as prone to such vacillations because of the severe conditions associated with the clayey soils.

No persisting stumps of original-growth pines are seen on these savannahs. They obviously contain their original vegetation and their origins cannot be attributed to the burning of swamps, as in North Carolina.

Disturbance Through Fire Suppression. Fire suppression as a national policy began in earnest in the Southeast in the 1920's and continued for about two decades before policies for controlled burning gradually began to be formulated. This period was marked by the publication of blatant anti-burning propaganda in the technical literature (e.g., Howell 1932) and rebuttals by those who perceived the impropriety of fire suppression (e.g., Eldredge 1935). The overriding effect of fire suppression in longleaf pinelands during this period was the dramatic increase in woody growth, documented by Heyward (1939). Heyward said that until recently, probably 90 percent of all longleaf pinelands were burned once every 3-4 years but that fire protection became widespread by 1930. He visited 101 fire-protected stands of longleaf pine from South Carolina to Louisiana and described the brush invasion on them. Among the shrubs that increased with fire suppression are saw-palmetto (see p. 299), wax-myrtle (Terry and White 1979), and probably gallberry (see p. 301). The invasion of species that were previously restricted to less frequently burned habitats initiated several seral trends, depending on site conditions. These trends were noted by several authors and summarized by Garren (1943).

Intentional suppression, coupled with the construction of roads and other impediments to the spread of fire, recently caused the formation of man-made ecotones where none existed previously. These ecotones are all the result of plants of adjacent habitats encroaching into longleaf pinelands. Laurel oak, mockernut, and other species common to well drained slopes and bluffs along streams and rivers commonly mix with adjacent stands of longleaf pine on adjacent uplands. Scattered plants of bracken, runner oak, and saw-palmetto on the uppermost slopes of river bluffs suggest that the longleaf pinelands once occupied such sites.

An excellent example of hardwood invasion in unburned longleaf pineland was observed on the Spring Hill Plantation south of Thomasville, Georgia. A magnolia-beech hammock was bordered on higher ground by mesic longleaf pineland, which had been kept free of destructive fires for several decades. Longleaf pines of perhaps 90-100 feet fall formed the typical open overstory. Laurel oaks (Quercus hemisphaerica) grew beneath them, their crowns not quite reaching the canopy of longleaf pines. Beneath the laurel oaks were large saplings of other hardwood trees, notably among them were southern magnolia and beech. This stand was logged shortly after its discovery and was not able to be studied further. A similar hardwood invasion was described following about 20 fire-free years in Jefferson County (see Research Summary 10). Beckwith (1967) described a similar stand in Hernando County, Florida that had been fire-suppressed for 34 years. Monk (1965), in a survey of 60 stands which were studied for the characterization of southern mixed hardwood forests in northern peninsular Florida, included five sites that contained wiregrass and at least one contained longleaf pine. Evidently these stands represented stages in the development of hardwood forest on fire-protected longleaf pinelands.

Similar instances are known of titi swamps overtaking flatwoods in the absence of fire. Coultas et al. (1979) described one such instance in southwestern Leon County. The titi zone bordered a creek which drained a longleaf pine flatwoods. The titi swamp occurred at a higher elevation on one side of the creek than the other. The soil type in this more elevated titi stand differed from that elsewhere in the titi swamp. A single longleaf pine grew well within this elevated titi stand and must have seeded-in there before the development of the titi swamp. When a path was cut through the elevated titi swamp, plants of Sarracenia psittacina quickly appeared and bloomed within a year. It is doubtful that a mature pitcher-plant could have developed so quickly from seed. Robust plants of other species typical of boggy flatwoods also appeared on the path. It seems likely that the elevated titi swamp invaded boggy longleaf pine flatwoods during the 1930's or 1940's.

Wherever sand pine scrubs border fire-excluded longleaf pinelands, sand pine quickly spreads into the longleaf pineland. The results of this process are easily observed near Carrabelle in Franklin County, where sand pine-covered beach ridges abut against longleaf pinelands north of U.S. 98.

As mentioned above, hardwood invasion is insignificant for about 20-30 years of fire-suppression. A resumption of frequent burning restores the typical aspects of longleaf pinelands without substantial changes in floristic composition or physiognomy. If fire suppression continued beyond that threshhold, irreversible changes occur, not the least of which is the elimination of wiregrass and other important components of the ground cover. The low reproductive capacities of these species, coupled with the reduction in fuel quality and the presence of invading hardwoods large enough to withstand fire, guarantee the irreversibility of these vegetational processes.

The threshhold of irreversibility may not be reached until later in longleaf pine savannahs within the bluestem range. Hodgkins and Nichols (1977) described a stand of longleaf pine growing on loamy sands in southwestern Alabama. Woody plants, other than longleaf pine, were sparse, and the usual complement of grasses, composites, and legumes were evenly distributed. This site had not been burned in over 40 years. I have seen similar stands within the bluestem range in Escambia County and adjacent Alabama with virtually no evidences of invading hardwoods. These stands must not have been burned for many years, because the pines lacked charred bark and several centimeters of litter and duff had accumulated. Heyward (1939) suggested that similar stands of his knowledge were too far removed from a hardwood seed source, but seed sources were readily available near the Escambia County pineland. A possibility is that the species of the ground cover in the bluestem range exert a remarkable control over the seedlings of trees other than longleaf pine. This situation begs investigation.

There is some evidence that the woody element of the ground cover in longleaf pinelands has increased over the past few decades as a result of the practice of controlled winter burning. The natural fire season corresponded with the summer thunderstorm season. Lovett Williams, the chief research biologist for the Florida Game and Fresh Water Fish Commission, observed that summer burning adversely affected saw-palmetto and wax-myrtle near Lake City, Florida. He wrote (personal communication 1979), "I am about 95% convinced that saw palmetto growth is curtailed by summer fire. This might account for Bartram's infrequent mention of saw palmetto when he speaks of the pine savannahs he traveled through."

Summer fires are known to cause some reduction in gallberry, as was mentioned on page 301. The present practice of winter burning apparently is promoting the proliferation of woody plants in the ground cover. Since a major reason for intensive site preparation in modern forestry is to reduce this woody component, one wonders if much of the need for intensive site preparation has stemmed from policies of winter burning.

Williams further observed that summer fires led to prodigious fruiting in runner oaks, blueberries, huckleberries, gopher apple (Licania michauxii), and blazing star (Liatris). Fruiting in wiregrass is also adjusted to summer fires (see Chapter 23). These observations tentatively suggest that sexual reproduction among the more important species of the ground cover may be geared to summer burning. If so, they have implications for wildlife management. A return to frequent summer fires would lead to increased mast production. The concomitant reduction in brush would promote the growth of grasses, legumes, and other herbaceous species with good forage values.

Effects of Soil Disturbance. Points that have already been established in this chapter and in Chapter 23 are that the ground cover is the most important and the only essential vegetational element in firelands, that wiregrass is the most important species in the ground cover of firelands in the panhandle, that wiregrass and some other species in the ground cover are susceptible to soil disturbance, that these species have exceedingly low reproductive capacities, and that they do not recolonize a site once the ground cover has been entirely removed. The questions remain, how much soil disturbance can be tolerated by wiregrass, and what are the ecological consequences of soil disturbances that affect but do not eliminate wiregrass? The emphasis is placed on wiregrass because more is known about it than its associated species in the ground cover and because what happens to wiregrass generally affects what happens to the other species.

Heavy mechanical equipment can be driven over the ground cover without any noticeable adverse effect, as long as no plants are uprooted or the soil is not scarified. Evidences for this observation are abundant. One instance in particular was the root raking effort at St. Marks Refuge (Chapter 23). Later that year the plants of the ground cover grew profusely and the wiregrass bloomed. Observations at the Big Woods (Research Summary 3) showed that wherever a clump of wiregrass was missing, a coppicing sprout of any of several hardwood trees usually had taken its place. Faint logging trails and other signs of minor disturbance could be seen at or near places where the clumps were missing. The regularized spacing of wiregrass clumps over vast areas makes it easy to observe where a clump had been removed. This regularized distribution is implied by the low standard errors of the mean densities of wiregrass in the 30 study sites from Research Summary 11.

At the longleaf pine savannahs at the Wade Place (Research Summary 4), coppicing hardwood sprouts were abundant, and wiregrass frequency was quite low (37 percent of the meter-square quadrats contained wiregrass).

Brush cutting had been substituted occasionally for burning, and the scars where the blade had dug into the soil were evident. (A brush cutter has a rotary blade like a power lawn mower; the blade cuts the soil if the machine is tilted, just as a lawn mower will ruin the turf if tilted.) The superficial soil disturbance evidently destroyed the clumps of wiregrass, and they were replaced by hardwoods.

The unburned longleaf pine savannah near Monticello (Research Summary 10) demonstrated the rapidity of growth of these hardwoods following release from fire. Within 20 years a tall hardwood understory had eliminated wiregrass and virtually all other plants of the original ground cover, at least where the shade was considerable. The significance of this change in vegetation is felt when it is recalled that the firelands may have occupied these study sites for at least the past 5,000 years (Chapter 15).

If minor scarification of the soil is sufficient to allow the invasion of hardwoods which will coppice indefinitely until released by fire suppression, what are the effects of more severe soil disturbance? Research Summary 11 provides some insight by comparing the abundance of several species in natural and disturbed habitats. In natural habitats, the mean densities of wiregrass per meter square were 4.6 in flatwoods, 4.8 in boggy sites, and 5.3 in longleaf pine-xeric oak woods. These values were determined at 10 study sites for each of the three habitat types. Each study site was paired with an adjacent pine plantation. Wiregrass densities were lower (significant at the 1 percent level) than in the natural habitats, with mean densities of 1.2 in boggy habitats and less in the other habitats. Soil disturbance in the pine plantations involved either chopping, disking, or bedding. Other species that suffered a loss in density were saw-palmetto, blueberry (Vaccinium myrsinites), and runner oaks. Plants that increased in density were panic-grasses, broomsedge, dog-fennel, and blackberry.

In no instance was wiregrass completely eliminated by soil disturbance during site preparation. Other species in the ground cover also survived. The results of Research Summary 7 showed that soil disturbance of this intensity may even cause a proliferation of the herbs of the ground cover, at least when these herbs had been suppressed previously from lack of recent fires. If sites were not subjected to any other treatment after the soil was chopped, disked, or bedded, it is likely that the ground cover would recover, as long as fires were frequent. Some of the more weedy species (broomsedge, dog-fennel, etc.) would be more abundant than before, and wiregrass and some other species would be a little less abundant, but the floristic composition and physiognomy would not be appreciably different. The greatest effect would be in the driest habitats, according to the results of Research Summary 11. Recovery is apparently impeded by dry soils and abetted by moist soils. (It should be noted, however, that cattle grazing has caused considerable floristic changes in boggy habitats (Pullen and Plummer 1961)).

Effects of Intensive Forestry. Terrain such as that described in Research Summary 11 is not chopped, disked, or bedded unless it is to be row-planted with pines or subjected to even more drastic land use such as improved pasture or row crops. As a result, the effects of soil disturbance must be evaluated along with the effects of row-planted pines. The inescapable observation is that any initial flourish of herbaceous vegetation that follows soil disturbance is eliminated by competition from the planted pines, as soon as canopy closure occurs. The pines are grown usually for at least another 15 years before they are harvested. If the pine plantation is thinned or burned during the rotation, plants of some or most of these herbaceous species survive, mostly in low densities.

The survival of these plants depends on the amount of light reaching the herbaceous vegetation and the length of time until the pines are harvested. An extreme example of the deleterious effects of pine plantations on the surviving ground cover is shown in the CRIFF C-3 study in Tate's Hell on Buckeye Cellulose Corporation lands, monitored by the University of Florida. One plot in boggy flatwoods had been bedded, heavily fertilized (P, N), and planted to slash pines. After 14 years (in 1976) the pines were about 40 feet tall with complete canopy closure. The mineral soil was covered by a layer of pine needles about 7 cm deep. There were no herbaceous plants of any species. A few shrubs, mainly wax-myrtles, were widely scattered. A control plot had been bedded and planted to pines but not fertilized. The vegetation of the ground cover was still extant, and wiregrass covered about 95% of the ground. (Wiregrass density was not determined; the propensity of the leaves of widely spaced clumps to elongate and overlap would account for the high percent cover, even if the densities were only one plant per meter-square, as could be assumed from the data in Research Summary 11.) The conclusion is that fertilization stimulated the growth of the planted pines, creating both shade and heavy leaf litter which eliminated the ground cover within 14 years.

If the pines of this fertilized plot were to be harvested, it would be expected that wiregrass and the many additional species of the original ground cover would not reappear. Whether or not they did reappear is almost academic, because it is a near certainty that these tree farms will be replanted with pines shortly after the crop has been harvested. It is doubtful that more than a token sample of the plants of the original ground cover would survive a second rotation, except under the most favorable conditions for their survival. Since such conditions are unfavorable for the economic production of pines, it is unlikely that many plantations will continue to support significant remnants of the original ground cover.

The only plausible conclusion from these observations is that pine plantation lands will not revert to the original firelands communities, even if these lands are lain fallow and managed in a way that would promote the survival of wiregrass and its associated species. The natural reproductive rates are too low to expect a proliferation of plants of these species. Even if their reproductive rates were much higher, there would not be enough acreage of original vegetation in the vicinity to serve as a seed source. Other weedy species and trees from other vegetational systems would invade these lands and eliminate the possibilities for a gradual return to original conditions. Plant succession will not return the land to its former condition. The conversion of firelands to pine plantation represent an irreversible and irretrievable loss of habitat.

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33. ACID SWAMP SYSTEM

The vegetation of acid swamps consists largely of trees and shrubs with evergreen or semi-deciduous, often coriaceous leaves. The soils are usually strongly acid, peaty, infertile, and waterlogged or shallowly inundated during wet seasons. Names that have been applied to the plant communities of acid swamps or their habitats include shrub-bogs, pocosins, titi swamps, bays, bayheads, bay branches, evergreen hardwoods swamps, and Carolina bays. The last three names sometimes apply to related vegetational systems as well as to acid swamps. Acid swamps are widespread throughout the panhandle and characteristically occupy the many isolated depressions and flat headlands of streams within pine flatwoods and grass-sedge bogs.

Community Organization. The communities display definite organization but not to the high degree as in firelands. This organization embodies two adaptive strategies. The first is the production of a highly acid and densely shaded substrate that virtually prohibits colonization by seedlings of other species. The second is a vegetational architecture that attracts infrequent and destructive crown fires. These fires serve in a homeostatic capacity, rejuvenating and perpetuating the community.

Species Richness. Few species are present in any given stand. Perhaps 10-30 species occur per hectare, with a few more on the borders adjoining firelands. Nearly all common species are woody. The total number of species inhabiting acid swamps in the panhandle is low. As a result, the floristic lists from one swamp to another are often quite similar.

Physiognomy. Acid swamps are thickets or forests ranging from about 2 to 25 meters tall, rarely taller. The taller the vegetation, the lower the frequency of fire, or at least the longer since the last destructive fire. The dominant species generally have broad, coriaceous, evergreen or tardily deciduous leaves. Among the more important species are sweetbay, black titi, swamp cyrilla, little-leaf cyrilla, swamp bay, fetterbush (Lyonia lucida), large gallberry (Ilex coriacea), myrtle-leaf holly (I. myrtifolia), and loblolly bay. Two needleleaved evergreen species are often present or dominant, slash pine and pond pine. Blackgum is the only deciduous broadleaved species that attains dominance with any frequency. Deciduous species, including pond-cypress, generally comprise a minor floristic element in any stand.

The taller stands are sometimes differentiated into a distinct overstory and understory. Usually there is no obvious stratification. The ground cover is absent as a distinct layer, except for occasional patches of peat moss (Sphagnum spp.) and except for some shrub bogs which are open enough to contain a distinct herbaceous stratum, generally of sedges.

Soils. The soil surface commonly consists of a distinct organic layer of decomposing litter and duff. This layer may be thin or nearly absent in those shrub bogs that serve as sloughs. In larger bay swamps the peaty soils are at least 2 meters deep (the maximum length of most hand-operated soil augers) and probably much deeper. Sand and clay is present in varying amounts in these peats and presumably was transported while suspended in sheet flow from surrounding uplands. Clays are sometimes most abundant at about 1.5-2 meters deep and may have been leached to that level.

Moisture. The water table is never far from the soil surface. Only in prolonged droughts will the water table drop below about 1.5 meters. Much of the moisture represents runoff from surrounding uplands and base flow which seeps from slopes that contain acid swamps. During rainy seasons the surficial soils remain saturated for days or weeks at a time. In the deeper swamps, standing water a few centimeters deep may persist for days or weeks. This water is probably removed mainly by evapotranspiration. Percolation is retarded by high water tables or pans. Many acid swamps are isolated in shallow depressions and cannot drain through creeks. Where acid swamps occupy headwaters, surface water moves by sheet flow or through braided channels, negating the possibility of the rapid removal of standing water into streams.

Fire. Most acid swamps experience irregular fires at a frequency of about once every 5 years along the edges of fireland communities to once or twice a century in the deepest bay swamps. The absence of graminaceous vegetation or other combustibles makes ignition very difficult except under the most favorable conditions. Should ignition occur, the leaves of the broadleaved trees and shrubs burn poorly, and the leaf litter is usually too moist for the fire to spread over large areas. When extreme droughts occur, crown fires sweep through the deepest bay swamps. Such fires may burn into the peat, creating a more hydric habitat thereafter. All trees except sometimes the larger pines are generally top-killed by fires. An occasional large sweetbay is seen that is fire-scarred. Such trees serve as evidence that not all hardwoods succumb to every fire.

Mineral Nutrients. Nutrient levels are quite low. The preponderance of plants with coriaceous leaves may reflect the low availability of nutrients. Some of the nutrients are likely made unavailable because of high acidity. The acidity is presumably responsible for high levels of aluminum which is toxic to plants of many species. Low nutrient availability and aluminum toxicity may be among the more important causes for the low species richness, along with low pH, poor aeration of the soil, and dense shade.

Maintenance. Plants of the more important broadleaved woody species and many of the other species readily coppice after fires. The well developed root systems give the coppicing sprouts of these plants a substantial competitive advantage over any plants that may have seeded-in from other areas. As a result, the community is reestablished without any intervening seral stages and essentially without the death of any individual plants. In this respect, the acid swamps resemble the fire-lands, except that the fires occur with less frequency.

The only question regarding the composition of the subsequent forest is the abundance of pine. Some of the larger pines may survive crown fires. Both pond pine and slash pine are adapted to seeding-in immediately following a fire (pages 249-252). The pine saplings generally grow more rapidly than the sprouts of hardwoods, allowing them to compete and eventually to form an overstory above a more slowly growing under-story of hardwoods. The density of pines surviving a fire and the availability of a source of pine seeds are unpredictable. The subsequent forest might be pine-dominated or, at the other extreme, pines might be entirely absent. Following the next fire on the same site, the density of pines may be entirely different than what they were after the previous fire.

The pines are relatively short-lived, and slash pines are known to become senescent after about 80 years (Hebb and Clewell 1976). If crown fires are very infrequent, the hardwoods will outlive the pines, and a pine-dominated stand may become a hardwood stand before the next fire.

After fires, the sprouts of titi and other shrubby species tend to grow more rapidly than the sprouts of sweetbay and other arboreal hardwoods. The stems of the tree species begin to overtop those of titi after 10-25 years. Titi and the other shrubbier species thereafter become the understory of a bay swamp.

Fires, perhaps coupled with oxidation not involving combustion, probably function to prevent peats from aggrading to the point that the habitat becomes mesic in wet seasons. In this respect, fires serve as a homeostatic mechanism by preventing the habitat from becoming dry enough to support a more diversified forest community.

Response to Disturbance. Acid swamps suffer very little disturbance in comparison to most other vegetational systems of the panhandle. Slash pines have been logged from nearly all stands, but their recovery in both size and numbers has been rapid. Sweetbays and other hardwoods are occasionally logged, but they recover from root sprouts. Perhaps the most severe disturbance has been the draining of acid swamps to lower water tables, thereby making more land available for pine plantations and for agriculture. If otherwise undisturbed, the deeper interiors of such stands will persist, although there will likely be a shift in composition favoring those species that prefer drier soils. This shift is facilitated by the oxidation of peats that are dry for longer periods than before ditching.

Mode or Origin. Many acid swamps today may have originated as water tables rose with rising sea levels about 5,000 to 7,000 years ago (p. 80). Relatively flat lands that were previously covered with fireland or scrub vegetation became increasingly hydric and were overtaken by acid swamp vegetation. Firelands and scrubs share very few species with acid swamps, which suggests that the transition to acid swamps must have been abrupt. This change in vegetation would have been most dramatic in firelands where wiregrass and other graminaceous species would have been killed by inadequate aeration of waterlogged soils and replaced by poorly burning woody plants. In such instances the mode of origin would be best explained in terms of the displacement model.

In lake basins, acid swamps may have originated gradually with the accumulation of peats and other sediments. As these basins filled, a hydrosere developed, beginning with aquatic herbs (species of *Nymphaea*, *Nuphar*, *Utricularia*, etc., of the palustrine system), which were replaced eventually by pond-cypress and blackgum (cypress-tupelo system). With continued aggradation of peat, sweetbay and other species of acid swamps replaced the cypress-tupelo vegetation.

Once established, the deep peaty substrate of acid swamps is subject to being burned to considerable depths by fires that occur only during droughts, perhaps with a frequency of once every one of few millenia in a given stand. The resulting habitat would again become ponded, allowing a hydrosere to develop, eventually returning the site to an acid swamp over the next few centuries or millenia, as was described for the Okefenokee Swamp (p. 202).

Ecotones. Acid swamps that contain a large proportion of blackgum and particularly pond-cypress may represent transitional stages in a hydrosere between a cypress-tupelo system and an acid swamp system. Fires burn with unequal intensities in different parts of an acid swamp, leaving an uneven surface of peaty substrate and perhaps allowing a few trees to survive. As a result, stands that seem to represent stages in a hydrosere may have had a more complex development.

The differentiation between firelands and acid swamps is usually distinct and sharply abrupt. This distinction is caused by the dense ground cover of grasses that regularly carries fires up to the edge of acid swamps. Generally there is a lack of flammable material in acid swamps, and the fires do not carry into them. During recent decades of fire suppression, the distinction between acid swamps and firelands has diminished, especially in seepage bogs. The vegetation of Tate's Hell is a good example, where once open grass-sedge seepage bogs and boggy flatwoods have become overgrown with woody species typical of acid swamps. Some of these species are typical of both systems, but were once kept in check in firelands by frequent fires. The shade and competition from plants of these species have reduced the ground cover to the point that it may not return, at least in localized areas. Such sites must now be classified as shrub bogs.

Other ecotones occur with hardwood forest systems. There is typically an intergradation between acid swamp vegetation in bayheads and hardwood forests on the floodplains a short distance down stream. The transitional vegetation is often called a branch bay which exists along a stream (the bay branch). The branch bay generally occurs upstream from the point of intermittency. That point is defined as the furtherest place upstream where base flow seeping from along the sides of the stream channel is sufficient to maintain a perennial flow of water in the channel between rainfall events during years of normal rainfall. The transitional vegetation is classified as belonging to the hardwood forest system rather than to the acid swamp system in order to emphasize the distinctiveness of acid swamp communities and their habitats. Bayheads with peripheral transition zones with hardwood forest communities also occur on seepages at the bases of bluffs, ravines, and steepheads.

Communities. The acid swamp system is divisible into three communities that are usually but not always distinct from one another: titi swamps, bay swamps, and shrub bogs. These communities and their habitats are briefly compared in Table 16. Two variants, based on floristic dominance, are recognized for titi swamps: pond pine swamps and myrtle-leaf holly swamps. The slash pine-hardwood swamp is a floristic variant of bay swamps. Wells and Boyce (1953) used the term, shrub bog, for all acid swamps in North Carolina. That term is restricted in the present classification to those acid swamps that adjoin grass-sedge bogs and associated boggy flatwoods.

TABLE 16. Conspectus of Acid Swamp Communities.

Communities	Soil Moisture in Summer Wet Season	Approximate Crown Fire Frequency	Vegetation
7. Titi Swamps	Often saturated but not inundated for long at a time after rains	5-20 years	Titi (any or all species), often pond pine, *Lyonia lucida*, and *Ilex coriacea* among the dominant species. Trees small, vegetation dense, no ground cover.
7a. Pond Pine Swamp			Pond pine common and generally the tallest tree.
7b. Myrtle-leaf Holly Swamp			Myrtle-leaf holly is either dominant or co-dominant with titi.
8. Bay Swamp (Bayhead if a headwater swamp)	Usually saturated, sometimes shallowly inundated	15-50 years	Sweetbay usually dominant or co-dominant; other prominent trees are usually slash pine, swamp bay, loblollybay, blackgum, titi, and sometimes pond-cypress and red maple. Overstory moderately or quite tall, sometimes with an understory but no ground cover.
8a. Slash Pine Hardwood Swamp			Slash pine dominant or co-dominant
9. Shrub Bog	Often saturated, usually not inundated for long at a time after rains except where occurring in shallow wet-weather sloughs or stringers.	5-20 years	Variable combinations of any above-listed species, also white cedar. Trees small or moderate height. If in a slough then the undergrowth not too dense and a sedge-dominated ground cover present.

7. *Titi Swamps*

The vegetation is often undifferentiated into strata. If a distinct overstory and understory exist, the overstory is comprised of an open stand or of irregularly spaced groves of pond pines or slash pines. Pond pine is the most common pine. When slash pines appear to grow with pond pines, the slash pines often occupy the slightly lower, wetter sites.

Broadleaved shrubs and small trees comprise the principle element of the vegetation, even when this element is the understory. At least one of the three species of titi is present and dominant: black titi, swamp cyrilla, and little-leaf cyrilla. The presence and dominance of these species varies seemingly at random from stand to stand, and their distribution might reflect the long term effects of initial floristic composition. Myrtle-leaf holly (Ilex myrtifolia) sometimes replaces titi as the principal dominant in small swamps at the heads of minor drainages. Lyonia lucida (fetterbush) and Ilex coriaces (large gallberry) are often abundant shrubs. Sweetbay is usually present but not abundant. Many other shrubs may be present, including Aronia arbutifolia, Arundinaria gigantea, Clethra alnifolia, Itea virginiana, Leucothoe racemosa, Lyonia ferruginea, Myrica heterophylla, M. inodora, Rhododendron serrulatum, Vaccinium australe, V. fuscatum, Viburnum nudum. Woody vines are common, particularly Smilax laurifolia, sometimes Gelsemium rankinii and Vitis rotundifolia.

The soils are highly organic sands, sometimes overlain with peat which may accumulate to about 30 cm deep. The soils are nearly always moist, but standing water is infrequent except shortly after heavy rains.

The frequency of fire is variable but usually does not exceed 20 years.

Titi swamps mostly occur on the higher, better drained sites of acid swamps. They commonly abut against pine flatwoods. Titi swamps have been largely ignored in ecological studies. One stand from Leon County was described by Coultas et al. (1979); this study is summarized in Research Summary 12. Coultas (1976) also described the soils of other titi swamps in the panhandle.

8. Bay Swamps

The overstory trees are moderately or quite tall in mature stands. Sweetbay is probably universally present and usually the dominant species. The only important exception to this rule occurs when slash pines are more abundant. Swamp bay is also almost invariably present and common but not as a principal dominant. Loblolly bay is often dominant in stands near the Suwannee River. Elsewhere it is uncommon or absent. Loblolly bay tends to occupy slightly higher terrain than sweetbay. Blackgum is usually represented by a few individuals, or in wetter bays it may assume co-dominance with other species. Less common species may include pond-cypress, white-cedar, red maple, diamond-leaf oak, water oak, sweetgum, and popash. The presence of more than a few scattered individuals of any of these species usually indicates an ecotone with a cypress swamp, cedar swamp, or a hardwood forest.

The understory is usually undifferentiated from the overstory, except when slash pines form a distinct overstory. Understory species are usually those woody species common in titi swamps, including all species of titi. A notable exception is pond pine, which is almost invariably absent from bay swamps. The understory is usually quite dense, however, occasional openings occur in mature stands. These openings may be covered by sphagnum. Why they never become colonized by woody plants has not been answered. Herbs are usually rare.

Bay swamps occupy those portions of acid swamps that are wetter and less frequently burned than titi swamps. The titi swamps serve as a buffer zone which protects the trees of bay swamps from the fires that burn on occasion a short distance into these acid swamps. Research Summary 13 describes an undisturbed, original-growth bay swamp of the slash pine-hardwood variety.

9. Shrub Bogs

The overstory and understory are usually not clearly differentiated. The trees are often about 10-20 meters tall. The trees and shrubs are sometimes dense, and at other times they form rather open stands, particularly where shrub bogs occur in sloughs. These open stands contain a distinct ground cover, often with sedges dominating. Such stands probably burn more frequently than most acid swamps. The biomass of the ground cover is probably insufficient to sustain a fire hot enough to be damaging to any but the smallest woody plants.

The more common trees are sweetbay, blackgum, slash pine, wax-myrtle, pond-cypress, popash, and occasionally white-cedar. These species often occur haphazardly without as much tendency towards zonation as in titi and bay swamps. The more common shrubs and vines include *Clethra alnifolia*, *Smilax laurifolia*, *Rubus argutus*, *Lyonia lucida*, and the species of titi. Among the herbaceous species, Scleria baldwinii is sometimes abundant, often with Eriocaulon spp. intermixed.

In sloughs the soil does not always contain a pronounced "O" horizon of litter and duff nor much organic matter in the "A" horizon. The soils are flooded briefly after rains in isolated depressions or for longer periods in sloughs where the water is slowly moving by sheet flow.

Shrub bogs are associated with grass-sedge bogs and commonly occupy low sites that are too wet to support grass-sedge vegetation. Those shrub bogs that occupy sloughs often intergrade with cypress-blackgum strands or with creek swamps. In the larger sloughs, the shrub bogs sometimes occupy the shallow edges and flank cypress-blackgum strands which assume a deeper, more central position.

Discussion

Soils. The characteristics of the soils of two acid swamps are compared in Table 17. The vegetation of these swamps is described in Research Summaries 12 and 13. The high acidity and low nutrient availability are readily apparent from the data. The depth of the "O" horizon and the high percentages of organic C attest to the slow decomposition of detritus under conditions of poor aeration and high acidity.

Vegetation. Monk (1966) described nine bay swamps that lacked appreciable quantities of pine from north-central Florida. The exact locations were not given, but it is possible that some of these stands were located in the eastern panhandle. The tree with the highest importance value (107 out of nearly 300) was loblolly bay. Sweetbay was the second most important species (importance value = 69). Other species

TABLE 17. Soil Properties of Two Acid Swamps.

	TITI SWAMP (Coultas *et al*. 1979)	SLASH PINE-HARDWOOD SWAMP (Hebb and Clewell 1976)
Great Group	Humaquept	Paleaquult
Depth of "O" Horizon (cm)	8	10
All Horizon (root zone)		
Texture	sandy clay-loam	fine sand
Depth (cm)	12	51
Organic C (%)	12.56	8.4
pH	3.4	3.8
Total N (%)	1.04	NA
Extractable Cations (meg/100g)		
Ca	0.0	0.15
Mg	0.4	0.21
K	0.1	0.03
Na	0.1	NA
P	NA	< 0.01
CEC (meq/100g)	43.5	NA
Al (ppm)	NA	120
Fe (ppm)	NA	2
Texture at 1.5-2.0 meters	sandy clay-loam	sandy clay-loam

in descending order of importance were swamp bay, sweetgum, blackgum, red maple, water oak, slash pine, bald-cypress (or pond-cypress ?), dahoon (Ilex cassine), Leucothoe sp., wax-myrtle, diamond-leaf oak, and Sambucus simpsoni. This list suggests that some of the stands were transitional to the creek swamp community of the hardwood forest system.

Carolina Bays. Carolina bays are elliptical depression generally with a northwest-southeast orientation and with a sandy ridge along the southeastern end. They occur on the coastal plain from North Carolina to southern Georgia near Valdosta, just above the Madison County line. Over 1,000 exist in Georgia, where they collectively comprise 250,000 acres (Wharton 1977). They have not been described from the panhandle but are close enough to be of interest. They often contain acid swamps and occasionally marshes and lakes.

The interest in Carolina bays stems not so much from their vegetation, but from their origin. Three theories explain their occurrence, and the advocates of each theory have joined in a vigorous debate in the literature. One theory states that the bays arose from the impact of meteorites. Wells and Boyce (1953) championed this theory while Buell (1939, 1946a, b) argued that solution activity associated with the aquifer was responsible. These authors supported their cases with botanical and paleoecological evidences. Whitehead (1973) supported the theory that the bays were formed by aeolian action. The matter is not settled, and future work aimed at the question of the origin of Carolina bays will certainly advance our knowledge about acid swamp vegetation and southeastern paleoecology.

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34. CYPRESS-TUPELO SWAMP SYSTEM

The vegetation of cypress-tupelo swamps is dominated by deciduous trees belonging to species of Taxodium (needleleaved conifers) and species of Nyssa (broadleaved hardwoods). These species occupy the most deeply flooded habitats of any forested vegetation in the panhandle.

Community Organization. The communities are organized very simply. One or few species of trees comprise the overstory. Virtually all other plants grow on hummocks around the bases of the overstory trees. The soil of hummocks is held in place by the fine roots of the trees. Presumably this soil is better oxygenated than the soils elsewhere, and the hummocks often provide the only habitat suitable to plants of the undergrowth. As a result, the community is largely organized around the hummocks.

Species Richness. Few species are present in any given stand. The cypress-tupelo communities that grow in peaty acid habitats have a very different floristic composition than the cypress-tupelo communities on alluvial floodplains. In peaty swamps, the species in the undergrowth are usually the same as those in the acid swamp system. In alluvial swamps, the species are the same as those in hydric hardwood swamps. Trees other than species of Taxodium and Nyssa are generally limited both in the species represented and the number of individuals. The number of herbaceous species is sometimes augmented by the presence of large slowly decaying logs which provide an elevated substrate for colonization.

Physiognomy. The overstory is the most important and conspicuous element of the vegetation. Overstory trees vary from about 2 meters tall in dwaft pond-cypress swamps to in excess of 30 meters tall in alluvial river swamps. The overstory is often closed, but is sometimes represented by rather widely scattered trees. An understory may be present or absent. Shrubby undergrowth is prevalant in stands that are not subjected to inundation for extended periods and is particularly common in the many cypress heads of the panhandle that have been partially drained by ditching. An herbaceous stratum is absent except sometimes in sloughs which are inundated only by shallow and very slowly flowing water.

Soils. Cypress-tupelo swamps occur on a variety of substrates from deep peats to sands or clays. Clay strata, either within the root zone or deeper, are often present and are important in retarding percolation and prolonging flooded or saturated conditions. Peats and mucks are characteristic of isolated swamps, headwater swamps and back swamps, but not of floodplains subject to regular overflow. Organic detritus may accumulate to a limited extent in oxbow ponds where the flushing action of floodwaters is not particularly forceful.

Moisture. Cypress-tupelo swamps are characterized by prolonged hydroperiods, longer than in acid swamp communities and hydric hardwood forests. The soil is usually inundated at least for several weeks every year and often for six months or more. The maximum depth of inundation varies considerably between habitats. Many cypress-tupelo swamps experience a brief dry period during most years when the water table drops well below the soil surface. The soils desiccate and if clayey they become fissured.

Fire. Fires are generally rare or absent, particularly on floodplains where topographic features and the lack of fuel minimize both the fire hazard and fire damage to the trees, even in the most severe droughts.

In peaty headwater swamps and in isolated swamps, fires may burn through the acid swamp vegetation that typically isolates the firelands from the cypress-tupelo swamps. The dry surface layer of peat contributes to the fuel. Since the undergrowth is generally sparse, the heat experienced by the trunks of the overstory trees is not sufficient to cause damage. If the undergrowth is thick or if the peat is dry enough to burn well into the root zone, fire scarring may occur or trees may be killed. In general, fire is a rare event, or at least it is not catastrophic except in localized areas called hot spots.

Mineral Nutrients. Nutrient levels are exceedingly low in the peaty swamps of headwaters and isolated depressions and exceedingly high on floodplains of major rivers.

Maintenance. The duration of the hydroperiod, often coupled with deep flooding, precludes the possibility of species of other communities successfully colonizing cypress-tupelo swamps. Cypress trees are noted for their longevity, and tupelos either live long or have vegetative methods of replacing their shoot systems, depending on the species. As a result, sexual reproduction is important to stand replacement only at long intervals.

Response to Disturbance. Catastrophic natural disturbances are rare and usually take the form of a single tree being lightning-struck or wind-thrown. Fires rarely kill trees. Prolonged droughts apparently have no affect, other than causing temporary stress on the trees. Cypress may survive droughts by sending some roots deep to a water table. A pond-cypress tree in a bayhead was removed during an excavation in Desoto County, and I observed an apparantly living root about 2 cm thick that was 3 meters deep in the soil. Presumably this root could supply water to the shoot during a severe drought. Mature cypress trees tolerate permanent inundation indefinitely, although their seedlings are unable to survive in such habitats.

Draining cypress-tupelo swamps has been practiced widely, causing a lowering of the water table and the invasion of acid swamp species in former cypress domes.

Mode of Origin. For a cypress-tupelo swamp to develop, all that is needed is for trees of at least one species of these genera to become established on a freshly available habitat. Such a habitat might be a newly formed alluvial deposit or the margin of a recently formed sinkhole pond. Once established, no other trees are able to tolerate the hydric conditions, and the forest will persist indefinitely. This forest is the result of initial floristic composition. Undergrowth would develop in time but would not be essential for the recognition of the community. A cypress-tupelo community could also replace another community because of a radical change in environmental conditions, i.e., in accordance with the displacement model. For example, solution activity may lower the land surface, or rising mean sea level might raise the regional water table. In either instance, a cypress-tupelo community could replace whatever less hydric vegetation may have occupied the site previously.

Cypress-tupelo swamps may also develop as part of a hydrosere. Peat from aquatic vegetation may aggrade to the point that cypress and tupelo seedlings are able to become established during a drier than normal year when water levels are depressed. Establishment can also be initiated by chunks of peat lifting off the bottom of ponds, owing to the pressure from methane (presumably) which accumulated beneath the peat. These chunks become floating islands on which cypress seedlings germinate. They send tap roots through the peat, the water column, and into the lake bottom, stabilizing the floating island and allowing peat to accumulate until the island is connected with the bottom or the shoreline. Although this mode of origin probably accounts for a small fraction of cypress-tupelo swamp acreage, the process accentuates the variety of ways that such vegetation can become established.

Ecotones. In peaty acid depressions, cypress-tupelo swamps usually occupy the deeper interior sites and bay swamps, the shallower, exterior sites. Intergradations sometimes occur, particularly between pond-cypress swamps and bay swamps. The cypress-tupelo swamps in headwaters are often distinct but intergrade with bay swamps along the edges and creek swamps along the upper reaches of defined streams. On floodplains further down stream, the cypress-tupelo communities occasionally intergrade with hydric hardwood forests dominated by species other than those of *Nyssa* and *Taxodium*.

Communities. Cypress-tupelo swamps fall into two distinct ecological and taxonomic categories. The first encompasses the peaty acid depression and headwaters where pond-cypress (*T. ascendens*) and blackgum (*N. biflora*) predominate. The second encompasses the alluvial circumneutral river swamps where bald-cypress (*T. distichum*) and water tupelo (*N. aquatica*) predominate. These two categories sometimes intergrade in the upper reaches of rivers where alluvial deposition is slight and the presence of tannins in the water is pronounced. Ogeechee tupelo (*N. ogeche*) is sometimes of importance in these transition zones and also in some strictly alluvial river swamps. Transitions also occur where back water swamps of blackgum intergrade with alluvial swamps of bald-cypress and water tupelo.

Three cypress-tupelo communities are recognized in the synoptic descriptions of Table 18. The first two communities are peaty acid swamp communities, and the last is an alluvial river swamp community.

10. Pond-Cypress Swamps

The overstory consists of pond-cypress, exclusively or nearly so. Other trees that may be present include blackgum, slash pine, sweetbay, loblolly bay, and other species of acid swamps and creek swamps. With the exception of blackgum, these other trees are likely growing on hummocks where the hydroperiod is not prolonged. These other trees typically are not as tall as the larger cypress trees. Spanish moss (*Tillandsia usneoides*) is often an abundant epiphyte.

The understory is absent or consists of blackgum or other species typical of bay swamps, creek swamps, and in strands, shrub bogs. Tall shrubs such as Virginia-willow (*Itea virginica*) and fetterbush (*Lyonia lucida*) are often common on hummocks at the bases of the overstory trees (Schlesinger 1978). Other species common in acid swamps may grow on these hummocks.

A ground cover is usually absent, except sometimes in strands where species of *Scleria*, *Rhynchospora*, and *Eriocaulon* may be common, also sawgrass (*Cladium jamaicense*) near the coast. Otherwise, herbs are generally limited to a few plants here and there on hummocks, with

TABLE 18. Conspectus of Cypress-Tupelo Swamp Communities.

Communities	Habitat	Soil Moisture	Fire	Vegetation
PEATY ACID SWAMPS				
10. Pond-Cypress Swamps	Isolated peaty acid depressions (domes or heads) and sloughs (strands)	Nearly always moist or wet (rarely dry) often inundated for weeks or months at a time, the water table often fluctuating widely	Moderate or rare	_Taxodium ascendens_. The undergrowth open, shrubby, or with sedges in strands.
10a. Cypress-Blackgum Swamps				_T. ascendens_, _N. biflora_, both in the overstory or sometimes one (usually _N. biflora_) forming a tall understory. Undergrowth shrubby, open.
11. Blackgum Swamps	Peaty acid backwater swamps or headwater swamps	Inundated most of the year to about 0.3 m deep, the water table not fluctuating widely	Rare	_Nyssa biflora_, the undergrowth very open, shrubby.
ALLUVIAL RIVER SWAMPS				
12. Bald-cypress-Tupelo Swamps	Alluvial floodplains subject to inundation at each river floodstage, often in oxbows and in depressions between levees, the soils often clayey, not strongly acid	Inundated much or all of the year	Rare of absent	_T. distichum_, _N. aquatica_, sometimes _N. ogeche_, the undergrowth sparse, shrubby.
12a. Bald-cypress Swamps				Overstory (almost) entirely _T. distichum_.
12b. Tupelo Swamps				Overstory (almost) entirely _N. aquatic_ and/or _N. ogeche_.

chain-ferns (Woodwardia areolata, W. virginica) commonly being conspicuous. A floristic variant of the pond-cypress community is the cypress-blackgum community. Pond-cypress and blackgum share the dominance in the overstory or sometimes blackgum comprises a tall dense understory just beneath the canopy of cypress.

The soils are variable with regard to the depth of the surficial organic horizon, the presence or absence of a spodic or an argillic horizon, and other attributes. The values for pH and mineral nutrients, though, are generally quite low (Table 19).

The water table fluctuates above and below the soil surface according to the season of the year. Most of the water is attributable to runoff and baseflow above the hardpan which is commonly present. Inundation may exceed 2 meters in depth in spring-fed ponds but usually not for more than several weeks at a time. Maximum depths in headwater swamps and isolated depressions commonly reach no more than about a meter. In most years, there is at least one period of one or several weeks in which the soil is not flooded nor saturated.

Fires are irregular or rare in occurrance. The thick-barked pond-cypresses are usually not affected, although fire-scarred trees are not uncommon. Fires, when they occur, are much more damaging to other trees species and may be responsible for keeping pond-cypress swamps from developing into cypress-blackgum swamps.

Pond-cypress swamps often assume the form of a dome or head particularly in isolated depressions. The largest trees are in the center and those towards the periphery are progressively shorter, as described on pages 318-321. Research Summary 14 describes the

TABLE 19. Soil Characteristics at Two Elevations in a Cypress Dome in Alachua County (Coultas and Calhoun 1975).

	Lower Site	Upper Site
Great Group	Umbraquult	Ochraquult
O Horizon depth (cm)	8	5
A Horizon		
Depth (cm)	89	25
Texture	sand to sandy loam	sand or loamy sand
B Horizon Texture	loamy sand to sandy clay loam	sand to sandy clay loam
Uppermost Stratum of A Horizon		
pH	3.7	3.8
Organic C (%)	8.82	7.4
Total N (%)	0.495	0.275
Extractable P (ppm)	7	11
Extractable Cations (meq/100g)		
Ca	0.12	0.15
Mg	0.30	0.21
Na	0.32	0.24
N	0.14	0.10

pond-cypress swamp community in the Okefenokee Swamp. Mitsch and Ewel (1979) described a dome in Alachua County in which 80% of the trees were cypress. There were 720 cypress trees/ha with a mean diameter of 21 cm.

11. Blackgum Swamps

Overstory. Blackgum forms a tall overstory, either exclusively or with a few scattered individuals belonging to other species. The canopy is closed or nearly so. The understory is absent or is open and consists of trees of various species common to other hydric communities. The ground cover is sparse or absent because of prolonged inundation.

The soils generally are overlain by an organic horizon and are moderately to strongly acid. The water table is generally more stable and less subject to fluctuation than in pond-cypress swamps. Water levels tend to remain constant for long periods and reach a maximum depth of about 30 cm. Flooded conditions continue for months and the soils remain saturated, or nearly so, for a long time after surface waters disappear. The habitat is probably more hydric than in most pond-cypress swamps, even though peak flooding may be much deeper in the latter. Fires are rare or absent.

The blackgum swamp community occurs essentially in two habitats. The first is in broad headwater swamps. Here the community occupies the lowest elevations in the center of the swamp and is generally enclosed by the pond-cypress swamp community. The low elevation of blackgum swamp accounts for the prolonged flooding and saturated soils. The breadth of the swamp reduces the depth of flooding by allowing the water to spread over a large area. Runoff entering the swamp from rainfall is removed by sheetflow towards the stream that issues from the swamp. This flow also prevents the water from becoming deep, but is slow enough to prevent the total drainage of the swamp except after a prolonged period without rain.

The second major habitat of the blackgum swamp community is in back water swamps on broad floodplains where river overflow does not reach except at exceptionally high flood stages. Such swamps are fed by rainfall, runoff, and sometimes by springs. Hall and Penfound (1939) described such a spring-fed swamp along the Pearl River in Louisiana. The same authors (1943) described a similar spring-fed back water swamp along the Alabama River in Alabama which contained blackgum, water-tupelo, and bald-cypress. The latter two species were particularly important in deeper water and blackgum nearer the shallow margins.

12. *Bald-Cypress - Tupelo Swamps*

The overstory is quite tall and is dominated by bald-cypress and water tupelo and/or ogeechee tupelo. Other hydric hardwoods of river floodplains may be present, such as popash and red maple. These other species, when present, are often smaller and contribute to the usually sparse understory. The ground cover is usually lacking as a distinct stratum because of the prolonged periods of flooding. Tree girths are usually enormous, as is apparent from a collective basal area value of 77.9 m^2/ha for a swamp in Louisiana (Hall and Penfound 1939).

Leitman (1978) observed that a stand along the Apalachicola River was inundated about 35-40% of the year from river overflow, as estimated from the stage-duration curve, and that inundation continued for an indefinite period after floodwaters receded because of runoff from rains. The soils reported by Leitman (1978) were clays with high cation exchange capacities (Research Summary 15). Fires are probably absent from lack of fuel as well as from hydric conditions and topographic irregularies that would hinder the spread of fire on a floodplain.

Two variants of the bald-cypress - tupelo swamp community are recognized, the bald-cypress swamp in which tupelo is absent or nearly so and the tupelo swamp community in which cypress is absent or nearly so. Penfound (1952) claimed that tupelo swamps usually resulted from the harvest of cypress.

Discussion

Wharton (in Wharton *et al*. 1977, p. 88) described a blackgum community in a back swamp of the Escambia River floodplain at the S.R. 184 bridge. His description is quoted below. He used the colloquial names of swamp black gum for *N. biflora* and tupelo gum for *N. aquatica*. The reference indicated was the Ph.D. thesis (Duke University) by R. A. Klawitter on a bottomland forest in South Carolina.

> "Even along alluvial rivers such as the Escambia, backswamps are found a distance from the river itself. Ponded by old natural levees, they develop into characteristic forests growing on highly acid, organic black mucks and peats, thus strongly resembling the swamps of blackwater streams. The Escambia locality, dominated by swamp black gum, has surface and deep peat zones over a dense clay. Trapped beneath the

deeper clay is an aquifer in which old roots are present...."

"Tupelo gum is found on the central Escambia floodplain. Klawitter (33) has shown that swamp black gum grows with less inorganic matter (silt-clay 42-56%) and more acidity (pH 3.6-4.1), while tupelo grows with more inorganics (silt-clay 56-80%) and under less acid conditions (pH 4.4). On the Escambia, the bulk of the silt-clay is probably being deposited nearer the mainstream. A shallow clay-rich zone in the Escambia backswamp suggests deposition when the main river was much nearer and occupied the abandoned slough. The presence of a hard clay layer acting as an impervious seal relates backswamps to swamp black gum ponds beneath which such a layer may also exist."

I accompanied Wharton when he examined the Escambia River blackgum swamp. The trees of the overstory were about 33 meters tall. About 95% of the overstory trees were blackgums up to about 60 cm in dbh. The other trees were bald-cypress and slash pines. The understory was discontinuous with dahoon and red maple dominant. Netted chain-fern (*Woodwardia areolata*) was the most conspicuous species in the ground cover. Other species present were cane (*Arundinaria gigantea*), hazel-alder (*Alnus serrulata*), Virginia willow (*Itea virginica*), St. John's-wort (*Hypericum galioides*), water oak, Carolina holly (*Ilex ambigua*), black titi, swamp cyrilla, sweetbay, sweetgum, swamp bay, greenbrier (*Smilax laurifolia*, *S. bona-nox*), muscadine (*Vitis rotundifolia*), cross-vine (*Bignonia capreolata*), royal fern (*Osmunda regalis*), sedge (*Carex* sp.), and golden-club (*Orontium aquaticum*).

Conner and Day (1976) described a cypress-tupelo swamp near the Mississippi River in Louisiana in which red maple was the only other important species besides bald-cypress and water tupelo. They made comparisons of productivity of cypress swamps, based on the literature. Net primary productivity in bald-cypress river swamps is as much as six times that in pond-cypress in domes. Mitsch and Ewel (1979) also noted a lower growth rate of cypress in domes than in other habitats, including creek swamps along small rivers where a mixture of tree species occurred with cypress. Mitsch *et al*. (1979) determined the phosphorus budget in a bald-cypress swamp in southern Illinois and presented data on water tables and sediment deposition.

Root and shoot biomass estimates were made in a cypress swamp by Mitsch and Ewel (1979) in their study in Alachua County. Root biomass was estimated for a cypress swamp and other swamp communities in the Great Dismal Swamp in Virginia (Montague and Day 1980).

Among the most fascinating cypress swamps are the dwarf pond-cypress sloughs in the southwestern Apalachicola National Forest and Tate's Hell Swamp. The trees are diminutive in height and proportionately reduced in girth and crown spread. One stand covers a large acreage near Whiskey George Creek in Tate's Hell and consists of a dense stand of cypress trees that are about two meters tall. The annual rings can scarcely be discerned with a hand lens, and these trees must be exceedingly old. It is not known why these trees are dwarfed. A phosphorus deficiency may be involved, as it is with grass-sedge bogs in the general vicinity (see p. 381).

Much of the Florida panhandle consists of longleaf pinelands (or other firelands system communities) which are interrupted by swampy depressions. These swamps, if deep enough, typically contain four communities as zones along an elevational gradient. These communities are a titi swamp (fringing the firelands at the higher and drier elevations), then a bay swamp, a pond-cypress swamp and a blackgum swamp. One or more of these communities may be missing because of the steepness of the gradient which results in a compression of the vegetational zones. The soils are acid and peaty.

In developing a system of classification for the vegetation of the panhandle, the vegetation dominated by cypress and tupelo could be treated satisfactorily in two entirely different ways. The alternative way, which was rejected, would have been not to recognize cypress-tupelo communities as comprising a separate system. Instead, the pond-cypress and blackgum communities would be included within the acid swamp system. This option is logical because of the close juxtaposition of pond-cypress and blackgum vegetation with acid swamps and because these communities are all characterized by peaty acid soils. The distinction between pond-cypress and blackgum communities and acid swamp communities becomes tenuous in sloughs where cypress strands are often not easily separable from bay swamps. If this alternative were opted, then the bald-cypress water tupelo community of alluvial floodplains would be incorporated into the hardwood forest system. This community resembles hydric hardwood forests because of the abundance of Nyssa spp., and this community intergrades with these hydric hardwood forests.

The decision to separate all Taxodium-Nyssa communities into a separate system was based on similarities of life form, floristic composition, and ecological preference for the most hydric sites. Unlike acid swamp communities, Taxodium-Nyssa communities lack species with persistent, coriaceous leaves. They contain cypress with its distinctive deciduous needle leaves which sets them apart from hydric hardwood forests. Although species of Taxodium and Nyssa occur in communities of other vegetational systems, they are never dominant because of the ability of trees of other species to compete successfully in these less hydric habitats.

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35. SCRUB SYSTEM

The scrub vegetation of Florida is distinctive and occurs only sparingly in adjacent states. Scrubs with the species composition typical to those of Florida also occur as isolated stands in the sandhills of Georgia and along the coast northward into South Carolina and westward into Mississippi. Within the panhandle scrubs are common near the coast west of the Ochlockonee River. In peninsular Florida, scrubs occur primarily along the higher energy coastlines and in the interior ridge country south nearly to the Everglades.

Much of the interest with respect to scrubs has centered on their highly contrasting floristic composition to that of the longleaf pine-xeric oak community (high pineland) which often exists side by side with scrubs. Nash (1895) wrote:

> "The 'scrub' flora is entirely different from that of the high pine land, hardly a single plant being common to both; in fact these two floras are natural enemies and appear to be constantly fighting each other.... I spoke above of the antagonism of these two floras. This is so marked that there is no mistaking it. Wherever they come together, the line of division is very distinct. A bare space of pure white sand usually separates the two. On one side you will see the tall *Pinus palustris* as far as the eye can reach, and on the other the diffusely branched *P. clausa* of much lower stature. You may look in vain in the 'scrub' for plants occurring in abundance just over the line in the high pine land, and *vice versa*. The strip of bare white sand dividing the two is neutral ground,

and each seems to jealously guard against the other's gaining a foothold there."

Several qualitative descriptions of scrubs have been published, among them that of Webber (1935) being particularly notable. Mulvania (1931) published the densities of scrub species in a quadrat study in Orange County. Kurz (1942) correlated scrubs and other vegetation types with coastal landforms throughout Florida, including Cochran's Beach in Franklin County and Beacon Hill in Bay County. He included species lists with cutaway profiles of each study location. Laessle (1958) presented quadrat data for a stand in Highlands County. He correlated the distribution of scrubs in peninsular Florida with geological formations and with soils data, primarily particle size distributions. He contrasted the differences in geology and soils between scrubs and sandhills. Laessle (1968) showed the spatial distribution of 25 species along a transect from a sandhill into a scrub near Ocala.

Organization. Scrubs have been called a fire-fighting association by Webber (1935). The life forms represented by the species present serve to discourage fires from carrying into scrubs from adjacent communities. The arrangement of the plants in terms of density and shade discourages the invasion of plants of potentially competetive species from other systems. "Fire-fighting" and the spatial arrangement that offers effective resistance to invasion are the only apparent attributes of the rather simple community organization in scrubs.

Species Richness. Scrubs are noted for their paucity of species. It is difficult to find more than about 15-30 species in a given stand without including weedy introductions in disturbed sites or species of adjoining communities in transition zones. There are no species that are always present in every scrub community, but there are a few species that occur almost exclusively in scrub systems. The latter include sand pine, myrtle oak, Chapman oak, rosemary (Ceratiola ericoides), the woody mint, Conradina canescens, and to a lesser degree, sand-live oak. Other species typical of scrubs include slash pine, saw-palmetto, and staggerbush (Lyonia ferruginea). Herbaceous species are often fewer in number than woody species in any given stand. Fruticose lichens sometimes form a dense and spectacular ground cover. Two of the most common terrestrial lichens in the panhandle according to Kurz (1942) are Cladonia leporina (British-soldier, a thick-branched plant with red, knob-like terminal spore bodies) and C. pycnoclada (deer-moss, a delicately and much-branched gray plant with an irregularly rounded habit).

Physiognomy. The most characteristic attribute of scrubs is the occurrence of a low thicket or ground cover of woody plants. These plants range in size from low shrubs about 3 dm tall to small trees about 3 meters tall. This stratum is the scrub proper, and any additional stratum is secondary in defining the vegetation as belonging to the scrub system. This stratum is open on dry dunes and quite dense where moisture is more readily available. The life form of the predominant plants in the scrub stratum is characterized by a highly branched but compact stem system and by broad, coriaceous, evergreen leaves. Myrtle oak, sand-live oak, and staggerbush all display these characteristics, and other species such as rosemary have most of them. Plants of these woody species are often rhizomatous and slow growing.

An open to rather dense overstory of sand pines or slash pines (but not both) may be present. Herbs are generally sparse and grow as individuals or in patches rather than as a distinct stratum.

Rosemary grows in open areas and has a distinctive zone of unvegetated white sand around each bush. Kurz (1942) suggested that the shallow lateral roots, which are 15-20 feet long on a bush five feet tall, keep the sand clean of herbs by preempting the water from near the soil surface. Another possibility is that the pungent aromatic substance produced by rosemary is a powerful allelopathic agent that inhibits the growth of any plants nearby.

Soils. The soils are always sandy with little or no organic matter, silts and clays present in the upper horizons. Laessle (1958) said that the sands of scrubs were always strongly washed and sorted, more so on the average than in sandhills covered by the longleaf pine-xeric oak community. Internal drainage is rapid and not impeded by spodic or argillic pans, except occasionally in scrubs containing slash pines. Geologically these soils occur on dunes and beach ridges near the coast and on relic shoreline features inland. Laessle (1958) identified these relic land forms as (1) Pleistocene beaches and bars; (2) hilltops that were submerged by the Okefenokee Sea, during which time the sands were washed and sorted; (3) sand deposits that had been washed and sorted by marine currents at a time of higher mean sea level; and (4) wave-washed lake shores and lake bottoms exposed as lake levels receded following limestone solution. The latter three land forms are common to peninsular Florida and not the panhandle.

Moisture. The loose dry surface soils of most scrubs suggest a xeric habitat. Scrubs with slash pine may approach these dry conditions or may be mesic. The water table in the xeric sites is often nearer the surface than one would expect, particularly in dune fields on barrier islands. It is likely that the dominant woody species have deep roots that are able to exploit the moist soil horizons just above the general position of the water table. It is possible that many other species, particularly herbs, do not grow in the scrub, because they are unable to produce such deep roots. If they do have this capability, a recently germinated plant would have succumbed from drought or competition before attaining sufficient downward root extension.

Fire. Fires are rare or absent in some scrubs and moderately frequent in others. The lack of grasses and other flammable herbs is a major reason why fires are often uncommon (Harper 1927). The dry sterile habitats retard plant growth and, therefore, the quantity of living biomass and detritus which could serve as fuel. The decomposition of the detritus is rapid and does not allow the accumulation of much flammable leaf litter.

Slash pine stands which have a dense undergrowth of saw-palmettos are exceptional and may burn fairly regularly, perhaps as frequently as every 10 years under natural conditions. The frequency would be even greater if it were not for the topographic irregularities of coastal habitats which isolate these slash pinelands into small stands. As a result, a single fire cannot sweep over great areas as had been typical in the firelands inland. Instead, ignition must result from a direct lightning strike or from a fire spreading into a scrub from an adjacent tidal marsh. The fires in slash pine-scrubs are usually surface fires, although needle-singe of the crowns is common because of the accumulation of fuels between fires.

In sand pine-scrubs the frequency of fire is lower, and the fires are generally crown fires which kill all of the pines. As a result, the fire frequency is once in the life time of sand pines, which usually is no more than 50-60 years (see page 260). Nash (1895) said that the soil of sandhills and sand pine-scrubs,

> "...was apparently originally the same pure white sand. That in the high pine land is now darker in color, being probably due to the charcoal deposited there by the annual fires. This seems to be the only difference. As fires are of rare occurrence in the 'scrub', the plants have made no provision against it, and so when a fire does go through, it causes great havoc, almost entirely killing the pines and oaks."

Garren (1943) said that these fires usually burned only in the spring at times of high winds. Laessle (1968) observed a lightning strike which ignited a mature stand of sand pine. He said the dense festoons of Spanish moss burned readily, contributing to the conflagration.

An important reason why sand pine-scrubs are immune from more frequent fires is the strip of barren sand that separates these scrubs from adjacent, nearly annually-burned sandhills. This strip serves as an effective natural fire break. Webber (1935) described this strip in the Ocala region.

> "Forty years ago the writer rode for many miles over this natural fire break of the great Etonia scrub north of Altoona....It seems probable that the extensive surface spread of the roots of the scrub vegetation combined with those from

> the trees of the high pine forest so thoroughly occupies this neutral territory that the grasses and herbs of the pine land cannot get started."

He said that in recent times grasses tend to cover this natural fire break, and that fires burn through these grasses and ignite the scrub in dry years. He proposed that the reduction in root competition resulting from the harvest of pines allowed these grasses to invade the natural breaks.

Scrubs lacking a pine overstory on coastal dunes experience fire very infrequently. The vegetation is unevenly distributed because of topographic irregularities, making it almost impossible for a fire to spread for any distance.

Mineral Nutrients. The deep sands of scrubs are deficient in nutrients, and the loss of soluble nutrients by leaching must be high. Much of the nutrient pool is likely incorporated in the living biomass at any given time. Laessle (1968) obtained values for extractable phosphorus of about 4.5 and 5.0 ppm in two stands. In another stand which had not been burned for 20 years he obtained the following values (ppm): K - 29, Ca - 290, Mg - 110. The pH in another unburned stand was 4.6.

Weathering of silica will not yield nutrients. Along the coast the sands contain some shell materials which provide nutrients upon weathering. The shell content in the sands along the coast in the panhandle is generally lower than elsewhere in Florida. Kurz (1942) showed a positive correlation between pH and shell content. He listed sand-live oak, which is abundant in scrubs in the panhandle, as an indicator of soils largely devoid of shell materials.

The most likely source of nutrients for scrubs along the coast is from meteorologic input. Aerosols of salt spray are intercepted by coastal plants and the soil as winds move on shore from the Gulf. These aerosols are rich in nutrients. The importance of meteorologic inputs has been documented in a hardwood forest on a barrier island off Long Island where this input alone was about equivalent to the nutrients available from all sources in several inland communities (Art el al. 1974). Additional nutrients are likely imported by overwash during hurricanes.

Maintenance. Plants belonging to most species of the panhandle would be unable to tolerate the inclement environments of scrubs, which includes very low nutrient levels, periods of very low soil moisture, and, near the coast, a constant exposure to saline aerosols. Seedlings of invading grasses and herbs encounter strong root competition and shade from the well established plants of the scrub stratum (Webber 1935). Trees of coastal hammocks do invade but are usually killed by crown fires or hurricanes while they are still saplings.

Plants of the scrub are adapted to survive fires or to take advantage of a recently burned site for reproduction by seed. As a result, the scrub persists indefinitely, at least at sites protected from drastic changes in landform by hurricanes.

Response to Disturbance. Nearly all woody plants of the scrub stratum coppice following fire, reestablishing the scrub without an intervening seral stage. Both pines are adapted to seeding-in following fire (see Chapter 20). Rosemary is completely fire-killed and does not coppice. Its seedlings are seen occasionally, and it likely is dependent on sexual reproduction for survival.

Stoneburner (1978) showed that the diametric growth rate of slash pines was greater than average during the few years following hurricanes on the barrier islands of coastal Mississippi. He noted that overwash during these storms removed all but the largest oaks of the scrub stratum. He proposed that pine growth was stimulated after being released from competition from the oaks. The overwash also exposed mineral soil which is needed for pine seedling establishment.

One of the many puzzling aspects of the vegetation of barrier islands is the near absence of a scrub stratum in some, but not all, slash pine forests for no apparent ecological or historical reason. Stoneburner's observations provide a hypothesis. Portions of scrubs that receive the brunt of hurricane overwash may have their scrub stratum scoured away. This stratum does not return, perhaps from lack of a seed source, lack of an appropriate seed bed, competition from the surviving overstory pines, or continual and excessive exposure to the harsh physical conditions of the environment. Whatever the reason, an open pineland is the result.

Scrubs are susceptible to burial in active dune fields. Some of the most scenic areas in the panhandle were created in groves of slash pines whose trunks were entirely buried, allowing a person to walk through the canopy. Kurz (1939, 1942) described how slash pines, sand-live oaks, and other woody species survive deep burial by the production of adventitious roots from trunks and branches. As a result, a root system is established within the well oxygenated layers of the soil. These trees and shrubs persist after a dune has moved slowly but completely through a site, exposing the original soil surface. Kurz (1942) said that it takes about a century for a dune to move into an area, bury the trees, then move on, exposing the trunks of the trees in their entirety.

Taller dunes often have a dense ground cover of oak sprouts only a few decimeters long. These sprouts usually represent the uppermost twigs of the crown of a buried tree which actually may be upwards to about 8 meters tall. Drifting sand is arrested by the twigs and accumulates around them. Stem growth must keep pace with this accumulation if the tree is to survive.

Dune growth and stabilization in the panhandle are attributable primarily to the presence of these trees. They trap drifting sand, causing a dune to form, and then they serve as a skeleton which holds the dune in place or at least retards its movement. Dune buggies pose a severe threat to dune stabilization because they kill the exposed crowns of buried trees. The barren, drifting sands on the eastern end of St. George Island serve as evidence of the result of dune buggy traffic. The few persisting dunes are capped with living woody vegetation. The sides have been blown away, leaving only the columnar central portion in tact. The drifting sands have moved nearly to the northern shoreline. The leading face of this sand mass is steep like a glacier and is rapidly burying trees in its advance.

Some of the barren openings of scrubs along the coast are the result of blowouts. The configurations of the dunes cause winds to be focused on small areas of perhaps only a few meters across. The erosion of sand by aeolian forces undermines the vegetation and leaves a depression of loose dry sands. Colonization of blowouts is made difficult by the continual shifting of these sands.

Webber (1935) has questioned whether or not a scrub can survive severe disturbance by man. He wrote,

> "It seems probable that thoroughly cleared scrub land under the conditions now existing in most parts of central Florida would never go back to scrub unless uncleared scrub surrounded the cleared area, and it would even then be doubtful."

Mode of Origin. Kurz (1942) and other authors contended that a scrub stratum generally becomes established on the bare sands of coastal habitats soon after grasses and creeping vines have stabilize the substrate. Later, sand pines invade to form an overstory. Once established, a scrub may persist indefinitely, even when isolated inland following a drop in mean sea level. Laessle (1968) speculated that the Red Hill scrub in Highlands County may date to the Pliocene or even the late Miocene, "...a most striking example of the scrub's persistence."

If scrubs indeed invade dunes recently stabilized by grasses and vines, one would expect to find seedlings of scrub species present in stands of this vegetation today. With the exception of seedlings of pines and rosemary, seedlings of scrub species are rarely seen in any habitat. The loose sands of a dune which is elevated well above the water table seems like an improbable seed bed for all but the most opportunistic weeds.

The persistence of dune-buried trees suggests an alternate hypothesis. These trees are always rooted on what was once a flat near sea level and the water table. Of common occurrence on flats and in interdunal swales is detritus, much of it from a flotsam or wrack of seagrasses, stranded by storm tides. After the leaching of sea salts by rains, this organic matter would provide the nutrients and hold the moisture capable of sustaining seedling oaks and other scrub species. Later, decomposition and percolation would remove this organic matter, and drifting sands would cover any remaining traces of evidence.

If this hypothesis correctly explains the establishment of the oaks and other dominant species of the scrub stratum, then the mode of origin of scrubs is by initial floristic composition and follows the tenents of the displacement model. If an intervening seral stage of grasses and vines indeed occurs, then the displacement model is partially applicable. The herbaceous vegetation merely serves to stabilize the substrate and does not contribute substantially to the improvement of the soil or to the ameliorization of the harsh fluctuations in temperature and moisture, as is typical in seral development.

Ecotones. Transition zones occur between scrubs and coastal hammocks, such as hammocks that border sloughs entering lagoons on the leeward side of barrier islands. The cordgrasses (especially Spartina patens) and other graminaceous species of tidal marshes may encroach a short distance into slash pine-scrubs from tidal flats on the margins of these lagoons.

Not all slash pine woods along the coast are scrubs. Some are better considered coastal slash pine flatwoods (firelands system) because of the abundance of herbs, especially grasses like Muhlenbergia capillaris (hairgrass) and Schizachyrium maritimum (sand bluestem) which are quite flammable. Those stands with a sparse but flammable herbaceous stratum are transitional between the slash pine-scrub community and coastal slash pine flatwoods.

Coastal prairies dominated by sea oats, sand bluestem, or any of a number of herbaceous species may also contain individuals or thickets of woody plants typical of scrubs. Such prairies might be transitional from a seral viewpoint or they may represent old dune fields that were leveled by storms, causing the demise of a scrub that once occupied the site. If so, then the woody plants are likely relicts that persisted since before the colonization of herbaceous species on the physically altered site.

Many sandhills near the coast contain a mixture of longleaf pine-xeric oak species (including wiregrass, turkey oak, and bluejack oak) and scrub species (including sand pine, myrtle oak, sand-live oak, and rosemary). The early literature stressed the fact that the scrub and high pineland communities were never mixed. Webber (1935) said that he could not remember seeing turkey oaks in scrubs in 1892. Now turkey oaks and other sandhills species are occasionally mixed with scrub communities. It is the concensus of Webber (1935), Kurz (1942), and Laessle (1968) that such stands were once longleaf pine-xeric oak communities in which fire was suppressed following the logging of the pines. In the absence of fire, sand pines and other typical scrub species expanded into former sandhills from adjacent scrubs, largely overtaking the longleaf pine-xeric oak community. Laessle (1968) wrote,

> "The rapid spread of sand pines to the sandhill islands in the Ocala National Forest is nearly everywhere evident since fires have been prevented....The invasion of sandhills by the typical scrub oaks, Q. myrtifolia and Q. chapmanii is apparently much slower but their occurrence there with decreasing frequency as one moves further from adjacent scrubs is evident from the transects."

In the panhandle such transitional communities are common along the north side of U.S. Route 98 in Franklin County and elsewhere.

Kurz (1942) did not believe that longleaf pine-xeric oak vegetation invaded sandhills. Laessle (1968) wrote,

"I have observed no evidence of succession toward sandhill vegetation from scrub....I have never observed the invasion of Pinus palustris in the scrub."

Communities. Three scrub communities are recognized, the coastal scrub community, the sand pine scrub community, and the slash pine-scrub community. These communities are briefly described and compared in Table 20.

13. *Coastal Scrub Community*

The overstory is absent, although slash pines or sand pines may be present as widely scattered individuals. The undergrowth or scrub stratum is the only vegetational element of importance. It is usually 1-2 meters tall. A few sand-live oaks or small trees of other species may attain a somewhat taller size. The number of species is usually lower than in the other scrub communities. Myrtle oak and sand-live oak are often dominant and rosemary conspicuous.

Table 21 lists some of the species common in the coastal scrub on St. George Island. Plants colonizing blowouts and other openings were Hypericum reductum, Polygonella polygama, Cnidoscolus stimulosus, and Cladonia spp. Some species were common only on the leeward side of the foredune: Ilex vomitoria, Juniperus silicicola, Serenoa repens, Panicum amarum, Schizachyrium maritimum, and Uniola paniculata. Research Summary 16

TABLE 20. Conspectus of Scrub Communities.

	Soil Moisture	Fire	Vegetation
13. Coastal Scrub Community	The surface of well drained sands; the site seemingly xeric	Uncommon or rare	Low woody thickets with myrtle oak and/or sand-live oak among the dominants. Other shrubs commonly present or dominant include *Lyonia ferruginea*, *Ilex vomitoria*, *Ceratiola ericoides*, *Quercus chapmanii*, *Conradina canescens*. Herbs sparse.
14. Sand Pine-Scrub Community	The surface of well drained sands; the site seemingly xeric	Uncommon or rare; usually crown fires	Overstory of sand pines; undergrowth of species of the Coastal Scrub Community. Herbs sparse.
15. Slash Pine-Scrub Community	The surface of rather dry to rather wet sands, the site broadly mesic	Uncommon to rather frequent; usually surface fires	Overstory of slash pines; undergrowth in drier sites as in the Coastal Scrub Community and in the wetter sites with dense saw-palmetto, *Lyonia lucida*, *Ilex glabra*, and other shrubs common to pine flatwoods. Herbs sparse.

TABLE 21. Some Species of the Coastal Scrub Community on St. George Island.

WOODY SPECIES	HERBACEOUS SPECIES
Bumelia lanuginosa	Andropogon capillipes
Ceratiola ericoides	Cenchrus tribuloides
Chrysoma pauciflosculosa	Chamaesyce ammannioides
Conradina canescens	Cnidoscolus stimulosus
Hypericum reductum	Croton punctatus
Ilex vomitoria	Cyperus lecontei
Juniperus silicicola	Heterotheca subaxillaris
Opuntia drummondii	Lythrum lineare
Pinus elliottii	Muhlenbergia capillaris
Quercus chapmanii	Panicum amarum
Quercus geminata	Paronychia erecta
Quercus myrtifolia	Polygonella polygama
Serenoa repens	Polypremum procumbens
Smilax auriculata	Rhynchospora megalocarpa
	Schizachyrium maritimum
	Scirpus pungens
	Seymeria cassioides
	Uniola paniculata

compares the densities of coastal scrub and slash pine-scrub communities at St. George Island.

Laessle (1968) described a stand of the coastal scrub community in Highlands County. He proposed that sand pines had once occupied the site and that the pines had become senescent and disappeared. Lack of fire for decades prevented the preparation of an adequate seed bed, providing that seeds could be disseminated from the nearest stand of sand pines a mile away. There was no seed source nearby of hammock species like southern magnolia and dogwood that would otherwide invade the fire-free site. The scrub stratum of the former sand pine-scrub community persisted and is best called a coastal scrub community for lack of an overstory. The stand is exceptional, because inland scrubs typically have a pine overstory.

Scrubs in the sandhills of Georgia also lack pines. Wharton (1977) described what he called an evergreen scrub forest and an evergreen scrub-lichen forest from Tattnall and Emanual counties. Common species were myrtle oak, Chapman oak, sand-live oak, staggerbush, saw-palmetto, Chrysoma pauciflosculosa, and Rhynchospora megalocarpa.

Penfound and O'Neill (1934) described a coastal scrub on Cat Island, Mississippi, in which the most frequently occurring species were Helianthemum arenicola and Chrysoma pauciflosculosa. Woody species were rosemary, slash pine, Clinopodium coccineum, and Ilex vomitoria.

14. Sand Pine-Scrub Community

The overstory consists of sand pines which are usually short to moderately tall and rather dense. The undergrowth is essentially the same as in the coastal scrub community. Table 22 lists some species

TABLE 21. Some Species of the Sand Pine-Scrub Community, Based on Kurz (1942), Laessle (1958), and Snedaker and Lugo (1972).

WOODY SPECIES	HERBACEOUS SPECIES
Calamintha coccinea	Cnidoscolus stimulosus
Ceratiola ericoides	Paronychia erecta
Chrysoma pauciflosculosa	Petalostemum feayi
Conradina canescens	Polygonella polygama
Ilex ambigua	Rhynchospora megalocarpa
Ilex vomitoria	Selaginella arenicola
Lyonia ferruginea	
Osmanthus amerianus	
Persea borbonia	
Pinus clausa	
Quercus chapmanii	
Quercus geminata	
Quercus myrtifolia	
Serenoa repens	
Smilax auriculata	
Vaccinium arboreum	
Vaccinium myrsinites	
Vaccinium stamineum	
Yucca aloifolia	

that have been considered typical of this community throughout Florida. This table omits species endemic to scrubs of the peninsula and species typical of sandhills which have been overtaken by scrubs in the absence of fire.

This community commonly occurs on beach ridges and other, relatively mature coastal upland land forms.

15. *Slash Pine-Scrub Community*

The overstory consists of a tall stand of slash pines. The undergrowth may contain some or most of the species common to the coastal scrub and the sand pine-scrub communities but usually contains other species, particularly where the soil is moist. Research Summary 17 compares the percent cover of the species in the undergrowth in a dry and in a wet site at St. George Island. The wet site was dominated by saw-palmetto, gallberry, wax-myrtle, and dwarf blueberry, none of which were important in the dry site.

Slash pine-scrubs often occupy interdunal swales and swales between beach ridges. The demarcation between this community and the sand pine-scrub community on the slopes of the same dunes is generally pronounced and without transition. In swales the scrub stratum is dominated by saw-palmetto, gallberry, and other wet site species. These species contrast to the oak-rosemary assemblage beneath the sand pines.

The term "slash pine-scrub" has not been employed before, and authors usually refer to slash pine communities on barrier islands and coastlines as flatwoods. The fact cannot be ignored, though, that slash pine-scrubs have the same scrub stratum as sand pine-scrubs on dry sites and that they lack an herbaceous ground cover on dry and moist sites. There is a tendency among ecologists to apply the term, scrub, only to the sand pine-scrub community. This application denies the floristic and especially the structural integrity of all vegetation with a scrub stratum. It also overemphasizes the overstory pines, which are not as important a floristic element in the community as the scrub stratum.

Kurz (1942) recognized what appears to be a slash pine-scrub community in interdunal swales at Beacon Hill. The floristic list contains wiregrass and other bog species, and the community is better considered as a boggy flatwoods. The origin of this flatwoods is unknown. It may have been more extensive but had been partially covered by dunes.

Pessin and Burleigh (1941) described a slash pine-scrub community from Horn Island, Mississippi. The pines were about 170 years old. Sand-live oak was present, and rosemary grew where fires were infrequent. Penfound and O'Neill (1934) described a slash pine community on Cat Island, Mississippi which contained sand-live oak, myrtle oak, and saw-palmetto. This stand is probably best considered a coastal slash pine flatwoods, rather than a scrub, because of the high frequency of grasses in meter-square quadrats: *Schizachrium maritimum* (69%), *Cynodon dactylon* (55%), and *Panicum repens* (55%).

Discussion

Reasons for Permanence. The quotation of Nash at the beginning of this chapter raised the question as to why two entirely different communities, sand pine-scrub and longleaf pine-xeric oak, could occur side by side indefinitely and maintain their sharp floristic discontinuity.

Webber (1935) said he had no evidence that the borderline between any given pair of undisturbed communities ever changed. Laessle (1968) suggested that stands of sandhill and scrub vegetation have maintained their same positions since the Pleistocene or earlier.

Whitney (1896) attempted to explain why these communities remained distinct:

> "...there is no apparent reason, from the chemical or physical examination, to account for this difference in the native growth on scrub as compared with the high land or the hammock, and as far as our investigations show, there is no difference in the soil. The only explanation for the difference in the character of the vegetation is that it is accidental and that one kind of crop or another received a start and simply spread; the two kinds of vegetation not being capable of growing together."

Laessle (1958) was unable to accept this explanation, which was precociously based on the theory of initial floristic composition. After an exhaustive and rewarding attempt to correlate scrubs with geomorphological features, he was still unable to demonstrate conclusively any other reason for the distinctness of scrub and sandhill communities. Perhaps out of desperation he wrote,

> "On circumstantial evidence it is concluded that the tremendous contrast in the flora of these communities is related largely to nutrition, and that a certain element is, or particular elements are lacking in the severely washed and sorted sands supporting scrub....Published analyses of soils supporting

these two communities are rather inconclusive."

Laessle (1968) later recanted and, in my opinion, correctly deduced that, "...the differential frequency of fire...has played the major role in maintaining their most contrasting floristic and structural characteristics."

Scrubs, Acid Swamps, and Chaparral. Scrubs and acid swamp communities share important structural features. First, both lack an herbaceous ground cover. Second, they both contain an undergrowth of woody plants mainly with coriaceous, persistent broad leaves. Third, an overstory of pines is sometimes present. Both communities grow on sterile, acid soils. Both burn infrequently. The shoot systems of most plants are fire-killed and are replaced by coppicing. In short, acid swamps are hydric scrubs. It would be entirely logical to combine them into a single system, and tradition was the only reason for not doing so in this treatment.

Scrubs have also been compared with chaparral and other broadleaf-sclerophyllous vegetation of Mediterranean climates. Chaparral differs by the presence of an herbaceous ground cover in which annuals are important and through which fires burn with a higher natural frequency than in most scrubs. The wet summers and high annual rainfall in Florida contrast with Mediterranean climates elsewhere. The physiognomic similarities are not echoed by taxonomic similarities. In summary, the comparison between Mediterranean-type vegetation and scrubs is not strong.

Relic Slash Pine-Scrub. Research Summary 18 described a slash pine-scrub community isolated 25 miles inland from the Gulf in Liberty County. It is the only large pure upland stand of non-coastal slash pine known from the panhandle that did not develop in response to timber harvest (see page 391) or other impacts of man's activities. The 48-hectare site was actually an island elevated 5 meters above the surrounding and broad cypress sloughs of Rowletts Creek. Sand-live oak was the principal dominant of the well defined scrub stratum, and staggerbush was also dominant. Herbs were sparse. The flora consisted on only 52 species. Some species were typical of acid swamps which were able to migrate from the lowlands of Rowletts Creek onto the site in the absence of frequent fires. Other species were typical of mesic hardwood forests and were also able to invade because of the low incidence of fire. The cypress swamps served as a fire break, and fires could be ignited only by a direct lightning strike. Most direct strikes would not be expected to result in a fire because of the lack of flammable vegetation and litter.

The site occurred along the Pamlico shoreline which dates to the most recent interglacial stage (see page 80) and may have acquired a scrub cover at that time. With the subsequent recession of mean sea level, the site was isolated inland. Scrubs were widespread throughout the panhandle until about 5,000 BC (see page 194), when regional tables rose in response to a more recent rise in mean sea level. The most parsimonious explanation of what may have happened thereafter is as follows. The increased soil moisture stimulated rank growth in the scrub stratum to the point that fires became more frequent and widespread. These fires, in turn, weakened the woody plants of the scrub and allowed grasses to invade, increasing the flammability of the habitat. The scrub was soon displaced by wire-grass-dominated firelands vegetation.

This sequence of events did not take place in the study site because of the low incidence of fires, and the scrub persisted to the present.

Some of the typical coastal species, such as myrtle oak, if present, were crowded out by the woody species from acid swamps. If one accepts the proposition that acid swamps are hydric scrubs, this species replacement does not distort the conceptualization of the vegetation on this site as representing a true scrub.

This senario is strictly hypothetical but fits existing paleoecological and autecological facts. At the risk of employing circular reasoning, this stand gives some insight into the events that led to the widespread displacement of scrub vegetation by firelands vegetation.

The soil is also unusual, according to the findings of P. E. Avers. It belongs to an undescribed series of Ultic Haplaquods and contains a distinctive brittle, red spodic horizon beginning about 30 cm deep.

Salt Spray Effects. Sand-live oaks and other woody plants of the scrub stratum appear as if wind-sheared along the Gulf coast. The crowns are flat to gently rounded and sloping with the tallest part of the crown away from the Gulf. The crowns are also very smooth and densely leafy, owing to the profuse branching of the short twigs. Wells and Shunk (1937) said that these plants were not wind-sheared but rather were growing in response to injury from salt spray. Any twig that grew above the rest of the crown was exposed to an excessive dose of saline aerosols, and its living tissues were killed by plasmolysis. Upon the death of the shoot, apical dominance no longer inhibited lateral growth, and fascicles of new twigs sprouted a little lower on the stem. As this process continued, the entire crown developed its nearly flat, densely leafy aspect.

Wells and Shunk (1938) elaborated:

"It was repeatedly noted on the repressed sea-front shrubs that, where the young and tender shoots were slightly depressed in the compact surface of the fastigiate twig mass, little or no injury occurred. So shoots of approximately equal surface area were taken from exposed and slightly depressed positions and carefully washed with equal amounts of distilled water. A few drops of silver nitrate solution were added to each of the washings. That from the exposed shoot gave a strong chloride precipitate, while that from the depressed shoot gave barely a trace. Why shoots so slightly depressed should escape from the spray was puzzling, until it was realized that a strong wind playing over a porous surface would set up a suction effect comparable to that familiar in atomizers, an effect which would result in a slight elevation of the spray-laden wind above the short spring growth slightly depressed in the shrub mass. A similar effect would keep the spray from falling behind the shrub mass, permitting the leeward lateral shoots to grow unimpeded. This phenomenon means that during the period of strong winds from the sea, there is set up a ground air current toward the sea. This air moves up through the interlacing branches and not only keeps the spray from settling into the shrubs but actually elevates the spray-laden wind slightly above their sloping surfaces. This effect is naturally most pronounced nearest the sea where the wind velocity is the highest, and where the spray is most concentrated."

Other authors maintained, though, that wind and its enhancement of transpiration were more important factors than salt spray in causing the peculiar forms of coastal trees and shrubs. These opinions were reviewed by Oosting (1954).

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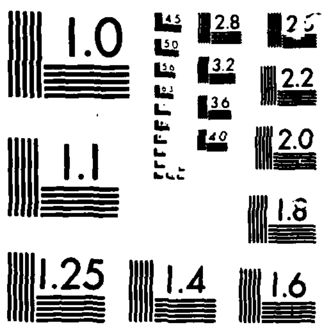

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36. COASTAL PRAIRIE SYSTEM

The coastal prairie system encompasses all herb-dominated vegetation of mesic and xeric habitats that are subjected to impaction by salt-spray or to overwash by storm tides. This vegetation occurs on beaches above the mean high tide mark, on dunes, and on flats associated with dune fields. These flats (or slacks as they are sometimes called) consist of interdunal swales and of low terrain where dunes are low, widely separated, or absent.

Community Organization. The communities are scarcely more than species populations with little or no interrelationships. On dunes only one species is essential, a vigorous rhizomatous grass which serves as a baffle trapping sand and which sends tillers upwards to keep from being buried. This process causes dunes to accrete. The principal species in the panhandle responsible for this process is sea oats (Uniola paniculata). The life history and dune-building capabilities of this species were described in Chapter 28. The sand bluestem (Schizachyrium maritimum) may also serve effectively in dune building, but confirmational studies are lacking. In flats, the dune-building function is not required. Plants representing an indefinite species composition grow there and collectively serve to stabilize the substrate, reducing erosion from wind and overwash. Otherwise, no interrelationships are evident or seem necessary for the persistence of the community.

Species Richness. Most communities contain approximately 10-30 species. The higher the number of species present on dunes, the greater the proportion of annuals. These annuals tolerate the harsh environmental conditions, taking advantage of the open, incompletely colonized habitat. Most of these same species have become widespread weeds in ruderal habitats throughout the panhandle. The total number of species and the proportion of perennial to annual species is generally higher on flats than on dunes.

Physiognomy. The only stratum of consequence is the ground cover, consisting largely or entirely of herbs. This stratum is sometimes subdivided into a taller layer of erect grasses and a shorter layer of annuals and repent perennials. Shrubs may occur for several reasons. First, sand-live oaks, red cedar, yaupon, saw-palmetto, and other woody species of coastal scrubs and hammocks often develop in depressions behind foredunes. The dunes grow in size or migrate inland, partially burying the woody plants and bringing sea oats and other species of the coastal prairies in close proximity to these woody plants. In this instance, the woody plants are not part of the coastal prairie vegetation, rather, the prairie was superimposed on top of the woody community. Second, blowouts and overwash may destroy dunes dominated by coastal scrub vegetation. A coastal prairie will replace the scrub, but an occasional woody plant that survived the destruction of the dune will persist as a relic in this prairie. Third, an older, stabilized flat may be invaded by woody plants of the coastal scrub community. The initial stage of this successional trend presumably is a prairie in which small shrubs or small trees are intermixed.

Several distinct life forms are represented among the herbs in dunes. These include (1) the rhizomatous grasses that are responsible for dune-building and which help to hold a dune together by their multilayered and highly branched rhizomes; (2) other erect or decumbent and often deep-rooted perennial herbs (Cnicoscolus stimulosus, Cenchrus tribuloides, Oenothera humifusa); (3) scandent creeping plants (Ipomoea stolonifera, Cynanchum angustifolium); (4) stoloniferous plants with rootstocks at or near the soil surface (Hydrocotyle bonariensis); and (5) annuals. Some or all of the deep-rooted perennial herbs may have seeded into the habitat in the early stages of dune development and then grew in concert with the dune. Studies are needed to test this possibility. The scandent and stoloniferous species may have seeded into high beaches, flats, or depressions and clambered up the sides of the well developed dunes, or they may have seeded into the incipient or developing dune along with the other perennials. These species are sand binders, although their importance in dune accretion and stabilization is not known. It is possible that Hydrocotyle bonariensis may have nearly as important a role as the rhizomatous grasses. If so, its role may be to grow into recently accreted sands and keep them from drifting during the next major wind storm. The decumbent and sprawling perennials also offer resistence to sand movement.

The diversity of life forms is less pronounced in flats and swales. Most species are cespitose or rhizomatous perennials.

Soils. The term, soil, is scarcely appropriate, because little or no modification of the parent material has occurred which has resulted in the formation of soil horizons. The substrate is quartz sand with little or no shell material, organic matter, silt, or clay. The sand is deposited by aeolian forces to form dunes and by wind or by water to form the substrates of flats and swales. Sands that are carried by storm tides and deposited onto flats are called overwash (or washover) fans.

Moisture. The water table is at least two meters below the soil surface at all seasons in dunes and nearer the surface in flats and swales (Ranwell 1972). Soil moisture is likely available to plants in flats and swales because of the proximity of the water table and the lack of pans or other impediments to downward root extension. Living roots of plants on taller dunes may not extend to the water table, and even if they did, water deficits occur because of high salinities and excessive evapotranspiration. The upper 20 cm of sand in dunes contains a rather constant moisture content of 3-4% (Ranwell 1972, van der Valk 1974a). Ranwell said that dew was an important source of water for dune plants. He presented some evidence for the hypothesis that additional moisture is made available by the condensation of interstitial water vapor onto the surfaces of sand grains. van der Valk (1974a) showed that soil moisture (and soil temperature) did not differ signifcantly from one part of a dune to another.

Mineral Nutrients. Nutrients are made available principally by meteorologic input from salt spray, as described in the previous chapter. Hurricane overwash also supplies nutrients which are utilized by plants (Schroeder et al. 1979). Salt-spray deposition diminishes with distance from the Gulf, because the larger aerosols tend to fall quickly. van der Valk (1974b) showed that the seaward side of a foredune received 55% of the salt spray deposit, the top 34%, and the landward side 11%. The nutrients in this salt are available to plants as long as the salt concentration is not lethal. Tolerance to salt concentration is quite variable among species. van der Valk (1974a) showed that plants of *Conyza canadensis* were killed by the salt concentrations on the seaward side of foredunes, but that plants of *Croton punctatus* and *Solidago sempervirens* were tolerant of these concentrations.

Fire. Fires are essentially absent from dunes because of topographic irregularities and sparcity of plant cover. Fires may occur occasionally on low, densely vegetated flats. The effect of such fires on the vegetation is unknown, but is probably not deleterious.

Maintenance. Dunes are temporary landforms which are constantly threatened by erosion and other alterations by wind and waves. The vegetation on dunes is likewise temporary, and long-term maintenance is not an important issue. As was discussed in Chapter 28, the vigor of sea oats depends on the accumulation of nutrients during the active accretion of sand. The supply of sand and the velocities of the wind along the Gulf coast limit the maximum height and size of the dunes. The period of accretion and thus the vigor of sea oats populations are governed by these limitations. Since nutrient import is correlated with sand accretion for sea oats, it stands to reason that plants of other species are also dependent on this same process. If accretion is arrested, then nutrient levels may drop to the point that the vegetation becomes senescent. Thereafter the ability of the vegetation to stabilize the dune would diminish, inviting wind erosion. These possibilities beg verification.

Flats are potentially more permanent habitats than dunes, although they are also subject to severe modifications such as scouring or burial by overwash or burial by dune migration. Salt spray and occasional inundations by storm tides may reduce the number of species that can tolerate such habitats and thus increase the likelihood that the species composition will not change with the invasion of species from inland habitats. Overwash and perhaps fire may also limit the possibilities for invasion by woody species.

Schroeder _et al_. (1979) studied flats on a barrier island along the Maryland-Virginia coast 12 years after a major storm had deposited overwash fans over many areas. These areas were dominated by herbs at the time of the study. Adjacent areas that escaped overwash deposition contained a substantially greater cover of woody species. The conclusion was that the overwash deposition arrested the succession from herb-dominated vegetation to shrub-dominated vegetation. The woody plants along that coast line are not tolerant of burial. None of the species which survive burial in the panhandle were present on the mid-Atlantic coast, such as sand-live oak, myrtle oak, saw-palmetto, yaupon, and slash pine. The results of studies from that region are not necessarily applicable in the panhandle.

Response to Disturbance. Natural disturbances of coastal prairies include blowouts, burial from dune migration or deposition of overwash fans, scouring during overwash, and occasional salinity shocks when storm tides inundate habitats which otherwise are characterized by low salinities. The survival and recovery of the vegetation is dependent on the degree of the disturbance. Plants of some species are capable of withstanding considerable disturbance. For example, sea oats and _Spartina patens_ are able to survive and grow through freshly deposited overwash fans (Schroeder _et al_. 1979). If the disturbance destroys the community, but the habitat remains essentially the same, then the community may become reestablished from nearby seed sources. If the habitat is changed, another community may colonize the site.

A key to recovery or to the establishment of vegetation of newly formed dunes is the ability of a sprout from a germinating seed to reach the soil surface. Drifting sand may bury seeds so deeply that the sprouts die before they can emerge from the sand. van der Valk (1974a) showed that this was the principal reason why several species (*Croton punctatus*, *Physalis viscosa*, *Solidago sempervirens*) were unable to colonize the seaward side of foredunes.

Schroeder *et al*. (1976) assessed the impacts of a man-made dune in North Carolina on coastal prairies nearby. The artificial dune was constructed to prevent storm damage to a barrier island. This dune caused natural vegetation behind it to be sheltered with respect to the impaction of salt spray, to sand movement, and to overwash. Colonization of the herbaceous vegetation by woody plants was the most apparent response of the vegetation.

Hosier and Eaton (1980) reported on the impacts of dune buggies on coastal prairies in North Carolina. Vehicular traffic caused a reduction in the number of species present and in the vegetational cover. These changes increased the vulnerability of the habitat with regard to erosion during washovers. The vehicles also caused a compaction of subsurface sands, retarding percolation. Instead of leaching, salts began to accumulate in the surface soils, causing a change in species composition in favor of halophytes.

Mode of Origin. Coastal prairies are generally considered as representing the initial or pioneer stage in primary succession. Seeds of the plants of these prairies, though, do not necessarily germinate in mineral sand. Presumably, an important seed bed is the wrack, comprised mainly of seagrasses, which becomes stranded in swales and flats by storm tides (Ranwell 1972, Oertel and Larsen 1976). Since organic matter is present, the succession is not strictly primary. In any event, the coastal prairies largely represent the results of initial floristic composition. Harsh environmental conditions and periodic disturbances often prevent further successional development, although the potential is present for seral elaboration.

Ecotones. Ecotones are common between coastal prairies and brackish tidal marshes, wherever the prairies border on lagoons. Similar transition zones occur where coastal prairies grade into emergent fresh water marshes in wet swales. On the mainland in the western panhandle grass-sedge bogs commonly occur near the coast and form transition zones with coastal prairies.

Other transitional vegetation may occur as stages in seral development. The potential succession from coastal prairies to coastal scrubs has been mentioned previously, although clear examples of vegetation in the midst of this transition have not been identified in the panhandle. There is evidence, though, that suggests that slash pine flatwoods have become established on account of the invasion of coastal prairies by slash pines. The slash pine flatwoods near the lagoon to the east of the causeway on St. George Island are dominated largely by herbs common to coastal prairies, such as *Eragrostis refracta* and *Muhlenbergia capillaris*.

Coastal prairies on similar flats nearby contain many of the same species. Shrubs are decidedly uncommon in both communities. The only substantial difference between them is the presence or absence of slash pines. It seems logical that these pines simply invaded coastal prairies. The conditions required for successful invasion are unknown. The lack of young pines on coastal prairies adjacent to a pine seed source suggests that the conditions for invasion are exacting.

Communities. Two communities are easily defined from coastal prairie vegetation: 16. Dune Prairie Community and 17. Overwash Prairie Community. The dune prairie community occupies xeric dunes, and the overwash prairie community occupies mesic interdunal swales and overwash flats. Table 23 lists some of the more common species of each community.

These two communities have been defined sufficiently in the preceding paragraphs, and formal descriptions of each have been omitted. Research Summary 19 gives relative densities in three dune prairies in the panhandle.

Discussion

Zonation of plant communities along the coastal strand in the Southeast has been described by many authors, some of whom have already been cited. As an introduction to the literature pertaining to coastal prairie and coastal scrub vegetation, the following list of papers is presented: Virginia, Tyndall and Levy (1978); North Carolina, Brown (1959), Burk (1962), Au (1974), van der Valk (1975); South Carolina, Salter (1974); Georgia, Johnson et al. (1974), Hillestad et al. (1975), Oertel and Larsen (1976); Florida, Kurz (1942), Davis (1975), Carlton (1977),

TABLE 23. Some Common Plants of Coastal Prairies.

Dune Prairies	Overwash Prairies
RHIZOMATOUS GRASSES	GRASSES
Cenchrus tribuloides	Andropogon virginicus var. glaucopsis
Dichanthelium aciculare	Chloris petraea
Panicum amarum	Eragrostis refracta
Paspalum distichum	Muhlenbergia capillaris
Schizachyrium maritimum	Setaria geniculata
Uniola paniculata	Spartina patens
STOLONIFEROUS HERBS	SEDGES
Cynanchum angustifolium	Cyperus lecontei
Hydrocotyle bonariensis	Dichromena colorata
Ipomoea stolonifera	Fimbristylis castanea
Phyla nodiflora	Fuirena scirpoides
ANNUAL HERBS	SHRUBS
Cakile edulenta	Baccharis halimifolia
Croton punctatus	Ilex vomitoria
Atriplex arenaria	Myrica cerifera
Bidens pilosa	
Helenium amarum	PERENNIAL HERBS
Heterotheca subaxillaris	Aster tenuifolius
Rumex hastatulus	Limonium carolinianum
SHRUB	Solidago sempervirens
Chrysoma pauciflosculosa	
PERENNIAL HERBS	
Chrysopsis gossypina	
Cnidoscolus stimulosus	
Helianthemum corymbosum	
Oenothera humifusa	
Physalis angustifolia	
Physalis viscosa var. maritima	

Mississippi, Penfound and O'Neill (1934), Pessin and Burleigh (1941), Huguley and Eleuterius (1976); Louisiana, Montz (1976).

The study by Huguley and Eleuterius (1976) compared the vegetation of Horn Island with that in similar habitats on the mainland. Ninety-eight species were tallied. This paper is mentioned because it attempts to account for the entire flora. Most ecological studies of any habitat tend to ignore the less common species or those species that are not evident or identifiable at the season that the study was conducted. Authors who attempt to treat the entire flora should be given special recognition.

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37. HARDWOOD FOREST SYSTEM

The hardwood forest system belongs to the deciduous forest formation as described by Braun (1950) in her magnificent monograph of that forest complex in eastern North America. Recent authors often refer to this vegetation in the southeastern coastal plain as the southern mixed hardwood forest.

In the panhandle this vegetation originally was restricted to riverine habitats and occasionally to protected habitats along the coast and around some lakes and sinks. With fire protection and other human interference with natural processes, this vegetational system has spread into other areas, often at the expense of the firelands system. The hardwood forest system is quite variable in species composition and habitat preference. Some of the component vegetation types, particularly the pine-oak-hickory woods and the coastal swamps, are transitional to other vegetational systems.

Community Organization. The vegetation appears to be well organized with pronounced vertical stratification and a variety of life forms. This organization results in several benefits, including a scarcity of fuel that could carry fire, a microclimate which ameliorates diurnal extremes, and a conservation of moisture owing to the protective canopy of the overstory.

Species Richness. The number of species present in a given stand is usually moderate to high. No single species is characteristic of all vegetation types of the hardwood forest system. Many species are restricted to one or few related types. A number of woody species are typically present. Herbaceous species are also numerous, but some of them may be represented by only a few individuals in a given stand.

Physiognomy. The most prominent stratum is the canopy formed by the overstory trees. The canopy is often closed or nearly so. The height of the canopy is variable but may exceed 30 meters in some stands. The understory may comprise a distinct stratum, or it may be continuous with the overstory. Saplings of overstory trees are usually common in the understory. Trees of small stature that rarely attain sufficient height to enter the canopy are also characteristic of many stands. The understory is often sparse in taller forests with closed canopies. It is dense in low or open forests. The ground cover consists of shrubs and herbs and may be separable into more than a single stratum. The density of the ground cover is often rather low, but it varies considerably from stand to stand.

Broadleaved hardwoods are usually the most important arboreal element; however conifers (pines, white-cedar, southern red-cedar) or cabbage palms may dominate some stands. In this respect, the hardwood forest system in the panhandle differs from hardwood forests further north. Evergreen and tardily deciduous species of hardwoods are usually present and sometimes more abundant than the deciduous hardwoods. Southern magnolia is a particularly abundant evergreen hardwood in many stands. American holly and live oak are commonly occurring species that are tardily deciduous. Outside of the southeastern coastal plain nearly all hardwoods are strictly deciduous. The tendency towards evergreenness tends to keep the ground shaded continually. The flush of spring wildflowers prior to the leafing-out of the trees, is not as pronounced in the panhandle as it is further north. The more constant shade may reduce the abundance of herbaceous plants and thus the profusion of spring wildflowers.

Soils. Hardwood forest vegetation occupies a large variety of soils. They often have well differentiated horizons and a distinct organic horizon of leaf litter and duff. Peats do not accumulate. The soil reaction is usually slightly to moderately acid.

Moisture. Hardwood forest sites vary from nearly xeric to nearly hydric. On floodplains the forests may experience inundation regularly from river overflow. The duration of inundation is usually brief, and hydroperiods are rarely prolonged.

Fire. Fires are generally uncommon to rare. When they do occur, fires often creep into a stand, burning the leaf litter which is often the only widely available fuel. Such fires kill the undergrowth, leaving an open, park-like overstory of fire-scarred trees. At other time, destructive crown fires kill nearly all trees and most other plants. Two, somewhat atypical hardwood forest types experience surface fires more frequently without suffering much damage, the pine-oak-hickory woods and the cabbage palm hammocks.

Mineral Nutrients. Hardwood forest system are generally richer in available nutrients than most other vegetation in the panhandle, particularly forests growing on alluvial soils. Nutrient cycling occurs primarily through the decomposition of detritus by invertebrate animals, fungi, and bacteria. Mycorrhizal fungi are common.

Maintenance. Root competition and the shade afforded by the closed canopy virtually preclude the survival of seedlings of most species, including those of trees in the overstory. Microsuccession occurs, though, in gaps formed by the demise of individual overstory trees. Dense thickets of woody reproduction are common in the early stages of gap succession. The trees and other plants that survive this process are not necessarily of the same species as those that occupied the site previously. As a result, the species composition and particularly the abundance of given species are fluid over a period of one or several centuries in any stand. Reproduction of most species is by seed; however, southern magnolia and some other species are capable of coppicing after being top-killed.

Response to Disturbance. Following crown fire, clear cutting, or other severe disturbance, hardwood forests are generally replaced by other hardwood forests. Replacement may not occur directly, and a seral community or two, dominated by non-arboreal species or pines, may occupy the site before hardwood dominance is asserted. The species composition and the dominant species of the new forest may be quite different than in the previous forest.

Mode of Origin. Hardwood forests typically undergo seral development. The effect of initial floristic composition on subsequent vegetation development is less pronounced in hardwood forest vegetation than in any other vegetational system in the panhandle. The displacement model is not applicable.

Ecotones. Pine-oak-hickory woods are transitional with the longleaf pine savannahs and with longleaf pine-xeric oak woods. Creek swamps and cedar swamps are transitional with acid swamps in bayheads. Some bottomland hardwood forests grade into cypress-tupelo forests. Coastal hammocks are sometimes transitional with scrubs. Tidal river swamps often grade into brackish marshes. Coastal hammocks and cabbage palm hammocks sometimes grade into slash pine flatwoods.

Hardwood forests commonly invade firelands which are kept fire-free and swamps and other aquatic habitats that are drained. Transitory communities occur in such sites and contain a mixture of the original vegetation and the invading hardwood vegetation.

Table 24 lists and compares the communities for the hardwood forest system.

TABLE 24. Conspectus of Hardwood Forest Communities.

Communities	Moisture, Soil	Fire	Salinity	Vegetation
18. Pine-Oak-Hickory	Dry-mesic, loamy	Rather frequent	None	Shortleaf pine, Spanish oak post oak, mockernut hickory
19. Mesic Hardwood Hammock 19a. Laurel Oak Woods 19b. Beech-Magnolia Hammock 19c. Mixed Hardwood Hammock	Mesic (the laurel oak woods well drained); sands or loams	Rare	None	Laurel oak, white oak, beech, southern magnolia, sweetgum, spruce pine
20. Bottomland Hardwood Forest 20a. Loblolly Pine - Hardwood Forest 20b. Mixed Bottomland Hardwood Forest 20c. Creek Swamp 20d. Cedar Swamp 20e. Point Bar Thicket	Wet-mesic to hydric, often considerable seasonal fluctuation in water table; sands loams, clays	Rare or absent	None	Loblolly pine, sweetgum, water oak, diamond-leaf oak, overcup oak, water hickory, red maple, green ash, pumpkin ash, white-cedar, sweetbay, black willow
21. Coastal Hammocks	Mesic sands with limestone or shell within root zone	Rare	Salt spray sometimes; tidal inundation in hurricanes	Live oak, southern mangolia, cabbage palm, southern red cedar, slash pine
22. Coastal Swamps 22a. Tideland Swamps 22b. Cabbage Palm Hammocks	Wet-mesic to hydric; limited seasonal fluctuation of water table; loams or peaty sands	Rare or, in cabbage palm hammocks, frequent	Salt spray sparingly; tidal inundation in hurricanes	Cabbage palm, pumpkin ash, red maple, sweetbay, blackgum, southern red cedar, loblolly pine, slash pine

15. Pine-Oak-Hickory Woods

The overstory consists primarily of shortleaf pine, Spanish oak (Quercus falcata, also called red oak), post oak, and mockernut hickory. The proportion of these species varies considerably between stands. Several other species are typically present, but usually in low densities. Sourgum and black oak are two of the most representative incidental species because they occur almost exclusively in this community. White oak and pignut hickory sometimes grow in the more moist pine-oak-hickory woods, especially where the severity of fire is minimal. The occasional presence of loblolly pine, sweetgum, water oak, and live oak in contemporary stands is probably the result of minor disturbance or of prolonged fire suppression rather than of natural processes. The canopy is usually moderately to quite tall and somewhat open, more so than most mesic hardwood hammocks on flat terrain.

The understory is absent in frequently burned stands or consists of thickets or of a continuous but sparse stratum in less frequently burned stands. The primary species are saplings of overstory species and dogwood. Blackjack oak (Quercus marilandica) is sometimes present in low numbers on drier sites and is largely restricted to pine-oak-hickory woods in the panhandle.

The ground cover is prominent and continuous. The density is inversely proportional to the density of the understory (Hodgkins 1958). Coppicing root crowns of oaks and hickories are abundant. Low shrubs are common (e.g., Ceanothus americanus, Collinsonia serotina), as are woody vines (e.g., Gelsemium sempervirens, Rhus toxicodendron, Smilax glauca, Vitis aestivalis). Grasses comprise an important floristic element (e.g., Andropogon spp., Sorghastrum spp., Schizachyrium tenerum, Tridens flavus, Dichanthelium commutatum). Many herbaceous dicots are present, primarily composites and legumes (e.g., species of Aster, Solidago, Desmodium, and Lespedeza, Amphicarpa bracteata, Clitoria mariana, Cassia nictitans, Elephantopus elatus, Kuhnia mosieri) and also species of other families (e.g., Dyschoriste oblongifolia). The total number of species is quite high and approaches that of fireland communities. Many of the species also occur in upland longleaf pinelands.

Soils are well drained sandy loams and loamy sands. Surface fires are infrequent but fairly regular. Harper (1943) suggested that the frequency of fires in prehistoric times was about once every ten years on the average.

Pine-oak-hickory woods occur in the Northern Highlands of the panhandle and extend into adjacent Georgia and Alabama. In the Piedmont and other interior provinces of the Southeast, the pine-oak-hickory woods assume a somewhat different species composition, but otherwise are similar to the pine-oak-hickory woods in the panhandle.

Agriculture and other land uses have reduced the previously extensive stands of pine-oak-hickory woods in the panhandle, and the few remnants have been largely altered by selective logging, grazing, and too much or too little burning. The best examples with which I am familiar are described in Research Summaries 20-22.

Early authors wrote that pine-oak-hickory woods covered some hills in the Northern Highlands and occupied the slopes of other hills which were capped by longleaf pine savannahs or longleaf pine-xeric oak woods. The bottomlands and ravines of these same hills contained various mesic hardwood hammocks characterized by trees such as loblolly pine, live oak, water oak, diamond-leaf oak, sweetgum, and southern magnolia. Today these species have largely replaced those of the original pine-oak-hickory forests on the uplands. Suburban Tallahassee has spread into these forests, and the larger shade trees in Tallahassee are primarily of these bottomland species rather than of Spanish and post oaks, mockernut, and sourgum.

Since the pine-oak-hickory woods are scarcely represented in the panhandle today, the following historical account is presented as a supplement to the description of the community given above.

Young (1818) was perhaps the first to describe the pine-oak-hickory woods from the Tallahassee Hills:

> "The distinguishing features of the two kinds of hills are - the oak and hickory, with a thick undergrowth of the one - and the predominance of pine, without undergrowth on the other. The pine hills [longleaf pine savannahs] are well timbered, and perfectly open, except in places where there are spots overgrown with low, scrubby oak bushes [longleaf pine-xeric oak woods]. But the fertile hills called high-hammock-land [pine-oak-hickory woods], have a very mixed growth of forest trees, and are generally covered with a various growth of vines, shrubs and bushes. The thickets in this part prevent the luxurient growth of grass, and on the score of pasturage, being always covered with a dense herbage, which by frequent burning affords the most nutritious food for cattle....

"It has already been mentioned that the fertile upland is called hammockland, what the name is taken from could not be ascertained, but it is always approximated to two kinds of soil - the one high with growth of oak, hickory and thicket [pine-oak-hickory woods] - the other, low, but dry, with a growth of bay, oak, large magnolia, beech, laurel, etc., with a variety of vines and other undergrowth [various bottomland hammock communities]. The high hammock is almost always fertile. The low has often too much sand as is seen at Sahwannee."

Williams (1823) described the area now occupied by Lake Seminole as containing timber principally of oaks, hickories, dogwood, tulip-poplar, and sourgum. His accompanying species list included those from pine-oak-hickory woods and from bottomland hammocks.

Vignoles (1823) explored the Tallahassee Hills and wrote that the oak and hickory,

"...lands produce almost exclusively those two kinds of forest trees, with occasional gigantic pines: the underbrush is generally composed of sucker saplings of the oak and hickory; this description of land is generally disposed on the exterior edges of the high hammocks and separate them from the pine lands."

This statement inferred that the pine-oak-hickory woods served as a buffer between the longleaf pinelands and the other hammock lands. The frequent fires in the longleaf pinelands burned into the pine-oak-hickory woods, causing the coppicing (suckering) of the oaks and hickories, but did not continue into the hammocks containing less fire-tolerant trees.

Smith (1884) described the natural vegetation on the brown loam lands of Leon and Jefferson counties:

> "The timber comprises the usual varieties of upland oaks, such as post, red, and Spanish, with blackjack [Q. laevis?] on the poor spots and hickory, shortleaf pine, with sweetgum, along the slopes and in the valleys. As this class of soil grades into the sandier varieties, so the shortleaf pine and upland oaks are gradually replaced by longleaf pine and blackjack, there being all gradations between the pure oak and hickory uplands and the genuine pine woods."

Smith's description reiterated the observation that pine-oak-hickory woods separated longleaf pinelands from moist hammocks. He also showed that the pine-oak-hickory woods intergraded with longleaf pinelands.

Smith (1884) restated this observation while describing longleaf pinelands:

> "In this subdivision are included all those high pinelands which usually skirt the oak uplands, or which rather occupy the ridges separating the oak upland areas from each other."

He said that the pine-oak-hickory lands and the longleaf pine ridges occupied about equal areas in Leon and Jefferson counties. Tucker and Grantham (in Smith 1884) said that these pinelands occurred in irregular bodies over northern Jefferson County and generally occupied the higher lands, separating areas of oak uplands.

Mohr (1901) described similar vegetation for Alabama:

> "The highest ridges are capped with siliceous deposits, where the shortleaf pine mingles with the hardwood trees, while the

longleaf pine makes its appearance on the most abrupt of their summits."

Harper (1943) later described the hills in southeastern Alabama as having longleaf pine on the sandy hill tops. The redder soils of the dry uplands had shortleaf pine, blackjack oak, red oak, post oak, black oak, and hickory. He said:

"The mixed forests of shortleaf pines and oaks on dry uplands have a good deal of grassy undergrowth and we may guess that in prehictoric times they were burned over about once every 10 years on the average."

Jones (1907), Bennett and Mann (1909), and Harper (1914) all wrote of the forests of shortleaf pine, oaks, hickory, and dogwood in the uplands of the Tallahassee Hills. Absent from their descriptions was mention of loblolly pine, water oak, and diamond-leaf oak.

The first authors to write of a more mixed forest on the uplands of the Tallahassee Hills which contained these bottomland hardwoods and the trees typical of pine-oak-hickory woods were Gano (1917) and Kurz (1944). Kurz recognized the pine-oak-hickory woods as an indefinitely arrested successional forest which would develop eventually into a beech-magnolia hammock in the absence of fire, assuming no logging or grazing. He described his pine-oak-hickory association as containing shortleaf pine, Spanish oak, post oak, black oak, and mockernut hickory, and also included two species typical of other communities, diamond-leaf oak and water oak. He also noted the abundance of grasses and coppicing hardwoods in the undergrowth.

Golden (1979) described pine-oak-hickory vegetation from the lower Piedmont of east-central Alabama. Quantitative descriptions and species lists were prepared for two segregate types, a mixed oak-hickory forest and an oak-pine forest. A discussion of the pine-oak-hickory woods in Leon County was written by Clewell (in press). In this paper is a map of northern Leon County showing the distribution of pinelands and pine-oak-hickory woods in 1824, based on the copious botanical notes of land surveyors. This map is presented here as Figure 42. The pine-oak-hickory woods were concentrated in areas that were once occupied by large populations of Apalachee Indians. These areas were near lakes and along the Cody Scarp. The Apalachees may have caused the conversion of longleaf pinelands to pine-oak-hickory woods through their agricultural practices or through other land use which reduced the frequency of fire. Evidence is presented in Research Summary 23 that a reduction in fire can initiate such a conversion.

Turner (1935) observed that nearly pure stands of even-aged shortleaf pine developed in Arkansas following the destruction of pine-oak-hickory woods by tornadoes. Such stands were called "hurricane forests" locally.

19. Mesic Hardwood Hammocks

The trees and shrubs characteristic of mesic hardwood hammocks are listed in Table 25. Representative vines and herbs are listed in Table 26. The overstory of a given stand generally consists of 5-12 species. The understory consists of saplings of overstory species and usually of several small trees that rarely if ever attain overstory status. The ground cover

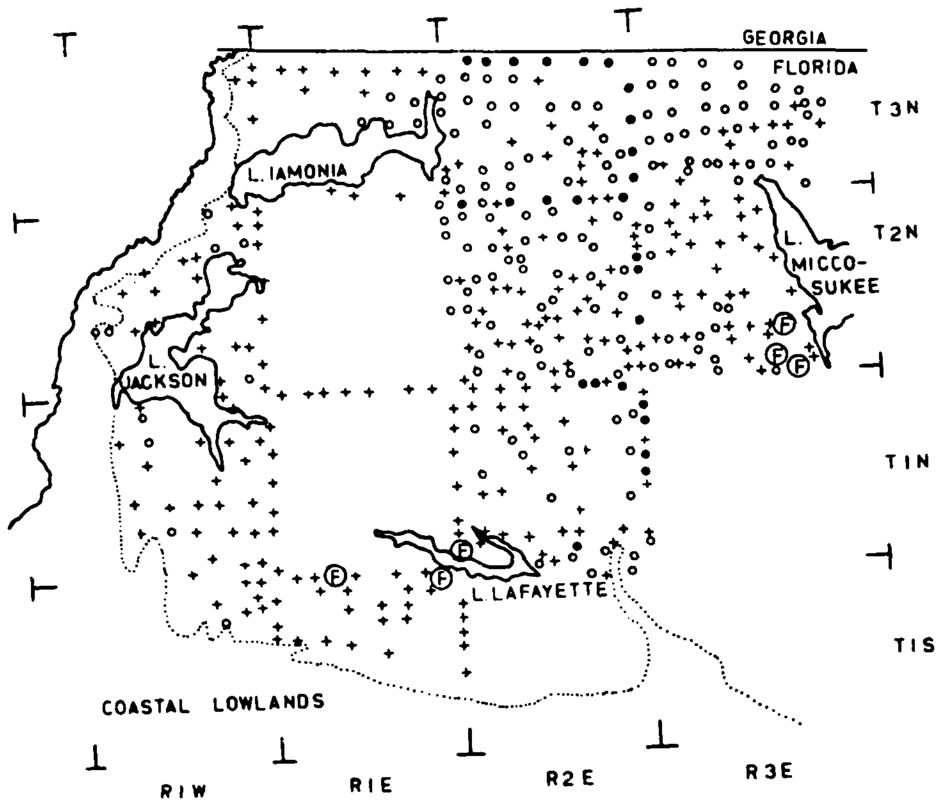

Figure 42. Vegetation of Leon County above the Cody Scarp (dotted line) in 1824, based on surveyors' field notes. Solid dot - longleaf pineland; open circle - pineland, the species unknown; plus sign - pine-oak-hickory woods; circled letter F - recent Indian agricultural field.

TABLE 25. Most Trees and Shrubs of Mesic Hardwood Hammocks.

OVERSTORY TREES

Acer saccharum
Carya glabra
Carya pallida
Carya tomentosa
Fagus grandifolia
Fraxinus americana
Liquidambar styraciflua
Liriodendron tulipifera
Magnolia grandiflora
Magnolia virginiana
Morus rubra
Nyssa sylvatica
Oxydendron arboreum
Pinus glabra
Pinus taeda
Prunus serotina
Quercus alba
Quercus austrina
Quercus falcata
Quercus hemisphaerica
Quercus laurifolia
Quercus michauxii
Quercus muhlenbergia
Quercus shumardii
Quercus stellata
Quercus velutina
Quercus virginiana
Sabal palmetto
Sassafras albidum
Tilia caroliniana
Tilia heterophylla
Ulmus alata
Ulmus americana
Ulmus rubra

UNDERSTORY TREES AND SHRUBS

Aesculus pavia
Amelanchier arborea
Aralia spinosa
Asimina triloba
Asimina parviflora
Bumelia lanuginosa
Bumelia lycioides
Bumelia reclinata
Callicarpa americana
Carpinus caroliniana
Celtis occidentalis
Celtis tenuifolia
Chionanthus virginica
Cornus florida
Crataegus plucherrima
Crataegus marshallii
Crataegus spathulata
Crataegus uniflora
Diospyros virginiana
Dirca palustris
Euonymus americanus
Forestiera acuminata
Forestiera ligustrina
Halesia diptera
Halesia tetraptera
Hamamelis virginiana
Hydrangia quercifolia
Ilex decidua
Ilex longipes
Ilex opaca
Ilex vomitoria
Juniperus silicicola
Kalmia latifolia
Linderna benzoin
Magnolia ashei
Mangolia pyramidata
Malus angustifolius
Myrica cerifera
Osmanthus americana
Ostrya virginiana
Persea borbonia
Prunus caroliniana
Ptelea trifoliata
Rhamnus caroliniana
Rhapidophyllum hystrix
Rhododendron austrinum
Sebastiana fruticosa
Staphylea trifolia
Stewartia malacodendron
Styrax grandifolia
Symplocos tinctoria
Taxus floridana
Torreya taxifolia
Vaccineum arboreum
Vaccinium elliottii
Viburnum acerifolium
Viburnum dentatum
Viburnum rufidulum

TABLE 26. Representative Herbs and Woody Vines of Mesic Hardwood Hammocks.

WOODY VINES

Ampelopsis arborea
Bignonia capreolata
Decumaria barbata
Gelsemium sempervirens
Parthenocissus quinquefolia
Smilax bona-nox
Smilax tamnoides
Smilax smallii
Toxicodendron radicans
Vitis aestivalis
Vitis rotundifolia
Vitis vulpina

HERBS

Agrimonia microcarpa
Apios americana
Aquilegia canadensis
Arisaema dracontium
Arisaema triphyllum
Aristolochia serpentaria
Asplenium platyneuron
Aster sagittifolius
Aster vimineus
Boehmeria cylindrica
Botrychium dissectum
Botrychium virginianum
Carex crebriflora
Carex floridana
Chasmanthium latifolium
Chasmanthium laxum
Chasmanthium sessiliflorum
Clematis catesbyana
Conopholis americana
Desmodium glutinosum
Desmodium laevigatum
Desmodium nudiflorum
Dichanthelium commutatum
Dicliptera halei
Dioscorea quaternata
Elephantopus carolinianus
Epifagus virginiana
Galium aparine
Galium circaezans
Galium pilosum
Galium tinctorium
Hexastylis arifolia
Lobelia puberula
Matelea gonocarpa
Mitchella repens
Monotropa uniflora
Oplismenus setarius
Panicum anceps
Passiflora lutea
Phaseolus polystachios
Phlox carolina
Phryma leptostachya
Polystichum acrostichoides
Ruellia caroliniensis
Sanguinaria canadensis
Sanicula canadensis
Sanicula marilandica
Senecio obovatus
Smilax lasioneuron
Solidago arguta
Solidago auriculata
Solidago brachyphylla
Solidago caesia
Solidago discoidea
Spigelia marilandica
Thelypteris normalis
Thelypteris ovata
Thelypteris quadrangularis
Tipularia discolor
Trillium underwoodii
Uvularia perfoliata
Viola floridana
Viola sororia
Viola triloba

is sparse, and only a few species of herbs are plentiful in most stands.

The species composition and the patterns of dominance are quite variable between stands. Three segregate vegetation types are recognizable, 19a) Laurel Oak Woods, 19b) Beech-Magnolia Hammocks, and 19c) Mixed Hardwood Hammocks.

The laurel oak woods occupy drier habitats, especially the upper portions of bluffs and well drained uplands which have been kept fire-free and undisturbed for several decades. Laurel oak (*Quercus hemisphaerica*) is often the most important species in the overstory. Other common species include mockernut hickory, sourgum, Spanish oak, post-oak, black oak, live oak, and in the understory dogwood, dwarf-thorn (*Crataegus uniflora*), crab-apple, and sparkleberry. Except for the prominance of laurel oak, this woods is scarcely distinguishable from pine-oak-hickory woods. The latter, though, experiences regular fires, contains a more prominent ground cover, and tends to occupy slightly drier sites.

The beech-magnolia hammocks are dominated by American beech and southern magnolia. They often represent more than half of the density and basal area of the overstory trees. Sweetgum is usually prominent among the other overstory species. American holly is conspicuous in the understory. Beech-magnolia hammocks occupy rather moist sites on the lower portions of bluffs and ravines. These hammocks are common in the Tallahassee Hills where fires and land use have been minimal and soil moisture adequate.

The mixed hardwood hammocks constitute all other combinations of mesic hardwood hammock vegetation. One of the many floristic elements comprising this mixed hardwood hammock assemblage is a forest dominated largely by white oak. This assemblage often forms a narrow zone on bluffs between the laurel oak woods and the beech-magnolia hammocks. Other floristic assemblages occupy lower slopes on bluffs and well drained levees on floodplains. These forests often intergrade with bottomland hardwood forests.

Some woody species are short-lived and grow in disturbed sites or in gaps created by the demise of an overstory tree. Sassafras, persimmon, and devil's-walking stick (Aralia spinosa) are examples. Spruce pine also appears to be opportunistic (see page 258-259) but often persists as an overstory dominant. It grows rapidly in diameter but rarely attains the girth of old-growth loblolly and slash pines, suggesting that it is relatively short-lived.

The ground cover is disappointing to observers who are used to the spectacular display of wildflowers in the Appalachians and elsewhere in the eastern deciduous forest region. The hammocks in the Marianna Lowlands and the bluffs of the Apalachicola River area are exceptions and contain a more pronounced display of herbs. Many of the common wildflowers of more northerly areas reach their southern limits of distribution in these two areas (Kurz 1933). Table 26 could be lengthened considerably if some of these species were added to it.

Many extant mesic hardwood hammocks have developed as a result of fire suppression in pinelands or from secondary succession on formerly disturbed or cleared lands. Harper (1911) was the first to point out the relationship between hardwood hammocks and the lack of fire. Harper (1914), Monk (1960), and Veno (1976) all gave examples of dry longleaf pinelands or scrubs in various stages of conversion to hammocks in the absence of fire. Quarterman and Keever (1962) studied 93 mesic upland stands on the coastal plain from South Carolina to eastern Texas and showed the results of the conversion of natural and old field pinelands to hammocks.

The reproductive abilities of southern magnolia and beech have been a topic of comment by several authors. Kurz (1944) said that these were the most shade tolerant trees of hammocks. He continued,

> "I have seen no perpetuation of either magnolia or beech in a closed mature magnolia-beech climax, and all my observations indicate that a new start must be made under trees that are not magnolias or beeches."

Reproduction in magnolia was already discussed in Chapter 22. Observations by Doren (in Blaisdell et al. 1973) yielded some insight into reproduction by beech. After a wildfire through a mature hammock, the litter and undergrowth had been removed, but the overstory trees only suffered fire scarring. Large numbers of beech seedlings soon appeared. Doren inventoried this crop of seedlings four growing seasons after the seed fall following the fire. There were up to 4.1 four-year-old beech seedlings per m^2. In two other hammocks, both unburned, there was about one beech seedling per acre. Doren concluded that fire either prepared an adequate seed bed or that fire stimulated an extraordinarily heavy seed crop, more seeds than could be consumed by the animals present. It appears that beech can either reproduce under its own cover following surface fires or that it must reproduce in competition with the seedlings of other tree species in gap succession.

It is the common opinion that mesic hardwood hammocks represent a climax community. The generalized composition of this community as it occurs in northern peninsular Florida was presented by Monk (1965, 1967, 1968), based on data compiled from the study of many diverse stands. Quarterman and Keever (1962) made a similar compilation for much of the southeastern coastal plain.

Research Summaries 24-30 describe several stands. Beech-magnolia hammocks are characterized in Research Summary 24. Mixed hardwood hammocks are characterized in Research Summaries 25 and 29. Mesic hammock zonation is shown for bluffs and ravines in Research Summaries 26, 27, and 30. Hammock vegetation is described within a sinkhole in Research Summary 28.

Several other publications provide additional descriptions of mesic hardwood hammocks. Harper (1925) listed the major species and qualitatively described a hammock on a slope of Lake Miccosukee in Jefferson County. *Ribes echinellum* was discovered there and is known otherwise from one other location in South Carolina. A mixed hardwood hammock in Alachua County was studied thoroughly by several investigators. Lugo *et al*. (1971) estimated the biomass of the leaves, wood, roots, litter, and the organic matter of the soil. The amount of chlorophyll *a* was estimated from a vertical profile (Lugo *et al*. 1973). The meteorological input of mineral nutrients was estimated by Ewell *et al*. (1975). Golley *et al*. (1965) described a mixed hammock in South Carolina.

An inordinate amount of effort has gone into the study of mesic hardwood hammocks in Florida and adjacent regions. A principal rationale for much of this effort has been to prove that this community is the climax community on the coastal plain. It is unfortunate that a community that occupies such a small total area has attracted so much attention, particularly since other communities still await an adequate qualitative description.

The habitats of many mesic hammocks are sometimes called calcareous, referring to the proximity of limestone to the soil surface or merely to clayey soils that have more calcium than sandy soils. Calcareous hammocks are common along spring-fed rivers, on the sides of sinks, and on bluffs near limestone outcroppings. Calcium-loving species are present in such habitats and include cabbage palm, southern red cedar, and redbud.

20. Bottomland Hardwood Forests

Bottomland hardwood forests occupy wet-mesic to nearly hydric habitats that are usually but not always associated with the floodplains of permanent streams and rivers. Habitats of these forests are generally subjected to shallow inundation, sometimes briefly and irregularly or sometimes for prolonged periods annually. In dry seasons, the root zone of the soil is often well aerated. Soils range from coarse sand to clay. Habitats occupied by this forest are quite variable, owing to differences in the hydrological regime, the substrate, and perhaps water quality (tannic, spring-fed, etc.).

Floristic variability parallels the variability in habitats and considerably exceeds the floristic variability of mesic hardwood hammocks. Table 27 lists most of the trees and some of the shrubs of bottomland hardwood forests. Research Summaries 32 and 35 list some of the woody vines and herbs. The diversity of herbaceous species is very high for

TABLE 27. Most Trees and Some Shrubs of Bottomland Hardwood Forests.

Acer negundo	Itea virginica
Acer rubrum	Juglans nigra
Acer saccharinum	Juniperus silicola
Alnus serrulata	Kalmia latifolia
Arundinaria gigantea	Leucothoe racemosa
Baccharis glomeruliflora	Liquidambar styraciflua
Betula nigra	Liriodendron tulipifera
Callicarpa americana	Magnolia virginiana
Carpinus caroliniana	Morus rubra
Carya aquatica	Myrica cerifera
Carya cordiformis	Nyssa aquatica
Catalpa bignonioides	Nyssa biflora
Celtis laevigata	Nyssa ogeche
Cephalanthus occidentalis	Osmanthus americanus
Chamaecyparis henryae	Ostrya virginiana
Chionanthus virginicus	Persea palustris
Cornus amomum	Pinckneya bractaeta
Cornus foemina	Pinus taeda
Crataegus aestivalis	Planera aquatica
Crataegus crusgalli	Platanus occidentalis
Crataegus marshallii	Populus deltoides
Crataegus spathulata	Populus heterophylla
Crataegus viridis	Quercus laurifolia
Cyrilla racemiflora	Quercus lyrata
Diospyros virginiana	Quercus nigra
Forestiera acuminata	Quercus michauxii
Fraxinus caroliniana	Quercus phellos
Fraxinus pauciflora	Quercus virginiana
Fraxinus pennsylvanica	Sabal palmetto
Fraxinus profunda	Sabal minor
Gleditsia aquatica	Salix caroliniana
Halesia diptera	Salix nigra
Halesia tetraptera	Styrax americana
Hamamelis virginiana	Styrax grandifolia
Hypericum galioides	Symplocos tinctoria
Ilex amelanchier	Taxodium distichum
Ilex cassine	Ulmus alata
Ilex decidua	Ulmus americana
Ilex opaca	Ulmus rubra
Ilex verticillata	Viburnum dentatum
Ilex vomitoria	Viburnum nudum
Illicium floridanum	Viburnum obovatum

Other trees and shrubs typical of mesic hardwood hammocks and bay swamps sometimes occur in bottomland hardwood forests, especially in transition zones.

the community and quite variable between and within habitat types. The ground cover ranges from sparse to dense, depending to a large extent on the density of the woody cover. Floodplains which are flooded and devoid of herbs part of the year may attain a lush herbaceous stratum during periods of low river stage.

Several segregate vegetation types are recognized, although they exhibit considerable inter-stand variability and intergradation between types. They are, 20a) Loblolly Pine-Hardwood Forest, 20b) Mixed Bottomland Hardwood Forest, 20c) Creek Swamp, 20d) Cedar Swamp, and 20e) Point Bar Thickets. In addition, river bank vegetation is often distinctive, but its lack of width and its exceedingly variable floristic composition prevent this vegetation from being recognized as a segregate vegetation type.

The Loblolly Pine-Hardwood Forest consists of loblolly pine and several hardwoods, with sweetgum and water oak commonly among the dominants. This forest occupies better drained sites that are not subject to annual inundation. A common location of this forest is along larger rivers where gentle slopes (rather than bluffs) lead gradually to the upland. The loblolly pine-hardwood forest lies next to the upland vegetation which is typically a fireland community.

Clear-cut areas on the floodplain of the Apalachicola River generally are invaded by loblolly pines and sweetgum, even though other species may have been more prevalent previously. Such stands may be successional to a more diverse forest that would develop later. The woody species of the loblolly pine-hardwood forest have become abundant on the uplands in the Northern Highlands province following the cessation of agriculture and the suppression of fire early in this century.

The Mixed Bottomland Hardwood Forest is the major community on alluvial floodplains and is quite variable but diverse in arboreal composition. In a major study currently being conducted on the floodplain of the Apalachicola River, H. M. Leitman (personal communication 1980) is recognizing three variants of the mixed bottomland forest type. The first variant occupies the wetter sites and consists of a forest in which at least 50% of the basal area is contributed by the following species: water-tupelo, ogeche-tupelo, blackgum, bald-cypress, popash, and planer-tree. The other trees belong to any other species of bottomland forests. The second variant occurs in less wet habitats and is composed of a forest in which at least 50% of the basal area is contributed by water hickory, green ash, overcup oak, and diamond-leaf oak. The third variant occupies even better drained habitats, and at least 50% of the basal area is contributed by sweetgum, water oak, hackberry, ironwood, and possum-haw. Absent from these forest variants is the overcup oak-water hickory community which is well defined in the Mississippi River area but which does not extend as far east as the Florida panhandle.

Other species that are common in the mixed bottomland hardwood forests are red maple, water locust, sycamore, swamp cottonwood, swamp-chestnut oak, willow oak, and American elm. Research Summaries 30 and 32 describe mixed bottomland hardwood forests from the Apalachicola River floodplain, and Research Summary 33 describes another from the St. Marks River. Research Summaries 34 and 35 describe this forest type from spring-fed rivers (Wacissa, St. Marks). The prevalence of pumpkin ash in these latter two stands is probably related to the habitat conditions of these swamps, which are characterized by being calcareous and by having constant water levels.

Creek swamps occupy largely colluvial floodplains bordering small perennial streams. Creek swamps may continue downstream where alluvial deposition is evident but not extensive. The forest composition is a combination of mixed bottomland hardwood forest species and species from bay swamps. These small streams typically terminate in a bayhead. If white cedar is conspicuous, then the creek swamp is termed a cedar swamp. Research Summary 31 describes a creek swamp along Bear Creek, which is dominated by sweetbay but is otherwise characterized by species more typical of alluvial habitats. A forest at the bridge of S.R. 4 and Sweetwater Creek (Santa Rosa County) displays a more balanced combination of mixed bottomland and bay swamp species. This stand is dominated by white-cedar, a species which is largely confined to creek swamps. The other common overstory species are typical of more alluvial habitats forested by mixed bottomland hardwoods: water oak, diamond-leaf oak, loblolly pine, and red maple. Other species common in bay swamps are abundant in undergrowth: swamp cyrilla, black titi, sweetbay, swamp bay, large gallberry, Myrica heterophylla, and Leucothoe axillaris.

Most of the forest along the Blackwater River is a cedar swamp. White-cedar is the dominant overstory tree on the levees for most of the length of the river. American holly dominates the understory. Other common trees are water oak, live oak, southern magnolia, swamp bay, loblolly pine, and swamp cyrilla.

Point bar thickets occupy sandy aggrading point bars on the outside curves of alluvial rivers. Black willow (or Carolina willow in the eastern panhandle)is often the only tree species. On the Apalachicola River some point bars contain black willows nearest the river, cottonwoods (Populus deltoides) behind the willows, and sycamores behind the cottonwoods. The large ascending trunks of willows often recline with age or break at the base. They become partially or entirely buried with newly deposited sands and sprout new branches from the trunks. Vegetative reproduction is thereby accomplished, quickly colonizing the expanding tip of the point bar. Willows and cottonwood are shade intolerant (Maisenhelder 1958) and are rare in the interior of the floodplain. Willows are further restricted to habitats where their seedlings experience moist or wet soils (McLeod and McPherson 1973).

Typical species of river banks include hazel alder, river birch, silver maple, ogeche tupelo, planer-tree, willow, bald-cypress, and flase-indigo (Amorpha fruticosa). None of these species is ubiquitous or even common along most rivers. River birch is abundant on the Apalachicola River but only above Ft. Gadsden. It is common along the Withlacoochee River but not the physiographically similar Suwannee River into which it flows. Ogeche tupelo is common on the banks of the Apalachicola River below the Chipola Cutoff, abundant along the Suwannee River, but uncommon along the Withlacoochee River. Black willow is common along the Ochlockonee and many other rivers, but rare along the Blackwater River. These inconsistencies in river bank vegetation are apparent when observed from a canoe.

Local disruptions in bottomland hardwood forests are caused frequently by the activities of beavers. Water is ponded behind beaver dams on floodplains and along creeks, causing many trees to die or be stressed from lack of aeration of the soil. Smaller trees are severed by the beavers. The forest canopy may become sparse over these ponds, allowing light to penetrate which stimulates the development of a marsh (Wharton 1977).

Kurz (1938) gave a brief description of the floodplain and bluff communities of the Apalachicola River and included lists of typical species. These descriptions apply primarily to the east side of the river above Bristol where the bluffs occur. Monk (1966) characterized the deciduous hardwood swamps in northern peninsular Florida by presenting average importance values of trees from 23 stands. Soil nutrient data were given and correlated with tree species. Gemborys and Hodgkins (1971) inventoried 49 creek swamps in southern Alabama near Pensacola. They did not describe communities but rather determined the relative position of each woody species along a moisture gradient.

Excellent descriptions and photographs of bottomland hardwood forests in the Southeast were provided by Putnam et al. (1960). Principal tree species were compared with regard to growth rates, tolerance to competition, seed bed requirements, susceptibility to fire, habitat preferences, and other criteria.

21. *Coastal Hammocks*

Coastal hammocks are mesic hardwood forests near the coast. They are usually subjected regularly to salt spray and/or to overwash during hurricanes. The overstory is variable in composition but almost invariably contains live oak (*Quercus virginiana*) as a dominant or at least as a conspicuous tree. Southern magnolia is the most important tree in some stands and is absent from other stands. Southern red cedar is usually present, although it has yet to recover its former prominance prior to its exploitation by pencil manufacturers. Saw mill operators virtually eliminated all merchantable red cedar trees which once dominated extensive stands along the coast of the eastern panhandle (Garber 1877, Harper 1912, 1921). Slash pines are often present as isolated individuals or in groves. Other overstory trees occasionally include pignut hickory, laurel oak and red mulberry. In moist sites, cabbage palm and sweetbay may assume dominance, and American elm and red maple may be common.

Understory trees and shrubs typically include yaupon (*Ilex vomitoria*) and wax-myrtle (*Myrica cerifera*). Other common species may include red bay, wild olive (*Osmanthus americanus*), black-haw (*Bumelia lanuginosa*), saw-palmetto, American holly, and Hercules'-club (*Zanthoxyllum clava-herculis*). Poison-ivy is among the most common woody vines. Herbs are rather sparse or at least unimportant in comparison to the woody element of the flora. St. Augustine-grass (*Stenotaphrum secundatum*) is often present and is indigenous only in coastal hammocks. Two other species which are rather commonly observed in coastal hammocks are *Galium hispidulum* and *Vicia acutifolia*.

Coastal hammocks often occur next to scrubs, with which they may intergrade. As a result, several shrubs and trees of scrubs occur on the edges of some coastal hammocks and include sand-live oak, myrtle oak, Chapman oak, fetterbush, and staggerbush.

Coastal hammocks commonly border tidal marshes and coastal sloughs. Such hammocks may occur as narrow strands on protected beaches or as extensive forests in the Gulf Hammock region of the eastern panhandle. Coastal hammocks also occur in dune fields on barrier islands and on shell middens.

The habitats of coastal hammocks share two features, besides subjection to saline conditions. First, they are largely protected from fire, although multiple trunks in some stands suggests fire may not always be absent. Second, limestone or shells occur within the root zone. Degradation of these calcareous materials has been thought responsible for increased nutrient availability (Ca, Mg, P, K) in the otherwise nutrient-deficient sands (Norman 1976). Calciphilous species are favored, including southern red cedar, cabbage palm, and yaupon. Live oak may be favored over sand-live oak because of this nutrient availability (Kurz 1942). Tesar (1973) inventoried the archeological sites in the western panhandle for the Gulf Islands National Seashore. He said (personal communication 1976) that coastal hardwood hammocks invariably occurred where shell middens, deposited by Indians, were shallowly covered by sand.

Shell middens are curious botanically for their diversity of species, including many tropical species that reach their northernmost limits of distribution on coastal middens in Florida. Soapberry (Sapindus marginatus) is known no further north than St. Vincent's Island in Franklin County, where it grows in a coastal hammock on the extensive middens along the northeastern shore. Eleocharis interstincta grows abundantly in an adjacent swale and is otherwise known from southern peninsular Florida. Small (1928) attributed such range extensions to Indians who may have planted useful tropical species at their settlements. Norman (1976) alternatively suggested that such species are continually being introduced by long distance dispersal and that shell middens offer the only suitable coastal habitats available for colonization by calciphilous plants. Curtiss (1879) described the vegetation on the middens in the mouth of the St. Johns River and elaborated on the hardships suffered during the exploration. Coastal hammocks occur on isolated dunes on Santa Rosa Island. One such dune was visited in 1977 west of Navarre Beach. The partially buried overstory trees were southern magnolia (up to 40 cm in dbh), southern red cedar, and live oak with a few slash pines on the edges. This tall dune was the only prominent topographic feature in an extensive low dune field dominated by a sparse coastal scrub community. It was apparent that the dune formed as drifting sands were arrested by the trees. According to the aforementioned comments by Tesar, the trees were present because Indians created a shell midden there.

Shrubs at the Santa Rosa site were beauty-berry, yaupon, black-haw, laurel cherry, winged sumac, persimmon, wax-myrtle, saw-palmetto, and cabbage palm. Vines were poison-ivy, Virginia creeper, Vitis rotundifolia, Ampelopsis arborea, and Smilax bona-nox. Erythrina herbacea and Pteridium aquilinum were the only herbs of note, except for the epiphytic Polypodium polypodioides.

Another coastal hammock occurs on a midden on Hog Island at the mouth of the Suwannee River. The trees and shrubs that were seen on a visit in 1976 were soapberry, sweetbay, cabbage palm, red mulberry, pignut hickory, southern red cedar, live oak, laurel oak, yaupon, Hercules'-club, beauty-berry, laurel cherry, red bay, saw-palmetto, and Walter viburnum (Viburnum obovatum). Other species were Vitis rotundifolia, Smilax bona-nox, and Galactia spp.

Kurz (1942) described coastal hammocks dominated by southern magnolia at Lanark and Carrabelle in Franklin County. Other species in these hammocks were sand-live oak, pignut hickory, laurel oak, Chapman oak, American holly, wild-olive, staggerbush, fetterbush, saw-palmetto, and beauty-berry He considered southern magnolia, rather than live oak, to be the dominant tree of the coastal climax community represented by these stands. Research Summary 36 describes a similar coastal hammock on St. George Island.

Penfound and O'Neill (1934) described a fire-free live oak-dominated forest on a barrier island in Mississippi and considered it a climax. Wells (1939) described a live oak forest at Cape Fear, North Carolina, and called it a salt spray climax. He wrote that this forest differed from climax forests inland because salt spray allowed the survival of only a limited number of tree species. A few cabbage palms grew with the live oaks, and red cedar (Juniperus virginiana) was once common before being logged. The undergrowth included much American holly, also tree-sparkleberry, wax-myrtle, yaupon, wild-olive, red bay, dogwood, laurel cherry, and beauty-berry. Wells suggested a sere beginning with sea-oats, continuing with a woodland of red cedar, yaupon, and wax-myrtle, and ending with live oak.

Oosting (1954) reviewed the literature on southeastern coastal vegetation and briefly described coastal hammocks.

Laessle and Monk (1961) described eight hammocks dominated by live oak in northeastern Florida. Three of these hammocks were near the Atlantic coast, and the oaks exhibited the typical sheared appearance from salt spray. The others were inland stands which resembled coastal hammocks but which were really artifactual communities developing in response to prolonged fire suppression. The habitats were formerly scrubs, sandhills, and scrubby flatwoods. Both coastal and inland stands owed their existence to the absence of fire. Cabbage palm and yaupon were common in the stands along the coast and were thought to be stimulated by the calcium released by the decomposition of coquina shells.

22. *Coastal Swamps*

Coastal swamps occur along floodplains of rivers within the zone of tidal influence and along the inland margins of tidal marshes. These regions are subject to salt water inundation and moderate or heavy salt spray during hurricanes. Otherwise, fresh water conditions prevail. Elevations near sea level cause water tables to be near the soil surface constantly. The proximity to the coast causes the rapid dissipation of flood waters and negates the possibility of deep or prolonged flooding at times of river overflow.

Table 28 lists many of the trees and shrubs that have been observed in coastal swamps. This list is not as long as those presented earlier for other hardwood forest communities. The paucity of species is not for want of nutrients, which are present at high levels. These nutrients are transported in river water, or they are released as limestone and shell degrades in the root zone. Occasional salinity shock may prevent the occurrence of some species. The rather uniform hydrological conditions may discourage other species which prefer more seasonally variable moisture regimes.

TABLE 28. Common Trees and Shrubs of Coastal Swamps.

OVERSTORY TREES	
Acer rubrum	Persea palustris
Celtis laevigata	Pinus elliottii
Fraxinus caroliniana	Pinus taeda
Fraxinus profunda	Quercus laurifolia
Juniperus silicicola	Quercus virginiana
Liquidambar sytraciflua	Sabal palmetto
Magnolia grandiflora	Taxodium ascendens
Magnolia virginiana	Taxodium distichum
Morus rubra	Ulmus americana
Nyssa biflora	
UNDERSTORY TREES AND SHRUBS	
Alnus serrulata	Ilex vomitoria
Baccharis halimifolia	Leitneria floridana
Cephalanthus occidentalis	Myrica cerifera
Cornus foemina	Sesbania punicea
Forestiera acuminata	

The species in Table 28 are a curious combination of those from coastal hammocks, mixed bottomland hardwood forests, and bay swamps. Coastal swamps intergrade with the first two communities. The presence of species common in bay swamps might be fostered by the constant soil moisture conditions which mimic those of seepages and back swamps on floodplains and in ravines where bayhead species are common. The abundance of bay swamp trees could also be in response to high tannin concentrations in river water. The arboreal composition of coastal swamps of the Suwannee River (described later) could be explained by tannic waters.

A conspicuous species which is commonly present and sometimes dominant in coastal hammocks is cabbage palm. It is favored by the calcareous soils and its ability to tolerate saline conditions and high winds. On the boundary between tidal marshes and coastal hammocks, cabbage palms often form pure thickets. These thickets probably lack other arboreal species because of relatively frequent salinity shocks and also fire. Fires in tidal marshes burn into these hammocks with some frequency, likely killing trees of most species but not the highly fire-tolerant cabbage palms.

Cabbage palms help give a floristic continuity to the coastal swamps, which otherwise consist of whatever hardwoods might be in the vicinity that can tolerate moist soils and occasional salinity shocks. The cabbage palm hammocks are quite distinctive and are hereby recognized as a variant of the coastal hammock community. Two variants are distinguished, 22a) Tideland Swamps which include any mainly hardwood assemblages, and 22b) Cabbage Palm Hammocks which are dominated by that species. Since cabbage palms are not hardwoods, it can be argued easily that cabbage palm swamps should be assigned to another system. None of the systems recognized in this work is more appropriate than that of hardwood forests. The only option would be to describe a new vegetational system for this minor vegetation type. Since a primary rationale of the present classification is to show relationships rather than differences between vegetation types, cabbage palm hammocks are assigned, albeit somewhat uncomfortably, to the coastal swamp community of the hardwood forest system.

The importance of salinity shock was discussed by Little et al. (1958) who studied the effects of a hurricane in 1954 along the coast of Maryland. They mentioned that salt spray seldom kills healthy forest trees. The 1954 storm caused an extremely high tide that traveled inland and became trapped in topographic depressions. The total deposits in these low spots may have exceeded 9,000 pounds of salt per acre, most of which had not leached below the root zone eight months later. Hardwoods, particularly sweetgum, were soon killed by the accumulation, but loblolly pines were less susceptible than the hardwoods.

Research Summary 37 documents the tideland swamps in the Gulf Hammock lands bordering the tidal marshes in the eastern portion of the St. Marks National Wildlife Refuge.

The coastal swamps of the Apalachicola River delta were explored between the railroad tressle and the causeway of U.S. 98 in 1978. Most of this region is tidal marsh. The low levees, though, contained shrubby thickets of *Sesbania punicea*, primarily, with lesser amounts of corkwood (*Leitneria floridana*) and buttonbush. The higher levees, which are much lower than those up river, contained a dense forest with trees mostly 12-22 m tall. Although measurements were not taken, these trees appeared to have relatively large diameters for their heights. The overstory consisted of red maple, sweetbay, cabbage palm, swamp bay, baldcypress, and popash. The shrubs included hazel alder, wax-myrtle, and *Baccharis halimifolia*. Woody vines included poison-ivy, *Ampelopsis arborea*, and *Rosa palustris*. Lizzard's-tail (*Saururus cernuus*) was an abundant herb. Other herbs included *Iris virginica*, *Hymenocallis crassifolia*, *Commelina virginica*, *Carex intumescens*, *Justicia ovata*, and *Samolus parviflorus*. Black willow formed a buffer zone between this swamp and the tidal marshes of saw-grass to the interior.

Coastal swamps were examined at the mouth of the Suwannee River in 1976. A dense swamp with trees mostly 15-22 m tall occurred within 1.5-2 miles of the Gulf. Tidal marshes occurred along the Gulf coast, and a gradual transition zone from marsh to swamp began about a half mile up river from the Gulf, beginning with a few short spindly trees mixed with marsh grasses. The coastal swamp proper consisted of sweetbay, swamp bay, blackgum, pumpkin ash (*Fraxinus profunda*), pond-cypress, cabbage palm, wax-myrtle, and southern red cedar. Trees along the river bank were of smaller diameter than those to the interior. Much cypress and red cedar had been harvested from the interior, as evidenced by stumps. Common trees in the interior were blackgum, hackberry (on higher ground), and diamond-leaf oak. Non-arboreal species included leather fern (*Acrostichum danaeaefolium*), lizzard's-tail, *Mikania scandens*, *Ampelopsis arborea*, and *Aster caroliniana*.

Penfound and Howard (1940) described a coastal swamp dominated by water oak and live oak in a bayou near New Orleans. The site was an abandoned distributary of the Mississippi River. Hackberry was rather common, and other species included American elm, white ash, and honey locust (*Gleditsia triacanthos*).

Observations in the St. Marks Refuge suggest a successional trend which appears to be associated with a slight change in mean sea level. This trend could go in either direction, depending on whether or not sea level was rising or falling. Assuming a falling trend in sea level, a tidal marsh of needlerush is invaded by sawgrass, and, if fires are fairly frequent, this is invaded in turn by pond-cypress to form an open woodland of sawgrass and cypress. As peat accumulates or as sea level continues to fall, slash pines and/or cabbage palms also invade. If the site is sheltered from frequent fires, the sawgrass marsh is invaded by hardwoods rather than cypress to form a coastal swamp. This swamp replaces the sawgrass and, as the drying trend continues, a mesic coastal hammock replaces the swamp. This hypothesis could be tested by paylonological analyses of the peaty soils in coastal swamps and marshes.

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38. TIDAL MARSH SYSTEM

Tidal marshes occur along the Gulf coast on beaches protected from wave action, on regularly and periodically inundated tidal flats, in bays and inlets, and on flats along brackish rivers. The most characteristic landscape of Gulf coastal tidal flats are the dark gray-green prairies of needlerush (Juncus roemerianus). These needlerush prairies are vast in the eastern panhandle. Looking eastward from the St. Marks lighthouse in Wakulla County, needlerush extends to the horizon and beyond.

Tidal creeks, flanked with dense yellowish-green bands of cordgrass (Spartina alterniflora), interrupt the needlerush prairies. Salt flats and barrens occupy the highest terrain, which is usually elevated only a few centimeters above the surrounding needlerush flats. The salt falts contain a low, sometimes sparse growth of saltgrass (Distichlis spicata) and succulents (Batis maritima, Salicornia virginica). The barrens are unvegetated patches of white sand.

Near the border with the upland forest of slash pine flatwoods and coastal hammocks, the marsh consists of a more diversified flora. Grasses and sedges are prominent, and couchgrass (Spartina patens) often forms a distinct zone. Shurbs form a narrow ecotone at the edge of the upland forest. Common species of shrubs include Iva frutescens, Baccharis halimifolia, and Ilex vomitoria.

The vegetation types just described collectively comprise what are called salt marshes. These marshes are often continuous with brackish marshes which occur primarily along rivers in the intertidal zone. Nearest the coast these brackish marshes are characterized by needlerush.

In contrast to the salt marshes though, cordgrass is absent at the water's edge, and salt flats and barrens are missing. Sawgrass (*Cladium jamaicense*) becomes intermixed and co-dominant with needlerush a short distance further upstream. Cattails (usually *T. domingensis*), reedgrass (*Phragmites australis*), and big cordgrass (*Spartina cynosuroides*) are among the more conspicuous coarse perennial graminaceous species in these marshes, although plants of several smaller, much less conspicuous species may be more abundant (e.g., *Lilaeopsis chinensis*, *Sagittaria subulata*).

The vegetation of tidal marshes consists of relatively few species representing little variation in life form and little if any distinct stratification. In contrast, the ecological conditions that control this vegetation are made complex from tidal influence. Because of this complexity, the description of the tidal marsh system is prefaced by the following section on intertidal environments.

Intertidal Environments. Parrondo *et al*. (1978) summarized the principal reasons for the harshness of the tidal marsh environment in two terse sentences:

> "High salinity affects plant growth osmotically, by direct toxicity, and by creating nutrient imbalance....Periodic tidal flooding of the sediment creates an anaerobic environment around the root system which few species can tolerate."

The effects of these environmental conditions are made even more severe in some habitats by abrupt changes in salinity and soil moisture. Plants of these habitats must be tolerant of widely fluctuating environmental parameters. In addition, the herbaceous vegetation of tidal marshes is exposed directly to sunlight and coastal breezes without the benefit of a protective forest canopy. As a result, the potential for evapotranspiration is great, and diurnal changes in temperature are considerable. Occasional hurricanes impose additional stresses and sometimes cause physical alterations of the habitat.

Brackish marsh habitats are not as stressful as salt marsh habitats. The salinity values are lower, and the fluctuations in salinity and soil moisture are not as extreme. Brackish marshes continue up river nearly to the limit of tidal influence. With increasing distance from the coast, the halophytic species are gradually replaced by those typical of fresh water environments. Ultimately, the brackish marsh is replaced by the riparian fresh water marsh. The latter is treated in the next chapter as a community of the flowing water system. Because of the transitions between salt marshes, brackish marshes, and riparian fresh water marshes, all three are compared in Table 29.

The zone of tidal influence is defined as that stretch of river which is noticeably pulsed by tides. The lower reaches of rivers contain brackish water that is well mixed. Further up stream the fresh water tends to flow on top of the heavier salt water without much mixing. A wedge of salt water is forced up stream at each high tide along the bottom beneath the fresh water. This wedge extends about 12 miles up stream from the coast in the St. Marks-Wakulla river system (Thompson 1977).

Tidal pulsing occurs even further up river, causing waters to rise with each high tide on the flats along the rivers. This pulsing guarantees that the marshes on these flats will have near-saturated soils continually. These hydric conditions extend up stream into flats occupied by riparian fresh water marshes. Tidal pulsing has been recorded

TABLE 29. Conspectus of Salt Marsh and Brackish Marsh Communities (Tidal Marsh System) and the Riparian Fresh Water Marsh Community (Flowing Water System).

	HABITAT	SALINITY	VEGETATION
23. Salt Marsh	Gulf coast on protected beaches and tidal flats with widths from several meters to several kms, depending on the elevational gradient. Barrens and salt flats common.	Interstitial soil water saline. Surface water either constantly and moderately saline or quite variable in salinity over a period of a few days or weeks.	Spartina alterniflora Juncus roemerianus Distichlis spicata Salicornia virginica Salicornia bigelovii Batis maritima Borrichia frutescens Limonium carolinianum
24. Brackish Marsh	Along tidal rivers and bays where fresh river water and runoff from upland contact the vegetation more than salt water. Rather narrow or, at the mouths of major rivers, quite broad. Barrens absent; salt flats uncommon or absent.	Interstitial soil water fresh or nearly so; surface water usually fresh except briefly during storm tides.	Cladium jamaiscense Typha domingensis Juncus roemerianus Phragmites australis Spartina cynosuroides Scirpus spp. Lythrum lineare Sagittaria subulata Sagittaria lancifolia Sporobolus virginicus Spartina patens
25. Riparian Fresh Water Marsh	River banks upstream from brackish marshes. Narrow, becoming interrupted or absent above the zone of tidal influence where the hydroperiod is not maintained during dry seasons or where prolonged deep flooding occurs at flood stage.	Interstitial and surface water fresh.	Pontederia cordata Polygonum punctatum Zizania aquatica Zizaniopsis miliacea Sagittaria lancifolia Physostegia purpurea Cicuta maculata Lobelia cardinalis Juncus polycephalus

as far inland as Wakulla Springs, but these pulsations become negligible from a vegetational standpoint 15 river miles from the coast at the U.S. 98 bridge over the Wakulla River (Thompson 1977).

Salt marshes occupy a vertical gradient of about 1-1.5 meters. The lowest marsh zone begins about at mean sea level (msl) and consists of cordgrass. Kurz and Wagner (1957) determined the lowest elevations at which cordgrass grew at nine locations from Santa Rosa to Wakulla counties. At one extreme cordgrass grew as much as 17 cm below msl, and at the other extreme cordgrass grew no lower than 3 cm above msl. The highest predicted tides at these locations were from 0.5 to 0.9 m above msl. The boundary between the upper limit of salt marshes and forested uplands is usually 1.2-1.5 m above msl but may be as low as 0.8 meters.

The salt marshes from Wakulla County eastward are often as much as 1-2 km wide and exceedingly flat. The elevational gradient is around a meter per kilometer or much less than one percent. Adjacent Apalachee Bay is correspondingly shallow with depths of as little as 3 m as far as 15 km offshore. Waves are dissipated from friction with the bottom, and the quiet conditions necessary for marsh development are met. The coast has been called a zero energy shoreline for the absence of waves (c.f. page 73).

Wave energy is slight along the coast of Wakulla and Jefferson counties and has been sufficient to deposit sands along the shoreline. These sands have formed a beach upwards to 1.7 m above msl, separating Apalachee Bay from the tidal flats. Tidal creeks interrupt this beach at frequent intervals. Wave energy is insufficient to deposit a beach from Taylor to Dixie counties, and the tidal flats begin directly at the shoreline.

Incoming tides run up the tidal creeks and rivers causing saline waters to overflow the banks and spread as sheet flow onto the tidal flats. In areas where no beaches separate estuaries from tidal flats, saline waters at high tide flood the marshes directly, as well as through tidal creeks. Tidal sheet flow is usually quite shallow. Cordgrass is often nearly covered briefly at high tide. Other marsh zones occur at higher elevations and typically receive no more than a few centimeters of inundation.

The return of tidal water at low tide into creeks and estuaries is sometimes physically retarded by the dense growths of needlerush and cordgrass. Kurz and Wagner (1957) noted that some tidal creeks are lined by low levees or berms up to 9 cm tall, which delay the return of surface waters into these creeks. The effectiveness of these levees in detaining surface waters is made possible by the exceedingly flat topography in tidal marshes. After particularly high tides, some water may become impounded in very shallow, saucer-shaped depressions in the higher marsh areas that are otherwise infrequently inundated. If these depressions contain an impervious bottom that retards percolation, the water will remain for several days until it evaporates.

Community Organization. Tidal marsh vegetation is not organized into integrated communities. Rather, the species occur in zones which are typically defined by the salinity regime and the soil moisture regime.

Species Richness. In the more saline habitats each zone consists of only one or few species. In the more brackish habitats, the number of species is greater. Sometimes only one species is dominant in a zone, and all other species are incidental or rare. Tidal marshes are floristically depauperate. Few species tolerate the harsh conditions. These species are typically abundant for want of competition from other species. Large acreages of needlerish marshes apparently contain only plants of that species, although careful searching might reveal a few plants of two or three additional species. No other terrestrial landscape in the panhandle contains so few species on so large an area.

Physiognomy. Tidal marshes are characterized by graminaceous plants (grasses, sedges, rushes) which generally grow in dense stands. Average plant heights range from about 6-250 cm, depending on the habitat conditions. More often than not, plant height is inversely proportional to salinity. The most saline habitats may be dominated by succulents (species of Salicornia, Batis, Borrichia), rather than graminoids. The transition zones between tidal marshes and forested communities consist largely of shrubs 1.5-2.5 m tall, sometimes with an herbaceous ground cover.

Soils. Tidal marsh soils vary considerably in texture, composition, stratification, salinity, and nutrient availability. Surface soils range from sands to clay-loams or to peats and mucks up to 3.3 m deep. Table 30 compares 10 surface soils in salt marshes in Apalachee Bay for several parameters. These soils represented very discrepant great groups, including psammaquents, haplaquods, haplaquolls, ochraqualfs, natraqualfs, and sulfaquents. Two additional great groups were reported in the brackish marshes of the Apalachicola River estuary: sulfihemists and fluvaquents (Coultas 1980). The values in Table 30 represent a wide range of conditions for most parameters.

TABLE 30. Salt Marsh Surface Soil Parameters in Wakulla County (Coultas 1969, 1970), Taylor County (Coultas and Gross 1976), and Dixie County (Coultas, 1978).

Dominant Vegetation	pH	CEC me/100g	Extractable Cations (me/100g) Ca	Mg	K	Na	Percent N	C	Silt-Clays
Spartina alterniflora	6.3	76	42	16	1.8	1.2	1.2	16	76
Spartina alterniflora	7.7	27	8	7	1.0	8.9	0.7	7	47
Spartina alterniflora & Juncus roemerianus	7.2	27	11	23	0.8	4.2	0.6	7	19
Juncus roemerianus	7.0	10	5	3	0.3	0.8	0.3	1	17
Juncus roemerianus	5.1	10	3	6	0.5	1.9	0.2	2	19
Juncus roemerianus	4.6	10	4	3	0.2	0.5	0.2	3	14
Juncus roemerianus	7.2	4	2	4	0.2	0.5	0.1	2	22
Distichlis spicata	6.1	5	2	3	0.2	0.7	0.1	1	26
Distichlis spicata	5.5	7	3	4	0.4	1.2	0.1	2	21
Spartina patens	7.1	4	1	2	0.1	0.2	0.1	1	14

Clayey soils are common at the mouths of rivers. The silts and clays predominate in the uppermost horizons, and sands become more abundant with depth. The predominant soils in the Apalachee Bay region are sandy loams or sands with a silt-clay content of 6-30%; however, a clay-loam with 76% silt-clay was reported from Taylor County (Table 30). These soils are much sandier than salt marsh soils along the Atlantic coast. Clay minerals are the same as those in adjacent upland soils and are thought to be of local origin. Surface soils show considerable mixing by burrowing animals and by water movement. Spodic and argillic horizons are sometimes present. Nutrients are generally abundant. The most easily extractable bases are Mg and Ca. Values for pH range from a low of about 3.5 in peats to a high of about 8.5 in the most saline habitats (barrens) and in tidal creeks.

The brackish marshes of the Apalachicola River estuary contain soils with a surficial silt-clay content of up to 99% (Coultas 1980). The clay minerals differed from those seen in the marshes in Apalachee Bay and presumably were transported as alluvium from interior provinces. The pH values for these soils ranged from 5.0 to 6.4 in the uppermost horizon. Plant nutrients were plentiful, salinity low, and the percentages of organic carbon were high. The sulfur content was high in soils of these marshes and those at the mouth of the Suwannee River (Coultas 1978, 1980).

Moisture. Water enters tidal marshes through tidal inundation, through rainfall, and as runoff or as base flow of the groundwater from adjacent uplands. Tidal inundation may occur with every high tide at low elevations or periodically with particularly high tides at higher elevations. There are usually two tides daily in the northeastern Gulf of

Mexico with a tidal amplitude of about 0.5 to 1.1 meters.

Predicted tides are not always attained. Onshore winds or low barometric pressure cause higher than predicted tides. An onshore wind of 40-60 mph once caused a 2.6 m tide instead of a predicted 1.1 m tide (Kurz and Wagner 1957). A 30 mph onshore wind is sufficient to push a tide over the top of the taller beaches that separate Apalachee Bay from the expansive tidal flats in Wakulla County. Sustained offshore winds can prevent a predicted high tide from being attained. Kurz and Wagner (1957) noted that a strong seaward wind once held a predicted 0.7 m high tide below mean low water, exposing seagrass beds a kilometer offshore. These conditions commonly occur in winter shortly after cold fronts pass across the Gulf coast.

The influx of fresh water as rainfall, runoff, and base flow is important at higher marsh elevations where tidal inundation is infrequent. These fresh waters prevent the marsh soils from dessicating between tidal inundations, and they dilute the saline waters that percolate into the soil after these inundations.

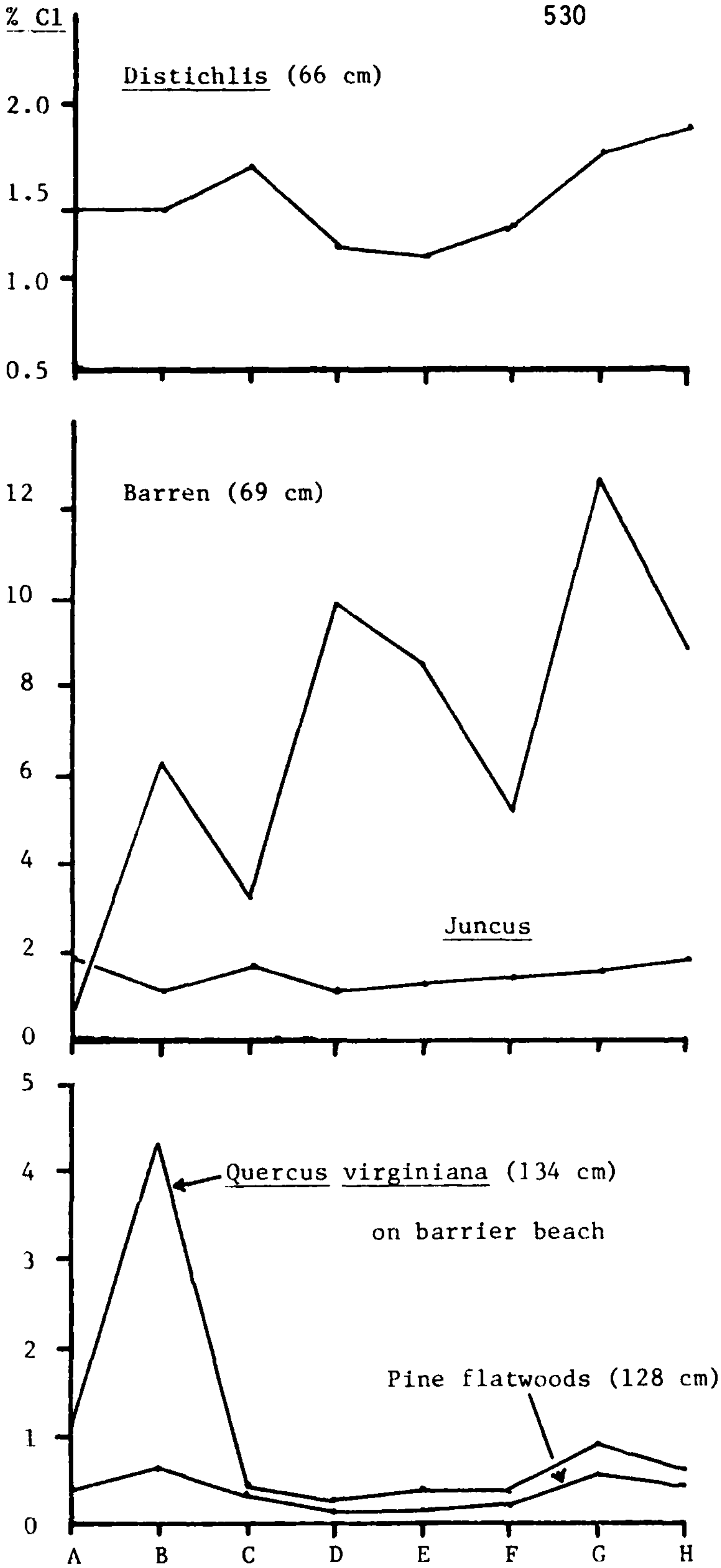
Water percolation is slow in mucks and loams and wherever the water table or an impermeable soil horizon is near the surface. Percolation is rapid in sands, particularly at higher marsh elevations where the water table and impermeable strata are relatively deep in the soil. Percolation and aeration are augmented in sands when burrowing animals, particularly fiddler crabs (Uca spp.), excavate tunnels.

Salinity. The salinity of the open Gulf is approximately 35 parts per thousand (o/oo) and is rather constant. Tidal creeks entering Apalachee Bay vary in salinity from about 15 to 27 o/oo (Subrahmanyan and Drake 1975). At lower elevations on tidal flats where tidal inundations are of daily occurrence, salinities are moderate and tend to reflect those of the tidal creeks. At higher elevations where tidal inundations are of periodic occurrence, salinities are quite variable. Between these periodic inundations, the salinity will decrease if diluted with rainfall, runoff, or base flow of ground water. On the other hand, salinities increase with the evaporation of salt water, as long as rainfall is negligible and there is no source of runoff or base flow nearby.

The highest salinities occur at the higher elevations where tidal inundations occur approximately once a month and where the soil is particularly well drained and aerated. Salinities may become so high that salt crystals are observed on the soil surface. After heavy rains or a tidal inundation, the salinities drop abruptly.

The widely fluctuating salinities and the frequently hypersaline soil water preclude plant growth, other than algae. Such sites are called barrens. Kurz and Wagner (1957) recorded chlorinity values for the soil water in barrens that were 8 times greater than in tidal creeks. (They expressed salt content as percent chlorinity of the soil water, rather than o/oo of salinity.) Slightly less saline habitats which are vegetated are called salt flats. Barrens and salt flats also occur in shallow high marsh depressions from which impounded tidal waters evaporate between the infrequent tidal inundations.

The interrelationships between the periodicity of tidal inundations and rainfall were studied by Kurz and Wagner (1957) at Live Oak Point in Wakulla County. Some of their data are summarized in Figure 42. The middle graph shows how chlorinities are relatively low and constant in a



A	10-1	5 days after hurricane.
B	10-24	after 23-day drought.
C	10-27	after hard rain.
D	12-3	after rain.
E	2-11	110-cm tide but no rain in last 3 weeks.
F	3-4	rain.
G	5-1	rain and 92 cm tide.
H	7-1	6 days of 92-107 cm tides but no rain.

Elevation above msl is given in cm.

Figure 42. Percent soil chlorinity on selected days in 1953-54 in several habitats at Live Oak Point, Wakulla County (after Kurz and Wagner 1957).

needlerush marsh (Juncus) and usually much higher and widely fluctuating in a barren. The fluctuations were mostly attributable to the periodicity of rainfall events and tidal inundations, but the lack of continuous measurements for these parameters made a precise correlation impossible.

The salinity (or chlorinity) of the water in the intersticies of the soil is not always the same as that of the water inundating the soil surface. The soil water is more constantly saline and is in contact with plant roots. As a result, soil water measurements are probably a better reflection of environmental conditions for plants than surface water measurements. Table 31 gives the approximate range and the maximum values for soil water chlorinity for the common salt marsh species and for a few freshwater species of near-coastal environments in Florida and Louisiana. Table 32 gives the surface water salinities for marsh species in Louisiana.

Fire. Tidal marshes burn occasionally, particularly needlerush and sawgrass zones where the fuel is plentiful and dense. Moist or inundated soils prevent the combustion of the lowest portion of the culm. Regrowth of shoots from the undamaged rootstocks is rapid, and the general aspect of the unburned marsh is regained within a year. The occurrence and frequency of fire has no apparent effect on species composition, plant zonation, and patterns of dominance. A temporary decrease in biomass is the only notable effect. Lightning is the usual source of natural fire. Viosca (1931) reported a probable instance of spontaneous combustion in a heavy accumulation of detritus in a brackish marsh in Louisiana.

Mineral Nutrients. As mentioned above, nutrients are generally plentiful in tidal marshes, although the efficiency of absorbtion of

TABLE 31. Percent Chlorinity of the Soil Water for Selected Species, Based on Penfound and Hathaway (1938) in Louisiana and Kurz and Wagner (1957) in Florida.

Approximate Ranges in Florida	Maximum in Florida	Maximum in Louisiana
0 - 0.5		
Andropogon glomeratus		
Quercus minima		
Serenoa repens		
0 - 1		
Ilex vomitoria	2.2	
Juniperus silicicola	2.2	
Magnolia grandiflora		
Muhlenbergia capillaris		
Myrica cerifera	0.9	
Panicum virgatum		
Pinus elliottii	1.0	
Quercus virginiana	4.3	
Setaria geniculata		
0 - 2		
Baccharis halimifolia	1.8	2.0
Fimbristylis castanea		1.9
Lycium carolinianum		
Solidago sempervirens		1.9
Spartina patens	5.4	3.9
Spartina spartinae		
0 - 2.5		
Aster tenuifolius		2.3
Iva frutescens	2.5	2.3
Juncus roemerianus	3.0	4.4
Sabal palmetto	2.2	
Spartina alternifolia	4.6	5.0
0 - 3.5		
Distichlis spicata	3.9	5.0
Batis maritima	4.9	5.0
Borrichia frutescens		4.4
Limonium carolinianum		
0.5 - 5.5		
Salicornia virginiana	5.1	
0.7 - 12.6		
Barrens	12.6	

Maxima in Louisiana for other species: Scirpus robustus - 3.9; Spartina cynosuroides - 2.0; Phragmites australis - 2.0; Panicum virgatum - 2.0; Ipomoea sagittata - 2.0; Scirpus americanus - 1.7; Lythrum lineare - 1.7; Typha latifolia - 1.1.

TABLE 32. Water Salinity Around Tidal and Fresh Water Marsh Plants in Louisiana (from Chabreck 1972).

	Salinity (o/oo)		Number of Observations
Batis maritima	24 ±	10	13
Spartina alterniflora	15	8	95
Juncus roemerianus	14	8	63
Distichlis spicata	13	7	80
Borrichia frutescens	12	9	5
Iva frutescens	12	9	5
Fimbristylis castanea	10	7	4
Spartina cynosuroides	9	5	27
Ruppia maritima	9	6	26
Scirpus robustus	9	5	61
Spartina patens	9	6	173
Baccharis halimifolia	8	6	31
Scirpus americanus	7	5	63
Eleocharis parvula	7	4	29
Pluchea camphorata	6	6	47
Lythrum lineare	6	4	23
Ipomoea sagittata	5	5	23
Leptochloa fascicularis	5	3	9
Cladium jamaicense	4	3	5
Bacopa monnieri	4	2	29
Spartina spartinae	4	1	4
Paspalum distichum	3	4	16
Phragmites australis	3	4	29
Cyperus odoratus	3	3	61
Panicum virgatum	3	4	17
Echinochloa walteri	3	2	44
Alternanthera philoxeroides	3	5	30
Kosteletzyka virginica	3	1	10
Sagittaria lancifolia	2	2	64
Panicum repens	2	1	6
Scirpus californicus	2	1	20
Osmunda regalis	2	1	6
Zizaniopsis miliacea	1	2	13
Myrica cerifera	1	1	14
Panicum hemitomon	1	1	43
Salix nigra	1	0	23
Cephalanthus occidentalis	1	1	13
Utricularia cornuta	1	1	10
Najas guadalupensis	1	0	7
Nymphaea odorata	0	0	5
Juncus effusus	0	0	2
Lymnobium spongia	0	0	4
Rhynchospora corniculata	0	0	2
Saururus cernuus	0	0	3

these nutrients by roots may be impaired because of saline conditions. The nutrients are imported in sea water, both from tidal inundation and also some from aerosols. Other nutrients are imported in river water which floods brackish marshes at high tide. Still other nutrients are made available by decomposition *in situ* or by combustion during fires.

Maintenance. Tidal marshes and the vegetational zones therein are maintained indefinitely by the salinity and soil moisture regimes. Changes in elevation and type of substrate are very gradual and are caused by changes in mean sea level, by the aggradation of sediments carried from streams onto flats at times of tidal overflow, by the erosion of sediments from adjacent uplands, and by the accumulation of peat.

Response to Disturbance. Any activity that interrupts the salinity or moisture regime is likely to cause a rapid and permanent change in the vegetation. The removal or accretion of surficial materials by hurricanes, dredging, or filling all cause such changes. Ditching sometimes affects the water regime in such a way as to influence the vegetation. Burning and the application of herbicides have been used effectively to encourage the spread of grasses for purposes of converting needlerush marsh into pasture. Following any kind of disturbance, the species best adapted to the new moisture and salinity regimes quickly colonize the site. Following colonization, the invading plants persist as long as the substrate is stable. The invasion of exotic species or of species from other systems is a rare event. The stringencies of tidal marsh conditions preclude the establishment of species other than those indigenous to tidal marshes.

Mode of Origin. The species that invade a new tidal marsh habitat generally persist as long as environmental conditions remain constant. When those conditions change, there is a concomitant change in the vegetation. Since there are few species present in any given site in a tidal marsh, the vegetational changes, when they occur, are dramatic. Succession does not occur. The initial floristic composition determines the vegetation of a site. Subsequent changes are in accordance with the displacement model.

Ecotones. The transition between brackish marshes and riparian fresh water marshes has been mentioned. The transitional shrub zones represent ecotones between tidal marshes and upland vegetation, mainly slash pine flatwoods, coastal hammocks, and coastal swamps. Otherwise, tidal marshes are well differentiated from other communities.

Communities. Two communities are recognized, salt marshes and brackish marshes.

23. Salt Marshes

Salt marshes comprise the most prominent coastal vegetation from the Ochlockonee River eastward in the panhandle. To the west, wave action is greater and all tidal marshes are restricted to protected coves and inlets, such as those that occur along the northern shores of barrier islands.

Salt marsh zonation is diagrammed in Figure 43, and Table 33 describes and compares the seven prominent vegetational zones in salt marshes of the panhandle. Figure 43 also gives frequencies of tidal

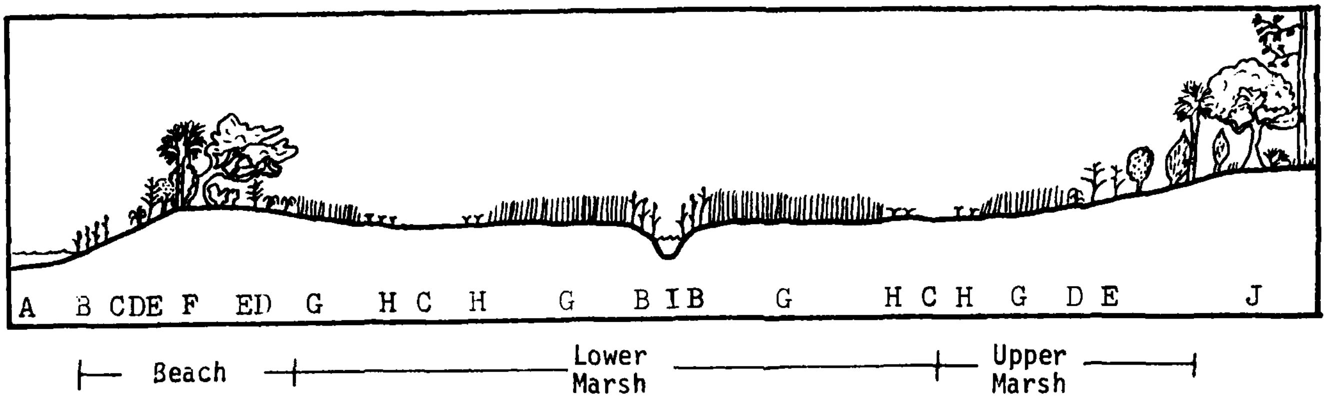


Figure 43. Generalized salt marsh zonation (after Kurz and Wagner 1957).

A Gulf of Mexico
B Cordgrass Zone (Spartina alterniflora)
C Barren
D Couchgrass Zone (Spartina patens) and/or Transitional Marsh Zone
E Transitional Shrub Zone
F Coastal Hammock
G Needlerush Zone (Juncus roemerianus)
H Salt Flat (Distichlis spicata, Salicornia spp.)
I Tidal Creek
J Coastal Pine Flatwoods

	Tide necessary to inundate (cm)	Predicted inundations*
Cordgrass Zone	52	694
Needlerush Zone (lower marsh)	98	81
Barren	104	38
Needlerush Zone (upper marsh)	107	21
Transitional Shrub Zone	122	0

	Average rate of soil water percolation (cm/minute)
Needlerush Zone	2.8
Salt Flat	4.3
Barren	7.7

*Live Oak Point, Wakulla County, 1954

TABLE 33. Conspectus of Vegetational Zonation in Salt Marshes.

	LOCATION	MOISTURE & SOIL	SALINITY	VEGETATION
23a. Cordgrass Zone	Protected beaches and tidal creeks at elevations essentially between mean sea level and the highest predicted tide.	Soil constantly saturated and usually inundated daily. Mucky sands, silts, clays.	Rather constantly moderately saline, the salinity approximating that of bay water.	*Spartina alterniflora* (tall form).
23b. Needlerush Zone	Tidal flats and beaches above mean high tide; also extending into brackish marshes.	Soil usually moist but aerated; inundated by exceptional tides. Needlerush germinating on sands and later producing deep fibrous peat.	Moderate to low; in high marshes, the soil salinity probably kept low by fresh water runoff and base flow from nearby uplands.	*Juncus roemerianus*, sometimes *Aster tenuifolius*, *Lilaeopsis chinensis*, & *Spartina alterniflora* (short form).
23c. Salt flats	Higher elevations on beaches & tidal flats where inundation by tides is infrequent.	Moist, aerated sands.	Quite variable within a period of a few days or weeks, from nearly fresh to hypersaline due to evaporation.	*Distichlis spicata*, *Salicornia* spp., *Batis maritima*, *Borrichia frutescens*, *Limonium carolinianum*, *Monanthochloe littoralis*.
23d. Barrens	Slightly higher elevations than saltflats or else shallow depressions in salt flats where water from exceptionally high tides collects and evaporates.	Moist, well aerated sands.	Quite variable as in salt flats but with higher salinities.	No vascular plants. Bluegreen algae and diatoms on soil surface.

TABLE 33, continued.

	LOCATION	MOISTURE & SOIL	SALINITY	VEGETATION
23e. Couchgrass Zone	Elevations higher than salt flats and barrens where tidal inundation is usually much less than once a month.	Mesic sands.	Low to moderate, the interstitial soil water probably kept fresh in part by runoff and base flow from uplands nearby.	_Spartina patens_, sometimes with species of the transitional marsh zone intermixed.
23f. Transitional Marsh Zone	As in couchgrass zone, which is merely a conspicuous floristic variant of the transitional marsh zone.	Mesic sands.	Low to moderate, as in couchgrass zone.	Variable, often with some of the following: _Spartina patens_, _S. spartinae_, _S. bakeri_, _Eleocharis cellulosa_, _Fimbristylis castanea_, _Andropogon glomeratus_ _Chloris petrea_, _Elyonuris tripsacoides_, _Panicum virgatum_, _Muhlenbergia capillaris_, _Solidago sempervirens_.
23g. Transitional Shrub Zone	Ecotone between marsh and the upland vegetation.	Mesic sands.	Very low; briefly subjected to some storm tides.	_Iva frutescens_, _Baccharis halimifolia_ _B. angustifolia_, _B. glomeruliflora_ _Lycium carolinianum_, _Myrica cerifera_, _Ilex vomitoria_

inundations for several marsh zones and some rates of percolation of the soil water. The landscape shown in Figure 43 depicts that just east of the St. Marks lighthouse in Wakulla County.

Since the several vegetational zones are usually limited to an elevational relief of no more than 1.5 m, each zone is restricted to a much narrower elevational range. Kurz and Wagner (1957) reported that all usual salt marsh zones from cordgrass through the transitional shrub zone occupied a vertical gradient of only 0.93 m at St. Joseph's Bay in Gulf County. Slight differences in elevation are accompanied by much greater differences in the soil moisture regime and the salinity regime and thus the vegetation. All zones are present and well developed where vertical gradients are gradual. Occasionally the slope is steep, perhaps as much as 2-3% on some beaches, and some zones are contracted or absent.

Figure 43 shows a well developed beach which has a narrow strip of coastal hammock on top. Such hammocks only occur at elevations of 1.5-1.7 m above msl. Beaches of lower elevations are capped by the shrub transition zone, and yet lower beaches by herbaceous marsh vegetation. Barrens on the seaward side of beaches often contain a few summer annuals which become established in the "tidal hay" of sea grasses which is often stranded on the barrens by particularly high tides. Common species include Atriplex arenaria, Cakile constricta, Chenopodium berlandieri, and Suaeda linearis. These annuals do not grow on barrens in the marshes behind these beaches. A succulent perennial, Sesuvium portulacastrum, sometimes grows at the upper edge of barrens on beaches. The shrub transition zone on beaches commonly contains (among others) Lycium carolinianum and, much less commonly, Baccharis angustifolia. Neither of these shrubs have been reported from shrub transition zones except on beaches. The transitional marsh zone is quite variable in floristic composition on the landward slope of beaches. Spartina spartinae and Sporobolus virginicus may be abundant.

The tidal flats, rather than the beaches, contain the vast expanses of salt marsh in the panhandle. The vegetation on these flats is often divided by a zone of barrens into the lower marsh (from tidal creeks to the barrens) and the upper marsh (from the barrens to the forested upland). Ecological conditions in the lower marsh are controlled primarily by tidal inundations, which are frequent. Ecological conditions in the upper marsh are controlled both by the infrequent tidal inundations and by the influx of fresh water from rain, runoff, and base flow.

In the lower marsh, the cordgrass zone largely occurs within the areas that are inundated by tidal flow daily or nearly so. The needlerush zone occurs at a slightly higher elevation where tidal inundation is periodic and the soils aerated at times. The needlerush zone is almost invariably the largest zone and typically occupies more area than all other zones combined. Salt flats occur at a slightly higher elevation than the needlerush zone, where evaporation of the soil water between the infrequent tidal inundations creates periodic hypersaline conditions. Wherever these conditions are extreme, no vascular plants can survive, and the site is a barren.

Kurz and Wagner (1957) noted that the peats occupied by needlerush in the lower marshes are relatively impermeable to water. The sands of adjacent salt flats were much more porous. As a result, sheetflow, pushed by the in-coming tide, glides across the peats in the needlerush zone and into the salt falts, where the water is readily absorbed by the sands. The sheet flow does not always continue onto the adjacent barren (assuming a sufficiently high predicted tide), because its velocity was reduced from friction against the dense stalks of needlerush.

There are three ecological effects from these circumstances. First, the soil under needlerush does not absorb as much salt as would be expected. Second, the salt flats absorb correspondingly more salt than would be predicted. Third, the hypersaline soil water in the barrens is not diluted by tidal inundation as frequently as would be expected. All three of these effects reinforce the moisture and salinity regimes that control the vegetation in these marsh zones.

Kurz and Wagner (1957) made an observation that might explain the formation of some saucer-shaped depressions containing barrens, which are surrounded by less saline salt flats at slightly higher elevations. They noted a barren 9 m across that occupied such a depression. Glasswort (Salicornia spp.) surrounded this depression, and peat from glasswort occurred in the soil of the barren. They suggested that glasswort once occupied the area that is now a depression. Upon the demise of the glasswort, the sand was no longer tightly held by living roots. Thereafter, sand was eroded by sheet flow, causing the depression to form. Tidal sheet slow became impounded in the depression at very infrequent intervals and evaporated, causing a higher soil salinity than in the surrounding ring of glasswort.

The zonation of upper marshes is often the reverse of that in lower marshes. With increasing elevation, the barrens yield to salt flats and these in turn to needlerush marsh, then transitional marsh, transitional shrubs, and finally the forested upland. Tidal inundation is very infrequent, less so than in the barrens. The salt flats are more frequently inundated than the needlerush zone of the upper marsh, and the subsequent zones are even less frequently inundated. The infrequency of tidal inundations allows rains and runoff to leach below the root zone. Leaching is probably more efficient in the upper marsh than in the lower marsh, because the soils are sandier and the water deeper. In the absence of rain, fresh water base flow prevents the evaporation of the soil water and thereby prevents hypersaline conditions. The degree of impact of base flow is presumably a function of the distance to the forested upland.

Runoff causes erosion of sands from the edge of the uplands onto the upper edge of the marsh. Sometimes a miniature cliff of only a few centimeters in height separates the forest from the marsh. A correspondingly miniature talus of sand forms a toe at the base of this cliff. The degree of slope at these upper marsh extremities may be only 2-3 degrees, but they are enormously steep in relation to the rest of the marsh. Vegetational zonation is particularly contracted on these gradients. At Wakulla Beach the following zonation was evident within a horizontal distance of 3 or 4 meters: (1) Spartina patens, (2) Iva frutescens and Baccharis halimifolia, (3) Myrica cerifera and Ilex vomitoria, (4) Juniperus salicicola (5) Sabal palmetto, and (6) Quercus virginiana and Pinus elliottii. The last three zones are properly part of a coastal hammock community, but the species of this community respond to the salinity and moisture regimes as do the species of salt marshes proper. This kind of zonation is also common on beaches, including the separation of the shrub zone into a lower Iva-Baccharis associes and an upper Myrica-Ilex associes.

24. Brackish Marshes

Brackish marsh vegetation is more variable than that of salt marshes. Thompson (1977) made the only quantitative study of brackish marshes in the panhandle and listed 74 species from the flats along the St. Marks and Wakulla rivers. Sawgrass and needlerush were the dominant and most conspicuous species. Cattails (Typha domingensis) and reedgrass (Phragmites australis) were locally abundant, particularly in wetter sites. Less conspicuous but often intermixed were Lythrum lineare, Lilaeopsis chinensis, Scirpus americanus, Ludwigia repens, and Crinum americanum. Near the water's edge the common species were Sagittaria lancifolia, S. subulata, and Spartina cynosuroides. Near the adjacent forested upland, the species were more numerous and included those that are also typical of the transitional marsh zone of salt marshes. Some of these species were Sporobolus virginicus, Fimbristylis castanea, Mikania scandens, and Spartina spartinae. Thompson measured peats and mucks from 0.5 to 3.3 m deep throughout her study area. These organic soils were much deeper than those in salt marshes. Her study is summarized in Research Summary 40.

The extensive brackish marshes at the mouth of the Apalachicola River were visited May 16, 1978. These marshes generally were dominated by sawgrass. Large patches of needlerush interrupted the sawgrass in places, particularly near the channels of the river and its distributaries. Other herbs were also common within a few meters of the banks of the channels, especially Cicuta maculata, Ipomoea sagittata, Rumex verticillatus, Sagittaria lancifolia, Spartina patens, and Teucrium canadense. These and other herbs were generally incidental or absent in the interior expenses of the sawgrass marshes.

Growing in the water near the banks of the channels were plants of Pontederia cordata, Nuphar luteum, and Typha latifolia. The marsh at the extreme tip of the delta (at the mouth of the Little St. Marks River) was dominated by sawgrass and patches of Phragmites australis, Pontederia cordata, Scirpus californicus, Sesbania punicia, and Typha latifolia. Other species seen in these marshes were Apios americana, Asclepias lanceolata, Carex hyalinolepis, C. reniformis, C. stipata, Juncus megacephalus, Kosteletzyka virginica, Ludwigia palustris, Mikania scandens, Osmunda regalis, Peltandra virginica, Proserpinaca palustris, Saururus cernuus, Spartina cynosuroides, Smilax bona-nox, Thelypteris palustris, and Zizania aquatica. The woody vegetation of the levees was already described in Chapter 37 with the coastal swamp community.

The only other account of the Apalachicola marshes (and the only published vegetational study of brackish marshes in the panhandle) was by Harper (1910). He walked across the newly completed railroad tressle that spans the marsh and enumerated the species he could identify below.

The brackish tidal marshes on the zero energy shoreline at the mouth of the Suwannee River were visited on August 19, 1976. No beaches or barrier islands protected these marshes from the Gulf of Mexico. Needlerush formed a zone 1-2 m wide facing the open Gulf. Large expanses of sawgrass or cattails were behind this needlerush zone, with plants of Sagittaria lancifolia commonly intermixed. There were also some patches of Phragmites australis and Scirpus sp. Further up stream narrow marshes fringed the coastal swamp forests. Common species were sawgrass, Sagittaria lancifolia, Pontederia cordata, and Zizania aquatica (and/or Zizaniopsis miliacea).

Discussion

Panhandle Investigations. Salt marshes have been studied intensively in the Southeast. Much of this work has been done in recent years in response to environmental concerns voiced with regard to coastal habitats. A number of studies have been done in the panhandle. More is known about salt marshes than any other environment in the panhandle. These studies include the following: Jackson (1952) recorded vegetational zonation and associated habitat factors near the St. Marks lighthouse in Wakulla County. Kurz and Wagner (1957) published a detailed monograph in which they correlated vegetation with elevation, soil chlorinity, pH, soil moisture, and type of substrate. They studied marshes near St. Marks lighthouse, Live Oak Point, Shell Point (all in Wakulla County), Alligator Point (Franklin County), St. Josephs Bay (Gulf County), and Little Sabine Bay (Santa Rosa County).

Coultas (1969, 1970, 1978) described salt marsh soils in Wakulla and Dixie counties, and Coultas and Gross (1976) described soils in Taylor County. Turner and Gosselink (1975) estimated the standing crop of Spartina alterniflora in Gulf, Franklin, Wakulla, and Taylor counties. Clewell et al. (1976) described the ecological effects of fill-roads built across salt marshes in Wakulla, Taylor, and Dixie counties. Kruczynski et al. (1978) measured salt marsh productivity and decomposition near the St. Marks lighthouse. Ribelin (1978) studied nutrient transfer of decomposing detritus from salt marshes into Apalachee Bay.

Many other studies done elsewhere in the Southeast are pertinent to the panhandle, including descriptions of salt marsh soils from Hernando and Duval counties by Coultas and Calhoun (1976) and from Levy and Citrus counties by Coultas and Gross (1977).

In contrast, very little is known about the brackish marshes of the panhandle. The works of Harper (1910), Thompson (1977), and Coultas (1980) were already mentioned. A small marsh on St. George Island is described briefly in Research Summary 39. Otherwise, one must be content with descriptions of brackish marshes from other states. Research Summary 41 describes a brackish marsh in Alabama. Research Summaries 42 and 43 contain information from two of several published studies made recently in Louisiana and Mississippi.

General Southeastern Studies. Penfound (1952) reviewed the earlier literature. Cooper (1974) and Marshall (1974) made general descriptions of southeastern salt marshes. Godfrey and Godfrey (1974) discussed the development of salt marsh habitats. Carlton (1975, 1976) published a guide to the identification of salt marsh plants and prepared a rather comprehensive bibliography on salt marsh ecology.

Productivity. Many studies have been made on salt marsh productivity, both for marshes generally and for particular species. Some studies in North Carolina were by Waits (1967), Blum *et al.* (1978), and Gallagher *et al.* (1980), the latter two papers pertaining to cordgrass and needlerush. Some studies in Georgia were by Pomeroy (1959) on algal productivity, Teal (1962) on trophic structure, Odum and Fanning (1973) on *Spartina alterniflora* and *S. cynosuroides*, and Linthurst and Reimold (1978) on seven species. Williams and Murdock (1972) measured productivity in needlerush in eastern Florida. Two studies from Mississippi were by de la Cruz (1974), Gabriel and de la Cruz (1974). Two additional studies from Mississippi concerned belowground biomass and decomposition rates for needlerush and *Spartina cynosuroides* (de la Cruz and Hackney, 1977, Hackney and de la Cruz, 1980). In the latter paper, it was estimated that the loss of root and rhizome biomass for needlerush was 18% at a depth of 5 cm after 382 days. There was no loss at a depth of 25 cm. Productivity studies in Louisiana included those by Kirby and Gosselink (1976) on cordgrass, White *et al*. (1978) on four species, and Hopkinson *et al*. (1978) on shoot production in seven species.

Nutrients. Reimold (1972) studied the movement of phosphorus in salt marshes. Haines and Dunn (1976) measured the growth responses of cordgrass to three levels of N and Fe. Mendelssohn (1979) studied the responses of cordgrass to different applications of nitrogen in a marsh in North Carolina. Growth was greater with ammonium than with nitrate. Tall forms of cordgrass responded more than short forms to nitrogen. DeLaune *et al*. (1979) studied the relationships between soil properties and biomass production in cordgrass in Louisiana. Buresh *et al*. (1980) measured the growth responses of cordgrass to P and N in Louisiana.

Salinity. Kurz and Wagner (1957) discovered that plants of *Batis maritima*, *Salicornia virginica*, and *Borrichia frutescens* were much taller when growing in soils with low chlorinity than in soils with high chlorinity. For example, plants of *B. frutescens* were 4 cm tall when growing in soils with a chlorinity of 1.1% and 60 cm tall at 0.1%. They also noted a growth response to soil moisture when the chlorinity was constant. Plants of *B. frutescens* were 5 cm tall in soils with an 18%

moisture content and 33 cm tall with a 33% moisture content.

Hoese (1967) discussed various ecological aspects with regard to hypersalinity. Waisel (1972) prepared a general review on halophytes. Beal (1973) listed the maximum chlorinities of the water in which many marsh plants were growing in North Carolina. Hess et al. (1975) discussed the establishment of Scirpus americanus.[1]

Parrondo et al. (1978) discovered that root growth of Spartina cynosuroides was reduced significantly at relatively low salinities but that root growth in S. alterniflora was not reduced except at much higher salinities. They found that the dry weight of these plants is inversely correlated with the quantity of NaCl in the soil and that dry weight is positively correlated with aerated soils for both species. They further reported that the growth rate of Distichlis spicata was not affected by low or moderate levels of soil NaCl. The greatest dry weights were obtained when there were 16 g/l of NaCl in the soil. Plants of Spartina alterniflora suffered a reduction in biomass when the NaCl content rose above 8 g/l.

Hackney and de la Cruz (1978) studied surface water and soil water salinities in relation to needlerush and Spartina cynosuroides in Mississippi. They found that changes in the salinities of the surface water were reflected by corresponding changes in the salinity of the soil water. The salinity of the interstitial soil water was almost always

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[1] A. E. Schuyler, writing in Rhodora 76: 51-52, 1974, said that the type specimen of the name, S. americanus, is identifiable as a plant that authors almost universally have been calling S. olneyi. The name, S. olneyi, must be regarded as a synonym of S. americanus. Plants that have been called S. americanus are now called S. pungens. These changes have been made throughout this report.

higher than that of the surface water. Salinities in the soil ranged from 2.5 to 15.8 o/oo. Those in the surface water ranged from 0 to 11.5 o/oo. The constantly higher salinities of the soil were thought to be important in reducing potential competition from salt-intolerant species. Weiss et al. (1979) also made measurements of surface and soil salinities in Louisiana.

Gallagher (1979) discovered that growth in plants of Sporobolus virginicus was limited by increasing salinities and possibly by a lack of available nitrogen. Roots and rhizomes showed more inhibition to salinity than the shoots. A clear correlation between salinity and biomass was not demonstrated. Seedling survival was good at high salinity.

Cavalieri and Huang (1979) studied the physiological mechanism of salt tolerance in several salt marsh species. They found high concentrations of proline (an amino acid) in the cytoplasm. They concluded that proline maintained an osmotic balance in the cytoplasm just as sodium chloride did in the vacuole. They showed that this mechanism was particularly important in needlerush and Limonium carolinianum.

Seeds and Germination. Amen et al. (1970) elucidated the germination requirements for Distichlis spicata. Stalter (1973c) discussed seed variability in cordgrass. Stalter and Batson (1973) reported on the viability of seeds of several species. Dietert and Shontz (1978) studied the germination ecology of Scirpus robustus. Parrondo et al. (1978) reported finding no viable seeds in plants of Spartina patens in Louisiana.

Vegetational Zonation in Salt Marshes. Many authors have described the vegetational zones in southeastern salt marshes. Among them are the following: In Louisiana and Mississippi, Penfound and O'Neill (1934), Penfound and Hathaway (1938), Chabreck (1972), Eleuterius (1971, 1972, 1973), Gabriel and de la Cruz (1974), Montz (1975, 1976a,b, 1977). In northeastern Florida, Stalter (1976). In Georgia, Johnson et al. (1974) In South Carolina, Stalter (1973b). In North Carolina, Wells (1928), Reed (1947), Bourdeau and Adams (1956), Adams (1963), Cooper and Waits (1973), Godfrey and Godfrey (1974).

Hall and Penfound (1939) and Montz and Cherubini (1973), all working in Louisiana, discussed the tension zones between tidal marshes and coastal swamps. Research Summary 41 also addresses this topic, documenting the invasion of trees into a brackish marsh in Alabama.

A rather frequent sight in needlerush marshes are places where masses of detritus have concentrated, weighting down and sometimes smothering the needlerush. These "cowlicks", as they are called locally, are roughly 10-25 m^2 in area and are caused by an eddying of the tidal sheet flow over a large area of marsh. Coultas and Gross (1975) observed anomalous patches of cordgrass in needlerush marsh and suggested that the cordgrass may have become established after the needlerush was smothered in cowlicks.

Eleuterius and Eleuterius (1979) tried to determine why there was such a sharp line of demarcation between cordgrass zones and needlerush zones in lower salt marshes in Mississippi. This line occurred at 0.54 m above msl. The cordgrass zone was entirely inundated 139 times during the year of study (1975) and the needlerush zone only 16 times. Most high tides flooded the lower three-fourths of the cordgrass zone but did not reach the upper one-fourth, as determined by automatic gauges. The lower three-fourths of the cordgrass zone was flooded 35-87% of the total hours per year, depending upon the elevation above msl within that zone. The upper one-fourth was flooded about 10% of the total hours. In contrast, the needlerush zone was flooded 0.5-5% of the total hours of the year. They concluded that the line of demarcation between the cordgrass and needlerush zones was not related to the frequency or duration of inundation.

Storm Damage. Hurricane damage in the tidal marshes of the northern Gulf coast was described by Harris and Chabreck (1958), Gunter and Eleuterius (1971) and Chabreck and Palmisano (1973). The later authors said,

> "The loss of vegetation was mainly a result of the sweeping action of wind and water, and plants were either uprooted or ripped apart and carried away by the current. Water salinity increased with the hurricane but declined by the following year and appeared to have only slight effect on marsh vegetation."

Some species had not recovered a year after the storm, including Eichhornia crassipes, Panicum hemitomon, Sagittaria graminea (all fresh water species), Scirpus robustus, and Panicum repens. Other species were much more abundant a year after the storm, including Paspalum distichum, Crinum americanum, and Ruppia maritima. Most species were either relatively unaffected or were making a satisfactory recovery, including Distichlis spicata, Phragmites australis, Sagittaria lancifolia, Saururus cernuus, Scirpus pungens, and Spartina alterniflora.

Craighead and Gilbert (1962) described the extensive damage to the coastal vegetation of the Everglades from a hurricane in 1960. The deposition of marly silt sealed the soil and created anaerobic conditions lethal to mangroves and other plants. Leisions in roots were thought to have allowed the passage of toxic levels of H_2S from the soil into some plants. Live oak, slash pine, and particularly cabbage palm were noted as being particularly wind resistant.

Marsh Paleoecology. Marshes are not static. Kurz and Wagner (1957) cited several evidences that suggested recent changes in salt marshes. One was a spodic horizon that began in the soil profile of the beach near the St. Marks lighthouse and continued seaward. They discovered woody roots preserved in this horizon 69 meters offshore. They observed rooted tree stumps offshore from marshes and other coastal environments---the relicts of an actively eroding coast. They described miniature cliffs, mentioned earlier, at the transition between the upper marsh and the pine flatwoods that indicated undercutting and erosion from sheet flow. They mentioned the many pine "islands" which are surrounded by salt marsh. These islands appeared as if the marsh had moved inland, drowning most of a formerly continuous pine flatwoods but leaving unmolested the slightly elevated sites. They observed new rhizomes of needlerush that were invading adjacent salt flats, as if these flats were becoming less saline. They noted sandy barrens covering peat, as if sands had been washed on top of formerly vegetated marsh and smothered the plants.

They attributed these changes to the effects of a gradual rise in sea level during recent decades and cited studies which documented this rise. They suggested that the marshes were encroaching into flatwoods, converting these habitats into new salt marshes. They claimed that the beaches were being pushed inland over former salt marshes as sea level rose. Recent geological evidence supports most of their contentions, but some of the changes that they cited began in late Holocene times rather than recently. Their hypothesis that beaches were migrating inland is not supported.

During the late Pleistocene, sea level was much lower (Figure 22). The terrain upon which the present marshes occur was upland habitat. Sea level gradually rose until 6000 BP and remained static temporarily at a point 2 m below present msl. During this sea level stand, a beach developed which is now submerged but still detectable as a low ridge system (Tanner and Bates 1965). By 4500 BP sea level had risen to a height 1.75 m above present msl, where it cut another beach into the sands of the Silver Bluff Formation (Murali 1976).[1] This height is only about a half-meter above today's highest predicted tides.

Later, sea level dropped below what it is today. Evidence of this drop is derived in part from kitchen middens buried beneath present salt marshes. Fibers from pot-sherd in these middens were C-14 dated to 1500 BP by Stapor (1973). Kurz and Wagner (1957) discovered a shell midden beneath a beach at Shell Point. They obtained a C-14 date of 1550 BP from the lowest stratum of peat in the marsh immediately behind this beach. That date closely corresponded with the 1500 BP dating by Stapor. The peat was 1.5 m deep and derived from cordgrass. Kurz and Wagner calculated the average rate of peat aggradation at 8.6 cm per century at Shell Point since 1550 BP.

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[1] R. S. Murali (verbal communication, 1979) suggested as an alternative explanation to the apparent 1.75 m rise in msl that wave action may have been locally greater in the eastern panhandle in 4500 BP than at present. The ecological consequences would have been the same with either explanation.

Stapor (1973) presented several evidences that mean sea level rose at the rate of at least 17 cm per century from 1500 BP to 700 BP. He also gave evidence for a rise in sea level during the first half of the present century. There is no indication that the present beaches are moving, in spite of rising sea level. They seem to be aggrading on top of another shoreline of the Silver Bluff Formation, midway between the -2 m shoreline and the +1.75 m shoreline. This intermediate shoreline must have developed between 6000 and 4500 BP when sea level corresponded to its present position. The ridge of this old shoreline would have stalled waves, causing sand suspended in the water to settle and build the present beaches, such as the one diagrammed in Figure 43.

Coultas (1969) discovered a pine log in a salt marsh 3 miles above the mouth of the St. Marks River, resting on a substrate 1.75 m deep and covered by peat. This log was carbon dated at 5280 BP. Current evidence would suggest that this log was buried beneath the first post-Pleistocene peats formed by salt marshes in this region. These peats were later submerged when sea level rose to its maximum height in 4500 BP.

This rise would account for the extension of the marsh inland and for the formation of the pine islands. When sea level subsequently dropped below the present level in 1500 BP, the marshes were reestablished and have persisted to present. The woody roots 69 m offshore from the St. Marks lighthouse theoretically would date to 1500 BP. The more recent increases in sea level since then would account for the miniature cliffs, the eroding coast, the stranded stumps offshore, and the invation of salt flats by needlerush.

Sheet flow is spreading the sandy talus of the miniature cliffs over the marsh, perhaps accounting for the sandy barrens that cover the peat. Sand is also imported by sheet erosion from the flatwoods and by creeks and rivers that carry particulates after heavy rains into the marshes. Much of this accretion of sand must be eroding almost immediately into the estuaries, or else the elevation of most marshes would be approaching that of mean high tide.

Needlerush occurs far up the St. Marks River where salinities are negligible except after hurricanes. It is also common at the heads of tidal creeks that extend well into the flatwoods. Needlerush seeds germinate in fresh water, but its seedlings would seem to be at a disadvantage from the competition afforded by the many species of brackish and fresh water marshes. It is possible that needlerush has persisted by vegetative propagation from rhizomes in these inland habitats since 4500 BP when sea level was higher and salinities were greater. If so, hurricanes may contribute salt water with sufficient frequency to curtail competition from fresh water species, thereby preventing the extinction of needlerush in these sites.

The Everglades. The Everglades of southern Florida are far removed from the panhandle both in distance and in climate. Nonetheless, the region is comprised to a large extent of brackish marshes dominated by sawgrass. *Eleocharis cellulosa* and many other species in the panhandle from brackish marshes and the transitional marsh zone are common in the Everglades. Insight into brackish marshes can be gained from various publications on the Everglades, among them being those of Egler (1952), Stephens (1956, 1974), Loveless (1959), Alexander (1971), Craighead (1972), Cohen (1974), Cohen and Spachman (1974), Gleason et al. (1974), and Hofstetter (1974).

Karst Features. Salt marshes east of the Ochlockonee River lie on a bed of limestone that is often less than 2 m below the surface and occasionally outcrops. The grass, *Monanthocloe littoralis* is often abundant in salt flats next to these outcrops. Sinkholes and ponds formed by sinkhole activity are common in salt marshes. A dragline cracked the limestone near the St. Marks lighthouse several years ago and created a fresh water spring from which water continues to flow.

Fill-Roads. The balance between salinity and soil moisture with reference to vegetational zonation suggests that most any disturbance in a salt marsh would have a pronounced vegetational impact. With that supposition in mind, a study was made in Wakulla, Taylor, and Dixie counties to assess the biological effects of fill-roads that had been built across salt marshes (Clewell et al. 1976). The comparison of recent and older aerial photographs provided evidence of change, as did field inspections. Four conclusions emerged from this study.

First, if a culverted fill-road cuts off the upper end of a salt marsh beyond the point where any tidal creeks have defined channels, the impact is noticeable within four years. The soil becomes drier, salinity decreases, and the species of transitional marsh and shrub zones invade the upper needlerush marsh, including *Spartina bakeri*, *Baccharis halimifolia*, *Juniperus silicicola*, and *Andropogon* spp.

Second, if an unculverted fill-road cuts off the upper end of a needlerush marsh, the marsh quickly becomes brackish and eventually fills completely with sawgrass. Third, if a fill-road cuts off the upper end of a salt marsh but the tidal creeks are bridged so as not to impede their normal flow, there may be no change after 40 years, except in the immediate vicinity of the right-of-way. If the channel of a tidal creek does not extend to the bridge, a connecting ditch may be required to facilitate tidal flow beneath the bridge.

Fourth, if a salt marsh occupies a peninsula which is inundated from an estuary on either side, and a fill-road is constructed on the highest terrain along the length of the peninsula, there will be no ecological consequences beyond the right-of-way, even if the road is not culverted.

Other Anthropomorphic Interventions. Fire has been used as a tool in tidal marsh management within the national wildlife refuges of the panhandle. Accounts have been written by Lynch (1941) and Zontek (1966).

Marsh drainage has been facilitated substantially in many salt marshes in Florida and elsewhere by ditching in an effort to control mosquito populations. Kuenzler and Marshall (1973) observed no effects on the vegetation in North Carolina marshes that were ditched. Clewell (1979) warned that the complexity of salt marsh ecology was becoming more apparent with each published study and that seemingly innocuous projects for mosquito control may be having profound impacts.

Salt marshes have been used for cattle pastures to a limited extent in the panhandle. Yarlett and Moore (1963) said that needlerush was useless for grazing but that it could be 95% eliminated by two consecutive mowings or burnings or by the application of 2, 4-D. After its removal, the needlerush is replaced in the eastern panhandle by more desireable species, including *Spartina alterniflora*, *S. cynosuroides*, *S. patens*, and

Distichlis spicata. McAtee *et al*. (1979) showed that burning or particularly shredding increased the forage biomass and the quantity of infloresences of *Spartina spartinae* in eastern Texas.

There has been a recent effort to vegetate coastal spoil islands with salt marsh plants, wherever moisture conditions allow. Initial plantings of several species on Drake Wilson Island by ecologists from Florida A. and M. University were highly successful. This large spoil island near Apalachicola was created in 1977. Natural colonization by tidal marsh plants was equally impressive. Nominal wave action, though, was causing rapid erosion in places. Substrate stabilization appeared to be the only threat to the ultimate success of the project. Coultas *et al*. (in press) said that erosion within the intertidal zone of a spoil island in Dickerson Bay, Wakulla County, caused poor survival among salt marsh plants. At higher elevations, *Spartina patens* and plants of several dune species spread rapidly and stabilized the substrate.

Other investigations of spoil islands were published by Woodhouse *et al*. (1972) in North Carolina and Eleuterius (1972) in Mississippi. The latter paper contained cutaway profiles of marsh topography and vegetation, showing the changes after spoils were deposited. Experiments and techniques for transplanting salt marsh plants were published by Stalter and Batson (1969), Stalter (1973a), Woodhouse *et al*. (1972, 1974), Broome *et al*. (1974), Seneca (1974), Knutson (1977), and Hunt (1979).

Some salt marshes in the St. Marks Refuge were impounded in the late 1930's and early 1940's creating brackish conditions favorable for overwintering waterfowl. In time, the needlerush and other salt marsh plants were replaced by sawgrass, cattails, and other coarse perennial species of brackish marshes. Wax-myrtle and other shrubs which later invaded these marshes were successfully controlled with fire. When the sawgrass, cattails, and other coarse graminaceous plants became too dense and interferred with waterfowl utilization, salt water was pumped into the impoundments by Refuge Biologist C. S. Gidden. The technique proved effective in suppressing the vegetation.

One of these impoundments was next to the St. Marks lighthouse and was dominated by Paspalum distichum (relative density 33%) and contained many fresh water species. The site was flooded with salt water during a hurricane in 1972. Two years later Paspalum distichum was still dominant, but tidal marsh plants had invaded or were much more prominent than before, especially Spartina bakeri, also Scirpus robustus and Spartina alterniflora.

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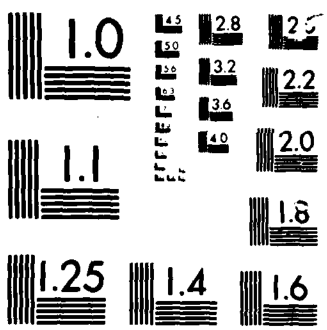

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39. FLOWING WATER SYSTEM

Flowing water environments include springs, perennial rivers, and estuaries. The vegetation in these environments consists primarily of submersed aquatics and emergent aquatics. Floating leaved aquatics and especially free floating aquatics are uncommon. The submersed aquatic vegetation is largely restricted to clear, relatively shallow waters where light regularly penetrates to the bottom. Black water rivers are darkened too much from tannins and are usually too shaded from a gallery of overhanging trees to support more than a few, isolated aquatic plants. Brown water alluvial rivers are too turbid to allow light penetration, and the swift currents and shifting substrates at flood stage further limit the possibilities for the establishment of aquatics. The only flowing water habitats of significance that could support aquatic vegetation in abundance are springs, spring-fed rivers, and estuaries.

Emergent aquatics are largely limited to habitats where the hydroperiod is continuous or nearly so throughout the year. This condition is met along the margins of springs and spring runs and on the banks of rivers within the zone of tidal influence. The continuous flow from springs insures nearly constant water levels along the edges of springs and spring runs. The damming effect of the tides keeps the banks wet along the tidal reaches of rivers in dry seasons. Further up river, the river banks are too dry to support emergent aquatics in dry seasons, or they are too deeply flooded during wet seasons. Nearer the coast the flood waters are dissipated rather than contained within a valley, and flooding is either shallow or brief.

Community Organization. The vegetation is not organized into distinct communities. One or few species tend to form zones along environmental gradients. In a given habitat, these zones collectively comprise the community. Only a single zone may be present in some habitats. The zones may be very broad, or they may be crowded.

Species Richness. Each aquatic community generally consists of only a few species, often less than ten. The emergent aquatic vegetation is floristically richer than the submersed aquatic vegetation, but the total number of species is low or moderate.

Physiognomy. The emergent vegetation is generally of slender, erect plants, these often graminaceous. There is little or no stratification. The submersed vegetation consists of two life form groupings. The first group consists of tape-grasses and other acaulescent plants which produce long slender leaves from rhizomes. These include *Vallisneria americana*, *Sagittaria kurziana* and *Thalassia testudinum*. The other group produces stems within the water column, and the leaves develop from nodes along these stems. Examples of nodal species are *Ruppia maritima*, *Najas guadalupensis*, and *Ceratophyllum demersum*.

Soils. The substrate varies considerably from mucks to sands or clays and seemingly has little influence on the vegetation. Most importantly, the substrate must be sufficiently permanent to provide anchorage. Rock outcroppings are typically devoid of vegetation, presumably because they are unsuitable for anchorage. Response to pH, nutrients, and salinity is variable.

Maintenance. The communities are seemingly permanent, although natural disturbances may frequently disrupt the vegetation in any given place. If the substrate is stable and not grossly modified by disturbance, the same species may be expected to return that occupied the habitat previously. Few species occur in these habitats, and the chances of community replacement after disturbance are thereby enhanced.

Response to Disturbance. Temporary changes in species abundance are experienced after hurricanes (see p. 551-2). Salinity shock, mechanical damage, and outright removal of plants are the primary types of hurricane damage. Channel dredging is a serious type of disturbance. Not only is the community destroyed at the site of disturbance, but also the substrate is disrupted. As a result, nearby aquatic vegetation is adversely affected by turbidity and sediment deposition. Turbulence is also caused by propellors in lanes frequented by motor boats. The intensity of these man-made disturbances to the substrate is not paralleled by forms of natural disturbance. Natural rates of sedimentation and erosion are so slow that the plants are able to adapt to new conditions without disruption.

Mode of Origin. Populations of the various species apparently colonize open habitats and persist. The vegetation in any given habitat, therefore, reflects the initial floristic composition rather than the product of seral development.

Ecotones. The emergent vegetation of the riparian fresh water marsh community intergrades with the brackish marsh community, as was described on pages 521-2. Many species of flowing water habitats also occur in habitats of the palustrine system, but these two systems are physically separated from each other.

Communities. Four communities are recognized: riparian fresh water marshes, spring run assemblages, tidal river assemblages, and seagrass beds. The riparian fresh water marshes include all emergent vegetation, and the other three communities include all submersed vegetation. The spring run assemblages occur in relatively clear fresh water. The tidal river assemblages occur in brackish water, usually where salinities are variable in any given place, but rarely above 24 o/oo. Seagrass beds occur in bays and estuaries with higher salinities. Some intergradation is observed between the three submersed aquatic communities as one goes up-river from an estuary. These communities are compared in Table 34.

Riparian Fresh Water Marshes

This community was described in the panhandle by Thompson (1977) along the Wakulla River near the bridge of U.S. 98. Table 35 gives densities of the plants at this site. Other results are shown in Research Summary 40. Thompson's study site 3 miles south of the U.S. 98 bridge contained vegetation primarily of this community, although brackish marsh species were also present. No other studies have been made in the panhandle.

Field notes pertaining to the riparian fresh water marsh community were made on several canoe trips. The Blackwater River contained patches of marsh well above the zone of tidal influence on recently deposited low levees that almost entirely blocked the mouths of several tributary creeks. Scirpus cyperinus and Andropogon virginicus were the most common species. Young red maple swamps were developing in the impounded waters behind these levees.

TABLE 34. Conspectus of Flowing Water System Communities.

COMMUNITY	HABITAT	VEGETATION
25. Riparian Fresh Water Marshes	Banks along spring runs and along rivers near the upper end of the zone of tidal influence. Patchy or absent elsewhere. No measurable salinity.	Cicuta maculata Juncus effusus, J. polycephalus Lobelia cardinalis Physostegia purpurea Polygonum punctatum Pontederia cordata Rumex verticillatus Sagittaria lancifolia, S. subulata Scirpus cyperinus, S. validus Sium suave Zizania aquatica Zizaniopsis miliacea
26. Spring Run Assemblages	Springs and spring-fed rivers in cool, fresh, and often swiftly flowing water.	Ceratophyllum demersum Najas guadalupensis Potamogeton illinoensis, P. pusillus Sagittaria kurziana, S. subulata Vallisneria americana
27. Tidal River Assemblages	Tidal rivers and bays with variable salinities, the mean about 1-8 o/oo.	Ruppia maritima Sagittaria subulata Vallisneria americana
28. Seagrass Beds	Estuaries and the open Gulf with salinities variable and mostly between 7 and 34 o/oo.	Halodule wrightii Halophila engelmannii, H. baillonis Syringodium filiforme Thalassia testudinum

TABLE 35. Densities of Riparian Fresh Water Marsh Plants along the Wakulla River at the U.S. 98 Bridge (from Thompson 1977).

	East River Bank	West River Bank
Number of Plants per Meter^2	108	137
	RELATIVE DENSITIES	
Cicuta maculata	< 1	< 1
Crinum americanum	0	3
Physostegia purpurea	6	8
Hymenocallis crassifolia	0	2
Isoetes flaccida	6	7
Juncus polycephalus	69	3
Ludwigia repens	0	< 1
Peltandra virginica	0	< 1
Polygonum punctatum	< 1	3
Pontederia cordata	12	2
Rhynchospora corniculata	0	< 1
Rumex verticillatus	0	< 1
Sagittaria lancifolia	2	1
Sagittaria subulata	2	65
Saururus cernuus	0	3
Scirpus validus	2	< 1
Zizania aquatica	< 1	< 1
	100	100

The Apalachicola River contained marshes along its banks southward of the confluence of the Brothers River, which is about 14 river miles from the Gulf coast. Juncus effusus and Zizaniopsis miliacea were both common. Nuphar luteum and some Pontederia cordata occurred in shallow waters along these banks in places. Brackish marsh species appeared just below the railroad tressle 6 river miles from the coast. North of the Brothers River, the river banks were lined with swamps, rather than marshes, except at abandoned woodyards which usually contained Juncus effusus in abundance.

The St. Marks River contained widely scattered patches of marsh along its banks between Natural Bridge and Horn Springs well above the zone to tidal influence. These marshes occurred wherever there were breaks in the forest canopy and were dominated by Pontederia cordata and Sium suave. Mikania scandens was common, and a few patches of Sagittaria lancifolia were conspicuous.

Mary Butler Davis (personal communication 1975) inventoried the vegetation at Wacissa Springs. Two kinds of marshes were present. One consisted primarily of Scirpus validus which was rooted in shallow flowing water along the river bank. Cicuta maculata was also present. The other consisted of floating mats of vegetation over the main spring boils. These mats were anchored on logs and were supported partially by masses of submersed aquatic vegetation. The mats consisted of plants of Eichhornia crassipes (water hyacinth), Limnobium spongia, Polygonum punctatum, Cicuta maculata, Hydrocotyle umbellata, Zizania aquatica, Hymenocallis crassifolia, and unidentified species of Panicum, Rhynchospora, and Lemnaceae. The water hyacinth generally grew in pure populations rather than with plants of the other species.

26. *Spring Run Assemblages*

As with the preceding community, this community was described in the panhandle by Thompson (1977) along the Wakulla River near the bridge of U.S. 98. The results of this study are summarized in Research Summary 44. The species present were as follows, listed in decreasing order of biomass: Vallisneria americana, Sagittaria kurziana, Sagittaria subulata, Potamogeton illinoensis, Najas guadalupensis, and Potamogeton pusillus. The total standing crop was 764 g/m^2, dry weight. Birkitt et al. (1979) also sampled for biomass at this site in 24, 0.25 m^2 quadrats and estimated the standing crop to be 1442 g/m^2. Biomass values for individual species were Sagittaria kurziana 963 g/m^2, Vallisneria americana 429 g/m^2, and Potamogeton illinoensis 50 g/m^2. Najas guadalupensis was present as a trace only.

This species assemblage is common throughout the panhandle in springs and spring-fed rivers. The tape-grasses (Sagittaria kurziana, Vallisneria americana) are particularly common in swiftly flowing water. The nodal species are more common in quieter waters. Two introduced species have become established in the spring-boil at the Wacissa River, Egeria densa and Hydrilla verticillata.

In the St. Marks River below Natural Bridge, the most common species was Potamogeton illinoensis. Some Najas guadalupensis was present, but tape-grasses were absent. Just below the delta of the Apalachicola River the bay is extremely shallow over wide areas. Vallisneria americana and Potamogeton pusillus were abundant in waters about 0.5 meters deep.

The latter is a fresh water species (Thompson 1977). Evidently, the enormous discharge of river water is sufficient to maintain fresh water conditions nearly into Apalachicola Bay.

27. *Tidal River Assemblages*

As with the preceding two communities, this community was described in the panhandle by Thompson (1977) along the Wakulla and St. Marks rivers. The community was dominated by Ruppia maritima where salinities were greatest, i.e., nearest the coast. This species extended into seagrass beds offshore from the mouths of rivers. With increasing distance up river from the coast, additional species occurred with R. maritima, presumably in response to less saline conditions. These species are also present in spring run assemblages. Vallisneria americana is abundant where salinities are sometimes as high as 24 o/oo. Potamogeton perfolitus was the only other species tolerant of those conditions in the St. Marks River. Not all species of spring run assemblages tolerate measurable salinities. Potamogeton illinoensis, P. pusilus, and Sagittaria kurziana are restricted to fresh waters.

Tidal river aquatics are subjected to the salinity "wedge" which is forced upstream along the river bottom at high tide (see p. 521). This wedge is clearly demonstrated in Thompson's data, which were recorded monthly for a year (Research Summary 44). At the U.S. 98 bridge, the salinities were less than 0.5 o/oo at all times, both top and bottom. Three miles downstream, the mean salinities at the surface were about 0.5 o/oo at the surface and nearly 2.5 o/oo at the bottom. Maximum salinities at this site were about 1 o/oo at the surface and 12 o/oo at the bottom. Further downstream, the mean and maximum salinities were regularly higher at the bottom than at the surface. Values for total hardness paralleled those for salinity. Odum (1953) cited evidence that not all of the salinity was attributable to tidal intrusion. He said that rivers in Florida as far west as the Wakulla were receiving a contribution of salt that was leaching from the surficial limestones. These rock formations had been saturated with sea water during the high sea level stands in the Pleistocene and still contained residual salts from that inundation.

Thompson (1977) reported that local residents claimed that the hurricane of 1972 virtually eliminated all aquatic vegetation from at least the brackish portions of the St. Marks and Wakulla rivers. It is not known if the plants were salt-killed or uprooted. Recovery was rapid, as was evidenced from the values for standing crop (Research Summary 44). These values were not as high as those recorded at the U.S. 98 bridge, though, because of channel dredging and turbidity caused by boat propellors.

28. *Seagrass Beds*

One or more of five species comprise the flora of seagrass beds. Turtlegrass (Thalassia testudinum) and manateegrass (Syringodium filiforme) are the most common. Shoalgrass (Halodule wrightii) is less abundant but widespread. Halophila engelmannii is much less common, and Halophila baillonis is rare and restricted to deep waters. Widgeongrass (Ruppia maritima) sometimes extends offshore from tidal rivers into seagrass beds. These species were described in Chapter 29.

Humm (1956 concluded that seagrass beds are nearly continuous in distribution throughout the panhandle. He said,

> "Shifting sands and river mouths are the two major factors responsible for minor interruptions in the distribution of sea grasses....In general the outer edge of sea grass beds seems to be determined by wave action and shifting sands or, in some places, by the level of extreme low tides. Sea grasses are often exposed at spring low tides, after which a killing of the leaves is evident."

Seagrass beds are extensive in the shallow flats of Apalachee Bay and were described by Gidden (see Research Summary 45). Humm (1973) estimated that only 10% of the seagrass beds were in estuaries because the fluctuations in salinity, temperature, and turbidity were limiting. Nonetheless, seagrasses are common at the mouths of the Suwannee and Ochlockonee rivers and near Alligator Point (Humm 1956). Only 7% of Apalachicola Bay contains seagrass beds, being limited there by high turbidity (Livingston _et al_. 1975). All six species are present there (Menzel 1971). Humm (1973) estimated that turtlegrass accounted for 60-75% of all the seagrasses in terms of cover or biomass in the eastern Gulf of Mexico.

Any of at least 30 species of benthic macrophytic algae may comprise part of the vegetation of seagrass beds in the panhandle. _Halimeda incrassata_ (a green alga) and _Digenia simplex_ (a red alga) were noted as dominants by Zimmerman and Livingston (1976a, b; Research Summaries 46, 47) off Taylor County. Humm (1973) estimated that the productivity of the seagrasses in the eastern Gulf may exceed that of all benthic algae or of the overlying plankton. He said that turtlegrass fixed about 900 g of carbon/m^2/year. Zimmerman and Livingston showed that the biomass of the benthic algae sometimes exceeded that of the seagrasses.

Soil. Seagrasses grow best on mucky sands or mucks. They become sparse or absent on hard-packed sands and on shell bottoms. Turtlegrass and manateegrass prefer rather sandy substrates, perhaps because mucky substrates contribute to turbidity which is especially detrimental for these species. The other seagrasses are less specific in their preference of substrates.

During the summer, the meadows of seagrasses prevent the current from stirring the muck. As a result, the water remains free of turbidity during the growing season. These meadows protect the substrate from erosion by storms and hurricanes. Low water temperatures in winter and exposure to cold air at low tide cause leaf-kills. The substrate is then exposed to currents, and the water becomes more turbid. Light penetration is further reduced by highly colored river water which is discharged into seagrass flats in large quantities with winter rains. High color and turbidity occur during the dormant season when their adverse effect on growth is minimal.

Ginsburg and Lowenstam (1958) gave evidence that seagrasses act as baffles and trap sand carried by the currents. Roots of the seagrasses grow into this newly deposited sand and stabilize it. This increment of sediment may be lost during storms. A severe hurricane caused sufficient erosion and sedimentation to uproot or bury 1,396 ha of seagrass beds near the sea islands of Mississippi Sound (Eleuterius and Miller 1976).

Water Parameters. Seagrass beds in shallower waters are exposed occasionally at low tide, particularly at spring low tides or when a strong offshore wind pushes the tide out beyond the predicted position. Phillips (1960) said that the predicted low tides at Tampa were identical for March 2 and 3, 1958. On March 2, the bottom was exposed nearly 100 m offshore because of a strong wind. On March 3 the bottom was exposed only 5 m offshore, and the wind was much calmer.

Strawn (1961) said that predicted spring low tides at Cedar Key were -1.0 m below msl. Offshore winds on September 18, 1947, caused a low tide of -1.4 m, the lowest recorded in an 11 year period. Strawn noted that the seagrass beds were extensive between mean low water (-0.8 m) and the lowest low tide. The lowest tides occurred in February when the bottom at -0.4 m was exposed 5% of the time. Seagrasses are not necessarily exposed to the cold, dry winds in February for as long as predicted. Drainage at low tide is impeded by bars, pools, and the friction from the dense seagrass shoots. Those species occurring in shallow water (especially shoalgrass) have flaccid leaves which lie flat at low tide, thereby remaining immersed as long as possible in the residual water. Those species occurring in deeper water (particularly manateegrass) have more stiffly erect leaves, which are less likely to bend in the current. Their erect habit keeps them better exposed to light but makes them more susceptible to exposure at low tide.

Salinity is variable but is generally lowest near shore, particularly near river mouths. Rains can lower salinities temporarily. Salinities offshore are generally 17-36 o/oo along the coast of the panhandle but drop to 6-10 o/oo after heavy rains. Full sea strength is about 35 o/oo.

Hypersaline conditions do not develop in the panhandle as they do along the Texas coast where the arid climate reduces stream discharge into estuaries and allows the concentration of salt water by evaporation.

Prolonged exposure to exceptionally high volumes of floodwater discharge from rivers during two consecutive winters killed 1,296 ha of shoalgrass near shore in Mississippi Sound. This discharge was so great that salinities in seagrass beds offshore near the barrier islands averaged 4 o/oo for three months. Turtlegrass and shoalgrass experienced heavy leaf-kills, and some manateegrass was entirely killed near these islands (Eleuterius and Miller 1976).

Discussion

Fresh Water Habitats. Odum (1957a) published one of the first major studies on trophic structure and productivity, based on extensive work at Silver Springs in Marion County. Much information was presented on growth rates and productivity of the tape-grasses. Mention was made of the aufwuchs community which consists primarily of epiphytic algae on tape-grasses. This periphyton becomes massive on older leaves. Odum (1957b) estimated primary productivity for 11 other springs in Florida.

Barko and Smart (1978) studied the growth of *Scirpus validus* and *Cyperus esculentus* under controlled conditions. They discovered that the growth of these two emergent marsh species was determined by the type of sediments in which the plants were rooted. Their work indicates that nutrients in the sediments, rather than in the water column, are important in determining growth and biomass characteristics.

Saline Water Habitats. Eleuterius (1971) reported that Vallisneria americana was common in the bayous and river mouths of Mississippi Sound in water up to a meter deep. This observation parallels that reported earlier with regard to the abundance of V. americana at the mouth of the Apalachicola River. Other observations on brackish aquatics are scarce. Radford (1976) listed the aquatics in the brackish portion of the Alligator River in Tyrrell County, N. C. Species present included Najas guadalupensis, Potamogeton perfoliatus, Ruppia maritima, Sagittaria subulata, and Vallisneria americana. Montz (1978) described the aquatics in Lake Pontchartrain, Louisiana. The salinity of this coastal water body varies but generally has a salinity of less than 5 o/oo. Species present included Vallisneria americana, Ruppia maritima, Najas guadalupensis, Zannichellia palustris, Potamogeton perfoliatus, and Eleocharis parvula.

Studies on seagrasses have been much more frequent. Those studies which pertain to the panhandle are the following, including some that were done elsewhere but which have pertinence to the understanding of the seagrasses in the panhandle. Thorne (1954) listed the seagrasses of the Gulf of Mexico. Humm (1956) noted the distribution of the seagrasses along the northern Gulf Coast. Ginsburg and Lowenstam (1958) established that seagrasses trap sand and increase sedimentation. Phillips (1960) summarized the literature on each of the seagrasses in the Gulf and presented many ecological observations on them from studies in the Tampa Bay area. Strawn (1961) presented detailed observations on the seagrasses at Cedar Key. Moore (1963) correlated the distribution of turtlegrass with environmental factors. Gidden (see Research Summary 45) conducted a quantitative inventory near the St. Marks lighthouse in Wakulla County.

McMillan and Moseley (1967) and McMahan (1968) studied salinity tolerances of seagrasses. Fuss and Kelly (1969) recorded the growth and survival of seagrasses under controlled conditions. den Hartog (1970) monographed the seagrasses of the world and gave ecological data. Eleuterius (1971, 1973) noted the seagrass distribution in Mississippi Sound. Menzel (1971) listed the seagrasses of St. George Sound. Humm (1973) reviewed the literature on seagrasses for the eastern Gulf of Mexico. McMillan (1974) discussed salt tolerances in seagrasses. Livingston _et al_. (1974) noted the extent of seagrasses in Apalachicola Bay. Eleuterius and Miller (1976) described the destruction of seagrass beds in Mississippi Sound following a severe hurricane and following unusually low salinities. Phillips _et al_. (1974) redefined the species of _Halodule_ taxonomically. van Breedlove (1975), Steller (1976), Phillips (1976) and Thorhaug (1979) experimented with transplanting seagrasses. Zimmerman and Livingston (1976a, b) made monthly determinations of biomass near the mouths of the Econfina and Fenholloway rivers off Taylor County. They correlated biomass and species distributions with physical factors and effluents from a kraft mill. McMillan (1976) gave phenological data on seagrasses with special reference to temperature. Thompson (1977) correlated the distribution of _Ruppia maritima_ with habitat factors in the lower St. Marks River. McMillan (1979) determined that chill tolerance was greatest for shoalgrass, least for manateegrass and intermediate for turtlegrass.

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40. PALUSTRINE SYSTEM

The palustrine system includes all vegetation associated with lakes, ponds, and wet weather depressions. In most parts of the world, lakes are considered to be permanent water bodies. In the panhandle, though, even the largest natural lakes become dewatered periodically, as was explained in Chapter 9. The organic sediments desiccate and sometimes catch fire. At other times, the lake basins become filled above their normal high water levels, thereby exserting control over the vegetation in adjacent, normally well drained habitats. As a result, the vegetation of a lake basin is exceptionally heterogeneous and even includes some forested areas.

Palustrine vegetation typically is differentiated into concentric zones along an elevational gradient. The more distinctive zones are identifiable as communities. The outermost zone is often a narrow ring of live oaks or other woody plants which separate the other palustrine zones from the surrounding upland vegetation. The upland vegetation is often a longleaf pineland and almost always contrasts sharply with the outermost palustrine zone.

The next zone to the interior of the ring of live oaks commonly consists of terrestrial herbs. Periodic flooding prevents this zone from becoming forested by upland species which, as a class, are intolerant of prolonged hydroperiods. On the other hand, flooding is too brief for aquatic plants to become established. As a result, this zone is colonized by a miscellaneous assemblage of annual and perennial herbs which tolerate or adapted to a wide range of moisture conditions.

The next zone is shallowly flooded much of the year or at least experiences prolonged hydroperiods. The marsh that occupies this zone commonly consists of plants representing three discrepant life forms. The first life form is characterized by erect emergent herbs (e.g., Juncus effusus, Typha latifolia). The second life form is characterized by shrubs (e.g., Hypericum fasciculatum, Decodon verticillatus). The third life form is characterized by repent herbs (e.g., Hydrocotyle umbellata, Ludwigia palustris) and mat-forming herbs (e.g., Eleocharis baldwinii, Juncus repens). The plants representing these various life forms may exhibit zonation within the generalized marsh community.

The next zone occurs where there is permanent standing water during most years of near-normal rainfall. The shallower areas tend to be occupied by emergent species (e.g., Pontederia cordata, Panicum hemitomon), somewhat deeper areas by floating-leaved aquatics (e.g., Nymphaea odorata, Nuphar luteum), and all areas by submersed aquatics (e.g., Ceratophyllum demersum, Utricularia floridana) and often free-floating aquatics (e.g., Lemna minor, Azolla caroliniana).

Some lakes are ringed by pond-cypress swamps and sometimes also by bay swamps. If these swamps are distinctly contained within a zone of live oaks (and/or a palustrine zone of terrestrial herbs or of emergent marsh plants), then the swamp zones may be considered part of the palustrine system. If such zones are lacking and the lakes are merely depressions within pond-cypress swamps and bay swamps, then the swamps may not be considered part of the palustrine system. In the latter lakes, only the aquatic herbaceous vegetation (any any associated shrubs) comprise the palustrine system.

Palustrine vegetation is highly diversified, but is held together into one system by the control exserted by the water regime within a confined basin. The steepness of the elevational gradient often contracts the zones into narrow rings and virtually superimposes one community on top of another. It is not uncommon to see the spreading branches of live oaks extending between the trees of very narrow bay swamp and pond-cypress zones until they terminate above the floating leaves of *Nymphaea odorata*.

The more distinctive zones are recognized as separate communities. Each community may, in turn, exhibit some internal differentiation into zones consisting of particular species or species-groups.

Community Organization. The communities are poorly to moderately organized. Some communities are little more than assemblages of opportunistic species with similar habitat requirements which colonize a site for a few months between inundations or dewaterings. Other communities seem to consist of a series of overlapping single species zones along an elevational gradient. The forested communities are usually better organized, sometimes with distinct stratification. Some stratification also occurs in the marsh and submersed vegetation.

Species Richness. The number of species is usually low in aquatic zones and low to moderate in terrestrial zones. The total number of species in an entire lake basin is often high.

Physiognomy. Community physiognomy is highly variable and ranges from forest to submersed vegetation.

Soil. Soils vary considerably from organic peats and mucks to sands and clays. The organic sediments sometimes form a distinct stratum and at other times consist of a watery ooze. Upon exposure to the atmosphere, the organic sediments quickly consolidate and oxidize.

Moisture. Moisture conditions range from nearly xeric to flooded for years or decades at a time. All natural basins dry out or drain completely at least two or three times a century because of prolonged droughts or the opening of a sinkhole. Sinkholes are common features of many lake bottoms. When organic or mineral debris loosens in a sinkhole, the water drains as long as the lake is above the piezometric surface.

Fire. Once a lake has dried out, fire is likely, particularly since droughts often cause dewatering and also create conditions promoting wildfires. Desiccated peats may smoulder for weeks until they become completely mineralized. At times of normal water levels, fires sometimes ignite and burn through dense emergent marsh vegetation, even over the water's surface.

Mineral Nutrients. Almost nothing is known about mineral nutrition in lakes in the panhandle. Presumably, those lakes that are surrounded by flatwoods and cypress swamps are rendered sterile from the acidity which interfers with the solubility and absorption of nutrients. Many other lakes contain prolific growths of aquatic vegetation and appear to have adequate supplies of nutrients. Some of these nutrients are undoubtedly supplied by runoff and seepage from the surrounding watershed. The periodic dewaterings allow the nutrients in organic sediments to be released at once by oxidation or burning.

Maintenance. All vegetational zones are maintained and perpetuated by the hydrological regime primarily and sometimes by fire secondarily.

Occasional periods of prolonged hydroperiods or inundations occur in the typically terrestrial zones, preventing the invasion of upland vegetation from other systems. Periodic dewatering in typically aquatic zones prevents the accumulation of peats and the invasion of trees (except pond-cypress). Fires accentuate the effects of dewatering.

Response to Disturbance. The ability of the vegetation to survive the stresses caused by the hydrological regime makes the palustrine communities virtually immune to any other natural disturbances. Efforts to stabilize water levels by constructing dams and blocking sinkholes are substantial disturbances. Research Summary 48 describes how Lake Miccosukee suffered from these efforts and how difficult it is to return the lake to its natural condition.

Mode of Origin. All communities appear to represent the results of initial floristic composition. Periodic cycles of draining and flooding prevent the elaboration of a hydrosere. Paylonological studies cited in Chapter 15 suggested that palustrine vegetation in the panhandle is best explained by the displacement model.

Ecotones. The communities of palustrine systems are distinct from vegetation in most other systems. Fresh water ponds sometimes occur in interdunal swales, and the palustrine marsh vegetation intergrades with that of overwash prairies. Ponds also occur with some frequency in sink-holes within tidal marshes. Brackish marsh vegetation mingles with that typically associated with the palustrine system.

The relationship between palustrine zonation and the vegetation of acid swamps and pond-cypress swamps has already been mentioned. Instances of these swamps forming palustrine zones cannot be construed as intergradation, but rather as convergence. This convergence resulted from the necessity of conceptualizing the various systems on the basis of different criteria. Palustrine zones dominated by live oak also represent instances of convergence with live oak-dominated forests in other systems, such as coastal live oak hammocks. The live oak zones in palustrine systems are usually floristically depauperate and can be distinguished easily from live oak-dominated forests elsewhere on the basis of the species composition.

Communities. Four communities are recognized: palustrine hammocks, palustrine terrestrial assemblages, palustrine marshes, and palustrine aquatic assemblages. As was mentioned above, two additional communities could be borrowed from other systems for purposes of mapping or discussing total palustrine complexes: (8) bay swamps and (10) pond-cypress swamps. The communities are compared in Table 36. These communities are based more on the hydrologic regime and resulting physiognomy than on species composition. Therefore, the floristic integrity of these communities is much lower than in most communities from other systems.

14. *Palustrine Hammocks*

This community usually consists of a ring of live oaks separating the uplands from the interior palustrine communities. Typically, the zone is very narrow, often a single tree in width. Sometimes the zone is wider and more like a forest, particularly where the live oak zones of lakes in close proximity are contiguous. An understory of myrtle-leaf holly is sometimes present, or, less commonly, myrtle-leaf holly is present but without live oak. Some wet depressions are characterized by

TABLE 36. *Conspectus of Palustrine System Communities*

COMMUNITY	MOISTURE	PHYSIOGNOMY	VEGETATION
29. Palustrine Hammocks	Dry to moist, generally well drained, rarely and only briefly flooded.	Forest or thicket, of broadleaved species.	*Quercus virginiana* *Ilex myrtifolia* *Crataegus viridis*
30. Palustrine Terrestrial Assemblages	Rather dry to moist, generally well drained, occasionally flooded for a few days or weeks but not necessarily every year.	Meadow of herbaceous plants, these variable in density, height and species composition.	*Eupatorium leptophyllum* *Ludwigia suffruticosa* *Rhexia mariana* *Diodia teres*
31. Palustrine Marshes	Shallowly flooded part or most of each year, the soil usually moist or wet when not flooded.	Marsh of erect emergent herbs (sometimes with shrubs intermixed) and often of repent or mat-forming shallow-water herbs.	*Juncus effusus* *Typha latifolia* *Scirpus erismanae* *Ludwigia palustris* *Eleocharis baldwinii* *Hypericum fasciculatum*
32. Palustrine Aquatic Assemblages	Flooded all year in most years of near-normal rainfall.	Aquatic herbs: emergent, floating-leaved, submersed, and free-floating.	*Pontederia cordata* *Panicum hemitomon* *Nymphaea odorata* *Lemna minor* *Ceratophyllum demersum* *Utricularia floridana*

thickets of hawthorns, rather than live oaks and hollys. Gano (1917) listed Crataegus viridis and C. aestivalis as the common species. Other vegetation is sparse or at least low in the number of species. Other plants may include Smilax bona-nox and Rhus copallina.

30. Palustrine Terrestrial Assemblages

This community occurs as a terrestrial zone around lakes which exhibit considerable fluctuations in water level, but which are not normally filled to capacity. The flora is a miscellaneous assemblage of opportunistic species. These plants either survive inclement moisture conditions as dormant rootstocks, or they die and recolonize the site later from seed. The species composition and the dominant species both vary considerably from one lake basin to another, likely reflecting local seed sources and habitat conditions.

If one species were to be identified as being representative of the community, Eupatorium leptophyllum would be the most likely nominee. This species is common, conspicuous, widespread, and occurs in no other native habitat. Other species represent a combination of common weeds (e.g., Diodia teres, Wahlenbergia marginata), species characteristic of adjacent uplands (e.g., Crotonopsis linearis, Rhexia mariana, both from longleaf pinelands), and species of the adjacent palustrine marsh community which are able to tolerate the drier habitats presumably because the competition is not severe (e.g., Sacciolepis striata, Cyperus globulosus). Many other species could be listed for this habitat. A few of them are: Eriocaulon lineare, Hedyotis uniflora, Lachnocaulon minus, Ludwigia suffruticosa, Polypremum procumbens, Scirpus cyperinus, Scirpus erismanae, Xyris elliottii.

31. Palustrine Marshes

Palustrine marshes share many species with both the palustrine terrestrial assemblages and the palustrine aquatic assemblages. It is difficult to list the species of palustrine marshes without overlapping considerably with the floras of the other two communities. In lakes where water levels are relatively constant except briefly during extreme conditions, the distinction between these communities is made easily floristically. In lakes where the water level fluctuates widely over a period of weeks or a few months, the communities are weakly separated at best. Many of the more common species in palustrine marsh communities are listed in Table 37 among the repent and mat-forming species and the erect species.

32. Palustrine Aquatic Assemblages

As with the palustrine marshes, the aquatic assemblages vary considerably in species composition from lake to lake. Zonation is often apparent, with erect emergent plants in the shallows, floating-leaved aquatics in deeper water, and submersed aquatics in the deepest water. Upon closer examination, this categorization is not always clear. Submersed aquatics usually occur in all zones. Maidencane (Panicum hemitomon, an emergent grass), is often a dominant in deep water (exceeding 2 m). Free-floating aquatics may occur in all aquatic zones. Mat-forming plants typically occur in shallows but sometimes extend as floating rafts over deeper water. Most of the species listed in Table 37 are likely to occur in palustrine aquatic assemblages, including all species listed as free-floating, floating-leaved, and submersed.

TABLE 37. Some Species of Palustrine Marshes and Aquatic Assemblages.

REPENT AND MAT-FORMING SPECIES

Bacopa caroliniana
Eleocharis baldwinii
Eleocharis robbinsii
Habenaria repens
Hydrochloa carolinensis
Hydrocotyle umbellata
Juncus repens
Limnobium spongia
Ludwigia arcuata
Ludwigia palustris
Proserpinaca palustris

ERECT SPECIES

Amphicarpum muhlenbergianum
Bidens mitis
Carex alata
Cephalanthus occidentalis*
Decodon verticillatus*
Dulichium arundinaceum
Echinochloa walteri
Fimbristylis scirpoides
Fuirena squarrosa
Hypericum fasciculatum*
Hypericum gentianoides
Juncus effusus
Panicum hemitomon
Paspalum dissectum
Paspalum distichum
Pluchea foetida
Polygonum hirsutum
Polygonum hydropiperoides
Polygonum punctatum
Pontederia cordata
Rhynchospora corniculata
Rhynchospora microcarpa
Sabatia dodecandra
Sacciolepis striata
Sagittaria graminea
Scirpus cyperinus
Scirpus erismanae
Syngonanthus flavidulus
Typha latifolia

FREE-FLOATING SPECIES

Azolla caroliniana
Lemna minor
Spirodela polyrhiza

FLOATING-LEAVED SPECIES

Brasenia schreberi
Nelumbo lutea
Nuphar luteum
Nymphaea odorata
Nymphoides aquatica
Potamogeton diversifolius
Utricularia inflata
Utricularia radiata

SUBMERSED SPECIES

Cabomba caroliniana
Ceratophyllum demersum
Eriocaulon decangulare
Mayaca fluviatilis
Myriophyllum laxum
Myriophyllum heterophyllum
Najas guadalupensis
Potamogeton illinoensis
Potamogeton pusillus
Sagittaria graminea var. chapmanii
Utricularis floridana
Utricularia foliosa
Utricularia purpurea

*Woody species.

Discussion

Palustrine vegetation is very poorly known in the panhandle as well as in most of the rest of the southeastern coastal plain. The comprehensive limnological studies that are available for lakes in northern states have not been made in Florida. The recent paper by Tarver (1980) for Lake Miccosukee is the first published study that gives any type of botanical overview of any lake in the panhandle. A few limnological studies are available for Florida (e.g., McDiffett 1980), and some governmental agencies record physical data regularly for particular lakes (e.g., the USGS at Lake Jackson). Other agencies maintain files on aquatic vegetation (e.g., the Florida Department of Natural Resources with regard to aquatic weed control). Nobody has yet to piece together the botanical and physical data available for any given lake to describe vascular plant composition, zonation, and habitat factors.

The palustrine marshes of the panhandle share many of the same species with the fresh water marshes that occupy shallow depressions in pine flatwoods in central peninsular Florida. Comparable flatwoods depressions in the panhandle are occupied by titi swamps. The species of titi do not extend into central Florida, and marshes dominated by a complex of emergent and mat-forming herbs replace these woody species.

When a lake dewaters, exposing the bottom for several weeks or months, a great array of plants quickly appears. The rapidity with which they sprout suggests that their seeds are always present in the sediments and that they remain viable for many years while submerged. Xyris longisepala is endemic to the panhandle and appears abundantly on dried lake bottoms. Rhexia salicifolia is another endemic which is particularly common in such habitats. Many other species typical of palustrine terrestrial assemblages also appear on exposed sediments.

The division of the species into the several categories in Table 37 is somewhat artificial and needs clarification. The species listed as having floating leaves, for example, include species which often hold their leaves horizontally some distance above the water (Nelumbo lutea), and others that are submersed but hold rather large leaves just beneath the surface (Brasenia schreberi, Utricularia spp.). Some species that are listed as being submersed (e.g., Cabomba caroliniana) have floating leaves which are very small and inconspicuous.

The free-floating species are sometimes stranded temporarily along the shoreline. Some of the erect species are actually diffusely or weakly branched (e.g., Polygonum hydropiperoides). Limnobium spongia is one of several species that could fit in more than one category. Nonetheless, the categorization is presented to emphasize the trends in life forms present.

Eriocaulon decangulare, which is common in bogs, is listed as a submersed aquatic in Table 37. It grows abundantly in sandhill ponds southeast of Tallahassee (e.g., Clear Lake) as rosettes at depths of 4 or 5 meters.

Aquatic weeds are a serious problem in the panhandle. Native species rarely are regarded as weedy in natural environments, but in lakes and reservoirs with stabilized water levels the growth of native species is sometimes exceedingly prolific (Research Summary 48). The formation of floating islands of peat is particularly prevalent in such habitats, and a hydrosere will develop on them (Hunt 1943). Several exotic introductions have added to the aquatic weed problem, especially water hyacinths (Eichhornia crassipes), hydrilla (Hydrilla verticillata), Brazilian waterweed (Egeria densa), alligator-weed (Alternanthera philoxeroides), and Limnophila sessiliflora.

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41. RUDERAL VEGETATION

Ruderal vegetation arises in response to disturbance of habitats by human activities. Virtually all existing vegetation in the panhandle has been impacted to some degree by man. The resilience of much of the vegetation has been sufficient to prevent noticeable or substantial changes in the species composition, physiognomy, and patterns of dominance. The term, ruderal, applies only to that vegetation which has been modified substantially or entirely. Unfortunately, there are no criteria for measuring degrees of disturbance in deciding what constitutes a "substantial" modification of the natural vegetation (see chapter 17 for further discussion).

Impacts that sometimes cause slight or moderate vegetational change include the following: 1) changes in the frequency or season of burning, 2) ditching which shortens the hydroperiod, 3) unintensive grazing by livestock, and 4) logging followed by natural regeneration by the same species that previously characterized the overstory. These impacts usually have not resulted in the development of ruderal vegetation unless the degree of impaction was severe.

Some impacts cause a permanent change in the environment which results in the original plant community being replaced by another natural plant community. The replacement community develops entirely because of human interference, but it mimics the natural vegetation typical of the new habitat conditions. Such replacement vegetation can scarcely be considered as ruderal. An example would be a titi swamp that extends into a pine flatwoods in the absence of fire (see page 394).

The term, ruderal, should designate vegetation which is noticeably and substantially different from any natural vegetation type in terms of species composition and dominance. A change in physiognomy is sometimes an apparent consequence of changes in species composition and dominance.

A common characteristic of most ruderal vegetation is the importance of exotic species. Natural, undisturbed vegetation rarely contains more than a few exotic species, usually less than 5% of the flora in those communities with moderate or high numbers of species and moderate to high community organization. Such exotic species are those which invade minor areas of disturbance within an otherwise natural community, e.g., a fire break in a fireland community or a trail side in a hammock. Exotic species gain importance in ruderal vegetation in terms of the number of species and/or the inclusion of dominant or otherwise conspicuous species. For example, 88,000 acres of phosphate strip mines that had been abandoned for 5-70 years were inventoried in Hamilton County and in central peninsular Florida. Over 22% of the 569 vascular plants on these lands were exotic species (Florida Bureau of Geology 1980). The large majority of these exotics were introduced inadvertently into Florida and have become naturalized.

As a general rule, the vegetational response to an environmental impact is proportionally greater in drier habitats than in wetter habitats. An example was presented on page 399 and Research Summary 11. Major environmental impacts in wetlands and aquatic habitats often result in temporary modifications of the vegetation. Within relatively few years, the original community reestablishes itself. If habitat conditions are permanently changed, a replacement community becomes established which cannot be discerned from the natural vegetation expected in such a habitat. Major environmental impacts in uplands are much more likely to result in the formation of ruderal vegetation.

Ruderal vegetation occurs in many habitats and is quite variable in species composition. Four general types of ruderal vegetation are sufficiently distinct and widespread so as to require recognition as communities: old field assemblages, pine-oak woods, pasture assemblages, and pine plantations. With the exception of the pine-oak woods, they lack permanence, either because of the rapidity of succession or because of the continuing impacts of land use. Nonetheless, they occupy sizeable areas, and vegetational mapping could not be accomplished without their recognition. The rest of this chapter will emphasize these communities, although it should be recognized that ruderal vegetation assumes other forms.

33. Old Field Assemblages

Agricultural fields which were planted to row crops and then lain fallow are commonly called old fields. During the time of cultivation, these fields contained various agricultural weeds, many of which were winter annuals. These germinated in the autumn after the crops were harvested and completed their growth and seed production before the fields were cultivated in the spring. These species and many additional species are commonly present during the first one or two years following the last harvest. Table 38 lists some of these, including the more common ones. Among them are many winter and summer annuals, a few biennials, many perennial herbs, and a few woody plants. Most of these same species are

TABLE 38. Some Species of First-Year Old Fields.

Acalypha gracilens	Heteropogon melanocarpus
Agalinis fasciculata	Heterotheca subaxillaris
Amaranthus hybridus	Hypericum gentianoides
Ambrosia artemisiifolia	Ipomoea hederacea
Andropogon virginicus	Ipomoea pandurata
Bidens bipinnata	Ipomoea quamoclit
Bulbostylis barbata	Jacquemontia tamnifolia
Carex albolutescens	Juncus dichotomus
Carex cephalophora	Lechea mucronata
Cassia fasciculata	Lepidium virginicum
Cassia nictitans	Lespedeza striata
Cassia obtusifolia	Linaria canadensis
Cenchrus echinatus	Mollugo verticillata
Cerastium glomeratum	Monarda punctata
Chamaesyce hyssopifolia	Oenothera biennis
Chenopodium ambrosioides	Oenothera laciniata
Cnidoscolus stimulosus	Oxalis dillenii
Corchorus aestuans	Paspalum boscianum
Coronopus didymus	Paspalum plicatulum
Crotalaria spectabilis	Paspalum praecox
Croton glandulosus	Paspalum urvillei
Cyperus globularis	Passiflora incarnata
Cyperus retrorsus	Physalis arenicola
Cyperus rotundus	Physalis virginiana
Daucus pusillus	Phytolacca americana
Desmodium tortuosum	Plantago virginica
Dichanthelium aciculare	Polygala grandiflora
Dichanthelium acuminatum	Polygala polygama
Dichanthelium boscii	Polypremum procumbens
Digitaria sanguinalis	Pyrrhopappus carolinianus
Digitaria villosus	Richardia scabra
Diodia teres	Rubus trivialis
Eragrostis hirsuta	Rumex hastatulus
Eragrostis spectabilis	Sagina decumbens
Erianthus contortus	Setaria geniculata
Erigeron strigosus	Silene antirrhina
Eupatorium capillifolium	Solanum carolinense
Eupatorium compositifolium	Solidago canadensis
Facelis retusa	Spermolepis divaricata
Geranium carolinianum	Stipulicida setacea
Gnaphalium falcatum	Tradescantia ohiensis
Gnaphalium obtusifolium	Trichostema dichotomum
Gnaphalium pensilvanicum	Triodanis perfoliata
Gnaphalium purpureum	Verbena urticifolia
Gnaphalium spicatum	Veronica perigrina
Haplopappus divaricatus	Wahlenbergia marginata
	Xanthium strumarium

present in other ruderal habitats, such as roadsides, lawns, abandoned mines, barrow pits, and fire lanes. Some of these species are also part of the flora of natural plant communities having definite community organization. Other species are present only in those natural habitats which are kept open by frequent natural disturbances, e.g., river banks and point bars, coastal prairies, and within palustrine terrestrial assemblages. Still other species are introduced species which are unknown in the panhandle except in strictly ruderal habitats.

Old field species are often said to be specialists which have forgone the ability to compete in closed habitats in order to concentrate on surviving in harsh environments. The strenuous conditions in these fields include exposure to direct solar radiation, greatly fluctuating diurnal temperatures and humidities, high rates of evapotranspiration, rapid soil erosion on slopes, and surface soil rearrangement by the pelting of rain drops. The soils are loose from cultivation and low in organic matter, facilitating wide fluctuations in soil moisture and temperature. These harsh conditions are not sufficient to prevent a surprisingly wide variety of plants from appearing during the first year or two, including tree species. Among them are shortleaf and loblolly pines, sassafras, black cherry, water oak, and live oak. Woody plants typically invade old fields later in succession, and they are not common during the first two or three years. In more northerly latitudes, the various stages of old field succession are more distinct than in the panhandle. Evidently, the moderate climate in the panhandle allows species to invade early in succession.

The floristic composition of first-year fallow fields is quite variable. Factors that control the composition include the following: 1) Previous Plant Cover. Seeds and rootstocks of the former agricultural weeds are likely to be present in abundance and will, therefore, likely be well represented in the years immediately following the cessation of cultivation. Woody plants with large rootstocks are sometimes present in agricultural fields and will persist, such as *Smilax bona-nox*, and *Campsis radicans*. Some crop plants or agricultural weeds may influence plant colonization by producing allelopathic substances that prevent the invasion of particular species the following year. 2) Surrounding Seed Source. New species will invade as long as there is a seed source within the dispersal range of their seeds. Other species will be absent. An example of this was observed at the Tall Timbers Research Station. Three corn fields, each about a mile apart on similar terrain and soils, were retired from cultivation the same year. The species composition was largely the same at all fields with an obvious exception. *Vulpia octoflora* was absent in and around two of the fields, but was present with a cover of 20% at the other. Seed source appeared to be the only explanation for its distribution at these fields.

3) Soils. Some species seem to be more abundant in sands and other species more abundant in loams. Some species prefer dry soils and others wet soils. Some species grow well in nutrient-deficient soil and others only in relatively fertile soils. Soil fertility is a function of the composition and amount of fertilizers used and also on the crop previously grown. Some crop plants deplete some or all mineral nutrients more than other crop plants.

4) Season of Last Soil Disturbance. A study at the Tall Timbers Research Station (Kay *et al*. 1978, Research Summary 49) showed that the month of the year that the field was last harrowed had a drastic influence on species composition and species dominance.

By the end of the second or third year following cultivation, most of the "weeds" are no longer abundant, and some species are absent or nearly so. Broomsedge (*Andropogon virginicus*, sometimes with lesser amounts of *A. ternarius*) usually is dominant by the end of the third year. Other species that are often common with broomsedge are dogfennel (*Eupatorium compositifolium* in drier areas, *E. capillifolium* on moist sites), goldenrod (*Solidago canadensis*), blackberry (*Rubus cuneifolius*), and dewberry (*Rubus trivialis*). Several other species may also be common, such as *Agalinis fasciculata*, *Eupatorium hyssopifolium*, and *Rhus copallina*. Once broomsedge has assumed dominance, the field will carry a fire. The species abundance may vary depending upon whether or not burning occurs. Trees also begin to invade in large numbers at the time that broomsedge assumes dominance, although it may be another year or two before the saplings are tall enough to be seen above the herbaceous cover. Shortleaf pine and loblolly pine are usually the first species to invade in abundance at least in the Northern Highlands. Slash pine and longleaf pine may invade, but usually much less abundantly. Spruce pine will colonize particularly moist areas. Hardwoods usually begin to invade in abundance after the young pines have overtopped the broomsedge. Among the first hardwoods species are sassafras, persimmon, Chickasaw plum (*Prunus angustifolia*), black cherry, water oak, live oak, and sweetgum.

The presence and abundance of any tree species depends on the adequacy of a seed source nearby. Striking examples of the relationship between seed source and tree invasion are seen at fallow fields which are bordered on one side by a forest. The saplings in the field are progressively more abundant and taller with proximity to the forest. Most seeds are dispersed short distances, thereby explaining the higher densities of saplings near the seed source. The taller trees grew from the first seeds to germinate after the field was suitable for colonization. Since most seeds are dispersed short distances, most taller trees are near the forest. The forest might also serve as a wind break, further promoting the establishment of saplings near it.

Research Summary 50 shows what happens after young tree saplings become established. Shortleaf and loblolly pines that were 8-12 years old were up to 3 m tall and were scattered in the field of broomsedge. Sweetgums and a few other hardwoods had also invaded. Nine years later, the pine canopy had nearly closed. The broomsedge was nearly gone, except in a few small openings. A few of the sweetgums were nearly as tall as the larger pines, but most hardwoods were still growing beneath the pines. Virtually no herbaceous plants of the old field assemblage were seen, and a few plants typical of mature forest undergrowth were present.

Old field assemblages are defined as the vegetation that occurs on fallow agricultural fields (or similarly disturbed sites) up until the time that the tree canopy begins to close. At the field just described, the process took approximately 20-25 years. The amount of time needed will vary, depending primarily on the physical site conditions.

The fence rows that border old fields develop a curious and conspicuous vegetation, dominated by woody plants which produce berries or drupes, such as species of Prunus, Diospyros, Sassafras, Juniperus, Rubus, Smilax, and Vitis. Birds eat the fleshy fruits and pass the seeds in their feces, often while perched on a fence. Digestive acids help scarify the seed coat, and the feces may contribute readily available mineral nutrients for the germinating seeds. Live oaks are also common along fence rows, and their acorns may also be bird-dispersed, although not necessarily ingested.

34. *Pine-Oak Woods*

After the tree canopy closes over an old field assemblage, the vegetation is forested and may be designated as a pine-oak woods community. One or more species of pines are usually the most conspicuous element of the canopy. Hardwoods appear soon thereafter in the canopy, particularly if fires are infrequent or absent. One or several species of oaks are almost invariably important among the hardwoods.

As with the previous stages in old field succession, the floristic composition of pine-oak woods varies widely because of physical site conditions and the availability of seed sources. Just because a seed source is nearby does not guarantee that a species will be well represented. Many trees produce seeds prolificly less than annually. Longleaf pine is very irregular in its seed production, and many forest trees produce large seed crops about every fourth year. The species that are most common in pine-oak woods are those that typically produce many seeds annually, such as shortleaf pine and black cherry. These species also have efficient seed dispersal mechanisms. Even if the seed crop of a particular species is abundant and well dispersed, a crop failure may ensue because of inclement weather or the presence of especially large populations of seed-eating animals.

The development of forests on old fields can be appreciated by the examination of Research Summaries 50 (Timberlane), 55 (Diehl's Woods), and 56 (Goodwood Plantation). The Timberlane site was already described with regard to the final developmental stage of old field assemblages. The site was approximately 25 years old. Diehl's Woods occupied a nearby tract with virtually identical site conditions. This former field had been lain fallow for about 35 years. The Goodwood old field was several miles away, had similar site conditions to Diehl's Woods, and had been lain fallow for at least 37 years. The three sites are compared with regard to density (trees/ha), basal area (m^2/ha), and the relative density (RD) and relative basal area (RBA) of all pines (as opposed to all hardwoods:

	AGE	DENSITY	BASAL AREA	PINE RD	PINE RBA
Timberlane	25	300	9.8	96	92
Diehl's Woods	35	739	25.7	43	58
Goodwood *	37	326	20.8	82	93

The principal species were shortleaf pine, loblolly pine, water oak, Spanish oak, sweetgum, and black cherry. The incidental species were slash pine, dogwood, mockernut hickory, post oak, laurel oak, live oak, and camphor tree (<u>Cinnamomum</u> <u>camphora</u>).

*Values in Research Summary 56 were calculated based on minimum tree diameters of 13 cm. The values were recalculated here based on 10 cm, which was the minimum diameter for the other two stands.

The comparison between Timberlane and Diehl's Woods shows a rapid increase in total tree density and basal area. The relative density and relative basal area of the pines dropped substantially, indicating that the increases in total tree growth were attributable more to hardwoods than to the pines.

The same trends were apparent in forest development at Goodwood, but the contrast between Timberlane and Goodwood was not as pronounced as between Timberlane and Diehl's Woods. Physical site conditions do not appear to be sufficiently different to explain this discrepancy. It seems that hardwoods did not develop as quickly at Goodwood as at Diehl's Woods. Two possibilities would explain this difference. First, the seed sources for hardwoods were not as plentiful at Goodwood. Second, a fire may have occurred at Goodwood at a time when the young sapling pines were large enough to survive, but not the sapling hardwoods. In either event, the pines would have had a greater advantage at Goodwood, and the development of hardwoods has been delayed temporarily.

The pines are unable to reproduce beneath their own cover. The hardwoods of the understory are more competitive as a group than the pines. Upon reaching their mature size, the pines lose branches and show other signs of stress from competition. Mortality is rather high among the pines, and they are replaced gradually by hardwoods until the pines are merely incidental in the overstory.

The initial hardwood overstory consists of species which, in turn, are able to reproduce little, if any, beneath their own cover. Other, more competition-tolerant saplings become conspicuous in the undergrowth, particularly those of southern magnolia. As mentioned on page 276, magnolia seedlings do not appear until the leaf litter has covered the soil for about 12 years.

As the hardwood overstory trees die, they are replaced by southern magnolias and the other, more competitive species. Kurz (1944) included the following trees among those in the second generation of hardwoods: southern magnolia, beech, pignut hickory, spruce pine, American holly, silverbells (Halesia diptera), and hophornbeam (Ostrya americana). This community is considered the climax community in old field succession and is identical to the naturally occurring mesic hardwood hammocks as described in Chapter 37. Kurz (1944) said that it would take at least 100-150 years under favorable conditions for a young beech-magnolia hammock to develop from an old field. He observed that no such hammocks had yet developed to that stage without having suffered from fire or other disturbances. Presumably, the mature hammock would be maintained indefinitely through gap succession.

A common practice in the Tallahassee Hills and elsewhere has been to burn off old fields annually or nearly so, as soon as the sapling pines are tall enough (about 2 m) to survive a surface fire. Some of these former fields have been burned regularly for a century or more. Research Summaries 52 (NB66) and 53 (Beadel Course) at the Tall Timbers Research Station are examples of old, essentially annually burned fields dating from the 19th century. The overstories of these pine-oak woods are dominated by pines, most of them being those that initially colonized the old fields. Oaks and other hardwoods are present as incidental species.

The understory of these open pinelands is essentially absent. The ground cover is dense and rich in species. Coppicing root crowns of hardwoods are abundant, particularly oaks. Some of these root crowns are quite old and may represent seedlings that invaded the old fields before they were initially burned. Broomsedge is still important, but many additional herbs have become established over several decades, most of them grasses, composites, and legumes. The herbs in the ground cover are a mixture of species characteristic of longleaf pinelands, pine-oak-hickory woods, and old field assemblages. Research Summary 54 shows that there are many floristic differences, though, between longleaf pinelands and frequently burned pine-oak woods.

Occasional hardwoods are able to become established in the overstory in spite of frequent burning. The coppicing root crowns of hardwoods often form patches in which the much more flammable grasses are largely excluded by competition. In years of low rainfall, the grasses produce insufficient biomass to carry a fire across these patches. As a result, the hardwood sprouts in the center may survive. The following year, these sprouts grow rapidly from the well established root systems of their root crowns. If subnormal rainfall continues for about two more years, these saplings will have grown tall enough to cast shade, produce a poorly burning leaf litter, and exert increasingly strong root competition for the limited soil moisture. All of these factors will weaken the grasses to the point that when normal rainfalls occur, the grass cover will not carry fire evenly through the thicket. The developing bark on the young hardwoods will be thick enough by that time to protect the trunk from heat. Thereafter, these hardwoods will be able to grow to maturation.

This process yields relatively few trees on former old fields that are near-annually burned. The probable consequence is a net loss of trees and the ultimate development of a savannah or prairie.

Perhaps the most common practice in pine-oak woods has been to burn the woods at irregular intervals. Many acres of pine-oak woods had once been annually burned, but were kept fire-free for a decade or two during the intensive national campaign during the 1920's and 1930's to prevent all forest fires. Irregularly burned stands such as these tend to have various mixtures of pines and hardwoods. Those stands that are burned rather frequently tend to be dominated by pines, and those stands that are burned less frequently are dominated more by hardwoods.

The hardwood trees arises as sprouts from root crowns during fire-free periods. After ten fire-free years, the NB66 plot (Research Summary 52) developed a dense understory of hardwoods, virtually all of which arose from established root crowns rather than from germinating seeds. Seedlings of shortleaf pine were also abundant in the more grassy openings, and many of them appeared to be growing sufficiently vigorously to survive and mature along with sapling hardwoods.

Research Summary 51 demonstrated the tendency of hardwoods to be favored over pines when a pine-oak woods is not burned. Several fire ecology demonstration plots had been established at the Tall Timbers Research Station in mature pine-oak woods that had previously been annually burned. These plots were scheduled to be burned at various intervals but less than annually. Those that had been burned at least once since the plots were established had greater proportions of pines to hardwoods than those that had not as yet been burned.

The pine-oak woods, particularly those that are irregularly burned, tend to resemble pine-oak-hickory woods in physiognomy, and they share many species in common with pine-oak-hickory woods. An important distinction between these two communities is the arboreal flora, including both the overstory trees and the understory or coppicing root crowns. The pine-oak woods invariably contain trees characteristic of the bottomland hardwoods community, particularly the loblolly pine-hardwood segregate (page 484). The Tallahassee Hills, particularly, were once heavily cultivated (page 38). When these lands were lain fallow, there were few upland forests that could serve as seed sources. The nearest seed sources were usually the wooded strands along creeks and rivers. Under original conditions, the trees of these bottomlands were unable to compete with upland species. The fallow fields, though, afforded an open habitat for colonization. Common invaders from the bottomlands were loblolly pine, sweetgum, water oak, and laurel oak. Less common but frequent invaders were slash pine, willow oak, and red maple. Live oak probably invaded from several sources, including bottomlands, around lakes, the many rural home sites, and fence rows.

In contrast, some typical trees of pine-oak-hickory woods are usually less common or absent, particularly post oak and mockernut hickory. Several herbaceous species common to pine-oak-hickory woods have not been observed in pine-oak woods, such as *Tephrosia virginiana* and *Pteridium aquilinum*. A patch of the latter species occurred next to the NB66 plot, but the area was later identified as a small, unmarked cemetary on land which had never been farmed.

Loblolly pine is not reproducing at NB66, but shortleaf pine, which is a dominant of pine-oak-hickory woods, is reproducing from seeds and from root crowns. Evidence cited on page 257 showed that loblolly pine seedlings are unable to compete successfully for water against other trees in upland habitats. It would seem likely that the seedlings of trees of other bottomland species may be similarly uncompetitive in uplands, or else those species would be represented in the natural pine-oak-hickory woods community. If this presumption is correct, then it would follow that irregularly burned pine-oak woods are gradually losing their trees that invaded from the bottomlands. These trees are likely being replaced by those typical of pine-oak-hickory woods. Whether or not a complete conversion is possible is speculative. Present demands for land may prevent that question from being answered.

Virtually all information on old field succession and pine-oak woods comes from the Tallahassee Hills, where agricultural activities have been intensive historically. Elsewhere, fallow fields are generally converted to pine plantations. Research Summaries 58 and 59 represent exceptions. Research Summary 58 describes an old homestead near the Wakulla River. The site is dominated by live oaks and other trees including loblolly pine. Research Summary 59 describes an old turpentine camp in the Apalachicola National Forest. The site has a forest of slash pines, loblolly pines, longleaf pines, and a few live oaks and water oaks. Both sites were cultivated in part.

Research Summary 57 describes two stands from the Northern Highlands near Thomasville. One occupies a former old field which had been burned regularly up until 50 years ago. The forest was comprised almost entirely of bottomland trees and was dominated by loblolly pine. The other stand was a longleaf pine savannah from which fire had been excluded for 60 years. Longleaf pine was still important, but loblolly pine and ten species of hardwoods had invaded the stand. The hardwoods were mostly typical of mesic hammocks rather than of bottomlands.

35. *Pasture Assemblages*

Pastures in the panhandle have been improved primarily with the introduction of bahiagrass (Paspalum notatum), which was introduced from South America. This grass has also been planted extensively along roadsides. It forms a dense, low turf which excludes plants of most other species, as long as it is grazed or mowed regularly. Its competitive abilities are enhanced with the application of lime and fertilizer. Other species which grow in pastures are primarily those listed in Table 38. Many improved pastures were formerly old fields which were planted with bahiagrass.

Research Summary 35 describes the conversion of a bahiagrass pasture into a prairie of native grasses following the exclusion of cattle and seven years of annual burning. Several native grasses were expanding their coverage at the expense of bahiagrass.

36. *Pine Plantations*

During the past 30 years, enormous areas of the panhandle have been converted from naturally regenerated, second-growth pinelands to pine plantations (see p. 45-48). All communities of the firelands system have been affected. Ditching has lowered the water table in many areas, enabling acid swamps to be planted to pines. Slash pine and some loblolly pine plantations were planted initially. Longleaf pines were avoided, because of the unpredictably long grass stage which diminished yields from pines grown in short rotations. More recently, failure of slash pine plantations on some sandhills has led to the planting of longleaf pines. Sand pines have also been planted successfully on sandhills.

Site preparation almost always includes clear cutting of the trees already present, burning, and some type of mechanical disturbance to the soil. Chopping is a favored technique on drier sites. Disking and bedding are favored on wetter sites. Rootrakes and KG blades have also been used. The effects of soil disturbance in intensive forestry were already described (p. 397-402). It should be reemphasized that the effects of soil disturbance are quite variable on the vegetation of the ground cover. The same treatment impacts the original ground cover more severely on drier sites than in wetter sites (see Research Summary 11). The composition of the ground cover after soil disturbance also varies with the type of equipment used, and probably the season in which the disturbance occurred.

The resulting vegetation is a mixture of native species and weedy species. The native species are often represented by plants which sprouted from rootstocks and which survived site preparation, such as wiregrass. The weedy species include plants that were previously present, either in low numbers (e.g., dogfennels) or as suppressed plants (e.g., broomsedge), and plants that invaded from other areas (e.g., Haplopappus divaricatus and many other species listed in Table 38). Some native species may be prolific the first year or two after site preparation, because their undamaged rootstocks are released from competition, such as species of Liatris. Some species, such as bracken (Pteridium aquilinum), may be very abundant or entirely absent, probably depending on whether or not its rhizomes were able to survive and then proliferate in the absence of competition. The annual partridge-peas (Cassia spp.) are also quite variable in abundance on recently site-prepared lands, reflecting the season of disturbance. In the study which determined the effect of the season of disturbance on old field assemblages (Research Summary 49), Cassia nictitans had a density in April of 26 plants per m^2 on a plot disked the previous October. In contrast, densities did not exceed one plant per m^2 on plots disked the previous August and the previous December.

In general, there is a flush of herbaceous growth in the first year or two after site preparation, with species of Andropogon, Dichanthelium, and sometimes Panicum among the dominants. This result was evident from the study by Moore and Terry (1980), summarized in Table 39. Thereafter, the herbaceous vegetation decreases in abundance and diversity in response to competition from shrubs (especially Ilex glabra in flatwoods sites) and the planted pines. This change in the undergrowth was demonstrated by Skoog (1980), whose work is summarized in Research Summary 63.

After about the tenth year, the herbaceous vegetation is nearly eliminated from woody competition and from the dense needle-drape produced by the sapling pines. Only a token of the herbaceous vegetation survives until the end of the rotation, unless the stand is burned or thinned. In future rotations, the herbaceous flora will likely consist only of the species common in old field assemblages (Table 38) and not of the species typical of the original fireland communities.

TABLE 39. Herbaceous Biomass in an Alachua County Pine Flatwoods Before and After Chopping (after Moore and Terry 1980)*.

	kg/ha	
	1976 Natural	1978 Chopped
GRAMINOIDS		
Panicum (Dichanthelium?) spp.	3	552
Andropogon capillipes	1	228
Panicum verrucosum	0	110
Andropogon virginicus	2	69
Rhynchospora spp.	0	54
Scleria spp.	3	46
Cyperus spp.	1	40
Andropogon stolonifer	1	19
Eleocharis vivipara	0	15
Other sedges	1	14
Aristida spiciformis	-	10
Aristida stricta	26	9
Other grasses, rushes	7	25
	45	1191
FORBS		
Pteridium aquilinum	145	250
Diodia virginiana	0	105
Cassia fasciculata	1	68
Eupatorium capillifolium	0	57
Osmunda cinnamomea	28	55
Erechtites hieracifolia	0	29
Pityopsis graminifolia	5	20
Pterocaulon pycnostachyum	0	13
Other forbs	21	79
	200	676
TOTAL (Graminoids + Forbs)	245	1867

*A 22-ha naturally regenerated second-growth, mature flatwoods, winter-burned and then sampled the next autumn (1976) in 132, meter-square clipped quadrats. Then double chopped the following year and resampled 13 months after the second chopping (fall of 1978).

Planted pine plantations resemble old fields in that both begin with a flush of herbaceous growth, often with broomsedge (*Andropogon* spp.) asserting dominance early in succession. Thereafter, pines and woody undergrowth become dominant. Unlike old field assemblages, the herbaceous vegetation contains a noticeable if not substantial quantity of residual native species. In subsequent rotations, these residual plants will be much less important or entirely absent.

Discussion

Old Field Studies. Two papers have been published specifically on old field vegetation in the panhandle. Kurz (1944) described the successional sequence from the first year of abandonment through the various forested phases. The paper is particularly valuable for its wealth of observations. The only point of disagreement is with his not distinguishing the pine-oak-hickory community from later old field seral stages. The other paper was by Kay *et al*. (1978), which correlated total vegetational cover to the month of disturbance. This study was done on the same plots at Tall Timbers Research Station that were used in the work reported in Research Summary 49.

Old field succession has been a popular subject for research in the southeastern United States and elsewhere. Some of the more important literature is as follows: in New Jersey, Bard (1952), McCormick and Buell (1957), Levin (1966), Buell *et al*. (1971), Hanks (1971, 1972, the latter paper also including data from North Carolina); in Tennessee, Quarterman (1957); in North Carolina, Crafton and Wells (1934), Billings (1938), Oosting (1942), and Keever (1950); in Georgia, Odum (1960), Odum _et al_. (1973), and Bakelaar and Odum (1978); in Louisiana, Bonck and Penfound (1945); in southern Illinois, Bazzaz (1968).

Oosting and Humphreys (1940) found evidence suggesting that seeds of plants typical of early stages of succession remain viable in the soil for many years. Seedlings of 18 species of open field herbs consistently sprouted in greenhouse flats from soils taken from fields lain fallow for up to 85 years or more. This study emphasized the importance of residual seeds in the soil in determining the initial floras of recently disturbed sites.

The germination ecology and autecology of some of the more important old field species have been determined by Keever (1950), Shontz and Oosting (1970), Holt (1972), and others. Ragweed (_Ambrosia artemisiifolia_) has received considerable attention by Bazzaz (1970, 1974), Pickett and Baskin (1973), Raynal and Bazzaz (1975), and others. _Aster pilosus_ was studied by Peterson and Bazzaz (1978). These and other studies have demonstrated some of the ecological processes which determine species abundance and the order of appearance in seral sequences in old fields. Allelopathic reactions are responsible for some of the competitive interactions between species. These have been studied by Blum and Rice (1969), Rice (1972, 1974), Rice and Pancholy (1972, 1973), and Gant and Clebsch (1975).

Forest Competition. Several studies have focused on the competition between pines (shortleaf, loblolly) and hardwoods in forest stands on former old fields. Much of this work was done in North Carolina. Korstian and Coile (1938) compared plant response in trenched plots and control plots in various forests. Trenching severs the roots of nearby trees and allows the herbs and saplings within the plot to grow without root competition from overstory trees. The study showed intense root competition for soil moisture but not for nitrogen.

Kozlowski (1949) followed with evidence that hardwoods were generally more efficient photosynthetically than pines, particularly at lower light intensities and at low levels of soil moisture. Oosting et al. (1952) found that light intensity was critical in determining whether or not pines would survive in pine-hardwood stands.

Korstian and Bilan (1957) presented further evidence for the importance of both light and soil moisture with regard to pine survival. If either light or moisture were too low, the pines lost in competition with hardwoods. Blair and Brunett (1976) documented the changes in forest composition after selective logging in pine-hardwood stands. Switzer et al. (1979) described changes in forest soil properties during the course of succession. Bower and Ferguson (1968) showed that the removal of an understory of hardwoods beneath shortleaf pines resulted in an increased growth rate in the pines during a drought year. The increase in growth was proportional to the degree of understory removal.

Pine Plantation Mensuration. Some studies of young pine plantations have given biased views of the herbaceous vegetation because of the experimental design and the uncritical interpretation of data. The improper choice of a control plot has reduced the value of several studies. Widely discrepant values for species abundance may be obtained for a natural pineland serving as a control, depending on the recent history of burning, as was nicely shown by Moore and Terry (1980). The proper selection of a control is particularly important in the assessments of wildlife carrying capacities, as can be seen from the data of Stransky and Halls (1979).

The uncritical interpretation of data is illustrated by wiregrass, which has been measured in several studies in terms of its frequency and density by line interception and in terms of its biomass in clipped quadrats. As was demonstrated in Research Summary 11 and discussed in Chapter 23, wiregrass drops significantly in density because of site preparation and does not reproduce thereafter. On the contrary, values of frequency, cover, and biomass often show that wiregrass increases in abundance within the next several years following site preparation. The explanation of this anomaly becomes apparent upon the understanding of the mode of growth of wiregrass. Shortly after site preparation or burning, the plant is merely a tuft of stubble 1-2 dm wide. During the next three years, the leaves elongate and arch, densely covering an area nearly a meter across. Values for frequency and cover substantially increase with this growth. Density, which has not been determined in most studies, remains constant.

One would expect that the values for biomass would increase moderately in proportion to leaf growth. On the contrary, the values for biomass are surprisingly high. The reason is that dead wiregrass leaves, which can scarcely be distinguished from live leaves, persist on the plant for a year or more before being shed. When biomass is determined, most of the weight represents dead leaves (i.e., litter), rather than living biomass.

A number of studies cited below have yielded valuable information with regard to the vegetation in pine plantations, although the data in some of them must be assessed in light of the preceding statements.

Plantations in Flatwoods. Pine plantations in the panhandle were studied in Tates Hell in Franklin County (see Research Summary 7) and in Hamilton County (White et al. 1975). Some plots in the Hamilton County study site were burned; other plots were bedded after being burned and disturbed with a KG blade. Measurements were made when the planted slash pines were nine years old. Shade from the pines reduced the light intensity two meters above the ground by 30% on the burned plot and by 85% on the bedded plot. Grasses amounted to 151 g/m^2 on the burned plot and only 50 g/m^2 on the bedded plot. The biomass of forbs was 11 and 4 g/m^2 on the burned and bedded plots, respectively. The frequency and biomass values for wiregrass, saw-palmetto, and dwarf-live oak were relatively high on the burned plots. The values for broomsedge, gallberry, and wax-myrtle were relatively high on the bedded plots.

Several studies were made in northern peninsular Florida, including that by Skoog (1980), which is summarized in Research Summary 63. Schultz and Wilhite (1974) reported their study in Baker County in a flatwoods that was logged, disked twice, and bedded. The ground cover was measured by interception two and four years after site preparation. Plants that were favored by the treatment included Aristida spiciformis, Sporobolus curtissii, and species of Rubus, Paspalum, and Panicum (Dichanthelium?). Broomsedge (especially Andropogon virginicus) gradually increased in response to site preparation. Species that decreased included wiregrass, saw-palmetto, runner oak, and dwarf-live oak.

White (1977) described a flatwoods in Union County that was clear cut in 1967, burned, KG-treated, disked, bedded, and fertilized. Biomass (kg/ha) was determined when the planted slash pines were five years old. Mean values were as follows:

Andropogon spp.	2198
Aristida stricta	559
other grasses	20
Carphephorus odoratissimum	16
Eupatorium capillifolium	9
other forbs	15
Ilex glabra	464
Rubus spp.	112
Serenoa repens	32
Vaccinium myrsinites	31
other shrubs	74

The total biomass was 3530 kg/ha. Eleven different applications of fertilizers were tested. Nearly all of them substantially reduced the biomass of wiregrass in comparison to the control plot which was not fertilized.

Ball et al. (1979) measured biomass in a pine plantation in Bradford County. Site preparation consisted of clear cutting, burning, chopping, and bedding. The studies were made in plots with planted slash pines that were 2, 5, and 10 years old. The more important grasses were Andropogon capillipes, A. virginicus, Sporobolus floridanus, Dichanthelium aciculare, D. sabulorum, and Paspalum ciliatifolium. The biomass of all grasses was 2190 kg/ha in the 2 year old plantation and 686 kg/ha in the 10 year old stand. There were many other herbs, among the more abundant were Rhexia mariana, Pityopsis graminifolia, Eupatorium leucolepis, Pterocaulon pycnostachyum, Euthamnia microcephala, Centella asiatica, Eleocharis albida, Scleria reticularis, and Rhynchospora fascicularis. The biomass of all forbs and sedges was 451 kg/ha in the 2 year old plantation and 114 kg/ha in the 10 year old plantation. In contrast to the herbs, the shrub biomass increased from 773 kg/ha at age 2 to 2700 kg/ha at age 10. The total living biomass (excluding planted pines) peaked at year 5 (4400 kg/ha) and delined thereafter.

Grelen (1976) studied a slash pine plantation in Louisiana, which also served as a cattle pasture. Plots within the plantation were burned, but the initial year of burning varied from age 5 to age 12 of the slash pines. The age of the stand at the initial year of burning did not affect the biomass of the herbaceous vegetation. Herbaceous biomass was inversely correlated to the basal area of the pines, regardless of the history of fire. All plots, including some that were not burned at all, had 90% less herbaceous biomass at age 13 than at age 6. Grelen suggested that the frequent removal of litter by burning may encourage the survival of grasses, thereby assuring their recovery after the planted pines are clear cut.

Plantations in Sandhills. Research Summaries 61 and 62 describe planted slash pine plantations in sandhills on fallow agricultural fields in Leon County. No site preparation preceded planting on these sterile sites. The herbaceous vegetation was quite sparce, reflecting in part the prior removal of the native vegetation when the fields were used for row crops. Research Summary 62 is note worthy, because turkey oaks and plants of other native species persisted in a fence row. These plants did not spread into the adjacent plantation, in spite of considerable opportunity to do so.

Many other studies on pine plantations in sandhills have been made at the Chipola Experimental Forest in Calhoun County (Hebb 1957, Scheer 1959, Woods 1959, Scheer and Woods 1959, Brendemuehl 1967, Burns and McReynolds 1972, Burns, 1972, Burns and Hebb 1972, Baker 1973). Of particular interest, though, was the study of Grelen (1962), who listed 93 species on sandhills that had been cleared, burned, and chopped within 1-4 years of the study. During the first summer after chopping, the dominant species was *Balduina angustifolia*, plants of which were vigorous and bushy. In the autumn, other species appeared in abundance, particularly *Petalostemum* sp. (perhaps *P. caroliniense*), *Dichanthelium ovale*, *Leptoloma cognatum*, and *Bulbostylis barbata*. Among the dominants appearing in the second year were *Conyza canadensis*, *Haplopappus divaricatus*, *Gnaphalium obtusifolium*, *G. pensilvanicum*, *Eupatorium compositifolium*, and *Andropogon virginicus*. In the fourth year, *Eupatorium compositifolium* was the most important dominant. Other important species which had appeared since the second year were *Croton argyranthemus*, *Hedyotis procumbens*, *Hypericum gentianoides*, *Lechea sessiliflora*, *Polygonella gracilis*, *Rhynchosia cytisoides*, and *Stylosanthes biflora*. Other species that were less abundant included *Andropogon ternarius*, *Digitaria villosa*, *Dichanthelium acicular*, *Euphorbia floridana*, *Krigia virginica*, *Schrankia microphylla*, *Paronychia patula*, and *Tragia* sp. (perhaps *T. urticaefolia*). The herbaceous flora on pine plantations in sandhills is quite different from that already listed for plantations in flatwoods.

Diseases in Plantations. Fusiform rust (*Cronartium fusiforme*) is a serious fungus disease in pine plantations. The economic impact was detailed by Powers *et al*. (1975) in the southern United States. The Florida Forest Service (1977) outlined the problem, drawing heavily on the experience of R. A. Schmidt. At the turn of the century, fusiform rust was rare, but now it causes an annual loss of $8 million in Florida slash pines. Before 1940, the forests were sparsely populated with older-aged pines. Intensive forest management restocked these forests with dense stands of young pines which are more susceptible to infection than older pines. Oaks are an obligate alternate host for fusiforme rust. The original habitats of slash pines were wet and essentially devoid of oaks. Slash pine plantations are often on drier sites where oaks are prevalent. Fire suppression in pine plantations has allowed the oaks to proliferate. These conditions have contributed to the severity of the incidence of fusiform rust.

Powers et al. (1974) showed that the incidence of fusiform rust was lower in natural stands of both slash pine and in loblolly pine than in plantations of these pines. Hollis et al. (1975) noted an increase of infection in response to fertilization (N, P) and other site amendments that ordinarily result in improved tree growth.

Another serious disease of pine plantations is pitch canker, caused by the fungus, Fusarium moniliforme. Severe outbreaks have been reported periodically, particularly in dense plantations of pines 11-23 years old (Dwinell and Phelps 1977). The incidence is highest on flat, sandy, wet, fertilized sites that have a history of fire. Drought and fertilization with ammonium nitrate may also increase the susceptibility to this disease. The incidence of the disease appeared to be less in natural stands than in plantations.

<u>Wildlife in Plantations</u>. The value of planted pine plantations for wildlife has been the subject of several studies in Florida, which have been cited in a bibliography by Harris (1978). Hebb (1971) inventoried the sandhills at the Chipola Experimental Forest and determined that site preparation decreased the abundance of game food plants. Harris *et al*. (1974) studied the same pine plantation that was inventoried by White *et al*. (1975) in Hamilton County. They concluded that the wildlife carrying capacity was reduced in comparison to natural flatwoods. The woody undergrowth and litter from pine needles in plantations suppressed the grasses, thereby lowering the amount of forage for such animals as cotton rats, rabbits, and quail. The decomposition of the leaf litter is slow in pine plantations, which depresses the populations of ground level arthropods and the animals that feed on them, including shrews, opossums, and armadillos. The dense canopy structure in plantations limits the utilization of plantations by birds.

Several studies of deer utilization have been made on pine plantations in the southeast. Beckwith (1964) compared uncleared and site-prepared sandhills in Citrus County, Florida. He noted an increase in available food plants on recently site prepared areas but an unexplained decline in the deer population. In a later study on this same site, Umber and Harris (1974) concluded that undergrowth favorable to much wildlife persisted for a longer time in pine plantations on sandhills than in flatwoods because of poorer tree growth and survival. Animals that dwell primarily on or near the ground were favored by this undergrowth. Birds and other animals that are dependent on vertical heterogeneity of the habitat were favored in natural pinelands, rather than in plantations.

Wolters and Schmidtling (1975) studied deer food plants in coastal Mississippi. They said that about 25% of the herbaceous species were eliminated by intensive cultivation in 12 year old plantations and that fertilization was particularly detrimental to production. Their data indicated that plantations were poor habitats for deer forage, but they concluded that the plantations were equal or better than the control sites. Blair and Enghardt (1976) studied loblolly pine plantations in Louisiana. They concluded that younger plantations up to 8-10 years old provided forage for deer. Thereafter, herbaceous and woody forage was too sparse.

In a general overview of wildlife values in managed forests, Harris and Smith (1978) pointed out that wildlife management in the past has been synonymous with game management. They emphasized that less than 10% of the vertebrates are game species, but all are wildlife. As a result, conclusions drawn with regard to wildlife values in plantations should specify the kinds of wildlife under consideration. They agreed with the conclusion of other authors that unburned pine plantations generally lose their value to wildlife quickly, e.g., in five years for quail and 10 years for deer. They said that site preparation affects wildlife more adversely than any other management operation and that mechanical site preparation is considerably more severe than chemical preparation.

Harris et al. (1979) proposed that large areas of managed forests be planned with wildlife values in mind. They argued that a diversity of forest practices should be used in a region in order to diversify the habitat for wildlife.

Commercial Forest Operations. General descriptions of industrial forest operations on lands owned by Buckeye Cellulose Corporation in the panhandle were written by Stevenson and Schores (1961) and by Jarvis and Beers (1965).

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42. ADDENDUM

After some chapters were written and typed, additional references were discovered that merited inclusion. In order to circumvent substantial rewriting and typing for relatively few entries, this addendum was prepared. The inclusions are presented in sequence by Chapter.

Chapter 1. On page 6, an unpublished manual for the identification of the aquatic plants of the southeastern states was mentioned. The first volume of this copiously illustrated work was published and treats the monocots (Godfrey and Wooten 1979). My manual for the identification of all vascular plants of the Florida panhandle was also mentioned. This work has been completed and is in press. The scientific names throughout the present report have been brought into compliance with the nomenclature of my manual. Ward (1978) published a detailed account of those Florida plant species which were considered to be rare and endangered by a panel of Florida botanists.

Chapter 4. In 1980, several parcels representing 675 acres at Eglin Air Force Base were returned to the U.S. Forest Service. These parcels now constitute the Choctawhatchee National Forest. They occur in Santa Rosa, Okaloosa, and Walton counties.

Another description of the shelterwood system for pine regeneration was prepared by Boyer (1979).

Chapter 5. Dohrenwend (1977) determined potential evapotranspiration in Florida based on the Holdridge bioclimatic classification system. The annual potential evaporation was about 1,000-1,050 mm for the panhandle. The estimated actual evapotranspiration was lower, about 850 mm. The water surplus (precipitation minus actual evapotranspiration) was about 500-700 mm.

Greller (1980) made a thorough study to determine whether or not the vegetation of Florida could be classified into climatic life zones. He could recognize only three, imperfectly defined zones which were based to a large extent on basal area data from forests consisting mainly of hardwoods. These zones were a mixed deciduous hardwood forest zone from the panhandle, a temperate broadleaved evergreen forest zone from central peninsular Florida, and a tropical forest zone from the southern tip of the peninsula. Broad transition zones occurred in intervening regions. Greller's work is of considerable service because it lays to rest the notion that Florida's vegetation can be classified satisfactorily on the basis of climatic criteria alone.

Greller's stand descriptions did not always pertain to a single community, and the values given for relative basal area were necessarily inflated for live oak and cabbage palm. Neither of these points detract from his conclusions, but his data should be used with an awareness of these points. The inflation of basal area data for cabbage palm is seen in Research Summary 37. Live oaks often have large basal areas because, unlike most hardwoods, they concentrate their woody growth in the expansion of girth rather than in height.

Chapter 6. Several recent papers have delt with changes in sea level since the Miocene. Kerr (1980) reviewed recent world-wide evidence from sediment analyses and reproduced a figure showing relative changes in sea level since the Paleocene. Geological epochs were dated approximately as follows:

Miocene	24 - 5.5 x 10^6 years
Pliocene	5.5- 2.9 x 10^6 years

Major periods of high sea level stands relative to present sea level occurred approximately 5.0, 1.8, 0.8, and 0.5 million years ago. Major periods of low sea level occurred approximately 6.8, 2.9, 1.7, 0.7, and 0.3 million years ago.

Gascoyne et al. (1979) working in the Bahamas, placed the Illinoian glaciation at 139,000 to 160,000 years ago with sea level lower than -42 m, probably much lower. They cited Shackleton and Opdyke (1973, Quat. Res. (N.Y.) 3:39) as placing the high sea level stand of the Sangamon interglacial stage at +12 m, 125,000 years ago. By 75,000 BP, sea level had dropped below -70 m. Cronin et al. (1981) working along the coast from Virginia to South Carolina confirmed the Sangamon estimate (+7.5 m, 120,000 BP), and presented evidence for other warm eras with sea levels of about +7 m at 188,000, 94,000, and 72,000 BP.

Clausen et al.(1979) worked at Little Salt Spring, a sinkhole 60 m deep near Charlotte Harbor in southwest Florida. They established mean sea level at -26 m at 12,000 BP, -1 m at 8,500 BP and -9 m at 5,500 BP. The Little Salt Spring paper further refined the rather well known post-Wisconsin sequences in sea level. The other papers showed that pre-Sangamon changes in sea level and the corresponding chronology remain imperfectly known.

Chapter 11. Rhue and Sartain (1978) reviewed the data from more than 4,000 soil tests of agricultural fields in Florida. Ranges were given for nutrients, pH, and other parameters for Entisols, Spodosols, and Ultisols. This survey is not directly applicable to soils of natural plant communities, but it provides a basis for assessing relative fertilities of these soils as they exist in Florida.

McKee (1980) studied the availability of nutrients in the soil solution of samples that were waterlogged and of other samples that were normally aerated. The soils were all silt loams from Louisiana taken from natural forests of longleaf and loblolly pines, scrub oaks, and Andropogon sp. The major impact of waterlogging occurred in those soils with low base saturation. Waterlogged soils had much higher levels of nutrients (divalent bases) than aerated soils. McKee warned that the higher levels did not necessarily mean that these nutrients were readily available to plants. He said that the results probably explained why soils with poor drainage and excess moisture often display wide ranges of site productivity.

Chapter 12. Two papers presented further evidence of the different effects of summer and winter burns on native vegetation. Ferguson (1958) reported the results of prescribed burns in eastern Texas in a forest of young shortleaf and loblolly pines which contained an undergrowth of sweetgum, post oak, and Spanish oak. The percent survival of shortleaf pine seedlings was calculated after one growing season during a year with subnormal rainfall. Survival was only 7% and 9% on plots that had been winter-burned 3 months and 10 months, respectively, following seedfall. Survival was 27% on a plot that was summer burned 8 months prior to seedfall. In Chapter 41, it was shown that shortleaf pines are less tolerant of drought conditions than are hardwoods. The conclusion from Ferguson's study is, then, that summer burning is more effective than winter burning in suppressing hardwood undergrowth.

Lewis and Harshbarger (1976) updated the results of the 20 year study of prescribed burning in the Santee Experimental Forest, Georgetown County, South Carolina. Prior results by Lotti and associates had been presented in Chapter 12 with regard to this study. The forest of loblolly pines contained a heavy undergrowth of hardwoods, especially sweetgum, sourgum, post oak, blackjack oak, willow oak, and Spanish oak. The site resembled NB66 (Research Summary 52). Repeated annual summer burning eliminated most woody undergrowth, more so than annual winter burning and periodic burning in summer or winter. Species that occurred only on plots that were summer burned were Andropogon ternarius, Carphephorus paniculatus, Centella asiatica, Muhlenbergia capillaris, and a species of Rhynchospora. Species occurring only on plots that were winter burned were Andropogon elliottii, Heteropogon melanocarpus, and species of Agalinis, Elephantopus, and Gymnopogon.

Chapter 14. White (1979) published a lengthy monograph on succession in naturally disturbed habitats. Much of what he said paralleled the sentiments outlined in Chapter 14. One of the more provocative comments was as follows:

> "A steady state is reached in which environmental gradients and community gradients continue to lace through the landscape....There is no ongoing trend to dominance by shade tolerant mesic species across the landscape. Rather, these species only dominate mesic situations where topography and soil texture insure moist and well-drained soils. The landscape remains gradient rich. The establishment of the gradients is the end point of succession."

This comment seems particularly apropos to the panhandle, where the vegetation types are often distributed along gradients into a regional mosaic.

Chapter 15. Interest in southeastern paleoecology has resulted in the publication of several recent papers. The conclusions of these papers confirm the general trends of the earlier works summarized in Chapter 15. Delcourt and Delcourt (1979) reviewed the evidence for vegetational changes in the Southeast since the full Wisconsin glaciation. The bluffland refugium hypothesis was upheld. These blufflands served as corridors for post-Wisconsin plant migration, beginning in 16,500 BP. A map showing the vegetation at the height of the Wisconsin glaciation in 18,000 BP was published and is reprinted with permission as Figure 44. Evidence for this figure came from several sources, including Delcourt et al. (1980) with regard to a study in the Mississippi embayment in Tennessee and Delcourt (1980) from a study in southeastern Alabama. The latter study described early Holocene oak-hickory forests which were replaced by pinelands. These pinelands became widespread on the sandy uplands by 4,700 BP. Delcourt and Delcourt (1980) also published a paper that discussed the reliability of paylonological data with regard to partially decomposed pollen grains.

Watts and Stuiver (1980) described the pollen profile from Sheelar Lake near Gainesville. From 23,880 to 18,500 BP the climate was dry and windy. Pines predominated, but the species were not able to be identified. Oaks, hickories, and other broadleaved trees were well represented and probably grew in localized stands. Prairie and sandhill herbs may have occupied unforested sites.

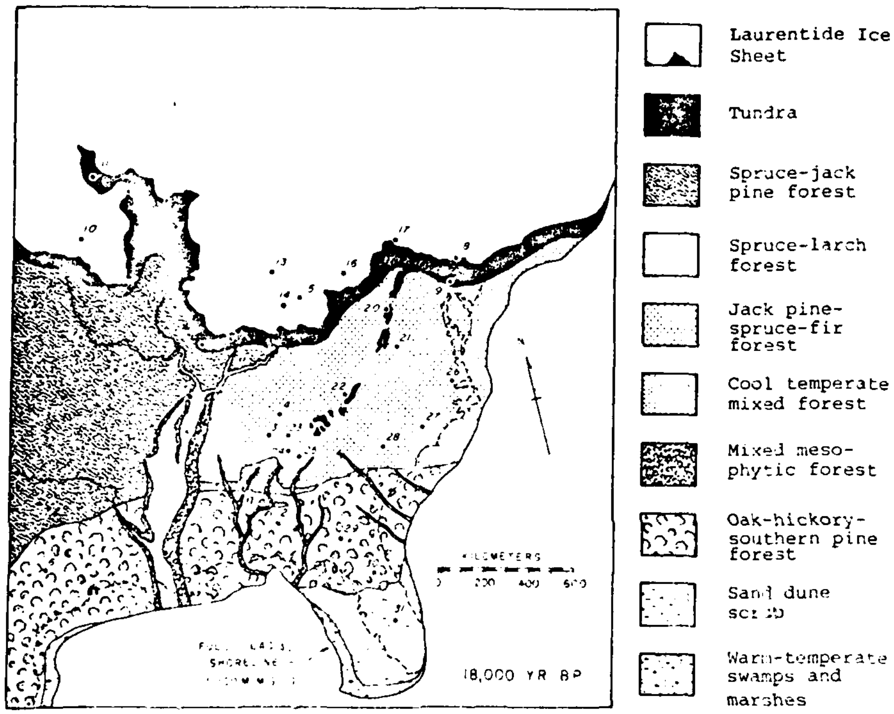

Figure 44. Full glacial vegetation. (Reprinted from Delcourt and Delcourt 1979.)

The climate became warm by 14,600 BP. Dry oak-hickory forests, which were interrupted by localized prairies, indicated dry conditions from 14,600 to 14,000 BP. Thereafter, the herbs were displaced by trees, indicating increased precipitation. Those trees included oak, hickory, hackberry, red or white cedar, and by 13,540 BP, considerable beech. After 13,000 BP, these trees were replaced by pines and herbs, indicating a drier climate with more fires. This change in the vegetation marked the beginning of the Holocene. Oaks became temporarily prevalent at the expense of pines from 9,500 to 7,200 BP, but later the pines regained their prominence and have persisted to the present. Cypress and swamp shrubs became increasingly important since 7,200 BP, indicating the development of acid swamps. Watts and Stuiver (1980) did not explain the reasons for the late appearance of acid swamps. Two possibilities would be higher water tables as mean sea level rose and the concomitant aggradation of peats in depressional terrain.

A new review of late Quaternary vegetation in the Southeast by Watts was announced, but I have yet to examine it (Ann. Rev. Ecol. Syst. 11: 387-410, 1980).

Chapter 17. White and Bratton (1980) elaborated on some of the practical problems of managing wilderness areas in order to maintain their primeval characteristics. Examples were given from the Great Smokey Mountains.

Chapter 19. Oliver (1978) made a substantial contribution to our knowledge of longleaf pine. He correlated site characteristics with longleaf pine growth in the sandhills of Kershaw County, South Carolina. The site index (which indicates how rapidly the pines grow) varied widely from 55 to 95 feet with little consistency to the soil series or to the soil texture. There were no correlations between site index and pH, extractable P, Mg, Ca, and K in either the A or B horizons.

The surface soil contained 65-95% sand and was from 1.5 to more than 15 feet deep. This soil was underlain by a stratum which contained at least 25% clay and which was impermeable to the percolation of water and the penetration of pine roots. The undulations of this impermeable stratum were inconsistent with the surface relief. Piezometer studies showed that the ground-water flowed downhill on top of the impermeable stratum. After a rain, peak water levels were measured in the piezometers at consecutively later time intervals downslope. Between rainfall events, the water table was below the root zone wherever the sands were deep. Low on the slope, though, the deeper sands contained ground-water nearer the surface because of accumulated base flow.

The site index was correlated with the depth to the water table, which in turn was correlated to the thickness of the surface soil and the position on the slope. Thin surface soils were not necessarily beneficial to the pines, though. In soils that were only 1.5 feet deep, the shallowly rooted pines were commonly wind-thrown.

Chapter 20. Pritchett and Lyford (1977) described the root system of slash pine. The tap root typically is 1-3 m deep. Up to 20 first-order laterals radiate from the taproot on mature trees. These laterals are 2-15 cm in diameter at their insertion and occur mostly at depths of 5 to 15 cm. The longest one measured was 18.7 m, but it terminated only 8.1 m from the tree base. Frequent abrupt changes in direction are responsible for laterals being closer to the tree base than their lengths would indicate. Sinker roots occur along these laterals and extend a short distance into the spodic horizon (Bh). Proliferation and mortality are high among the fine feeder roots.

Swindel et al. (1979) measured the biomass of slash pines in natural stands. Values were given for foliage, branches, and stems. The relationship between these values and basal area was estimated.

Chapter 23. The first documentation of natural seedling establishment of wiregrass (*Aristida stricta*) was presented in an unpublished file report by R. Glasgow at the St. Marks National Wildlife Refuge. Much of the field work was done by Mary Butler Davis and J. Reinman. The site was located in the n.w. corner of section 16, T5S, R2W, near Panacea in Wakulla County. A longleaf pine-xeric oak community occupied a sandhill which contained the usual compliment of wiregrass and other plants of the ground cover.

All trees and shrubs were cut early in 1977. Merchantable logs were removed, and all remaining woody materials were pushed with a rootrake into a brush pile. The operator kept the rootrake above the soil surface, so that disturbance to the soil and to the herbaceous vegetation was negligible. The brush pile was ignited in July, 1977, and the fire escaped, causing a summer burn over much of the study site. Wiregrass flowered prodigeously in response to the fire and produced seeds in abundance. Most seeds were shed by December, 1977.

Six, one meter-square plots were established to check for the reproduction of wiregrass. Three plots were in undisturbed areas and contained 3-6 mature clumps of wiregrass. These clumps were mapped and their diameters measured in December, 1977. The range in diameter was 1.2-7.0 cm. The other three plots were placed on disturbed sites which contained no wiregrass. Wiregrass seeds were scattered manually on these plots.

Two years later the plots were again observed. The three undisturbed plots all contained wiregrass seedlings, 12 in all. The original wiregrass plants were measured. The 13 surviving clumps (out of 14) had increased in diameter on an average of 39%.

The three disturbed plots contained 53 wiregrass seedlings. One plot had been placed in a firelane where the soil had been greatly disturbed. Three seedlings were recorded. Another plot had been placed where the brush had been burned and the soil had been subjected to intense heat and to compaction by heavy equipment. Thirty-five seedlings were recorded. The third plot had been subjected to light disturbance and contained 15 seedlings. The seedlings in two of the disturbed plots (firelane, burned) ranged from 0.8 to 5.3 cm in diameter. Those in the third plot (light disturbance) were smaller and not measured.

This study confirmed the tentative conclusions in Chapter 23 that wiregrass can reproduce by seed only following a fire during the growing season. Management designed to restore the ground cover in firelands must include summer burning.

Before recent disturbances resulting from land use, fireland communities were the most prevalent kind of vegetation in the southeastern coastal plain and probably occupied a majority of the land area. By far, the most important species ecologically in the firelands from southern North Carolina to Mobile Bay was wiregrass. It is amazing that the two most important studies on wiregrass are a master's thesis by Parrott (c.f. page 297) and file report in a wildlife refuge office, both unpublished.

On page 294, it was suggested that at least several herbs and low shrubs that grow in association with wiregrass have not been observed to reproduce. A recent review of the vegetation on abandoned phosphate mines helps confirm this suggestion (Florida Bureau of Geology 1980). More than 88,000 acres were surveyed in Hamilton County and in central Florida. Wiregrass and several associated species were observed only on lands adjacent to mines where disturbance had not been substantial. The associated species included Aristida spiciformis, Aster tortifolius, Balduina angustifolia, Carphephorus corymbosus, Lyonia fruticosa, Quercus laevis, Q. myrtifolia, and Rhododendron serrulatum. Subsequent to this study I discovered one plant of wiregrass growing on a windrow of mining spoils at a mine that had been abandoned for about 25 years in Hillsborough County. This plant and a few plants of scrubs (including Q. myrtifolia) were present in the same area, near the edge of the mine and near a scrubby flatwoods. It appeared that these plants had not seeded onto the site, but rather that the last load of spoils deposited on that windrow contained native topsoil with living rootstocks.

Chapter 27. Two papers appeared recently that elucidated the physiological differences between sourgum and blackgum (Keeley 1979, Keeley and Franz 1979). Upland trees (sourgum) were found to be very intolerant of flooded soils. After a year of flooded conditions, survival was poor, growth stunted, and rates of respiration low. In contrast, swamp trees (blackgum) were quite tolerant of flooding.

Floodplain trees from the Georgia Piedmont growing in drained soils were intermediate to the upland trees and the swamp trees in their physiological responses to flooding.

Chapter 32. Coultas (1976) prepared descriptions of soils which pertain to the discussion presented on page 388. One soil was described from a grass-sedge seepage bog along the west side of Bradwell Bay in Wakulla County. The other soil was described from a grass-sedge savannah in Liberty County. The latter soil is typical of the soils at the two savannahs characterized in Research Summary 9.

Conde *et al*. (1979) made biomass estimates of several trees characteristic of firelands and associated swamps, including longleaf pine, slash pine, sweetbay, swamp bay, loblolly bay, blackgum, bald-cypress, and myrtleleaf holly. Swindel *et al*. (1980) presented equations for predicting the green weights of some of these same species.

White (1979) discussed longevity of non-arboreal plants and made some observations which pertain to the discussion on page 362. He said that studies from the Great Plains and from British heathlands showed that herbs do not necessarily live indefinitely. Individual plants or populations eventually senesce and are replaced by individuals or populations representing other species. These replacements also become senescent in time and are replaced either by the first species or by a third species. The process is microsuccessional and mimics gap-phase succession as was described for hardwood forests in Chapter 37. It is not known whether or not the plants of the ground cover in firelands undergo such endogenous replacement, but the possibility should not be discounted.

Chapter 37. White (1979) made comments on riverbank vegetation, which pertain to the discussion on page 504. He said that *Acer saccharinum*, *Betula nigra*, *Populus deltoides*, and *Salix nigra*, all of which occur in the panhandle, share the following attributes which adapt them for survival on riverbanks. They produce large annual seed crops. The seeds are light weight and are easily dispersed by wind or water. Vegetative growth is rapid, and maturity is reached quickly. The damaged shoot system is capable of resprouting.. The plants are highly tolerant of flooding. These trees have "paid a price" for these attributes. They are short-lived, shade intolerant, and have low wood density.

Whipple (1980) described a stand of bottomland hardwoods from southern Louisiana. He calculated the regularity of dispersion for the individuals of the species present.

The study of H. M. Leitman on the Apalachicola River floodplain was mentioned on page 502. Subsequently, she sent me additional information (personal communication 1981). Forty-five tree species were encountered at 223 sampling points along 8 transects across the floodplain. These sampling points were placed in vegetation which included both the cypress-tupelo swamp system and the hardwood forest system. She found that water tupelo was the most common tree in the floodplain both in terms of density and basal area. The trees and forest types are being characterized in terms of the percentage of the year that the soils are flooded or saturated and the number of consecutive days that the forests experience flooding or saturated soils during the growing season. The report will be published soon and will be a major contribution to the knowledge of the vegetation of the panhandle.

Her discovery that water tupelo is more important than bald-cypress suggests that the Bald-Cypress - Tupelo Swamp Community (page 432) is better termed the Water Tupelo - Bald-Cypress Community.

Chapter 38. Mention was made on page 558 of the colonization of a spoil island, Drake Wilson Island, near Apalachicola. The report of that investigation was prepared by Kruczynski *et al*. (1978). The island was created in March, 1976 and planted with *Spartina alterniflora* and *S. patens* in July of that year. Growth was substantial and the effort successful. Spontaneous colonization was monitored. Forty-two species had invaded the island by September, 1977. Six additional species had been planted by the Army Corps of Engineers, including sand pine and cabbage palm.

Chapter 41. With regard to the management of lands for wildlife on pages 629-630, some comments by Lewis and Harshbarger (1976) are apropos. As mentioned earlier, their study was not done on pine plantations, but rather in pine-oak woods. They said,

> "Conditions favorable for both domestic and wild animals are best maintained in the South by retaining the understory vegetation in a subclimax condition through the use of fire. Periodic winter burning appeared to produce the best habitat for deer and turkey. However, the best quail habitat was produced by annual winter fires since forbs, especially legumes, were most abundant with this treatment."

Forage yields were best with annual winter fires and biennial summer fires.

On page 604, old field species were classified as "specialists" that survived the harsh open conditions of open habitats. Such colonizing plants are said to belong to "r" strategy species, which are characterized by being tolerant of environmental extremes and intolerant of competition, by high reproductive potentials and initially rapid growth, and by being short-lived. Competitive plants (e.g., wiregrass) are said to be "K" strategy species, which are characterized by being closely matched to habitat conditions, by strong competitive abilities, by low reproductive output and slow growth, and by a long life span (White 1979).

A final reference (Eyre 1980) pertains to several of the communities recognized in Part IV. About 28 forest cover types were described which occur in the panhandle. These forest types are mostly defined more narrowly than are the communities in the present report. For example, the two descriptions of forest cover types that I contribute to that work are both included within larger communities: the Slash Pine-Hardwood Type within the Bay Swamp Community and the Southern Redcedar Type within the Coastal Hammock Community.

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RESEARCH SUMMARY 1. THOMPSON'S WOODS

1. Longleaf Pine-Xeric Oak Woods

Unpublished data by A. F. Clewell

Dry sand ridge capping sandy loam hills, burned every few years, located on the west side of U.S. 319 just south of junction S.R. 3, Grady Co., Georgia, 4 miles north of the Leon Co., Florida line. Inventoried October 29, 1974.

OVERSTORY: All young second-growth longleaf pines upwards to 37 cm in dbh and 20 m tall. 180 trees/ha, as sampled in a 500 m^2 quadrat.

UNDERSTORY: 1340 trees/ha, as sampled in a 500 m^2 quadrat, with the following relative densities:

Pinus palustris	91.0
Quercus marilandica	4.5
Quercus laevis	1.5
Quercus incana	1.5
Diospyros virginiana	1.5
	100.0

GROUND COVER: There were 1300 coppicing rootcrowns/ha of tree species, as determined in a 100 m^2 quadrat, with the following relative densities:

Quercus laevis	46.2
Diospyros virginiana	15.4
Quercus stellata	15.4
Quercus falcata	7.7
Quercus nigra	7.7
Sassafras albidum	7.7
	100.1

The frequency of non-arboreal species was determined in 30 m^2 quadrats. The percentage of quadrats in which each of the species occurred was as follows:

Aristida stricta	100	Pityopsis graminifolia	30
Gaylussacia dumosa	83	Tragia urens	27
Dichanthelium commutatum	80	Chrysopsis mariana	23
Dyschoriste oblongifolia	73	Quercus pumila	23
Helianthus radula	70	Rhus copallina	23
Andropogon virginicus*	67	Schrankia microphylla	23
Vaccinium myrsinites	63	Agalinus pulchella	20
Pteridium aquilinum	57	Angelica dentata	20
Carphephorus odoratissimus	40	Ceanothus microphyllus	20
Rhynchosia reniformis	40	Elephantopus elatus	20
Ageratina jucunda	30	Hedyotis procumbens	20
Aster adnatus	30	Hieracium gronovii	20

*Plants stunted.

RESEARCH SUMMARY 1, continued.

Solidago odora	17	Tephrosia virginiana	7
Stylisma humistrata	17	Vaccinium stamineum	7
Gaylussacia frondosa	17	Andropogon gerardii	3
Aristolochia serpentaria	13	Asimina longifolia	3
Petalostemon albidus	13	Aster concolor	3
Sorghastrum secondum	13	Eryngium yuccifolium	3
Gymnopogon ambiguus	10	Eupatorium hyssopifolium	3
Lespedeza repens	10	Galactia macreei	3
Linum medium	10	Galium pilosum	3
Strophostyles umbellata	10	Hypericum stans	3
Scleria sp.	10	Ilex glabra	3
Eupatorium album	7	Polygala nana	3
Lechia minor	7	Aster tortifolius	3
Malus angustifolius	7	Tephrosia spicata	3
Rhus toxicodendron	7	Trichostemon dichotomum	3
Rhynchosia tomentosa	7	Verbesina aristata	3
Rubus cuneifolius	7	Vernonia angustifolia	3
Sorghastrum nutans	7	Viola sp.	3

Other species, not occurring in quadrats:

Andropogon ternarius
Asclepias verticillata
Aster dumosus
Aureolaria pedicularia
Carya tomentosa
Cornus floridana
Euphorbia pubentissima
Ipomoea pandurata
Lespedeza stuevei
Lobelia puberula
Myrica cerifera
Nyssa sylvatica
Pentstemon multiflorus
Pinus echinata
Polygala incarnata
Salvia azurea
Silphium simpsonii
Smilax glauca
Stylosanthes biflora
Vitis rotundifolia

There were 60 species recorded in the quadrats and 20 additional species observed in the ground cover. Nine tree species were listed, including those occurring as coppicing rootcrowns. In all, there were 89 species.

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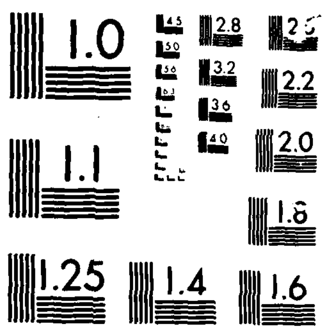


MICROCOPY CHART

RESEARCH SUMMARY 2. SANDHILLS NEAR SPRING HILL

1. Longleaf Pine-Xeric Oak Woods

Unpublished data of A. F. Clewell

Two stands 2 km apart in dry sandhills along Forest Road 358A, Apalachicola National Forest, nw section 23 and nw section 26 of T1S, R2W, Leon County. The stands were similar to each other and are burned about every 5 years. Inventoried in 1974 by J. Gibel, J. Herron, G. Roney, and B. Sabine.

OVERSTORY: The overstory consisted solely of longleaf pines about 15-20 m tall. Since the original-growth was clear cut about 1920, the overstory pines had not yet formed a distinct stratum above the understory oaks. As a result, trees exceeding 11 cm in dbh were considered as overstory trees. These were studied in quadrats comprising 1,000 m^2 at each of the two stands. There were 130 overstory trees/ha with a basal area of 7.7 m^2/ha.

UNDERSTORY: The understory was studied in the same quadrats as the overstory. There were 4674 trees/ha with the following relative density:

Quercus laevis	79
Quercus incana	12
Quercus margaretta	8
Vaccinium arboreum	1
	100

GROUND COVER: The frequency of non-arboreal species was determined in 20, 0.8 m^2 quadrats in each stand. The percentage of quadrats in which each of the more abundant species occurred was as follows:

Aristida stricta	100	Quercus minima	25
Pteridium aquilinum	48	Andropogon sp.	25
Tragia urens	43	Chrysopsis graminifolia	23
Dichanthelium spp.	30	Vaccinium myrsinites	20
Licania michauxii	25	Rubus cuneifolius	18
Quercus pumila	25		

Some other species were:

Asclepias verticillata	Desmodium floridanum
Asclepias tuberosa	Dichanthelium aciculare
Asimina longifolia	Dichanthelium ovale
Aster patens	Dryschoriste oblongifolia
Aster tortifolius	Eriogonum tomentosum
Baptisia lanceolata	Euphorbia curtissii
Bulbostylis ciliatifolia	Eupatorium album
Cassia fasciculata	Eupatorium compositifolium
Ceanothus americanus	Galium pilosum
Cnidoscolus stimulosus	Gelsemium sempervirens
Crotalaria rotundifolia	Gymnopogon ambiguus
Croton argyranthemus	Hieracium gronovii

RESEARCH SUMMARY 2, continued.

Hypericum gentianoides
Hypericum microsepalum
Indigofera caroliniana
Lechea minor
Lespedeza hirta
Liatris chapmanii
Muhlenbergia capillaris
Onosmodium virginianum
Palafoxia integrifolia
Petalostemum albidum
Petalostemum caroliniense
Polygonella gracilis
Rhus copallina
Rhynchosia reniformis
Ruellia ciliosa
Scutellaria integrifolia
Seymeria pectinata
Smilax auriculata
Solidago odora
Stillingia sylvatica
Stylisma humistrata
Stylosanthes biflora
Tephrosia florida
Tephrosia spicata
Vernonia angustifolia
Zornia bracteata

RESEARCH SUMMARY 3. BIG WOODS AT GREENWOOD PLANTATION

2. Longleaf Pine Savannah

Unpublished data of A. F. Clewell

Mesic, annually burned, original-growth stand on gentle slope along Pine Tree Blvd. between U.S. 84 and the Atlantic Coast Line Railroad tracks. Soil a fine sandy loam; pH 5.9; organic matter low; N very low; Ca 215 ppm; Mg 78 ppm; K 20 ppm; P 0.65 ppm. Inventoried June 1, 1968 by A. Clewell and R. Komarek.

OVERSTORY: All longleaf pines, up to 68 cm in dbh and 28 m tall. Stumps of trees that were removed after being lightning-killed often exceeded 100 years and sometimes 200 years old. The overstory was sampled in quadrats comprising 3600 m^2. There were 158 trees/ha with a basal area of 17.0 m^2/ha. There were 22 stumps/ha.

UNDERSTORY: Absent.

GROUND COVER: There were 85 coppicing rootcrowns/ha of tree species, as determined in quadrats comprising 81 m^2, with the following relative densities:

Diospyros virginiana	42.9
Quercus falcata	21.4
Prunus serotina	14.3
Quercus hemisphaerica	7.1
Quercus nigra	7.1
Quercus stellata	7.1
	99.9

The frequency of non-arboreal species was determined in 30, m^2 quadrats, placed where there was no evidence of soil disturbance. The percentage of quadrats in which each of 62 species occurred was as follows:

Aristida stricta	93	Sorghastrum secondum	30
Pteridium aquilinum	90	Schizachyrium tenerum	30
Aster adnatus	70	Ageratina jucunda	27
Pityopsis graminifolia	67	Aster tortifolius	27
Andropogon virginicus*	57	Euphorbia pubentissima	27
Vaccinium myrsinites	57	Vaccinium stamineum	23
Quercus minima, Q. pumila	50	Kuhnia eupatorioides	20
Dyschoriste oblongifolia	47	Rhynchosia tomentosa	20
Dichanthelium spp.	43	Desmodium lineatum	17
Gaylussacia frondosa	40	Chrysopsis mariana	17
Gaylussacia dumosa	33	Muhlenbergia capillaris	17
Rhus copallina	33	Myrica cerifera	17
Helianthus radula	33	Rhus toxicodendron	17
Solidago odora	30	Schrankia microphylla	17

*Plants stunted.

RESEARCH SUMMARY 3, continued.

Aster concolor	13	Sorghastrum nutans	7
Aster dumosus	13	Trichostema dichotomum	7
Carphephorus odoratissimus	13	Angelica dentata	3
Cassia nictitans	13	Aristida lanosa	3
Centrocema virginianum	10	Ceanothus microphyllus	3
Elephantopus elatus	10	Desmodium strictum	3
Gymnopogon brevifolius	10	Eryngium yuccifolium	3
Agalinus purpurea	7	Eupatorium hyssopifolium	3
Crotalaria purshii	7	Galactia macreei	3
Eupatorium album	7	Galium pilosum	3
Ilex glabra	7	Hibiscus aculeatus	3
Lechea minor	7	Lespedeza angustifolia	3
Lespedeza repens	7	Onosmodium virginianum	3
Polygala lutea	7	Rhexia alifanus	3
Rhynchosia reniformis	7	Smilax glauca	3
Rubus cuneifolius	7	Tephrosia spicata	3
Rubus trivialis	7		

The following 29 species were also present, but not in the quadrats:

Aronia arbutifolia
Asimina longifolia
Malus angustifolius
Gymnopogon ambiguus
Conoclinium coelestinum
Eupatorium compositifolium
Eupatorium linearifolium
Liatris squarrosa
Rudbeckia hirta
Vernonia angustifolia
Desmodium ciliare
Galactia erecta
Galactia volubilis
Lespedeza virginica
Petalostemum albidum
Psoralea psoralioides
Stylosanthes biflora
Tephrosia virginiana
Asclepias verticillata
Buchnera floridata
Cyperus filiculmis
Hypericum stans
Lechia mucronata
Phlox floridana
Polygala grandiflora
Polygala incarnata
Rhynchospora harveyi
Scleria ciliata
Tragia urens

There were 98 species recorded, including trees.

RESEARCH SUMMARY 4. WADE PLACE

2. Longleaf Pine Savannah

Unpublished data of A. F. Clewell

Well drained sandy loam slope on the south side of S.R. 122, 8 miles north of the Leon County, Florida, line and 3.8 miles south of junction U.S. 319 in Thomas County, Georgia. Inventoried June 1, 1968 by A. F. Clewell and R. Komarek.

The pines were original-growth, and only lightning-killed trees have been logged. One stump had 314 rings. The pine stand continued up slope from the study area and became a longleaf pine-xeric oak woods with an understory of Quercus laevis, Q. margaretta, Q. incana, and Castanea pumila. The pineland has been burned or sometimes brush-cut annually or nearly so. Brush-cutting has scarred the soil in places, causing a reduction in wiregrass density and allowing the establishment of many hardwoods which survive as coppicing rootcrowns.

OVERSTORY: All longleaf pines, these up to 60 cm in dbh and 34 m tall. In quadrats comprising 5400 m^2 there were 115 pines/ha with a collective basal area of 12.8 m^2/ha.

UNDERSTORY: Absent.

GROUND COVER: Non-arboreal plants and coppicing hardwoods were studied in 30, m^2 quadrats. The percentage of quadrats in which each of these 63 species occurred was as follows:

Pteridium aquilinum	90	Dichanthelium commutatum	20
Dyschoriste oblongifolia	80	Quercus incana	20
Tephrosia virginiana	60	Sassafras albidum	20
Rhus copallina	53	Andropogon gerardii	17
Quercus margaretta	50	Desmodium floridanum	17
Solidago odora	50	Erianthus alopecuroides	13
Sorghastrum secundum	47	Quercus laevis	13
Quercus pumila	43	Tragia urens	13
Gaylussacia frondosa	40	Clitoria mariana	13
Aster tortifolius	37	Ageratina jucunda	10
Vaccinium stamineum	37	Aster adnatus	10
Aristida stricta	37	Aster sagittifolius	10
Andropogon virginicus*	33	Euphorbia pubentissima	10
Vaccinium myrsinites	33	Verbesina aristata	10
Sorghastrum nutans	33	Aristida lanosa	7
Castanea alnifolia	33	Aristolochia serpentaria	7
Pityopsis graminifolia	27	Aster dumosus	7
Ceanothus americanus	20	Asimina longifolia	7
Centrocema virginianum	20	Cassia nictitans	7
Gaylussacia dumosa	20	Chrysopsis mariana	7
Myrica cerifera	20	Hieracium gronovii	7

*Plants stunted.

RESEARCH SUMMARY 4, continued.

Lespedeza virginica	7	Hypericum stans	3
Muhlenbergia capillaris	7	Lespedeza hirta	3
Quercus falcata	7	Nyssa sylvatica	3
Rhus toxicodendron	7	Quercus nigra	3
Smilax glauca	7	Rubus trivialis	3
Angelica dentata	3	Rhynchosia tomentosa	3
Desmodium obtusum	3	Scutellaria integrifolia	3
Desmodium strictum	3	Salvia azurea	3
Desmodium lineatum	3	Scleria sp.	3
Eryngium yuccifolium	3	Stillingia sylvatica	3
Helianthus radula	3		

There were 29 other species that did not occur in quadrats:

Cornus florida
Carya tomentosa
Pinus echinata
Pinus taeda
Prunus serotina
Quercus velutina
Castanea pumila
Ceanothus microphyllus
Gymnopogon ambiguus
Paspalum bifidum
Aster concolor
Cirsium horridulum
Eupatorium album
Eupatorium hyssopifolium
Liatris gracilis
Liatris graminifolia
Silphium simpsonii
Elephantopus elatus
Vernonia angustifolia
Crotalaria rotundifolia
Crotalaria purshii
Desmodium laevigatum
Desmodium paniculatum
Galactia macreei
Lespedeza angustifolia
Lespedeza stuevei
Strophostyles umbellata
Lobelia puberula
Pentstemon multiflorus

There were 93 species recorded in all.

RESEARCH SUMMARY 5. BUCKHORN FLATWOODS

3a. Longleaf Pine Flatwoods

Unpublished data of A. F. Clewell

Sandy moist flat with a spodic horizon, along the south side of Forest Road 305 about 2 or 3 miles west of the Buckhorn Hunt Camp, Apalachicola National Forest, Leon County (section 6 of T2S, R3W, and section 1 of T2S, R4W). Inventoried by A. F. Clewell and R. Komarek in the spring and early summer of 1970.

The woods are winter-burned about every 5 years. The longleaf pines represent natural second-growth following clear cutting in the late 1920's. (Persistent stumps of the original-growth pines revealed a former density of 103 trees/ha.) Many of the trees are leaning, presumably unable to tolerate competition. The trees are of many sizes and are not differentiated into an understory and overstory. The overstory was, therefore, defined arbitrarily as consisting of those trees of at least 10 cm in dbh. Smaller trees over 2 m tall comprised the understory. The trees were inventoried in 8 plots, each one a hectare in size.

OVERSTORY: All longleaf pines up to 40 cm in dbh and 23 m tall. There were 455 trees/ha with a collective basal area of 14.7 m^2/ha.

UNDERSTORY: All longleaf pine except one slash pine. There were 360 pines/ha with a collective basal area of 2.8 m^2/ha.

GROUND COVER: The non-arboreal species were sampled for frequency in 30, m^2 quadrats in each of the 8, one-hectare plots. The percentage of quadrats in which the more common species occurred were as follows:

Aristida stricta	98	Andropogon virginicus*	18
Quercus minima, Q. pumila	83	Cassia fasciculata	18
Ilex glabra	68	Seymeria cassioides	14
Vaccinium myrsinites	56	Lyonia lucida	10
Serenoa repens	43	Tephrosia hispidula	10
Pteridium aquilinum	38	Tragia urens	9
Hypericum hypericoides	37	Rhexia alifanus	9
Dichanthelium spp.	34	Gaylussacia frondosa	9
Smilax glauca	32	Lyonia ferruginea	9
Pityopsis graminifolia	29	Pterocaulon pycnostachyum	7
Balduina uniflora	26	Xyris caroliniana	7
Carphephorus odoratissimus	26	Syngonanthus flavidulus	7
Aster tortifolius	26	Aster eryngiifolius	6
		Aster adnatus	5

*Plants stunted.

RESEARCH SUMMARY 5, continued.

Less common species included:

Angelica dentata	Lespedeza repens
Asclepias cinerea	Liatris chapmanii
Asimina longifolia	Licania michauxii
Aster reticulatus	Lobelia paludosa
Baptisia simplicifolia	Myrica cerifera
Carphephorus pseudoliatris	Osmunda cinnamomea
Chrysopsis mariana	Panicum anceps
Cyrilla racemiflora	Pityopsis oligantha
Cleistes divaricata	Polygala nana
Crotalaria purshii	Polygala setacea ?
Cuscuta sp.	Sabatia difformis ?
Desmodium lineatum	Scleria nitida
Desmodium paniculatum	Scleria triglomerata
Drosera capillaris	Smilax auriculata
Eryngium yuccifolium	Smilax pumila
Eupatorium compositifolium	Stillingia sylvatica
Helianthus radula	Tofieldia racemosa
Hypoxis sp.	Vaccinium darrowi
Iles coriacea	Vitis rotundifolia
Ilex myrtifolia	Xyris caroliniana
Kalmia hirsuta	Zigadenus densus

There were 72 species, including the 2 pines.

RESEARCH SUMMARY 6. LIBERTY COUNTY FLATWOODS

3a. Longleaf Pine Flatwoods

Unpublished data by A. F. Clewell

Sandy flatwoods bordering grass-sedge savannahs (described in Research Summary 9) in the Apalachicola National Forest, T4S, R8W. One stand was in Section 4 along the north side of Forest Road 113 just west of Kennedy Creek. The other stand was in Section 17 along the east side of S.R. 379. Both stands were quadrated May 14 and October 24, 1970.

OVERSTORY: Second-growth longleaf pines.

UNDERSTORY: Absent.

GROUND COVER: The species were listed in 30, m^2 quadrats in each stand in May. Thirty additional quadrats were established in each stand in October, and only those species that were too young to identify in May were tallied. The numbers below are the percentages of quadrats in which each species occurred. Additional species are listed that did not occur in the quadrats but which were present in these stands or in similar flatwoods nearby.

	Section 4	Section 17
Agalinis aphylla	23	7
Ageratina aromatica	7	
Aletris aurea		
Aletris lutea		
Aletris obovata		
Angelica dentata	3	
Andropogon virginicus	27	50
Aristida stricta	97	100
Asclepias cinerea		
Asclepias longifolia	3	
Asclepias michauxii	3	10
Asimina longifolia		
Aster adnatus	63	33
Aster concolor	17	3
Aster dumosus	7	
Aster eryngiifolius		3
Aster linariifolius	33	33
Aster reticulatus		
Aster tortifolius		20
Aureolaria pedicularia		
Baptisia lanceolata		7
Baptisia simplicifolia		
Berlandiera pumila		
Callicarpa americana		
Carphephorus odoratissimus	13	27

RESEARCH SUMMARY 6, continued

	Section 4	Section 17
Carphephorus paniculatus		20
Carphephorus pseudoliatris	7	
Cassia fasciculata	7	
Cassia nictitans		3
Chrysopsis gossypina		
Chrysopsis mariana	17	10
Cirsium horridulum		
Cirsium lecontei		3
Cnidoscolus stimulosus	17	
Crotalaria purshii	7	10
Ctenium aromaticum		47
Desmodium ciliare		
Desmodium lineatum		10
Desmodium paniculatum		3
Dichanthelium acuminatum	43	23
Dyschoriste oblongifolia		
Elephantopus elatus		13
Erigeron vernus		
Eriogonum tomentosum		
Eryngium yuccifolium		13
Eupatorium album	3	
Eupatorium compositifolium		
Eupatorium rotundifolium		30
Eupatorium recurvans	3	
Eupatorium semiserratum		
Euphorbia inundata		20
Galactia erecta	13	13
Gaylussacia dumosa		
Gaylussacia frondosa	13	17
Gelsemium sempervirens		
Gnaphalium falcatum	3	
Hedyotis procumbens	3	
Heleanthemum carolinianum		13
Helenium pinnatifidum		13
Helianthus heterophyllus		3
Helianthus radula	30	67
Hibiscus aculeatus		
Hieracium gronovii		13
Hypericum fasciculatum	3	
Hypericum microsepalum	3	17
Hypericum myrtifolium		3
Hypericum tetrapetalum		
Hypericum stans		
Ilex glabra		30
Lacnocaulon anceps		13
Lespedeza capitata		
Lespedeza repens	13	
Liatris gracilis		20
Liatris tenuifolia		7

RESEARCH SUMMARY 6, continued

	Section 4	Section 17
Licania michauxii	47	53
Lobelia floridana	3	
Lobelia paludosa		
Lygodesmia aphylla		
Myrica cerifera	13	23
Myrica heterophylla		
Myrica inodora		
Nolina atopocarpa		17
Onosmodium virginianum	40	17
Osmanthus americana	3	
Paspalum sp.		3
Petalostemon albidum		13
Phoebanthus tenuifolia	70	50
Pityopsis aspera		3
Pityopsis graminifolia	60	63
Pityopsis oligantha		
Polygala crenata		
Polygala grandiflora		
Polygala incarnata	7	
Polygala lutea		
Polygala nana		7
Pteridium aquilinum	93	7
Pterocaulon pycnostachyum		
Quercus falcata		
Quercus incana		
Quercus laevis		
Quercus minima, Q. pumila	77	73
Quercus nigra		
Rhexia alifanus		27
Rhynchospora sp.	3	3
Rhynchospora mollissima		3
Rubus cuneifolius	3	13
Sabatia brevifolia		3
Salvia azurea	3	
Schrankia microphylla	47	23
Scleria hirtella	20	20
Scutellaria integrifolia	3	
Serenoa repens	3	7
Seymeria cassioides	30	13
Sisyrinchium arenicola	3	
Smilax auriculata	60	
Smilax pumila	10	
Solidago odora	17	40
Solidago stricta		
Stylisma patens	3	17
Stillingia sylvatica		13
Stylosanthes biflora	33	57
Tephrosia virginiana	17	3

RESEARCH SUMMARY 6, continued

	Section 4	Section 17
Tragia urens	83	57
Trichostema dichotomum	20	
Vaccinium darrowi	23	
Vaccinium myrsinites	3	10
Viola septemloba	23	20
Viola sp.	3	3
Vitis rotundifolia		
Xyris caroliniana	7	
Zigadenus densus		

133 species are listed (including longleaf pine), of which 60 occurred within the quadrats of Section 4 and 67 within those of Section 17.

4. Boggy Flatwoods

Conde, L. F., J. E. Smith, and C. A. Hollis. 1979. Effects of intensive reforestation activities on higher plant species diversity and frequency on a coastal pine-cypress-titi site: first years results. IMPAC Reports 2(1): 1-12. School of Forest Resources and Conservation, Univ. of Florida, and Southeastern Forest Experiment Station, USDA, Forest Service. (For follow-up see IMPAC Reports 5(3): 1-28, 1980).

The site was located on land belonging to the Buckeye Cellulose Corporation in Franklin County.

The site was divided into 2 plots. One was undisturbed and the other was logged, burned, bedded, fertilized, and planted to slash pines a year before the inventory. The undisturbed plot was described as follows:

OVERSTORY: Open, 20 m tall, of slash pine (with old turpentine faces), pond-cypress, and white cedar.

UNDERSTORY: Dense because of years of fire suppression, primarily consisting of black titi, little-leaf titi, fetterbush, large gallberry, and myrtle-leaf holly, mostly 3-6 m tall.

GROUND COVER: Limited to scattered small grassy openings. Species frequency was determined by interception along 3-meter-long line-segments. Wiregrass was intercepted by about 15% of these segments in the undisturbed plot and by about 60% in the year-old planted pine plantation (see 1980 report).

The following list contains 111 species (29 woody, 82 herbaceous) for both the undisturbed and the treated plots. (Other species were also reported, some of which were probably restricted to the borders of sloughs, and the others may have been introduced as weeds during site preparation.) Forty-nine species (46 herbs, 3 woody) were observed only on the treated plot. These species may have been overlooked on the undisturbed plot because of the dense understory, or the plants of some species may have been repressed entirely by competition from the understory and were surviving as dormant rootstocks. Plants of these species on the disturbed plot responded to release from competition or at least were more easily seen.

The authors did not offer this interpretation for the additional 49 species but suggested succession as an explanation without any discussion of details.

WOODY SPECIES

Aronia arbutifolia
Chamaecyparis henryae
Clethra alnifolia
Cliftonia monophylla
Cyrilla parvifolia
Cyrilla recemiflora
Gaylussacia mosieri
Gelsemium rankinii?
Hypericum brachyphyllum
Hypericum fasciculatum
Ilex coriacea
Ilex glabra
Ilex myrtifolia
Lyonia fruticosa
Lyonia lucida
Magnolia virginiana
Myrica cerifera
Myrica inodora
Nyssa biflora
Osmanthus americana
Persea palustris
Pieris phillyreifolia
Pinus elliottii
Rhododendron serrulatum
Smilax laurifolia
Styrax americana
Taxodium ascendens
Vaccinium fuscatum?
Vitis sp.

GRAMINACEOUS SPECIES

Andropogon glomeratus
Andropogon tenarius
Andropogon virginicus
Aristida stricta
Aristida virgata
Carex joorii
Ctenium aromaticum
Dichanthelium acuminatum
Fuirena squarrosa
Juncus marginatus
Juncus polycephalus
Panicum dichotomiflorum
Panicum rigidulum
Rhynchospora baldwinii
Rhynchospora cephalantha
Rhynchospora chapmanii
Rhynchospora corniculata
Rhynchospora filifolia
Rhynchospora gracilenta
Rhynchospora plumosa
Rhynchospora rariflora
Scirpus cyperinus
Scleria baldwinii
Scleria reticularis

FORBS

Agalinis linifolia
Agalinis purpurea
Aletris lutea
Aster chapmanii
Balduina uniflora
Bartonia paniculata
Calopogon pallidus
Carphephorus pseudoliatris
Chondrophora nudata
Coreopsis leavenworthii?
Cuscuta compacta
Dichromena latifolia
Drosera capillaris
Drosera filiformis
Eriocaulon decangulare
Eupatorium recurvans
Eupatorium semiserratum
Euthamia minor
Helianthus floridanus
Hypoxis hirsuta
Justicia crassifolia
Lachnanthes caroliniana
Lachnocaulon anceps
Liatris spicata
Lilium catesbaei
Lobelia floridana
Lophiola americana
Ludwigia linearis

RESEARCH SUMMARY 7, continued.

FORBS (Continued)

Ludwigia pilosa
Lycopodium alopecuroides
Lycopodium carolinianum
Oxypolis filiformis
Plantanthera ciliaris
Plantanthera nivea
Pleea tenuifolia
Pluchea camphorata
Pluchea foetida
Pluchea odorata
Pluchea rosea
Polygala cruciata
Polygala cymosa
Polygala lutea
Proserpinaca pectinata
Rhexia alifanus
Rhexia virginica
Sabatia quadrangula
Sagittaria graminea
Sarracenia flava
Sarracenia psittacina
Syngonanthus flavidulus
Utricularia cornuta
Utricularia juncea
Woodwardia virginica
Xyris ambigua
Xyris baldwiniana
Xyris elliottii
Xyris stricta
Zigadenus glaberrimus

RESEARCH SUMMARY 8. SEEPAGE BOG NEAR BLOXHAM

5. Grass-Sedge Seepage Bog

Unpublished data of A. F. Clewell

Hillside in the Apalachicola National Forest 2.5 miles south of Bloxham in Leon County and 160 m south of Forest Road 344C in section 33, T1S, R4W. Inventoried by D. Tober, W. Cooksey, and R. Gaskalla in 1974.

The lower of the accompanying diagrams shows the profile of the region. The area between Forest Road 344C and the titi swamp is now a young longleaf pine plantation. Grand Bay is a well developed bay swamp. The sand ridge contains a longleaf pine-xeric oak community. The bog separates the titi swamp from Grand Bay for about 130 meters. The bog is about 400 m long on its east-west axis which parallels the road.

Bog vegetation consists of a dense turf of wiregrass (Aristida stricta), sedges, pitcher-plants, clubmosses, and scattered small trees of species common to acid swamps. Some species present were:

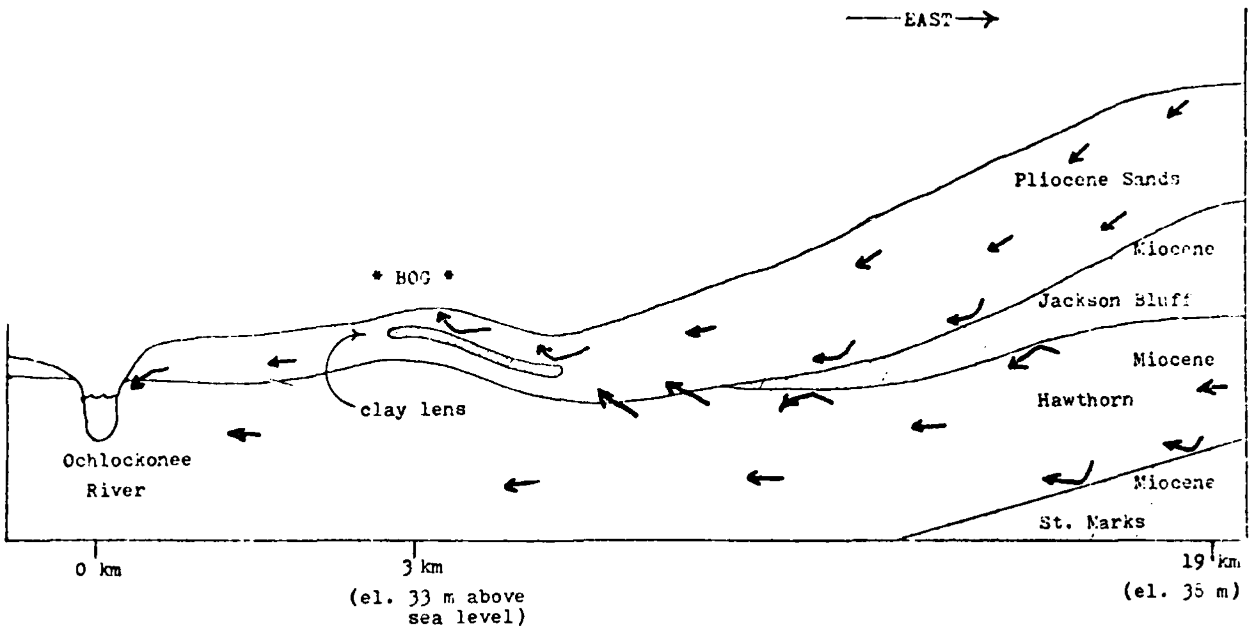
Woody Species	Herbs
Cliftonia monophylla	Drosera capillaris
Cyrilla parvifolia	Drosera tracyi
Hypericum fasciculatum	Eriocaulon compressum
Ilex glabra	Eriocaulon decangulare
Ilex myrtifolia	Lachnanthes caroliniana
Lyonia lucida	Rhexia alifanus
Lyonia mariana	Sarracenia flava
Magnolia virginiana	Sarracenia psittacina
Myrica heterophylla	Sphagnum sp.
Myrica inodora	
Pinus serotina	
Smilax laurifolia	

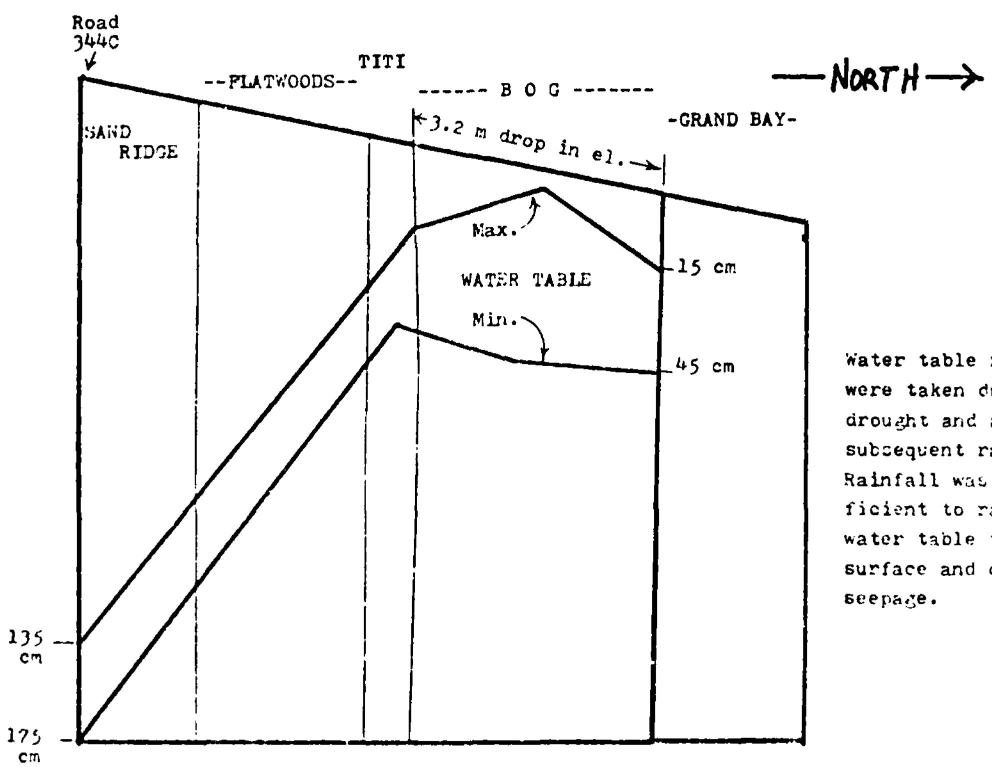
During wet seasons, water seeps upwards to the soil surface. When seepage occurs, the soil is a slightly quaking quicksand which is made firm by the dense herbaceous turf. The topsoil is a black peaty sand 9 dm deep at higher elevations and 3 dm deep downhill. The pH was 6.3. An argillic horizon is 122 cm deep at the west end of the bog. This horizon is 127 cm deep at mid-bog and 152 cm deep at the east end.

Pliocene sands were 15 m deep 3 km east of the bog (Fla. Geol. Surv. Bull. 47, 1966). These sands lie on the impervious Jackson Bluff Formation which is 3 m thick to the east but which does not extend beneath the bog.

The upper diagram suggests the reason for seepage. Ground water seeps westwards towards the Ochlockonee River. Part of this base flow is confined within the Hawthorn Formation beneath the Jackson Bluff Formation. This head of water is pushed upwards beneath the bog as soon as the Jackson Bluff Formation disappears. The argillic horizon is a clay lens that deflects the base flow towards the surface. The high value for pH suggests water from an aquifer rather than water which has been accumulating organic acids in an impervious basin.

HYPOTHETICAL DIAGRAM OF THE HILLSIDE BOG NEAR BLOXHAM





Water table readings were taken during a drought and after subsequent rains. Rainfall was insufficient to raise the water table to the surface and cause seepage.

6. Grass-Sedge Savannah

Unpublished data by A. F. Clewell

Wet clayey bogs in the Apalachicola National Forest, T4S, R8W. One stand was in Section 4 along the north side of Forest Road 113 just west of Kennedy Creek. The other stand was in Section 17 along the east side of S.R. 379. Quadrats were studied May 7 & 14, 1970.

OVERSTORY: Absent

UNDERSTORY: Absent

GROUND COVER: Recently burned. The trees and shrubs listed below were coppicing from rootcrowns, except for *Pinus elliottii* which survived fire as stunted saplings and *Hypericum fasciculatum* which were killed but still standing. Frequencies of species were determined in 30, m^2 quadrats in Section 17 and 60, m^2 quadrats in Section 4. Half of the quadrats were placed in lower, wetter areas than the other half in Section 17. The percentage of quadrats in which each species occurred is listed below. "High" signifies a species that was more frequent on high ground and "low" signifies a species that was more abundant on low ground in Section 17. Additional species are listed which were observed on these savannahs and in others nearby but not in any quadrats.

	Section 4	Section 17
Agalinis aphylla		
Agalinis filicaulis		
Agalinis purpurea		
Aletris aurea		
Aletris lutea	25 high	23
Andropogon sp.		33
Anthaenantia rufa		
Aristida affinis		
Aristida stricta	100	100
Arnoglossum ovatum		
Asclepias connivens		
Asclepias lanceolata		
Asclepias longifolia	2 high	
Aster adnatus		
Aster chapmanii		
Aster eryngiifolius	7 high	
Aster reticulatus		
Balduina uniflora		
Bigelowia nudata		
Calopogon pallidus	8 low	3
Calopogon pulchellus	8 high	
Carphephorus pseudoliatris		
Chaptalia tomentosa	42 low	67
Cirsium lecontei	2 low	3

RESEARCH SUMMARY 9, continued.

	Section 4	Section 17
Clethra alnifolia		
Coreopsis gladiata		
Coreopsis nudata		10
Ctenium aromaticum	15 low	30
Cyrilla parvifolia		
Dichanthelium acuminatum	35 high	87
Dichromena colorata	15 low	27
Dichromena latifolia		3
Diospyros virginiana		
Drosera capillaris	3 high/low	80
Erianthus giganteus		
Erigeron vernus	7 low	
Eriocaulon compressum	33 low	63
Eriocaulon decangulare	17 low	17
Eryngium yuccifolium		
Eupatorium leucolepis	3 high	
Eupatorium recurvans		
Eupatorium rotundifolium		
Euphorbia inundata	23 high	
Euthamnia minor		
Fraxinus caroliniana		
Fuirena squarrosa		
Gaylussacia dumosa		
Helenium pinnatifidum	28 low	13
Helianthus heterophyllus	23 low	23
Hypericum brachyphyllum		
Hypericum fasciculatum	73 high/low	
Hypericum microsepalum		
Hypericum myrtifolium		
Hypoxis hirsuta		
Hyptis alata		
Ilex coriacea		
Ilex glabra	3 high	
Ilex myrtifolia		3
Iris tridentata		
Liatris spicata		
Lilium catesbaei		
Lobelia brevifolia		10
Lobelia floridana		
Lobelia paludosa	3 low	17
Lophiola americana	2 low	37
Lycopodium alopecuroides		
Lycopodium prostratum		
Lyonia lucida		
Magnolia virginiana		
Muhlenbergia capillaris		
Myrica cerifera	3 high	
Myrica heterophylla		3
Nyssa biflora		
Osmunda cinnamomea		
Osmunda regalis		

RESEARCH SUMMARY 9, continued

	Section 4	Section 17
Oxypolis filiformis		
Panicum rigidulum		
Parnassia caroliniana		
Paspalum plicatulum	3 high	
Persea palustris		
Physostegia leptophylla		3
Pinguicula sp.		3
Pinus elliottii	7 high/low	
Pityopsis oligantha	12 high	
Plantanthera nivea		
Pleea tenuifolia		
Pogonia ophioglossoides		
Polygala baldwinii		
Polygala crenata	2 high	
Polygala cruciata	3 high	
Polygala cymosa		
Polygala harperi	3 high	
Polygala ramosa		13
Quercus nigra		
Rhexis alifanus	68 high/low	87
Rhexia lutea		3
Rhexia petiolata		
Rhynchospora corniculata		
Rhynchospora chapmanii		
Rhynchospora globularis		
Rhynchospora microcephala		
Rhynchospora plumosa		43
Rubus argutus	3 high	
Rudbeckia graminifolia		87
Rudbeckia mohrii		
Ruellia pedunculata		
Sabatia bartramii		
Sabatia stellaris		
Sarracenia flava	3 low	
Sarracenia psittacina	8 low	
Scleria baldwinii		17
Scleria hirtella		
Scleria reticularis		
Scleria sp. (reticularis?)	8 low	30
Seymeria cassioides	22 high	
Sisyrinchium arenicola	8 high	10
Smilax glauca		
Smilax laurifolia		
Spiranthes praecox		
Taxodium ascendens		
Tofieldia racemosa		
Utricularia juncea		37
Verbesina chapmanii	40 low	17
Vitis rotundifolia		
Xyris ambigua		
Xyris caroliniana		

	Section 4	Section 17
Xyris stricta		
Zigadenus densus		
Zigadenus glaberrimus		

128 species are listed, including 36 that were recorded in the quadrats of Section 4 and 33 in the quadrats of Section 17.

The soil of a similar savannah in the same vicinity was described by C. L. Coultas (1976 , Soils of the Apalachicola National Forest wetlands part I. Titi swamps and savannahs. Proc. Soil Crop Soc. Fla. 36: 72-77) in the s.w. 1/4 of section 4, T5S, R8W, 3 miles n.w. of Sumatra, Liberty County:

Great Group	Paleaquult
Profile	
O horizon	Absent
A horizon	clay-loam, 51 cm deep
B horizon	mottled clay, 100+ cm deep
All horizon	
Depth (cm)	10
Sand-Silt-Clay (%)	20-52-28
Organic C (%)	3.38
pH	4.6
Total N (%)	0.25
Extractable Cations (meq/100g)	
Ca	0.3
Mg	0.4
K	0.1
Na	0.2
CED (meq/100g)	17.9

RESEARCH SUMMARY 10. UNBURNED HIGH PINELAND, MONTICELLO

2. Modified Longleaf Pine Savannah

Unpublished data by A. F. Clewell

Mesic woods on gentle slope along the west side of S.R. 149A, 5.2 miles north of Monticello, in s.e. Section 32, T3N, R5E, Jefferson County. Inventoried October 23, 1967.

The soil was a fine sandy loam which became clayey below 30 cm. A dense hardwood understory reached to the base of the crowns of a more open pine overstory. The pines were up to 23 m tall. Since the overstory and understory were not clearly differentiated, overstory trees were defined as those with a dbh of at least 10 cm. Understory plants were smaller in dbh but were at least 2 m tall.

OVERSTORY: The overstory was inventoried in quadrats totaling 2700 m^2. There were 304 trees/ha with a total basal area of 20.4 m^2/ha. The species abundance was as follows:

	Relative Basal Area	Relative Density
Pinus palustris	71	67
Pinus taeda	19	16
Quercus falcata	10	12
Cornus florida	--	1
Magnolia grandiflora	--	1
Quercus hemisphaerica	--	1
Quercus nigra	--	1
	100	99

The pines were 16-43 cm in dbh. The largest hardwood was 45 cm in dbh, Q. hemisphaerica.

UNDERSTORY: The understory was inventoried in quadrats totaling 1350 m^2. There were 830 stems/ha:

	Relative Density		Relative Density
Quercus nigra	35	Magnolia grandiflora	3
Quercus hemisphaerica	18	Malus angustifolius	2
Quercus falcata	12	Quercus virginiana	2
Prunus serotina	8	Sassafras albidum	2
Cornus florida	6	Pinus palustris	1
Nyssa sylvatica	6	Vaccinium arboreum	1
Quercus stellata	4		
		TOTAL	100

Additional understory species not occurring in the quadrats were:

Acer rubrum	Ilex glabra
Callicarpa americana	Myrica cerifera
Crataegus (uniflora?)	Rhus copallina
Diospyros virginiana	

GROUND COVER: Aristida stricta (wiregrass) was evenly distributed except where the trees were most dense. There it was represented by depauperate plants or was absent. Other, more common species were:

Gelsemium sempervirens	Smilax glauca
Pteridium aquilinum	Vaccinium stamineum
Quercus pumila	Vitis rotundifolia

Additional species included:

Asimina longifolia	Rubus cuneifolius
Ageratina aromatica	Solidago odora
Kalmia angustifolia	Tephrosia spicata
Lespedeza repens	Vaccinium darrowi
Rhus toxicodendron	Vernonia angustifolia
Rhynchosia mollissima	

HISTORY OF THIS WOODS:

The original-growth longleaf pine was harvested about 1915.

Evidence:
1. "Fatwood" pine stumps with numerous very narrow rings were still extant and represented original-growth pines.
2. The oldest living pine is about 55 years old, as determined from six increment borings.

The last fire occurred about 1947-1950.

Evidence:
1. Saplings with charred bark were at least 20 years old (as determined by ring counts near ground level) and those without were no more than 17 years old.
2. The dense, shrubby undergrowth would not have survived a recent fire.
3. The leaf litter was 5-20 cm deep and would not have accumulated except for lack of fire.

A prolonged fire-free period occurred shortly after the timber harvest of 1915.

Evidence: 1. Trees of Pinus taeda (loblolly pine) were no more than 40 years old (determined by increment borings) and could not have survived fire as young saplings. Therefore, there were no fires from about the mid-1920's until the mid-1930's.

2. Many of the larger hardwoods had to have grown big enough by 1947 to have survived the fire that occurred in 1947-1950. Any fires before then would have killed most of these trees in the young sapling stage.

3. A magnolia tree grew with multiple trunks, presumably having been top-killed in the 1947-1950 fire and coppicing afterwards. This magnolia pre-dated the 1947-1950 fire. Magnolia seeds germinate only in soils with at least 9-12 years of accumulated leaf litter. Therefore, there was no fire at least since the mid-1930's until 1947-1950.

RESEARCH SUMMARY 11. EFFECTS OF SOIL DISTURBANCE IN FIRELANDS

Unpublished data of A. F. Clewell

Twenty-nine pairs of study sites were selected within the Apalachicola National Forest and one pair just beyond its borders, all in Leon, Liberty, and Franklin counties. The ten pairs were equally distributed between dry, moist, and wet habitats. One site of each pair contained natural, undisturbed vegetation in the ground cover (the trees were natural second-growth). The other site of each pair had been converted into a pine plantation. The two sites of each pair were in close proximity to each other with no apparent habitat differences other than that caused by site preparation and tree planting. The natural vegetation had been winter-burned about every fifth year, and some of the older planted sites had been burned at least once.

Densities were determined for seven important species. Percent cover was determined at each site for two species of runner oaks. The data were taken in 30, meter-square quadrats at each site by C. L. Hilty in 1974.

The ages since treatment and the principal treatment at the disturbed sites were as follows:

BOGGY FLATWOODS and BOGS	PINE FLATWOODS	LONGLEAF PINE-XERIC OAK WOODS
4 Bedded	1 Chopped	4 Chopped
5 Bedded	1 Chopped	4 Chopped
7 Bedded	2 Chopped	4 Chopped
8 Disked	2 Chopped	4 Chopped
9 Disked	2 Chopped	4 Chopped
9 Bedded	2 Chopped	6 Chopped
10 Disked	2 Disked	10 Chopped
11 Disked	2 Disked	10 Chopped
12 Disked	2 Disked	18 Chopped
30 Bedded	2 Bedded	21 Bedded

Data analysis showed no important correlations between density (or cover) and the number of years since site preparation or density (or cover) and the principal treatment. As a result, the values for each habitat were combined in the following table. Values in this table represent observations in 300 m^2 (30 quadrats at each of 10 sites). Values less than 0.05 were recorded as zero.

RESEARCH SUMMARY 11, continued.

	BOGGY FLATWOODS and BOGS		PINE FLATWOODS		LONGLEAF PINE-XERIC OAK WOODS	
	Natural	Disturbed	Natural	Disturbed	Natural	Disturbed
			Density/m^2			
Aristida stricta	4.8	1.2*	4.6	0.7*	5.3	0.5*
Serenoa repens	0.1	0	1.1	0.1*	0	0
Vaccinium myrsinites	0	0	2.1	0.7*	0.5	0.3
Dichanthelium spp.	0.1	3.0	0.1	12.2*	0	3.4*
Andropogon virginicus	0	2.4	0	2.3*	0.1	3.0*
Eupatorium compositifolium	0	0	0.1	0.6	0	2.3
Rubus cuneifolius	0.3	1.5	0	0.8	0.1	3.0*
			Percent Cover			
Quercus pumila	0	0	5.1	0.5	0.9	0.1
Quercus minima	0	0.1	7.8	1.0	1.7	0.1

*Significant at the 1% level between natural and disturbed sites (Wilcoxon sign-rank test).

The mean densities for Aristida stricta at each natural site ranged from 4.2 to 5.2 plants/m^2 in boggy habitats (with standard errors of 0.2 to 0.3), from 1.9 to 7.2 plants/m^2 in pine flatwoods (SE 0.3-0.5), and from 4.4 to 6.8 plants/m^2 in longleaf pine-xeric oak woods (SE 0.2-0.3).

The data show the following:

1. The principal habitat types for each species and their abundance under natural conditions.
2. The uniform density of Aristida stricta (wiregrass) in all natural habitat types.
3. The reduction in densities (or cover) after treatment for five species, and the increase in densities for four species.
4. The increasing severity of treatment on wiregrass from wet to dry habitats.

RESEARCH SUMMARY 12. TITI SWAMP IN LEON COUNTY

7. Titi Swamp

Coultas, C. L., A. F. Clewell, and E. M. Taylor, Jr. 1979. An aberrant toposequence of soils through a titi swamp. J. Soil Sci. Soc. Amer. 43: 377-383.

Titi stringer through pine flatwoods 1 km west of Clear Lake in the Apalachicola National Forest, Leon County, in nw 1/4 of section 34, T1S, R2W.

OVERSTORY and UNDERSTORY (undifferentiated): Trees were arbitrarily defined as those woody plants with a dbh of at least 2.5 cm. Trees were inventoried in quadrats totaling 522 m^2. There were 6015 trees/ha with a total basal area of 26.6 m^2/ha, distributed as follows:

	Relative Density	Relative Basal Area
Cliftonia monophylla	54	51
Magnolia virginiana	13	13
Cyrilla racemiflora	10	6
Pinus serotina	6	15
Myrica inodora	5	7
Ilex coriacea	4	1
Nyssa biflora	3	2
Lyonia lucida	1	--
Myrica heterophylla	1	--
Leucothoe racemosa	1	--
Vaccinium australe	1	--
Clethra alnifolia	--	--
Pinus palustris	--	5
	99	100

The single longleaf pine was atypical of the community. It persisted from a time when part of the site was a boggy flatwoods. Subsequently, fire suppression allowed the titi community to colonize the flatwoods.

Pond pines (Pinus serotina) were the largest trees, other than the longleaf pine, with heights to 12 m and diameters to 20 cm. The largest hardwoods were 9 m tall and 13 cm in dbh.

Shrubs and saplings were dominated by Lyonia lucida and to a lesser extent by Clethra alnifolia and Ilex coriacea. Smilax laurifolia and Sphagnum sp. comprised the rest of the flora in the central portions of the swamp. Cover was too dense to allow light for herbs.

The brushy borders adjoining flatwoods contained more species of shrubs and herbs. The most prominent were: Cliftonia monophylla, Ilex glabra, I. coriacea, and Rhododendron serrulatum. Others included Aronia arbutifolia, Gaylussacia frondosa, Myrica cerifera, Rhus toxicodendron, Serenoa repens, and several herbs.

RESEARCH SUMMARY 13. BRADWELL BAY

8a. Slash Pine-Hardwood Swamp

Hebb, E. A., and A. F. Clewell. 1976. A remnant stand of old-growth slash pine in the Florida panhandle. Bull. Torrey Bot. Club 103: 1-9.

Wet bay swamp in section 7, T4S, R3W, in the Bradwell Bay Wilderness of the Apalachicola National Forest, Wakulla County, about 8 miles nw of Sopchoppy. A 5 ha stand was studied in 1967-68.

OVERSTORY: The overstory consisted solely of *Pinus elliottii*. Charred bark was evidence of fire, perhaps dating to the 1920's. There were 151 pines/ha with a collective basal area of 34 m^2/ha, as determined in quadrats totaling 3560 m^2. Tree heights were 30-36 meters. Diameters ranged from 19 to 108 cm. Trees up to about 63 cm in dbh were about 85 years old, most with heartrot.

UNDERSTORY: Comprised of trees up to 12 m tall and arbitrarily defined as those trees at least 5 cm in dbh. These trees likely post-date the most recent fire. The trees were sampled in quadrats totaling 1780 m^2. There were 991 trees/ha with a collective basal area of 11.8 m^2, distributed as follows:

	Relative Density	Relative Basal Area
Magnolia virginiana	47	35
Persea palustris	16	11
Nyssa biflora	15	43
Cyrilla racemiflora	11	4
Pinus elliottii	9	6
Ilex coriacea	2	1
	100	100

UNDERGROWTH; Comprised of all woody plants under 5 cm in dbh and all herbs. Estimates of percent cover were made by interception along lines totaling 178 meters long. The most important species were:

	Percent Cover
Sphagnum sp.	56
Clethra alnifolia	19
Ilex coriacea	17
Cyrilla racemiflora	10

Herbaceous vascular plants collectively had less than 1% cover.

VASCULAR FLORA: Only 27 species occurred on the 5-hectare site, of which 14 were evergreen or tardily deciduous. All species sampled in the overstory and understory were evergreen or tardily deciduous except *Nyssa biflora*. The species were:

RESEARCH SUMMARY 13, continued.

Acer rubrum
Carex glaucescens
Clethra alnifolia
Cyrilla racemiflora
Gelsemium rankinii
Gordonia lasianthus
Ilex coriacea
Ilex myrtifolia
Itea virginiana
Leucothoe racemosa
Lyonia lucida
Magnolia virginiana
Myrica heterophylla
Nyssa biflora
Panicum tenerum
Persea palustris
Pieris phillyreifolia
Pinus elliottii
Pteridium aquilinum
Rhododendron canescens
Rhus toxicodendron
Rhynchospora chalarocephala
Smilax laurifolia
Taxodium ascendens
Vaccinium fuscatum
Vitis rotundifolia
Woodwardia virginica

RESEARCH SUMMARY 14. OKEFENOKEE CYPRESS SWAMP-FOREST

10. Pond-cypress Swamp

Schlesinger, W. H. 1978. Community structure, dynamics and nutrient cycling in the Okefenokee cypress swamp-forest. Ecol. Monogr. 48: 43-65.

Seventeen stands of cypress were studied near the Suwannee River in the Okefenokee Swamp, Georgia. A tall understory of Ilex cassine and Nyssa biflora grew beneath an overstory of 150-year-old pond-cypress. Standing dead trees of cypress were common. Evidences were seen of frequent fires in recent times.

All trees exceeding 4 cm in diameter were inventoried. There were 2,186 stems/ha of which 1,467 were cypress. These stems comprised 80.4 m^2/ha of basal area of which 69.4 was of cypress. Importance values were as follows:

Taxodium ascendens (live)	205	Magnolia virginiana	5
Taxodium ascendens (dead)	44	Lyonia lucida	1
Ilex cassine	20	Persea palustris	1
Nyssa biflora	17	Clethra alnifolia	1
Cyrilla racemiflora	6	Vaccinium spp.	1
			300

Shrubs were those woody plants less than 4 cm in diameter and greater than 1 meter high. There were 6,840 stems/ha with the following importance values, based on frequency and density:

Itea virginica	26	Cyrilla racemiflora	5
Lyonia lucida	21	Pieris phillyreifolia	5
Leucothoe racemosa	14	Taxodium ascendens	3
Clethra alnifolia	10	Decodon verticillatus	2
Ilex cassine	6	Nyssa biflora	1
Smilax walteri	6	nine species	1
			100

Cypress trees accounted for 98% of the above-water forest biomass. Net primary productivity was low. Most of the above-water biomass of cypress trees was in the boles and only 0.8% in the leaves.

The annual nutrient uptake in cypress trees is low and most goes to the foliage. From 73 to 91% of the annual nutrient uptake is lost by foliar leaching and leaf-fall. Only a small part of the annual uptake becomes a permanent addition to the wood. The wood contains large amounts of nutrients which are immobilized for use in the ecosystem. Nutrients in fallen leaves are largely lost to the system by their incorporation into peat. The atmospheric input of nutrients may be of special importance in this system. Nutrient uptake and storage is as follows; values are kg/ha:

RESEARCH SUMMARY 14, continued

	Ca	Mg	K	N	P
Above-water nutrient pool (mostly in boles)	666	111	230	996	46
Annual nutrient uptake (mostly to the folliage)	54	11	11	NA	2.3

12. Bald-Cypress - Tupelo Swamp

H. M. Leitman. 1978. Correlation of Apalachicola River floodplain tree communities with water levels, elevation, and soils. Thesis, Florida State University. 53 p.

Slough on the floodplain of the Apalachicola River near Blountstown, Calhoun County, in section 35 of T1N, R8W.

All trees exceeding 7.5 cm in diameter were inventoried in a .124-ha area. Trees with butresses above breast height were measured just above the buttress. There were 476 trees/ha with a collective basal area of 43.5 m^2/ha, distributed as follows:

	Relative Basal Area	Relative Density
Taxodium distichum	40	10
Nyssa aquatica	24	46
Nyssa ogeche	23	20
Fraxinus caroliniana	8	15
Quercus lyrata	5	3
Cephalanthus occidentalis	-	2
Gleditsia aquatica	-	2
Planera aquatica	-	2
	100	100

The upper 23 cm of soil was characterized as follows:

Sand (%)	1.4
Silt (%)	17.1
Clay (%)	81.5
pH	5.0
Total N (%)	0.112
Total Organic C (%)	1.38
CEC (me/100g)	28.21
Exchangeable Cations (me/100g)	
Ca	6.48
Mg	1.68
K	0.23
Na	0.14

The clay content did not drop below 70% in the upper 1.5 meters.

RESEARCH SUMMARY 16. SCRUBS ON ST. GEORGE ISLAND

13. Coastal Scrub
15. Slash Pine-Scrub

Unpublished data of A. F. Clewell

Low dunes and sandy flats behind the foredune to near the center of St. George Island, Franklin County, between the causeway to the mainland and Sikes Cut. Inventoried in 1977 by N. Raymond, W. Mrazek, and M. Borgman.

Densities were determined by interception in two habitats:

	COASTAL SCRUB	SLASH PINE SCRUB
Length of line (m):	80	22
Number of plants intercepted:	290	115
Relative Densities		
WOODY SPECIES		
Bumelia lanuginosa	0.3	0
Ceratiola ericoides	7.6	13.9
Chrysoma pauciflosculosa	2.4	7.8
Conradina canescens	1.7	7.8
Hypericum microsepalum	0.3	0
Ilex vomitoria	2.1	0
Lyonia lucida	0	4.3
Opuntia drummondii	0.3	0
Pinus elliottii	2.4	7.0
Quercus geminata	13.8	18.3
Quercus myrtifolia	38.8	0
Serenoa repens	4.1	17.4
Smilax auriculata	1.0	0
Smilax bona-nox	0.7	0
Vaccinium myrsinites	2.4	13.0
HERBACEOUS SPECIES		
Lythrum lineare	0	0.9
Rhynchospora megalocarpa	3.4	9.6
Schizachyrium maritimum	12.1	0
Uniola paniculata	2.4	0
	99.8	100.0

15. Slash Pine-Scrub

Unpublished data of A. F. Clewell

Mesic sandy flat on St. George Island, Franklin County, between the causeway to the mainland and Sikes Cut. Inventoried in 1974 by A. Clewell, G. Cruz, and G. Roney.

Two sites with an open slash pine overstory were inventoried, one site somewhat drier than the other.

OVERSTORY: Defined as all trees at least 10 cm in dbh (maximum was 33 cm); the pines mostly were taller than the oaks.

	Moist Site	Dry Site
Number of trees/ha	280	180
Relative Densities		
Pinus elliottii	100	61
Quercus geminata	0	39
	100	100

SAPLINGS: There were 710 sapling pines/ha in the moist site and none in the dry site. The saplings were 2-9 cm in dbh.

UNDERGROWTH: The percent cover of the non-arboreal plants (under 2 cm in dbh) was determined by interception along a line 100 meters long at each site:

	Moist Site	Dry Site
WOODY SPECIES		
Ceratiola ericoides	0.1	12.8
Chrysoma pauciflosculosa	0	0.9
Conradina canescens	1.4	0.8
Ilex glabra	20.4	0.2
Ilex vomitoria	0.1	0
Myrica cerifera	9.9	2.8
Pinus elliottii	0.3	0
Quercus geminata	0	22.0
Quercus myrtifolia	0	13.3
Quercus virginiana	0.1	0
Rhus copallina	0.4	0
Serenoa repens	42.5	8.6
Smilax auriculata	1.2	0
Vaccinium arboreum	0.4	0.2
Vaccinium myrsinites	9.5	0.3
Total Woody Plants	86.3	61.9

	Moist Site	Dry Site
HERBACEOUS SPECIES		
Andropogon virginicus	0.8	0.1
Aristida spiciformis	2.1	0
Fuirena scirpoides	5.5	0
Panicum sp.	0.4	0
Polygonella polygama	0	2.7
Rhynchospora megalacarpa	0	4.4
Seymeria cassioides	4.9	0.3
Total Herbaceous Plants	13.7	7.5
Total, All Plants	100.0	69.4

Other plants that were not intercepted included:

WOODY SPECIES

Hypericum reductum
Quercus chapmanii

HERBACEOUS SPECIES

Amphicarpum muhlenbergianum
Aristida virgata
Chamaesyse hyssopifolia
Cyperus polystachios
Cyperus retrorsus
Eragrostis refracta
Fimbrisylis castanea
Hedyotis uniflora
Juncus scirpoides
Muhlenbergia capillaris
Panicum repens
Paspalum setaceum
Paspalum urvillei
Setaria geniculata
Sophronanthe hispida

15. Slash Pine-Scrub

Unpublished data of A. F. Clewell

The 48-ha site was in the Apalachicola National Forest in Liberty County five miles south of Wilma and 25 miles inland from the Gulf coast, in nw section 36 of T4S, R8W. The site rose to 5 m in elevation above the broad cypress swamps of Rowletts Creek which surrounded the site. The site was burned in 1963 and in 1968. The inventory was made by P. E. Avers and A. F. Clewell in 1970 with additional observations in 1973.

The soil was sandy with a pH of 4.4 to 5.4 in the root zone. There were two notable horizons. At 21-30 cm deep the sand was cemented with organic matter into a brittle, dark reddish-brown spodic horizon. Below 100 cm there was 10-25% clay forming an argillic horizon. The soil represents a bisequm.

OVERSTORY: Soley of Pinus elliottii with a cover of 50%. The trees were 24-27 m tall and mostly 20-50 cm in dbh (maximum 75 cm). Most of the overstory was harvested in 1968. Ring counts of 27 stumps revealed various ages from 41 to 121 years.

The overstory trees were inventoried in a 0.24-ha quadrat. There were 246 trees/ha with a collective basal area of 23.3 m^2/ha.

UNDERSTORY: Sparse with a cover of 15%, which consisted of trees that coppiced from root crowns after being top-killed in the fire of 1963 but which survived the fire of 1968. Most trees were 3-12 m tall (some of Magnolia grandiflora were taller), many with multiple trunks. Relative densities were determined in two sites, one drier than the other:

	Dry Site	Moist Site
Area sampled (m^2)	2000	3600
Trees/ha	275	206
Relative Densities		
Quercus geminata	33	0
Magnolia grandiflora	24	24
Lyonia ferruginea	16	19
Pinus elliottii	9	8
Quercus nigra	7	4
Cliftonia monophylla	5	3
Osmanthus americana	4	4
Magnolia virginiana	2	16
Cyrilla parviflora	0	15
Quercus hemisphaerica	0	4
Gordonia lasianthus	0	1
Persea palustris	0	1
	100	99

UNDERGROWTH: Consisted of those woody plants that were top-killed by the fire in 1968 and had coppiced to a height of 1.5-2 m in 1970 and 2-4 m in 1973. Cover exceeded 90%. The few herbaceous species were widely scattered.

Relative densities were determined by line-interception. A line 122 m long was used at each site:

	Dry Site	Moist Site
Number of Plants Intercepted:	481	491
Relative Densities		
Gaylussacia dumosa	16	13
Lyonia lucida	15	26
Lyonia ferruginea	12	0
Ilex coriacea	10	31
Gaylussacia frondosa	10	2
Quercus geminata	8	0
Pteridium aquilinum	7	1
Ilex glabra	1	9
Vitis rotundifolia	1	4
19 additional species	20	14
	100	100

Only 52 species were seen on the entire 48-ha site, excluding trail-side weeds. Species not already listed were:

TREES, SHRUBS

Acer rubrum
Chamaecyparis henryae
Clethra alnifolia
Hypericum aff. exile
Hypericum fasciculatum
Hypericum microsepalum
Ilex opaca
Itea virginica
Liquidambar styraciflua
Myrica cerifera
Myrica heterophylla
Myrica inodora
Nyssa biflora
Quercus margaretta
Rhus copallina
Serenoa repens
Symplocos tinctoria
Vaccinium australe
Vaccinium fuscatum
Viburnum nudum

WOODY VINES

Smilax auriculata
Smilax glauca
Smilax laurifolia
Smilax pumila

HERBS

Carphephorus odoratissimus
Dichanthelium aciculare
Lachnanthes anceps
Mitchella repens
Osmunda cinnamomea
Polygala lutea
Polygala nana
Rhynchospora sp.
Scleria triglomerata
Seymeria cassioides
Woodwardia virginica

RESEARCH SUMMARY 19. DUNE VEGETATION

16. Dune Prairie

Carlton, J. M. 1977. A survey of selected coastal vegetation communities of Florida. Fla. Dept. Nat. Res., Marine Res. Publ. No. 30. 40 p.

Relative densities were determined by line interception. The transects began on the beach where vegetation was first encountered and continued inland. Densities were determined quarterly for one year. Mean values are given below.

County:	Escambia	Gulf	Franklin
Location:	Western Santa Rosa Island	Cape San Blas	Eastern St. George Island
Length of Transect-m:	76	57	38
Number of Species:	19	17	5
Uniola paniculata	30	71	9
Schizachyrium maritimum	25	6	89
Heterotheca subaxillaris	12		
Chrysoma pauciflosculosa	7	4	
Hydrocotyle bonariensis	6	8	
Oenothera humifusa	5		
Chamaesyce ammannioides	2	2	
Conyza canadensis	3	2	
Helianthemum corymbosum	3		
Chrysopsis gossypina	3		
Panicum amarum		1	1
All species < 1	4	6	2
	100	100	100

RESEARCH SUMMARY 20. WELAUNEE PLANTATION WOODS

18. Pine-Oak-Hickory Woods

Unpublished data of A. F. Clewell

Well drained upland woods on sandy loam soil, annually burned in recent years, located on the south side of S.R. 146, 2 miles n.e. of I-10 in Leon County (mostly in s.e. section 4, T1N, R2E). Inventoried in July-October, 1974, by A. Clewell, G. Roney, and B. Sabine.

STRATIFICATION: The overstory consisted of a semi-closed canopy about 20-30 m tall. The understory was essentially absent except for a few scattered saplings and small trees. The ground cover was dense and consisted of coppicing root crowns of trees and various herbs, low shrubs, and woody vines.

ARBOREAL VEGETATION: Trees (at least 10 cm in dbh) and saplings (2.5-9 cm in dbh) were inventoried in a quadrat 4,000 m^2. There were 190 trees/ha with a collective basal area of 14.1 m^2/ha. There were 72 saplings and 42,200 root crowns per ha. The woody plants were distributed among the species as follows:

	TREES		SAPLINGS	ROOT CROWNS
	Relative Basal Area	Relative Density	Relative Density	Relative Density
Carya tomentosa	48	65	72	19
Pinus echinata	30	9	0	0
Quercus falcata	14	9	11	47
Quercus stellata	6	16	3	29
Quercus nigra	2	1	0	0
Diospyros virginiana	0	0	7	2
Sassafras albidum	0	0	7	2
Celtis occidentalis	0	0	0	1
	100	100	100	100

NON-ARBOREAL VEGETATION: 46 non-arboreal species of the ground cover were recorded in 40, meter-square quadrats. The percentages of quadrats in which the more frequent species occurred were as follows:

Amphicarpa bracteata	85	Erianthus alopecuroides	25
Sorghastrum spp.	58	Tridens flavus	25
Clitoria mariana	48	Galactia volubilis	23
Parthenocissus quinquefolia	43	Dyschoriste oblongifolia	23
Smilax lasioneuron	38	Ceanothus americanus	18
Collinsonia serotina	35	Rubus cuneifolius	15
Andropogon virginicus	33	Smilax glauca	15
Schizachyrium tenerum	32	Viburnum rufidulum	15
Melanthera nivea	25	Vitis aestivalis	15
Elephantopus elatus	25	Vernonia gigantea	13

RESEARCH SUMMARY 20, continued.

FLORA: The flora of the stand, excluding weeds in fire lanes and other disturbed sites, consisted of the following 100 species:

TREES

Carya tomentosa
Diospyros virginiana
Pinus echinata
Quercus alba
Quercus falcata
Quercus nigra
Quercus stellata
Quercus velutina
Sassafras albidum

SHRUBS

Callicarpa americana
Castanea alnifolia
Ceanothus americana
Celtis occidentalis
Collinsonia serotina
Crataegus pulcherrima
Crataegus uniflora
Quercus pumila
Rubus cuneifolius
Rhus copallina
Vaccinium stamineum

WOODY VINES

Campsis radicans
Parthenocissus quinquefolia
Rhus toxicodendron
Smilax bona-nox
Smilax glauca
Smilax smallii
Vitis aestivalis

GRASSES

Andropogon gerardii
Andropogon virginicus
Dichanthelium commutatum
Erianthus alopecuroides
Gymnopogon ambiguus
Schizachyrium tenerum
Sorghastrum nutans
Sorghastrum secundum
Tridens flavus

COMPOSITES

Ageratina jucunda
Aster dumosus
Aster sagittifolius
Aster tortifolius
Chrysopsis mariana
Elephantopus elatus
Fleischmannia incarnata
Helianthus divaricatus
Hieracium gronovii
Lactuca canadensis
Liatris graminifolia
Melanthera nivea
Pityopsis graminifolia
Rudbeckia hirta
Silphium simpsonii
Solidago arguta
Solidago brachyphylla
Solidago odora
Solidago petiolaris
Verbesina virginica
Vernonia angustifolia
Vernonia gigantea

LEGUMES

Amphicarpa bracteata
Cassia nictitans
Centrocema virginianum
Clitoria mariana
Crotalaria rotundifolia
Demosidum cuspidatum
Desmodium fernaldii
Desmodium nudiflorum
Desmodium obtusum
Desmodium paniculatum
Erythrina herbacea
Galactia volubilis
Indigophora caroliniana
Lespedeza intermedia
Lespedeza procumbens
Schrankia microphylla
Strophostyles umbellata
Stylosanthes biflora
Tephrosia spicata

RESEARCH SUMMARY 20, continued.

OTHER HERBS

Agalinis tenuifolia
Angelica venenosa
Asclepias verticillata
Aureolaria flava
Cuscuta campestris
Cnidoscolus stimulosus
Dyschoriste oblongifolia
Euphorbia pubentissima
Galium pilosum
Hedyotis procumbens
Hexalectris spicata
Ipomoea pandurata
Polianthes virginica
Polygala grandiflora
Pteridium aquilinum
Ruellia caroliniensis
Salvia azurea
Scutellaria integrifolia
Smilax herbacea
Smilax lasioneuron
Stillingia sylvatica
Tillandsia usneoides
Tragia urticaefolia

RESEARCH SUMMARY 21. JONES COURSE

18. Pine-Oak-Hickory Woods

Unpublished data of A. F. Clewell

Upland, well drained woods on sandy loam soil and annually winter-burned for at least 20 years. Near Anders Branch at the Tall Timbers Research Station, northern Leon County (n-cent. section 16, T3N, R1E). Inventoried for trees in October, 1976 and for non-arboreal vegetation in April and October, 1974, by A. Clewell and R. Komarek.

AGE: Increment borings revealed ages of 125 years for *Pinus echinata* and 99 years for *Quercus stellata*. The larger oaks were likely much older, as evidenced by the partial ring counts from heart-rotted trees.

STRATIFICATION: The overstory was 20-25 m tall. Tree cover was variable, perhaps averaging 25%. Tree diameters ranged upwards to 78 cm in dbh. The understory was essentially absent. The ground cover consisted of a dense growth of coppicing root crowns, low shrubs, woody vines, and herbs.

ARBOREAL VEGETATION: Trees of at least 10 cm in dbh were inventoried in quadrats collectively comprising 7,650 m^2. Coppicing root crowns were tallied in 60, m^2 quadrats. There were 137 trees/ha, comprising 11.8 m^2/ha of basal area. There were 17,500 root crowns/ha. The species were distributed as follows:

	TREES		ROOT CROWNS
	Relative Basal Area	Relative Density	Relative Density
Pinus echinata	44	36	0
Carya tomentosa	19	32	17
Quercus falcata	10	5	24
Quercus stellata	8	12	12
Quercus alba	7	2	1
Nyssa sylvatica	5	5	0
Quercus velutina	4	3	39
Pinus taeda	2	1	0
Quercus marilandica	1	2	1
Cornus florida	(> 1)	2	1
Sassafras albidum	0	0	5
	100	100	100

NON-ARBOREAL VEGETATION: 70 non-arboreal species of the ground cover were tallied in 30, meter-square quadrats. The percentage of quadrats in which each of the more frequent species occurred was as follows:

RESEARCH SUMMARY 21, continued.

Dyschoriste oblongifolia	100	Aster tortifolius	33
Smilax glauca	90	Gymnopogon ambiguus	27
Andropogon virginicus	80	Centrocema virginianum	23
Solidago odora	63	Petalostemum albidum	23
Elephantopus elatus	57	Tephrosia virginiana	23
Cassia nictitans	53	Rhus copallina	20
Euphorbia pubentissima	47	Sorghastrum elliottii	20
Pteridium aquilinum	47	Andropogon ternarius	17
Vaccinium stamineum	47	Aristida virgata	17
Helianthus hirsutus	43	Aureolaria flava	17
Trichostema dichotomum	40	Callicarpa americana	17
Chrysopsis mariana	37	Galium pilosum	17
Dichanthelium commutatum	37	Rubus trivialis	17
Dichanthelium sp.	37	Smilax bona-nox	17
Bidens flavus	37	Verbesina aristata	17
Aristida lanosa	33	Crotalaria rotundifolia	13
Ceanothus americanus	33	Scleria sp.	13

FLORA: The 126 species observed in the stand are listed below. An asterisk (*) denotes species which occurred only in ravines where there was some fire protection.

TREES

Acer rubrum
Carya glabra*
Carya tomentosa
Castanea sp.
Cornus florida
Diospyros virginiana
Liquidambar styraciflua*
Malus angustifolius
Nyssa sylvatica
Pinus echinata
Pinus taeda*
Prunus serotina
Prunus umbellata*
Quercus alba
Quercus flacata
Quercus hemisphaerica*
Quercus laevis
Quercus margaretta
Quercus marilandica
Quercus nigra*
Quercus phellos
Quercus stellata
Quercus velutina
Sassafras albidum

SHRUBS

Callicarpa americana
Ceanothus americanus
Myrica cerifera
Rhus copallina
Quercus pumila
Vaccinium arboreum
Vaccinium stamineum
Viburnum rufidulum

WOODY VINES

Gelsemium sempervirens
Rhus toxicodendron
Rubus trivialis
Smilax bona-nox
Smilax glauca
Smilax smallii
Vitis aestivalis
Vitis rotundifolia

RESEARCH SUMMARY 21, continued.

GRASSES

Andropogon elliottii
Andropogon ternarius
Andropogon virginicus
Aristida lanosa
Aristida virgata
Dichanthelium commutatum
Dichanthelium sp.
Eragrostis hirsuta
Erianthus alopecuroides
Erianthus contortus
Gymnopogon ambiguus
Schizachyrium tenerum
Sorghastrum elliottii
Sporobolus junceus
Tridens flavus

COMPOSITES

Ageratina jucunda
Aster concolor
Aster dumosus
Aster patens
Aster sagittifolius
Aster tortifolius
Chrysopsis mariana
Conoclinium coelestinum
Elephantopus elatus
Helianthus angustifolius
Helianthus hirsutus
Kuhnia mosieri
Liatris graminifolia
Pityopsis graminifolia
Silphium simpsonii
Solidago arguta
Solidago austrina
Solidago odora
Solidago petiolaris
Verbesina aristata
Vernonia angustifolia

LEGUMES

Baptisia leucantha
Cassia nictitans
Clitoria mariana
Centrocema virginiana
Crotalaria rotundifolia
Desmodium cuspidatum
Desmoidum fernaldii
Desmodium floridanum
Desmodium marilandicum
Desmodium obtusum
Desmodium paniculatum
Desmodium perplexum
Erythrina herbacea
Galactia volubilis
Lespedeza hirta
Lespedeza intermedia
Lespedeza procumbens
Lespedeza repens
Lespedeza stuevei
Lespedeza virginica
Petalostemum albidum
Rhynchosia tomentosa
Schrankia microphylla
Stylosanthes biflora
Tephrosia spicata
Tephrosia virginiana

OTHER HERBS

Asclepias verticillata
Aureolaria flava
Cuscuta sp.
Cyperus retrofractus
Dyschoriste oblongifolia
Euphorbia pubentissima
Galium pilosum
Hedyotis procumbens
Ipomoea pandurata
Lobelia puberula
Mitchella repens*
Monotropa uniflora*
Phlox floridana
Polygala grandiflora
Pteridium aquilinum
Rhynchospora globularis
Ruellia caroliniensis
Salvia azurea
Scleria pauciflora
Scleria triglomerata
Stillingia sylvatica
Stylisma humistrata
Tillandsia usneoides
Trichostema dichotomum

RESEARCH SUMMARY 22. SAN LORENZO WOODS

18. Pine-Oak-Hickory Woods

Unpublished data by A. F. Clewell

Mesic hillside, somewhat loamy and annually winter-burned. Located on the Welaunee Plantation 4 miles south of Capps, Jefferson County. The hilltop was occupied in the 1600's by the San Lorenzo Mission, built by the Spanish in the midst of a village of agricultural Indians. Inventoried November 4, 1974.

STRATIFICATION: The overstory formed a rather closed canopy of fairly tall trees, none less than 10 cm in dbh. The understory was absent. The ground cover was rather sparse but continuous and consisted of the sprouts of coppicing root crowns, low shrubs, woody vines, and herbs.

ARBOREAL VEGETATION: All trees were inventoried in a 1,250 m^2 quadrat on the east-facing slope. Coppicing root crowns were tallied in a 100 m^2 quadrat. There were 260 trees/ha with a collective basal area of 19.3 m^2/ha. There were 10,500 coppicing root crowns/ha. The species were distributed as follows:

	TREES		ROOT CROWNS
	Relative Basal Area	Relative Density	Relative Density
Quercus falcata	58	37	19
Carya glabra	13	18	33
Carya tomentosa	10	12	4
Liquidambar styraciflua	5	6	0
Pinus echinata	5	3	0
Pinus taeda	4	3	0
Quercus virginiana	3	6	1
Quercus stellata	1	12	14
Nyssa sylvatica	1	3	0
Quercus nigra	0	0	14
Celtis tenuifolia	0	0	8
Diospyros virginiana	0	0	2
Tilia heterophylla	0	0	2
Prunus serotina	0	0	1
Quercus alba	0	0	1
	100	100	99

NON-ARBOREAL VEGETATION: 35 non-arboreal species of the ground cover were tallied in 30, meter-square quadrats. The percentage of quadrats in which each of the more frequent species occurred was as follows:

RESEARCH SUMMARY 22, continued.

Amphicarpa bracteata	80	Melanthera nivea	23
Dichanthelium commutatum	77	Polymnia uvedalia	23
Clitoria mariana	73	Ceanothus americana	20
Tridens falvus	50	Cyperus retrofractus	20
Sorghastrum elliottii	47	Erianthus alopecuroides	20
Cassia nictitans	40	Fleischmannia incarnata	20
Aster sagittifolius	37	Vitis rotundifolia	20
Helianthus hirsutus	27	Pteridium aquilinum	17
Vernonia altissima	27	Desmodium paniculatum	13
Elephantopus elatus	23	Phaseolus polystachios	13

FLORA: The 88 Species observed were as follows:

TREES

Carya glabra
Carya tomentosa
Celtis tenuifolia
Cornus foemina
Cornus florida
Diospyros virginiana
Liquidambar styraciflua
Nyssa sylvatica
Pinus echinata
Pinus taeda
Prunus serotina
Quercus alba
Quercus falcata
Quercus nigra
Quercus stellata
Quercus virginiana
Sassafras albidum
Tilia heterophylla

SHRUBS

Ceanothus americanus
Hypericum stans
Malus angustifolius
Quercus pumila
Rhus copallina
Vaccinium stamineum

WOODY VINES

Bignonia capreolata
Campsis radicans
Rhus toxicodendron
Rubus trivialis
Smilax bona-nox
Smilax smallii
Vitis aestivalis
Vitis rotundifolia

GRASSES

Andropogon virginicus
Chasmanthium sessiliflorum
Dichanthelium commutatum
Erianthus alopecuroides
Panicum anceps
Paspalum setaceum
Sorghastrum elliottii
Tridens flavus

COMPOSITES

Ageratina jucunda
Aster concolor
Aster sagittifolius
Chrysopsis mariana
Elephantopus elatus
Fleischmannia incarnata
Helianthus hirsutus
Kuhnia eupatorioides
Liatris graminifolia
Melanthera nivea
Pityopsis graminifolia
Polymnia uvedalia
Prenanthes serpentaria
Solidago odora
Vernonia altissima

LEGUMES

Amphicarpa bracteata
Cassia nictitans
Clitoria mariana
Crotalaria rotundifolia
Desmodium floridanum
Desmodium laevigatum
Desmodium marilandicum
Desmodium paniculatum
Erythrina herbacea
Galactia macreei
Lespedeza hirta
Lespedeza intermedia
Lespedeza stuevei
Phaseolus polystachios
Tephrosia spicata

OTHER HERBS

Acalypha gracilens
Agrimonia pubescens
Aristolochia serpentaria
Cnidoscolus stimulosus
Cuscuta sp.
Cyperus retrofractus
Cyperus tetragonus
Hedyotis procumbens
Ipomoea pandurata
Lobelia puberula
Onosmodium virginianum
Pteridium aquilinum
Ruellia caroliniensis
Scleria sp.
Smilax herbacea
Tillandsia usneoides
Trichostema dichotomum
Viola sp.

RESEARCH SUMMARY 23. SPRINGWOOD PLANTATION.

18. Pine-Oak-Hickory Woods
2. Longleaf Pine Savannah

Unpublished data by A. F. Clewell

Rolling well drained longleaf pinelands along U.S. 319 on the next hill north of junction S.R. 3 in Grady County, Georgia, near the Florida line on Springwood Plantation. Inventoried in the autumn of 1974.

The site was an annually burned, old second-growth longleaf pine savannah with trees upwards to 29 m tall and some in excess of 76 years old. A small depression was ringed by a fire lane, precluding most fires. Hardwoods and shortleaf pines were mixed with longleaf pine within the fire lane, forming a pine-oak-hickory woods.

Longleaf pine grew in the lowest ground in the depression. In times past, fires must have burned through the depression frequently enough to allow the establishment of longleaf pine. Therefore, the topographic features of the depression were not sufficient to explain the presence of the pine-oak-hickory woods. The study was undertaken to see if fire exclusion in recent years might have contributed to the establishment of floristic elements typical of pine-oak-hickory woods.

Tree density was determined on either side of the fire lane. The area sampled inside the fire lane was on flat ground between the lane and the depression to assure that the comparison reflected differences in fire frequency and not topography. Coppicing root crowns and non-arboreal species were sampled in 30, meter-square quadrats on each side of the fire lane.

	Longleaf Pine Savannah		Pine-Oak-Hickory Woods	
Area Sampled (m^2):	1,240		240	
DBH Class (cm):	4-15	16-40	4-15	16-35
	TREES PER HECTARE			
Pinus palustris	226	161	42	83
Pinus echinata	8	0	42	0
Carya tomentosa	8	0	83	42
Quercus falcata	0	0	0	83
Quercus stellata	0	0	292	83
	242	161	459	291

RESEARCH SUMMARY 23, continued.

PERCENTAGES OF M^2 QUADRATS IN WHICH ROOT CROWNS OCCURRED

	Longleaf Pineland	Pine-Oak-Hickory Woods
Carya tomentosa	0	10
Diospyros virginiana	3	17
Prunus serotina	0	7
Quercus falcata	13	10
Quercus stellata	7	10
Quercus virginiana	0	3
Sassafras albidum	3	33
Liquidambar styraciflua	0	3

PERCENTAGES OF M^2 QUADRATS IN WHICH NON-ARBOREAL SPECIES OCCURRED

	LL	POH
Acalypha gracilens	0	3
Ageratina aromatica	20	17
Andropogon ternarius	7	0
Andorpogon virginicus	40	73
Aristida stricta	70	17
Asclepias verticillata	3	3
Aster adnatus	7	0
Aster concolor	13	0
Aster dumosus	23	0
Aster tortifolius	33	33
Carphephorus odoratissimus	20	7
Cassia nictitans	43	43
Centrocema virginiana	3	3
Clitoria mariana	17	0
Desmodium marilandicum?	0	13
Desmodium paniculatum	13	0
Dyschoriste oblongifolia	87	53
Elephantopus elatus	30	7
Erianthus alopecuroides	7	23
Eryngium yuccifolium	3	0
Eupatorium album	23	13
Euphorbia pubentissima	10	27
Galium pilosum	0	27
Gaylussacia dumosa	30	27
Gaylussacia frondosa	17	17
Galactia macreei	60	97
Gelsemium sempervirens	0	17
Gymnopogon ambiguus	10	7

	LL	POH
Helianthus radula	43	3
Hypericum hypericoides	13	10
Lespedeza angustifolia	10	0
Lespedeza repens	0	7
Lespedeza virginica	0	10
Liatris graminifolia	3	0
Panicum anceps	23	47
Phlox floridana	0	3
Pityopsis graminifolia	23	23
Quercus pumila	100	17
Rhus copallina	23	0
Rhynchosia reniformis	23	0
Rubus cuneifolius	3	0
Ruellia caroliniensis	0	3
Salvia azurea	0	3
Schrankia microphylla	3	0
Scutellaria elliptica	3	0
Smilax glauca	0	33
Smilax smallii?	0	3
Solidago odora	20	13
Sorghastrum nutans, S. secundum	7	13
Stillingia sylvatica	3	0
Stylosanthes biflora	7	3
Tephrosia spicata	3	23
Tephrosia virginiana	83	47
Toxicodendron radicans	0	33
Tragia urens	7	10
Vaccinium myrsinites	0	10
Vaccinium stamineum	27	50
Vernonia angustifolia	0	13

RESEARCH SUMMARY 23, continued.

Tree density within the encircling fire lane was nearly twice that outside of the fire lane. Eighty three percent of the trees within the fire lane were hardwoods and shortleaf pines less than 16 cm in dbh, as opposed to 4% outside of the fire lane. The abundance of these small diametered trees within the fire lane suggested that the reduced frequency of fire has been the primary factor in allowing the colonization of trees other than longleaf pines and thus the conversion of a longleaf pineland to a pine-oak-hickory woods.

The abundance of coppicing root crowns within the fire lane and their rarity in the longleaf pineland further suggested colonization between infrequent fires. Herbs typical of pine-oak-hickory woods were more frequent within the fire lane (e.g., Erianthus alopecuroides, Galium pilosum), while herbs typical of longleaf pinelands were less frequent there (e.g., Aristida stricta. Helianthus radula).

19. Mesic Hardwood Hammock

Blaisdell, R. S., J. W. Wooten, and R. K. Godfrey. 1974. The role of magnolia and beech in forest processes in the Tallahassee, Florida, Thomasville, Georgia area. Proc. Ann. Tall Timbers Fire Ecol. Confr. 13: 363-397.

Two stands were studied in the Tallahassee Hills of northern Leon County. The Woodyard Hammock lies along the northern shore of Lake Iamonia at the Tall Timbers Research Station. Ireland's Woods borders a creek west of Lake Jackson. There was no evidence of appreciable disturbance in either stand.

In Ireland's Woods 45% of the trees of Magnolia grandiflora contained sucker sprouts from the roots.

Tree inventories yielded the following data:

	Relative Basal Area	Relative Density
WOODYARD HAMMOCK		
Magnolia grandiflora	44	43
Fagus grandifolia	31	29
Liquidambar styraciflua	7	9
Nyssa sylvatica	5	4
Pinus glabra	4	7
Quercus laurifolia	3	2
Carya glabra	2	3
Quercus michauxii	1	1
Magnolia virginiana	1	1
Ulmus alata	1	1
Ulmus americana	1	1
	100	101
IRELAND'S WOODS		
Magnolia grandiflora	55	57
Fagus grandifolia	19	21
Liquidambar styraciflua	15	15
Nyssa sylvatica	5	4
Pinus glabra	3	2
Magnolia virginiana	3	2
	100	101

RESEARCH SUMMARY 25. WAKULLA SPRINGS HAMMOCK.

19. Mesic Hardwood Hammock

Unpublished data of A. F. Clewell

Mature mesic forest bordering Wakulla Springs in Wakulla County (section 11, T3S, R1W). Inventoried in the summer of 1975 by B. E. Dusseault and B. A. More.

The site was nearly flat. The sandy soil was underlain by limestone which outcropped in many places and which was more than a meter deep in many other places. Values for soil pH were from 5.6 to 7.2. The overstory was mostly 27-33 m high. One tree was 40 m tall. Tree cover ranged from 70-95%.

Two stands within the same forest were inventoried. In one stand, all trees of at least 5 cm in dbh were tallied. In the other, all trees at least 15 cm were tallied.

Minimum dbh (cm)	5		15	
Area sampled (ha)	0.6		2	
Trees per ha	623		126	
Basal Area (m^2/ha)	31.4		14.5	
	Relative Basal Area	Relative Density	Relative Basal Area	Relative Density
Magnolia grandiflora	24	9	17	14
Carya glabra	19	18	29	30
Quercus alba and Q. austrina	14	8	6	6
Fagus grandifolia	10	5	25	19
Quercus michauxii	7	4	11	9
Tilia heterophylla	6	4	3	4
Ilex opaca	5	13	2	7
Liquidambar styraciflua	3	11	4	5
Carpinus caroliniana	3	13	-	2
Quercus nigra	2	2	0	0
Quercus shumardii	1	3	-	-
Nyssa sylvatica	-	-	-	2
Fraxinus americana	-	1	0	0
Cercis canadensis	-	2	0	0
Cornus florida	-	1	-	-
Sassagras albidum	-	-	0	0
Prunus serotina	-	1	.	-
Persea borbonia	-	-	0	0
Aralia spinosa	-	-	0	0
Crataegus sp.	-	-	0	0
Ulmus alata	-	-	0	0
Quercus laurifolia	0	0	1	-

A dash (-) signifies a value less than 1.

RESEARCH SUMMARY 25, continued.

Woody plants less than 5 cm in dbh and at least 6 dm tall that belonged to species that were not listed in the table above were inventoried in quadrats totalling 250 m^2:

	Density per 100 m^2
Smilax spp.	38
Hamamelis virginiana	26
Euonymous americanus	23
Ilex decidua	12
Callicarpa americana	10
Bumelia lycioides	9
Bignonia capreolata	8
Prunus caroliniana	5
Vitis spp.	5
Vaccinium arboreum	4
Sabal minor	3
Morus rubra	2
Parthenocissus quinquefolia	1
Symplocos tinctoria	1
Yucca flaccida	1
Viburnum rufidulum	1
Arundinaria gigantea	-
Asimina parviflora	-
Crataegus marshallii	-
Osmanthus americana	-
Pinus glabra	-
Toxicodendron radicans	-

A dash (-) signifies values less than 1

Some common herbaceous species were:

Arisaema dracontium
Aspelnium platyneuron
Conopholis americana
Dioscorea quaternata
Elephantopus nudatus
Epifagus virginiana
Galium hispidulum
Mitchella repens
Oplismenus setarius
Panicum dichotomiflorum
Polystichum acrostichoides
Pteridium aquilinum

RESEARCH SUMMARY 26. ROCK BLUFF.

19. Mesic Hardwood Hammock
8. Bay Swamp

Unpublished data of A. F. Clewell

Bluff of the Ochlockonee River about 2 miles south of the S.R. 20 bridge near S.R. 375 and about 100 m south of the public boat landing at Rock Bluff (section 30 of T1S, R4W) in Leon County. Inventoried in the summer of 1975 by L. Woodford.

The upland behind the bluff was covered by a longleaf pine-xeric oak woods. The bluff was densely forested and mesic. A bayhead (described below) occupied a wet creek bottom emanating from a small spring at the base of the bluff. The data below represent an inventory of all trees at least 4 cm in dbh:

Area Samples (m^2):	1,000		750		175	
Trees per ha:	3,080		1,413		1,943	
Basal Area (m^2/ha)	19.8		45.1		86.4	
	Upper Slope		Lower Slope		Bayhead	
	Relative Basal Area	Relative Density	Relative Basal Area	Relative Density	Relative Basal Area	Relative Density
Pinus palustris	1	5	0	0	0	0
Quercus margaretta	2	3	0	0	0	0
Vaccinium arboreum	1	9	0	0	0	0
Osmanthus americana	-	12	0	0	0	0
Vaccinium stamineum	1	6	0	0	0	0
Quercus hemisphaerica	71	44	9	23	0	0
Carya tomentosa	18	19	9	9	0	0
Pinus glabra	1	1	12	6	0	0
Quercus alba	-	2	21	11	0	0
Cornus florida	1	5	[illegible]	8	0	0
Magnolia grandiflora	0	0	25	8	0	0
Fagus grandifolia	0	0	17	4	0	0
Ilex opaca	0	0	2	4	0	0
Acer saccharum	0	0	-	5	0	0
Magnolia ashei	0	0	-	7	0	0
Chionanthus virginica	0	0	-	-	0	0
Persea palustris	0	0	2	10	46	24
Magnolia virginiana	0	0	0	0	38	18
Nyssa biflora	0	0	0	0	11	3
Gordonia lasianthus	0	0	0	0	4	9
Ilex coriacea	0	0	0	0	1	47

A dash (-) signifies a value less than 1.

RESEARCH SUMMARY 27. LITTLE SWEETWATER CREEK STEEPHEAD

19. Mesic Hardwood Hammock
8. Bay Swamp

Unpublished data of A. F. Clewell

Steep slopes at the head of Little Sweetwater Creek about 4 miles north of Bristol near S.R. 270 in Liberty County (central section 16, T1N, R7W). Inventoried in the summer of 1976 by N. Schobert and W. Sherwood.

A longleaf pine-xeric oak community once occupied the adjacent upland but was replaced by a slash pine plantation. The steepness of the sandy slopes prevented the accumulation of litter. Springs seeped from the steepheads and the bases of the slopes, feeding a small creek. The narrow creek bottom was occupied by a bayhead community, described below, which contained much shrubby Illicium floridanum.

Trees of at least 10 cm in dbh were tallied in two, 10-meter wide transects which ran from the rim of the upland down to the creek bottom and up the other slope. The total area sampled was 1,850 m^2. Relative basal areas for the trees were as follows:

	Relative Basal Area		
	Upland Rim & Upper Slope	Mid-Slope	Creek Bottom
Quercus hemisphaerica	38	21	0
Carya tomentosa	15	2	0
Quercus alba	15	7	0
Quercus virginiana	10	0	0
Tilia heterophylla	10	4	0
Diospyros virginiana	3	0	0
Amelanchier arborea	2	0	0
Cornus florida	1	0	0
Carya glabra	1	0	0
Quercus laevis	1	0	0
Pinus glabra	1	11	0
Osmanthus americana	1	1	6
Vaccinium arboreum	1	1	0
Quercus stellata	1	0	0
Magnolia grandiflora	0	33	0
Fagus grandifolia	0	12	0
Carya pallida	0	3	0
Oxydendrum arboreum	0	3	3
Persea borbonia	0	1	10
Acer rubrum	0	2	0
Nyssa biflora	0	0	55
Magnolia virginiana	0	0	25
Illicium floridanum	0	0	1
	100	100	100
Total Basal Area/ha (m^2):	23	28	19
Trees per ha:	580	320	220

RESEARCH SUMMARY 27, continued.

Other trees and shrubs included:

Aralia spinosa
Asimina parviflora
Bumelia lanuginosa
Calamintha dentata
Callicarpa americana
Celtis tenuifolia
Cercis canadensis
Chionanthus virginicus
Conradina glabra (upland rim)
Crataegus uniflora
Euonymus americanus
Halesia diptera
Ilex coriacea
Ilex opaca
Itea virginica
Juniperus silicicola
Leucothoe racemosa
Ostrya virginiana
Pinus taeda
Sassafras albidum
Sebastiana fruticosa
Styrax grandifolia
Symplocos tinctoria
Taxus floridana
Vaccinium fuscatum
Viburnum nudum

Some woody vines were:

Bignonia capreolata
Gelsemium sempervirens
Rhus toxicodendron
Smilax bona-nox
Smilax pumila

Some herbs were:

Aristolochia serpentaria
Clematis reticulata
Dichanthelium commutatum
Dioscorea quaternata?
Hexastylis arifolia
Lilium superbum
Mitchella repens
Polystichum acrostichoides
Tillandsia usneoides

19. Mesic Hardwood Hammock
20. Bottomland Hardwood Forest

Hardin, J. W. 1954. The vegetation pattern around a Florida sinkhole. Fla. State Univ. Studies 13: 6-17.

This large sink lies west of S.R. 369 in Leon County near the Wakulla County line in the Apalachicola National Forest (section 8, T2S, R1W). The rim of the sink is 250 feet in diameter. The sink narrows to an ellipse of 90-125 feet at the water's edge. Limestone (St. Marks formation) outcrops near the base. Ground water percolates through the overlying sands and seeps at the top of the limestone. A layer of marl on top of the limestone likely represents rock that is undergoing solution from acids carried by the ground water.

In one week in May, the relative humidity was constantly at 90% a meter above the water's surface but varied at the rim from 15% (afternoons) to 94% (early morning).

A longleaf pine-xeric oak woods covered the upland to the rim of the sink. A mesic hammock occupied the upper slope, and a woods similar to river bottom communities occupied the lower slope. Zonation was thought to be in response to changes in humidity, soil moisture, and substrate.

The upper slope supported 30 species, including:

Carya tomentosa
Clethra alnifolia
Cornus florida
Diospyros virginiana
Ilex coriacea
Liquidambar styraciflua
Lyonia lucida
Magnolia grandiflora
Myrica cerifera
Quercus laurifolia
Quercus nigra
Serenoa repens
Smilax laurifolia
Symplocos tinctoria
Vaccinium arboreum

The lower slope supported 13 species, including:

Adiantum capillus-veneris
Ilex cassine
Itea virginica
Magnolia virginiana
Morus rubra
Salix nigra
Woodwardia virginica

Other species at nearby sinks included Rhododendron canescens, Fagus grandifolia, and Quercus virginiana.

In 1967 recording thermometers were placed at the edge of the water in Big Dismal Sink and in the longleaf pine-xeric oak woods at the rim of the sink by P. Darst (unpublished). Night temperatures were nearly identical. Daytime high temperatures were 14-18° F higher in the pineland than in the sink.

19. Mesic Hardwood Hammock

Unpublished data by A. F. Clewell

Between Wakulla Beach and U.S. 98 in Wakulla County, bordering a low coastal slash pine flatwoods which in turn bordered a tidal marsh. The hammock was inventoried in April, 1970, in conjunction with the archaeological study of Indian burial mounds (500-2,000 years old) by D. Phelps.

Local residents knew of no disturbances other than fire for the last 60-70 years. Fire scars on magnolia limbs indicated a fire about 1955. Seven of 10 basswoods had multiple trunks, these with 45 annual rings, suggesting coppicing after a severe fire in the early 1920's. One tree (*Quercus hemisphaerica*) contained about 125 rings. The largest trees were scattered *Q. virginiana* up to about 100 cm in dbh.

All trees at least 10 cm in dbh were tallied in a quadrat 3,611 m^2, which was placed between the two large burial mounds. There were 465 trees/ha with a collective basal area of 27.0 m^2/ha. The species were distributed as follows:

	Relative Basal Area	Relative Density
Pinus glabra	18	14
Liquidambar styraciflua	17	21
Tilia heterophylla	17	8
Quercus hemisphaerica	14	6
Magnolia grandiflora	12	10
Carya glabra	9	6
Ostrya virginiana	5	14
Ilex opaca	2	7
Cornus florida	1	4
Quercus alba	1	2
Quercus austrina	[illegible]	2
Fraxinus americana	1	1
Sabal palmetto	1	1
7 Species	2	4
	100	100

The seven minor species in the quadrat were:

- Carpinus caroliniana
- Osmanthus americana
- Persea borbonia
- Prunus serotina
- Quercus nigra
- Quercus virginiana
- Viburnum rufidulum

RESEARCH SUMMARY 29, continued.

Other trees and shrubs at the site were:

- Acer rubrum
- Aesculus pavia
- Asimina parviflora
- Aralia spinosa
- Bumelia lanuginosa
- Callicarpa americana
- Cercis canadensis
- Cornus foemina
- Fagus grandifolia
- Hamamelis virginiana
- Ilex vomitoria
- Juniperus silicicola
- Osmanthus americana
- Phorodendron serotinum
- Quercus michauxii
- Rhus copallina
- Serenoa repens
- Vaccinium arboreum

Of these, Hamamelis virginiana and Ilex vomitoria were particularly abundant shrubs. Woody vines were common:

- Bignonia capreolata
- Campsis radicans
- Lonicera sempervirens
- Parthenocissus quinquefolia
- Rhus toxicodendron
- Smilax bona-nox
- Vitis rotundifolia

Herbs included:

- Arisaema dracontium
- Asplenium platyneuron
- Carex crebriflora
- Conopholis americana
- Dichanthelium sabulorum
- Elephantopus elatus
- Mitchella repens
- Polypodium polypodioides
- Tillandsia usneoides

RESEARCH SUMMARY 30. LOGAN HILL.

19. Mesic Hardwood Hammock (bluff)
20. Bottomland Hardwood Forest (floodplain)

Unpublished data of A. F. Clewell

Moist, shaded bluff of the Apalachicola River on Logan Hill near the primitive campground at Torreya State Park, Liberty County (southern section 17, T2N, R7W). Inventoried in the summer of 1976 by R. D. Kaplan and L. M. Kaplan.

The soil on the bluff was a well drained sandy loam which became clayey within a few decimeters of the surface. Loose limestone cobbles were mixed with the top soil near the base of the slope.

ARBOREAL VEGETATION: Trees of at least 10 cm in dbh were inventoried in a 20 by 200 meter transect which began at the narrow, level ridge top and extended down slope and 30 meters beyond the base of the slope on the floodplain. The angle of slope was 12-15 degrees. The data were as follows:

RESEARCH SUMMARY 30, continued.

	Ridge	Upper Slope	Lower Slope	Flood-plain	Ridge	Upper Slope	Lower Slope	Flood-plain
Area sampled (m^2):	1300	600	1400	700	1300	600	1400	700
Basal area/ha (m^2):	22.2	17.8	23.0	29.6				
Trees/ha:					338	250	321	314
	Relative Basal Area				Relative Density			
Carya tomentosa	16	0	0	0	29	0	0	0
Quercus velutina	15	0	0	0	13	0	0	0
Prunus umbellata	--	0	0	0	2	0	0	0
Cornus florida	2	0	0	0	5	0	0	0
Quercus stellata	7	0	0	0	5	0	0	0
Acer saccharum	1	0	0	0	5	0	0	0
Crataegus pulcherrima	--	0	0	0	2	0	0	0
Bumelia aff. lycioides	1	0	0	0	5	0	0	0
Pinus taeda	5	0	0	0	2	0	0	0
Quercus hemisphaerica	1	0	0	0	2	0	0	0
Pinus glabra	3	0	11	0	7	0	2	0
Ostrya virginiana	--	0	1	0	2	0	5	0
Liquidambar styraciflua	6	16	16	11	5	33	9	5
Carya glabra	--	0	1	0	2	0	5	0
Quercus alba	31	23	0	0	7	13	0	0
Tilia heterophylla	8	0	9	0	5	0	11	0
Persea borbonia	4	0	--	0	2	0	2	0
Fagus grandifolia	0	47	9	0	0	13	5	0
Ulmus alata	0	1	0	0	0	7	0	0
Ilex opaca	0	3	1	0	0	20	2	0
Liriodendron tulipifera	0	10	--	0	0	13	2	0
Magnolia grandiflora	0	0	9	0	0	0	7	0
Quercus michauxii	0	0	8	0	0	0	11	0
Morus rubra	0	0	2	0	0	0	7	0
Acer negundo	0	0	1	0	0	0	5	0
Halesia diptera	0	0	1	0	0	0	2	0
Fraxinus americana	0	0	22	8	0	0	9	5
Ulmus americana	0	0	1	14	0	0	5	27
Melia azedarach	0	0	1	0	0	0	2	0
Quercus nigra	0	0	1	0	0	0	2	0
Quercus shumardii	0	0	4	0	0	0	2	0
Carpinus caroliniana	0	0	3	7	0	0	7	18
Celtis laevigata	0	0	0	26	0	0	0	22
Carya aquatica	0	0	0	19	0	0	0	9
Fraxinus profunda	0	0	0	15	0	0	0	9
Ilex longipes	0	0	0	--	0	0	0	5
	100	100	101	100	100	99	102	100

RESEARCH SUMMARY 30, continued.

Several lightning-struck trees were observed in the transect. A stump sprout of Torreya taxifolia grew on the upper slope. Long-persisting logs of 4 Torreya trees were seen on the upper and lower slopes. These were once tall understory trees.

WOODY UNDERGROWTH: Rhapidophyllum hystrix was restricted to the lower slope where it formed dense thickets. Other woody vegetation was much less dense than higher on the slope, probably because of the density of needle-palm. Viburnum nudum grew only on the lower slope.

Woody species that did not reach 10 cm in dbh in the transect but which occurred on the ridge and upper slope were:

Bignonia capreolata	Parthenocissus quinquefolia
Celtis aff. tenuifolia	Smilax bona-nox
Cercis canadensis	Smilax glauca
Crataegus uniflora	Smilax pumila
Euonymus americanus	Smilax smallii
Hamamelis virginiana	Toxicodendron radicans
Hydrangia quercifolia	Viburnum dentatum
Nyssa sulvatica	Viburnum rufidulum
Osmanthus americana	Vitis rotundifolia

HERBACEOUS UNDERGROWTH: Since the study was undertaken in the summer, various spring- and fall-blooming species were not identifiable. Herbaceous cover was sparse on the bluff with a maximum cover in places of 20%. Cover was greater on the floodplain and reached 85%. A species list was not prepared for the floodplain, but Laportea canadensis was one of the common species.

Species confined to the ridge were Callicarpa americana, Desmodium glabellum, and Silphium simpsonii. Species that occurred on the ridge and/or slope were:

Agrimonia microcarpa	Polystichum acrostichoides
Aster lateriflorus	Ruellia caroliniensis
Chasmanthium sessiliflorum	Sanguinaria canadensis
Dichanthelium boscii	Sanicula marilandica
Dioscorea villosa	Smilax lasioneuron
Galium circaezans	Spigelia marilandica
Mitchella repens	Thelypteris normalis
Passiflora lutea	Tillandsia usneoides
	Tradescantia hirsutiflora

20. Bottomland Hardwood Forest

Unpublished data of A. F. Clewell

Terrace between Bear Creek and Hickory Hill near S.R. 65B and 500 m east of the S.R. 267 bridge over Bear Creek, about 8 miles south of Quincy, Gadsden County (section 41, T1N, R4W). Inventoried in 1976 by A. Redmond, S. Folensbee, and K. Sparks.

The loamy soil was wet from seepage at the base of the hill and contained much organic matter. Mats of *Sphagnum* covered about 10% of the ground.

The overstory averaged 25 m tall (max. 29) with a canopy closure of 85%. Trees of at least 10 cm in dbh were inventoried in a quadrat of 0.1 ha. There were 810 trees/ha with the following relative densities:

Magnolia virginiana	28
Liriodendron tulipifera	20
Liquidambar styraciflua	15
Carpinus caroliniana	11
Quercus laurifolia	10
Acer rubrum	5
Magnolia grandiflora	4
Fraxinus americana	4
Pinus glabra	1
Ilex opaca	1
Nyssa biflora	1
	100

Springy areas contained tall shrubby thickets of *Illicium floridanum*. With the exception of the following species, little else grew with *Illicium*: *Acer rubrum*, *Quercus laurifolia*, *Magnolia virginiana*, *Itea virginica*, *Mitchella repens*, *Decumaria barbata*.

Other woody species in the stand included:

Callicarpa americana	Pinckneya bracteata
Gelsemium sempervirens	Rhus toxicodendron
Hamamelis virginiana	Rubus argutus
Lyonia lucida	Viburnum nudum
Parthenocissus quinquefolia	Vitis rotundifolia

20. Bottomland Hardwood Forest

H. M. Leitman. 1978. Correlation of Apalachicola River floodplain tree communities with water levels, elevation, and soils. Thesis, Florida State University. 53 p.

Floodplain on the west side of the Apalachicola River near Blountstown in Calhoun County (section 35, T1N, R8W), and near Wewahitchka in Gulf County (section 16, T4S, R9W).

Levees at both sites were inundated by river overflow 9% of each year. The levee at Wewahitchka was lower in elevation with regard to mean river stage than the levee at Blountstown. (Floodstage is correspondingly lower at Wewahitchka, because the valley is broader there.) The low plane at Wewahitchka lay between the levee and a cypress-tupelo slough. This plane was inundated 25% of the year by river overflow and probably longer because of the temporary ponding of flood waters and rainfall.

Soil analyses were similar in all habitats, at least in the uppermost horizon:

Percent Silt-clay	94-95
Percent Organic Carbon	4-5
Percent Nitrogen	.27-.35
pH	5.1-5.2
Cation Exchange Capacity (me/100g)	33-39
Exchangeable Cations (me/100g)	
Ca	12-15
Mg	2.3-2.8
K	0.3-0.4

Trees were inventoried which were at least 7.6 cm in dbh:

RESEARCH SUMMARY 32, continued.

Habitat:	High Levee	Low Levee	Low Plane
Location:	Blountstown	Wewahitchka	Wewahitchka
Area Sampled (m^2):	3380	1130	1430
Trees/ha:	604	336	517
Basal Area (m^2/ha):	31.7	30.1	28.7

	RELATIVE BASAL AREA		
Acer negundo	2		
Acer rubrum		3	-
Betula nigra	1	-	3
Carpinus caroliniana	2		
Carya aquatica	8	40	1
Celtis laevigata	9	-	2
Crataegus viridis	-	-	-
Diospyros virginiana	-		
Forestiera acuminata		-	-
Fraxinus caroliniana			9
Fraxinus pennsylvanica	13	37	7
Ilex decidua	3	-	
Liquidambar styraciflua	39		
Morus rubra	1		
Nyssa aquatica			26
Planera aquatica		4	5
Platanus occidentalis	3		2
Populus heterophylla			22
Quercus laurifolia	6		
Quercus lyrata	5	16	20
Quercus nigra	1		
Taxodium distichum			3
Ulmus alata	1		
Ulmus americana	6		
	100	100	100

A dash (-) signifies a value less than 1.

Additional trees and shrubs included:

Cephalanthus occidentalis	Itea virginica
Gleditsia aquatica	Quercus hemisphaerica
Hypericum galioides	Salix nigra

Woody vines included:

Ampelopsis arborea	Rubus trivialis
Brunnichia cirrhosa	Smilax bona-nox
Campsis radicans	Smilax tamnoides
Cocculus carolinus	Vitis aestivalis
Gelsemium rankinii	Vitis rotundifolia
Parthenocissus quinquefolia	Vitis vulpina
Rhus toxicodendron	

Herbs included:

Asclepias perennis	Mikania scandens
Aster sagittifolius	Onoclea sensibilis
Boemeria cylindrica	Pilea pumila
Carex louisianica	Pluchea camphorata
Conoclinium coelestinum	Polypodium polypodioides
Cynoctonum mitreola	Saururus cernuus
Hymenocallis occidentalis	Senecio glabellus
Hypoxis occidentalis	Spilanthes americana
Hypoxis leptocarpa	Spiranthes cernua
Justicia ovata	Thelypteris quadrangularis
Lycopus americanus	Tillandsia usneoides
Lygodium japonicum	Triadenum walteri

20. Bottomland Hardwood Forest

Unpublished data of A. F. Clewell

West side of the St. Marks River, south of Natural Bridge, Wakulla County (n.w. section 32, T2S, R2E). Inventoried in 1977 by D. A. Rozar.

All trees of at least 10 cm in dbh were tallied in a quadrat 1010 m^2.

There were 574 trees/ha with a collective basal area of 26.2 m^2. The species were distributed as follows:

	Relative Basal Area	Relative Density
Carpinus caroliniana	22	33
Fraxinus pennsylvanica	14	10
Liquidambar styraciflua	11	12
Celtis laevigata	11	7
Pinus taeda	9	2
Acer rubrum	6	5
Taxodium distichum	6	5
Nyssa sp.	5	7
Magnolia virginica	4	5
Ostrya virginiana	4	3
Quercus laurifolia	3	2
Juniperus silicicola	3	2
Myrica cerifera	1	3
Cornus foemina	1	2
Ulmus americana	-	2
	100	100

Other woody species in the quadrat included:

- Cephalanthus occidentalis
- Ilex opaca
- Morus rubra
- Ilex vomitoria
- Parthenocissus quinquefolia
- Sambucus canadensis
- Toxicodendron radicans

RESEARCH SUMMARY 34. WACISSA RIVER HAMMOCK

20. Bottomland Hardwood Forest

Unpublished data of A. F. Clewell

East side of the Wacissa River about 30 m below the confluence of the Little River, Jefferson County (s.w. section 1, T2S, R3E). Inventoried in 1977 by D. A. Rozar.

All trees of at least 10 cm in dbh were tallied in a quadrat 1600 m^2.

There were 650 trees/ha with a total basal area of 31.5 m^2. The species were distributed as follows:

	Relative Basal Area	Relative Density
Acer rubrum	22	11
Nyssa aquatica	21	14
Fraxinus profunda	19	16
Magnolia virginiana	15	14
Liquidambar styraciflua	7	14
Carpinus caroliniana	7	10
Ilex cassine	2	8
Ostrya virginiana	2	4
Quercus nigra	2	1
Persea borbonia	1	3
Ilex opaca	1	1
Quercus michauxii	1	1
Quercus laurifolia	-	1
Carya glabra	-	1
Cercis canadensis	-	1
	100	100

The species in the quadrat that were represented by individuals less than 10 cm in dbh were:

Cornus foemina
Diospyros virginiana
Liriodendron tulipifera
Myrica cerifera
Pinus taeda
Taxodium distichum
Viburnum obovatum

Other woody species in the vicinity of the quadrat were

Callicarpa americana
Fraxinus caroliniana
Itea virginica
Lyonia fruticosa
Rhus toxicodendron
Sabal minor

12. Bald-cypress Swamp
20. Bottomland Hardwood Forest

Unpublished data of A. F. Clewell

West side of the Wakulla River just south of S.R. 365 at the "upper bridge", Wakulla County (n.e. section 2, T3S, R1W). Inventoried by M. McAuliffe and M. Benavides in 1977.

The river swamp was divided somewhat arbitrarily into three zones parallel to the river. The cypress swamp was along the river bank, and the bottomland hardwood forest was on the adjacent terrace and on the gentle slope leading to the upland. Trees at least 10 cm in dbh were inventoried:

Habitat:	Cypress Swamp	Bottomland Terrace	Hardwood Forest Slope
Area Sampled (m^2):	560	1,000	1,000
Trees/ha:	1,767	810	590
Basal Area (m^2/ha):	82.4	34.7	36.8

	Relative		Relative		Relative	
	Basal Area	Density	Basal Area	Density	Basal Area	Density
Taxodium distichum	39	13	1	3		
Fraxinus caroliniana } Fraxinus profunda	37	58	20	31		
Acer rubrum	12	13	15	10		
Quercus laurifolia	4	4	12	6	29	15
Quercus nigra	3	3	6	4		
Planera aquatica	3	4	11	10		
Persea palustris	1	4	16	8		
Cephalanthus occidentalis	1	1	1	3		
Nyssa biflora			7	4	1	2
Liquidambar styraciflua			7	7	2	5
Carpinus caroliniana			2	6	17	41
Myrica cerifera			2	6		
Quercus phellos			-	1		
Cornus foemina			-	1		
Magnolia virginiana					38	19
Ulmus americana					7	5
Carya glabra					3	3
Ilex opaca					2	7
Quercus michauxii					1	3
	100	100	100	100	100	100

RESEARCH SUMMARY 35, continued.

Other trees and shrubs present were:

Arundinaria gigantea
Baccharis sp.
Callicarpa americana
Celtis laevigata
Cercis canadensis
Euonymus americanus
Hypericum galioides
Ilex cassine
Ilex coriacea
Ilex vomitoria
Itea virginica
Morus rubra
Osmanthus americana
Styrax americana
Symplocos tinctoria
Vaccinium ashei

Woody vines included:

Ampelopsis arborea
Decumaria barbata
Ipomoea macrorhiza
Matelea sp.
Rosa palustris
Smilax bona-nox
Smilax tamnoides
Toxicodendron radicans
Vitis rotundifolia

Herbs included:

Asclepias perennis
Boehmeria cylindrica
Crinum americanum
Hydrocotyle umbellata
Hymenocallis crassifolia
Justicia ovata
Lobelia cardinalis
Mikania scandens
Mitchella repens
Osmunda regalis
Panicum anceps
Polygonum punctatum
Pontederia cordata
Rhynchospora corniculata
Ruellia caroliniensis
Rumex verticillatus
Sabatia calycina
Sagittaria lanceolata
Sium suave
Thelypteris normalis
Vallisneria americana

21. Coastal Hammock

Unpublished data of A. F. Clewell

Hammock bordering the slough that flows into Nick's Hole, eastern St. George Island, Franklin County. Inventoried in the spring of 1977 by N. Raymond, W. Mrazek, and M. Borgman.

The two study sites were on either side of a road that traversed the end of the slough. The south site was located at the head of the slough. The north site bordered either side of the slough. Where light was sufficient, sawgrass grew within the slough. Slash pine-scrub bordered the hammock on the upland. All trees of at least 10 cm in dbh were considered the overstory. Other trees and shrubs of lesser diameter but at least 3 dm tall were considered the understory (estimates of understory cover also included herbs, vines, and seedlings of trees and shrubs). Relative basal areas (RBA) and relative densities (RD) were determined for trees of each species.

	SOUTH SITE			NORTH SITE		
	Overstory		Understory	Overstory		Understory
Area Sampled (m^2):	1,200		48	1,000		100
Percent Cover:	60		30	25		50
Trees/ha:	650		39,375	480		19,200
Basal Area (m^2/ha):	25.1			26.8		
	RBA	RD	RD	RBA	RD	RD
Quercus virginiana	70	72	6	24	17	1
Magnolia grandiflora	12	4	1	1	4	3
Juniperus silicicola	9	10	1	24	31	1
Pinus elliottii	4	1	0	41	40	0
Diospyros virginiana	3	5	0	0	0	0
Quercus geminata	1	5	0	0	0	0
Prunus caroliniana	1	1	10	0	0	0
Persea borbonia	1	1	28	0	0	1
Myrica cerifera	0	0	26	1	2	14
Ilex vomitoria	0	0	20	0	0	44
Bumelia lanuginosa	0	0	5	0	0	1
Osmanthus americana	0	0	1	0	0	0
Sabal palmetto	0	0	1	9	6	15
Quercus myrtifolia	0	0	1	0	0	0
Ilex glabra	0	0	0	0	0	9
Baccharis glomeruliflora	0	0	0	0	0	8
Serenoa repens	0	0	0	0	0	2
Sambucus canadensis	0	0	0	0	0	1
	101	99	100	100	100	100

Other shrubs that were present but which did not occur in quadrats were:

Quercus chapmanii
Vaccinium arboreum
Vaccinium myrsinites

Woody vines included:

Parthenocissus quinquefolia
Rhus toxicodendron
Rubus trivialis
Smilax auriculata
Smilax bona-nox
Smilax walteri
Vitis rotundifolia

Herbs included:

Dichanthelium aciculare
Galium hispidulum
Hydrocotyle bonariensis
Ipomoea sagittata
Pteridium aquilinum
Rhynchospora megalocarpa
Solidago sempervirens
Stenotaphrum secundum
Vicia acutifolia

The next slough to the west was bordered by a hammock containing trees of exceptionally large diameters for this habitat on St. George Island. Measurements of dbh ranged upwards to 80 cm for Pinus elliottii, 74 cm for Quercus virginiana, 62 cm for Magnolia virginiana, and 53 cm for Juniperus silicicola. Multiple trunks on trees of Magnolia virginiana suggested a past history of fire.

22. Coastal Swamp

Thompson, S. K. 1980. Hammock vegetation in the northern gulf hammock region, Florida. Thesis, Fla. State Univ. 49 p.

Moist forest within 3.5 km of coastal salt marshes between S.R. 59 and the Aucilla River in the St. Marks National Wildlife Refuge, Wakulla and Jefferson counties (sections 14, 25 of T4S, R2E; sections 15, 20, 21, 22 of T4S, R3E). The area was logged for southern red cedar, cypress, and pine between 1915 and 1925.

Six stands, each 0.5 ha, were inventoried. Average tree height was 17 m, maximum 37 m. Canopy closure was about 75%. All trees at least 10 cm in dbh were inventoried in each stand. Tree density ranged from 552 to 1014 trees/ha (average 828). Tree basal area ranged from 46.3 to 58.1 m^2/ha (average 46.3). These values are high, because the abundant plants of Sabal palmetto in the undergrowth exceeded 10 cm in dbh.

Relative basal areas and densities are given below for trees. Relative densities are given for shrubs and saplings, defined as plants with stems 2.5-9 cm in dbh.

	TREES		SHRUBS & SAPLINGS
	Relative Basal Area	Relative Density	Relative Density
Sabal palmetto	44	43	0
Quercus laurifolia	11	10	5
Pinus taeda	10	6	2
Liquidambar styraciflua	5	10	10
Quercus virginiana	8	5	1
Acer rubrum	4	5	7
Magnolia virginiana	6	3	4
Ulmus americana	2	3	3
Fraxinus pauciflora	1	3	12
Juniperus silicicola	2	2	3
Quercus nigra	1	3	3
Nyssa biflora	2	2	2
Persea palustris	1	2	17
Morus rubra	1	2	1
Magnolia grandiflora	1	1	2
Myrica cerifera	-	1	9
Ilex cassine	-	-	5
Taxodium distichum	-	-	-
Pinus elliottii	-	-	0
Quercus shumardii	-	-	0
Osmanthus americana	-	-	0
Carpinus caroliniana	-	-	0
Ilex vomitoria	0	0	11
Cornus foemina	0	0	-

RESEARCH SUMMARY 37, continued.

Table, continued.

	TREES		SHRUBS & SAPLINGS
	Relative Basal Area	Relative Density	Relative Density
Lyonia fruticosa	0	0	-
Forestiera acuminata	0	0	-
Ilex coriacea	0	0	-
Celtis laevigata	0	0	-
Vaccinium arboreum	0	0	-
Baccharis halimifolia	0	0	-
Leitneria floridana	0	0	-
Euonymus americanus	0	0	-
	99	101	98

The importance of Sabal palmetto and especially Juniperus silicicola decreased with increasing distance from the coast. The importance of Liquidambar styraciflua increased with distance from the coast.

Limestone was less than a meter deep in 8% of the area of one stand, 66% of another stand, and intermediate in the other 4 stands. Values of pH were from 5.1 to 6.3. Soil nutrient values were high for Mg, K, and particularly Ca. Soil salinity was measurable but not limiting to plant growth.

Other species present included:

SHBUBS

Aesculus pavia
Arundinaria gigantea
Callicarpa americana
Cercis canadensis
Chionanthus virginica
Clethra alnifolia
Gleditsia aff. aquatica
Hypericum galioides
Ilex opaca
Ilex vomitoria
Itea virginica
Leucothoe racemosa
Lyonia lucida
Rhapidophyllum hystrix
Sabal minor
Serenoa repens
Yucca aloifolia

WOODY VINES

Berchemia scandens
Bignonia capreolata
Campsis radicans
Rubus trivialis
Smilax bona-nox
Toxicodendron radicans
Vitis rotundifolia

HERBS

Arisaema triphyllum
Boehmeria cylindrica
Chasmanthium laxum
Chasmanthium nitidum
Cladium jamaicense
Corton glandulosus
Cuscuta compacta
Cynoctonum mitreola
Dichanthelium commutatum
Elephantopus nudatus
Erechtites hieracifolia
Galium pilosum
Gnaphalum purpureum
Oplismenus setarius
Osmunda cinnamomea
Panicum rigidulum
Plantanthera clavellata
Ponthieva racemosa
Polypodium polypodioides
Pteridium aquilinum
Rhynchospora miliacea
Ruellia caroliniensis
Sabatia calycina
Samolus parviflorus
Saururus cernuus
Tillandsia usneoides
Viola floridana
Woodwardia areolata
Woodwardia virginica

RESEARCH SUMMARY 38. ST. MARKS SALT MARSH PRODUCTIVITY

23. Salt Marsh

Kruczynski, W. L., C. B. Subrahmanyan, and S. H. Drake. 1978. Studies on the plant community of a north Florida Salt Marsh. Part I. Primary production. Bull. Marine Sci. 28: 316-334.

A 600 meter transect was established from the East River to the upland at S.R. 59, 3.5 km north of the St. Marks lighthouse, Wakulla County, in the St. Marks National Wildlife Refuge.

Data were taken in the Low Marsh between the river and the zone of barrens and in the High Marsh between the barrens and S.R. 59. Pure stands of *Juncus roemerianus* and *Spartina alterniflora* were sampled in both low and high marshes. A salt flat of *Distichlis spicata* was sampled in the high marsh.

	LOW MARSH		HIGH MARSH		
	Juncus roem.	Spartina altern.	Juncus roem.	Spartina altern.	Distichlis spicata
Mean annual biomass - g/m^2	1237	400	601	100	
Max. biomass - g/m^2 (November)					610
Net productivity of shoots, Kcal/m^2/year in pure stand	5401	2646	1157	472	2268
Mean height - cm	102	85	78	48	
Living shoots/m^2	885		1692		
Dead shoots/m^2	776		3029		

Juncus roemerianus grows all year with both seasonal and annual fluctuations in productivity. The growth rate correlates with temperature.

Spartina alterniflora is dormant in the winter.

Other species occurring along the transect were:

- Aster tenuifolius
- Baccharis halimifolia
- Batis maritima
- Borrichia frutescens
- Ilex vomitoria
- Iva frutescens
- Lilaeopsis chinensis
- Limonium carolinianum
- Lycium carolinianum
- Sagittaria subulata
- Salicornia bigelovii
- Salicornia virginica
- Spartina cynosuroides
- Spartina patens
- Sporobolus virginicus
- Suaeda linearis

RESEARCH SUMMARY 39. NICK'S HOLE MARSH

23. Salt Marsh
24. Brackish Marsh

Unpublished data of A. F. Clewell

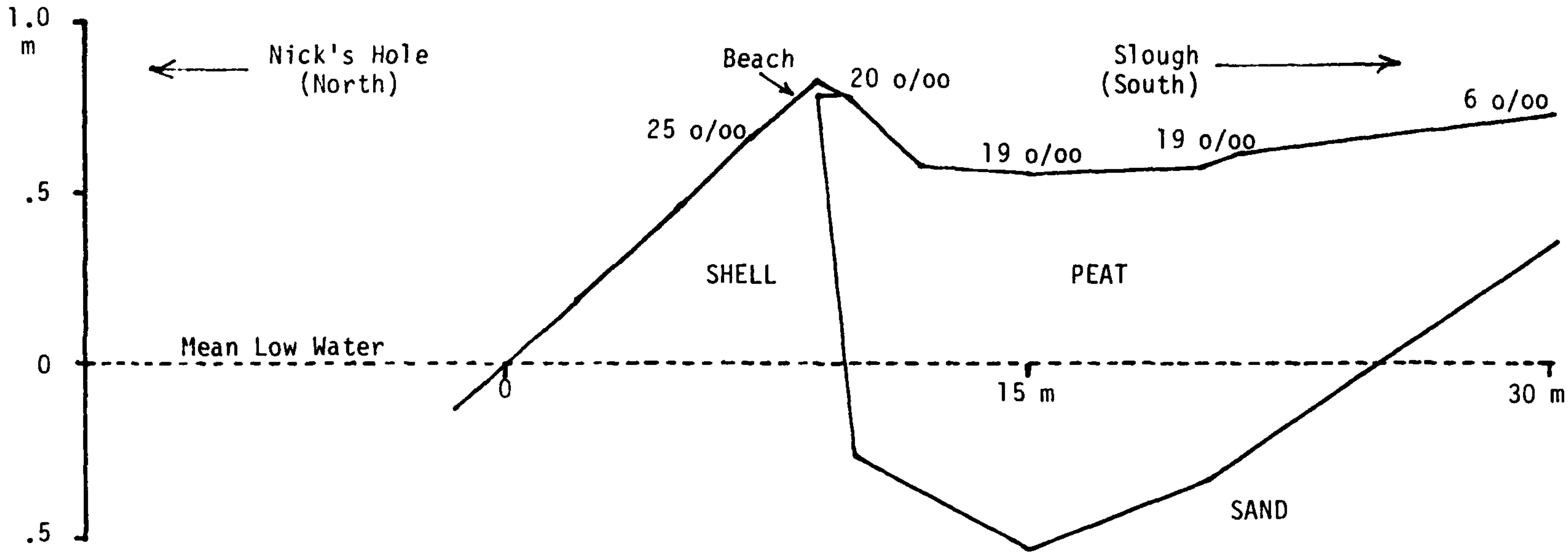
Nick's Hole is a "U"-shaped bay about 300 meters wide on the north side of St. George Island, Franklin County, about mid-way between the causeway and Sike's Cut. An oyster shell beach (presumably a kitchen midden) forms the southwestern "corner" of Nick's Hole at the bottom of the "U". This beach is 150 meters long and is capped with a thin layer of sand.

The basin behind this beach is a peaty tidal marsh. Fresh water enters this basin from a slough. This water is partially impounded by the beach, but a narrow break in the beach at its eastern edge serves as an outlet and allows a limited tidal exchange. Storm tides are driven over the beach into the basin at long intervals.

A transect was established with a rod and level at right angles to the beach in the spring of 1977 by N. Raymond, W. Mrazek, and M. Borgman.

The transect only extended about one-third of the distance from the beach to the back of the basin where the slough discharged. The vegetation at the southern end of the transect (sawgrass marsh) was characteristic of the vegetation in the unsampled portion of the basin. A few patches of pure *Typha domingensis* were the only important exceptions. A few plants of *Crinum americanum* and *Thalia geniculata* were observed at the mouth of the slough.

The data are summarized on the following page. Vegetational cover was determined by line interception. Values for pH ranged from 5 to 6.5 in the marsh. Mean low water was assumed to be the lowest point on the beach where *Spartina alterniflora* grew.



	PERCENT COVER							
Spartina alterniflora	40	40						
Juncus roemerianus		50	--	5	25	80	10	5
Borrichia frutescens		--						
Spartina patens			50	60				
Sesuvium portulacastrum			10	15				
Batis maritima				10				
Cladium jamiacense					25	40	80	90
Distichlis spicata			--	--	10			
Sporobolus virginicus			--					
Solidago sempervirens			--					
Iva frutescens			--					
Baccharis halimifolia			--					
Limonium carolinianum			--	--	--			
Salicornia virginica				--	25			
Aster tenuifolius					5			

RESEARCH SUMMARY 40. ST. MARKS-WAKULLA RIVER MARSHES

24. Brackish Marshes
25. Riparian Fresh Water Marshes

Thompson, S. M. 1977. Vascular plant communities and environmental parameters under tidal influence on the Wakulla and St. Marks Rivers, Florida. Thesis, Fla. State Univ.

Marshes were studied within the zone of tidal influence on the St. Marks River (river miles 5, 8, 10 from the coast) and its tributary, the Wakulla River (river miles 12, 15), both in Wakulla County. River mile 15 is at the U.S. 98 bridge.

Fresh water marshes occurred at mile 15. Marshes at mile 5 were borderline between salt and brackish marshes. The others were brackish. Marsh substrates were mucks 0.5-3.3 meters deep.

Study sites were established on both sides of the river at each of the five river-mile locations. One site was placed 10 m from the river bank and another 10 m from the woods bordering the marsh. A third site was establisned mid-way between the former two sites. The marsh was too narrow to establish more than one site at mile 15 and the east side at mile 12.

At each of the 24 sites, all plants were counted in 15, meter-square quadrats in the summer of 1976. A total of 74 species were observed in these marshes. The 4 or 5 species with the highest densities are listed for each site on the following page. Those species are listed below.

Cladium jamaicense
Crinum americanum
Distichlis spicata
Eleocharis cellulosa
Fimbristylis castanea
Juncus polycephalus
Juncus roemerianus
Lilaeopsis chinensis
Limonium carolinianum
Ludwigia repens
Lythrum lineare
Mikania scandens
Polygonum punctatum
Pontederia cordata
Physostegia purpurea
Sagittaria lancifolia
Sagittaria subulata
Saururus cernuus
Scirpus pungens
Spartina alterniflora
Spartina spartinae
Sporobolus virginicus
Zizania aquatica

Dominant species are listed in order of decreasing density.

Names are abbreviated from list on previous page.

Numbers are river miles from the coast.

Coastal Swamps and Hammocks			St. Marks River // Wakulla River (river mile)			Coastal Swamps and Hammocks
		Polygonum S. subulata Pontederia Physostegia	15	Juncus poly Pontederia Zizania S. subulata		
Juncus roem Crinum Lythrum Mikania	Cladium Juncus roem S. subulata Pontederia	Cladium S. subulata Juncus roem Pontederia	12	Juncus roem S. subulata Crinum Saururus		
Juncus roem Cladium Crinum Mikania	Juncus roem Cladium Crinum Mikania	Cladium Juncus roem S. subulata S. lancifol	10	Juncus roem Cladium Lythrum Saururus	Juncus roem Scirpus pun Lythrum Crinum	Juncus roem Mikania Lythrum Crinum
Juncus roem Mikania Ludwigia Crinum Cladium	Juncus roem Cladium Lythrum Mikania Crinum	*Cladium* S. subulata Ludwigia Pontederia	8	Juncus roem Scirpus pun Lythrum Cladium	Juncus roem Lilaeopsis Crinum Lythrum Cladium	Juncus roem Fimbristylis Limonium Mikania Cladium
Juncus roem S. spartinae Fimbristylis Sporobolus	Juncus roem Lilaeopsis Lythrum Cladium	Juncus roem Lilaeopsis Lythrum Distichlis	5	Juncus roem Lythrum S. subulata S. alternif	Juncus roem Lilaeopsis Distichlis Eleocharis	Juncus roem Lilaeopsis Distichlis Lythrum

RESEARCH SUMMARY 41. UPPER MARSH OF DEER RIVER

7. Titi Swamp
24. Brackish Marsh
25. Riparian Fresh Water Marsh

A. F. Clewell and J. Usher. Data obtained as biological baseline information in the preparation of a draft environmental impact statement for a new source NPDES Permit for Ideal Basic Industries, Inc., by the U.S. Environmental Protection Agency, Region IV (904/9-78-005).

The study site was located near the upper end of the North Fork of Deer River in southern Mobile County, Alabama. A broad sawgrass marsh was interrupted by an open grove of mainly blackgums, presumably in the process of invading the marsh. Near the upland edge of the marsh the sawgrass gave way to fresh water marsh vegetation. The toe of the slope of the upland contained a titi swamp. A longleaf pine savannah occupied the upland.

A short distance down stream from the site the trees were absent from the sawgrass marsh. Needlerush became increasingly important, and a band of _Sagittaria lancifolia_ 1-4 m wide lined the river bank. Species of _Spartina_ were absent this far from the coast.

The soil of the marsh consisted of a fibrous peat that exceeded 1.5 m in depth near the creek. The upper 5-15 cm of peat was intermixed with silt and clay, which probably eroded from the yellow clayey sands of the upland. The soil of the fresh water marsh and titi swamp was a deep silt-clay darkened with organic matter.

The sawgrass exceeded 2 m tall and was exceedingly dense with 100% cover in most places, except in the fresh water marsh and titi swamp. It was interlaced by long stems of _Smilax bona-nox_, which formed occasional massive tangles. The only other species with appreciable cover was _Ludwigia glandulosa_, which dominated the fresh water marsh with better than 25% cover.

A transect line 87 meters long was established in 1977 from the river bank through the titi swamp. Herbs and vines were tallied for frequency by line interception in contiguous meter-long segments along the transect line. The percentages of segments in which each species was intercepted are presented on the following page.

All trees and shrubs were tallied which grew within 2 meters of the transect line on either side. Densities were calculated for each species and presented on the following page.

RESEARCH SUMMARY 41, continued.

Habitat:	Sawgrass Marsh	Sawgrass-Blackgum	Sawgrass Marsh	Fresh Water Marsh	Titi Swamp
Meters along Transect:	1-39	40-46	47-58	59-78	79-88
	Percentage of Interceptions				
Cladium jamaicense	100	57	100	5	0
Sagittaria lancifolia	5	0	0	0	0
Smilax bona-nox	87	14	0	5	0
Hypericum nitidum	3	0	0	0	0
Lycopus angustifolius	3	0	0	25	0
Ludwigia glandulosa	0	14	0	90	20
Ipomoea sagittata	3	0	0	0	0
Osmunda regalis	21	0	0	45	0
Toxicodendron radicans	18	71	33	5	10
Mikania scandens	0	29	8	5	0
Peltandra virginiana	0	0	8	0	0
Pontederia cordata	0	0	0	35	0
Saururus cernuus	0	0	0	10	0
Crinum americanum	0	0	0	10	0
Woodwardia virginica	0	0	0	10	0
Panicum sp.	0	0	0	5	0
Polygonum hydropiperoides	0	0	0	5	0
Triadenium virginicum	0	0	0	5	0
Pteridium aquilinum	0	0	0	0	30
	Density per 100 m^2				
Acer rubrum	7.0	10.7	2.1	13.8	12.5
Ilex myrtifolia	1.3	0	2.1	0	0
Myrica cerifera	3.9	7.1	18.8	5.0	0
Nyssa biflora	0.6	39.3	14.6	32.5	5.0
Persea palustris	0	3.6	0	0	0
Pinus elliottii	0	3.6	9	2.5	17.5
Magnolia virginiana	0	3.6	6.3	10.0	7.5
Cliftonia monophylla	0	0	0	0	20.0
Clethra alnifolia	0	0	0	0	12.5
Serenoa repens	0	0	0	0	5.0
Symplocos tinctoria	0	0	0	0	5.0
Hamamelis virginiana	0	0	0	0	5.0
Rubus argutus	0	0	0	0	2.5
Myrica heterophylla	0	0	0	0	2.5
Diospyros virginiana	0	0	0	0	2.5
	12.8	67.9	43.9	63.8	97.5

RESEARCH SUMMARY 42. COASTAL MARSH ZONATION IN LOUISIANA

23. Salt Marshes
24. Brackish Marshes
25. Riparian Fresh Water Marshes

Chabreck, R. H. 1972. Vegetation, water and soil characteristics of the Louisiana coastal region. La. State Univ. Agric. Exp. Sta. Bull. No. 664.

Four vegetation-salinity zones were recognized: saline (salt marshes), brackish, intermediate (both brackish marshes), and fresh (riparian fresh water marshes). The more important species of each zone are given along with values for percent composition as compiled from studies at many locations.

SALINE

Spartina alterniflora	62
Juncus roemerianus	10
Distichlis spicata	14
Batis maritima	4
Spartina patens	6
12 other species	4

BRACKISH

Spartina patens	55
Distichlis spicata	13
Scirpus americanus	5
Spartina alterniflora	5
Juncus roemerianus	4
Ruppia maritima	4
Eleocharis parvula	2
Scirpus robustus	2
32 other species	10

INTERMEDIATE

Spartina patens	34
Phragmites australis	7
Sagittaria lancifolia	6
Bacopa monnieri	5

INTERMEDIATE continued

Paspalum distichum	4
Vigna repens	4
Echinochloa walteri	3
Panicum virgatum	3
Scirpus pungens	3
Alternanthera philoxeroides	2
Cyperus odoratus	2
Scirpus robustus	2
42 other species	25

FRESH

Panicum hemitomon	26
Sagittaria lancifolia	15
Eleocharis sp.	11
Alternanthera philoxeroides	5
Spartina patens	4
Phragmites australis	3
Ceratophyllum demersum	2
Cyperus odoratus	2
Hydrocotyle umbellata	2
Lemna minor	2
Myriophyllum spicatum	2
Utricularia cornuta	2
81 other species	14

RESEARCH SUMMARY 43. COASTAL MARSH ZONATION IN MISSISSIPPI

23. Salt Marshes
24. Brackish Marshes
25. Riparian Fresh Water Marshes

Eleuterius, L. N. 1972. The marshes of Mississippi. Castanea 37: 153-168.

Four vegetation-salinity zones were recognized with increasing distance from the coast up rivers. I-saline (salt marsh); II-brackish (brackish marsh); III-intermediate (brackish marsh); IV-fresh water (riparian fresh water marsh). Species in each zone are as follows:

	I	II	III	IV
Aster tenuifolius	x			
Distichlis spicata	x			
Salicornia bigelovii	x			
Suaeda linearis	x			
Sabatia stellaris	x			
Spartina alterniflora	x	x		
Spartina patens	x	x		
Spartina cynosuroides	x	x		
Limonium carolinianum	x	x		
Scirpus robustus	x	x		
Scirpus americanus	x	x		
Juncus roemerianus	x	x	x	
Ipomoea sagittata		x		
Asclepias lanceolata		x		
Sagittaria lancifolia		x	x	x
Cladium jamaicense			x	
Osmunda regalis		x	x	x
Phragmites australis			x	
Boltonia asteroides		x	x	x
Crinum americanum		x	x	x
Sium suave		x	x	x
Proserpinaca pectinata		x	x	x
Pluchea purpurascens		x	x	x
Polygonum setaceum		x	x	x
Lythrum lineare		x	x	x
Ludwigia sphaerocarpa		x	x	x
Iris virginica		x	x	x
Hymenocallis occidentalis		x	x	x
Bidens frondosa		x	x	x
Scirpus validus			x	x
Panicum virgatum			x	
Eleocharis obutsa				x
Eleocharis intermedia				x
Eleocharis tuberculosa				x
Eleocharis quadrangulata				x

RESEARCH SUMMARY 43, continued.

	I	II	III	IV
Saururus cernuus				x
Scirpus pungens				x
Pontederia cordata				x
Rhynchospora macrostachya				x
Ptilimnium capillaceum				x
Zizania aquatica				x
Sium suave				x
Juncus megacephalus				x

26. Spring-run Assemblages
27. Tidal River Assemblages

Thompson, S. M. 1977. Vascular plant communities and environmental parameters under tidal influence on the Wakulla and St. Marks Rivers, Florida. Thesis, Fla. State Univ.

The Wakulla River (Wakulla County) is a clear spring-run and a tributary of the St. Marks River. The St. Marks River is more turbid and tannin-laden, but essentially non-alluvial. The bottom consists of muck or mucky sand, except where limestone outcrops in deeper water.

Water parameters were measured monthly for a year at the surface and near the bottom. These parameters differed little from site to site with the exception of salinity and total hardness. As salinity increased, total hardness increased correspondingly.

pH ranged from 7.5-9.0
Temperature ranged from 12-29 with the mean about 20 C.
Dissolved oxygen ranged from about 5-13 ppm with a mean of about 8.
Alkalinity ranged from 68-205 ppm with a mean of about 140.
Total hardness ranged from 100-8500 ppm.
Salinity varied as shown below. Minimum salinities did not exceed 1.0 o/oo at each sampling station, both surface and bottom.

Vegetation was sampled in the late summer in foot^2 quadrats at 5-m intervals along 5 transects, each running from bank to bank across the river. The uppermost was 15 miles from the coast at the bridge at U.S. Route 98. The lowermost was below the town of St. Marks, 5 miles from the coast. The habitats at the two transects furthest upstream (at miles 12 and 15) were essentially fresh water and contained springrun assemblages. The others were brackish and contained tidal river assemblages. Storm tides reach all sites.

RIVER:	Wakulla			St. Marks	
MILES FROM COAST:	15	12	10	8	5
MEAN SALINITY (TOP/BOT):	0/0	0/1	1/2	2/3	4/8
MAX. SALINITY (TOP/BOT):	0/0	2/12	4/13	7/24	13/25
	Dry Weight (g/m^2)				
STANDING CROP:	764	759	267	324	63
Potamogeton illinoensis	79	0	0	0	0
Sagittaria kurziana	204	1	0	0	0
Potamogeton pusillus	2	1	0	0	0
Najas guadalupensis	44	154	2	0	0
Ceratophyllum demersum[3]	0	189	1	0	0
Sagittaria subulata[1]	193[2]	154	29	1	0
Vallisneria americana	242	209	143	111	0
Potamogeton perfoliatus	0	0	0	68	0
Ruppia maritima[1]	0	52	92	144	63

[1]Plants or some of them often exposed at low tide.

[2]Extrapolated from density value, based on the density & biomass values of *S. subulata* at mile 12.

[3]Abundant but patchy throughout the fresh water portion of the Wakulla River, thus the discrepant values at miles 15 and 12.

RESEARCH SUMMARY 45. SEAGRASSES, ST. MARKS LIGHTHOUSE

28. Seagrass Beds

Unpublished File Report, St. Marks National Wildlife Refuge, by C. S. Gidden, 1964.

The study was conducted within 5 miles on either side of the St. Marks lighthouse, Wakulla County, in water up to about 2.4 m deep at low tide. The bottom was clearly visible on calm days.

The substrate was muck and sandy muck. There were also some shell beds and areas of hard sand which were essentially devoid of vegetation. Salinity was 20-56% of sea strength, as determined at 5 stations. Salinity varied because of fresh water entering from the St. Marks River and from several creeks. Full sea strength is about 36 o/oo salinity.

Vegetation was sampled along 5 transects which began on the shore at the point of mean low water and extended seaward 1.7 to 2.3 miles. Four hundred seventy two, $foot^2$ samples were taken 110 feet apart on the 9.83 miles of transects.

Frequency was determined by dividing the number of samples in which a species occurred by 472. The mean dry weight (g/m^2) per species was determined for each transect. The maximum and minimum values for the 5 transects are given below.

	Frequency	Dry Weight
Thalassia testudinum	71	12 - 119
Syringodium filiforme	42	3 - 48
Halodule wrightii	63	3 - 9
Ruppia maritima	14	0 - 11
Halophila engelmannii	14	0.1- 1

Thalassia and Syringodium grew best in .6-1.8 m of water in sandy muck at higher salinities. Thalassia also grew in shallower water.

Halodule and Ruppia grew best in shallower water in soft muck at lower salinities. Ruppia was restricted to these conditions which were met at the mouth of the St. Marks River. Halodule grew under all environmental conditions.

Halophila seemed to prefer higher salinities, regardless of depth or substrate.

RESEARCH SUMMARY 46. EFFECT OF POLLUTION ON SEAGRASSES

28. Seagrass Beds

Zimmerman, M. S., and R. J. Livingston. 1976. Effects of kraft-mill effluents on benthic macrophyte assemblages in a shallow-bay system (Apalachee Bay, north Florida, USA). Marine Biol. 34: 297-312.

Data were obtained from 26 stations from within the intertidal zone to a distance of 5-6 km offshore between March, 1972 and April, 1973, Taylor County.

	Econfina River (natural)	Fenholloway River (polluate)
Total g/m^2	47,984	2,741
Number of Species	30	29
	Percent Biomass	
Thalassia testudinum	38	24
Syringodium filiforme	8	39
Halodule wrightii	1	13
Halophila engelmannii	-	10
Ruppia maritima	1	-
ALGAE		
Halimeda incrassata	43	1
Digenia simplex	5	1
All other species	4	12

Important Species of Algae

CHLOROPHYTA	RHODOPHYTA	PHAEOPHYTA
Anadyomene stellata	Digenia simplex	Padina vickersiae
Caulerpa ashmeadii	Gracilaria cervicornis	Sargassum filipendula
Caulerpa prolifera	Gracilaria verrucosa	Sargassum pteropleuron
Cladophora sp.	Laurencia intricata	
Halimeda incrassata	Laurencia poitei	
Penicillus capitatus	Polysiphonia harveyi	
Udotea conglutinata	Spyridia filamentosa	
Udotea flabellum		

RESEARCH SUMMARY 47. SEASONALITY OF SEAGRASSES, TAYLOR COUNTY.

28. Seagrass Beds

Zimmerman, M. S. and R. J. Livingston. 1976. Seasonality and physico-chemical ranges of benthic macrophytes from a north Florida estuary Apalachee Bay. Contrib. Marine Sci. 20: 33-45.

	Year	DRY WEIGHT (g/m^2)											
		Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
Thalassia	1972			866	408	1006	1789	549	1172	1744	3204	982	663
testudinum	1973	830	1518	1360	1271								
Syringodium	1972			176	221	170	330	551	643	394	468	189	144
filiforme	1973	339	330	54	211								
Halodule	1972			11	3	3	21	32	42	25	94	41	42
wrightii	1973	133	28	41	44								
Halophila	1972			12	5	26	27	27	3	12	36	16	21
engelmannii	1973	37	18	64	37								
Ruppia	1972			2	1	0	0	0	0	0	0	338	1
maritima	1973	3	2	0	1								
ALGAE													
Halimeda	1972			685	708	1238	2058	1722	2230	2462	3023	1174	227
incrassata	1973	1436	504	838	959								
Chlorophyta	1972			76	10	26	87	57	47	60	109	48	27
12 species	1973	58	44	45	17								
Digenia	1972			77	39	110	241	26	475	401	181	129	44
simplex	1973	88	113	106	149								
Rhodophyta	1972			58	26	15	65	23	108	45	100	51	16
16 species	1973	37	85	218	61								
Phaeophyta	1972			1	7	0	7	2	17	11	31	8	1
4 species	1973	1	3	1	1								
AV. ANNUAL TOTAL		2962	2645	2346	2090	2594	4625	2989	4737	5154	7246	2976	1186
PERCENT SEAGRASS		45	72	55	53	46	47	39	39	42	52	53	73

RESEARCH SUMMARY 48. LAKE MICCOSUKEE

32. Palustrine Aquatic Assemblages

Tarver, D. P. 1980. Water fluctuation and the aquatic flora of Lake Miccosukee. J. Aquat. Plant Manage. 18: 19-23.

Lake Miccosukee lies between Leon and Jefferson counties near the Georgia line. It has a surface area of 2954 ha and is fed mainly by seepage from ground-water. The lake is underlain by clays and sandy clays 15-20 m deep. Originally, a sinkhole at the north end periodically drained the lake. The lake last went dry in 1950 during a severe drought.

An earthen dam was placed around the sinkhole in 1954 to prevent the lake from draining. A low dam was placed at the outfall on the southern end of the lake to stabilize the water level. Subsequently, aquatic plants proliferated. A hydrosoil of peat and muck accumulated on the bottom, which was as much as 40 cm deep in 1977. Methane and hydrogen sulfide were produced by decomposition and became trapped within the hydrosoil. Periodically, these gases caused chunks of peat to become bouyant and float to the surface. These became floating islands and were quickly colonized by *Panicum hemitomon*, *Decodon verticillatus*, and, to a lesser degree, *Cephalanthus occidentalis*.

Floating-leaved aquatics (*Nymphaea odorata*, *Nuphar luteum*) were abundant, as were several submersed aquatics, particularly *Brasenia schreberi*. The latter was heavily utilized by ducks for food. The hydrosoil contained 200-800 seeds of *B. schreberi* per meter-square, and 14% of these germinated under laboratory conditions over 101 days.

In an attempt to consolidate the hydrosoil and to reduce undesirable populations of aquatic plants, the lake was 90% dewatered between February, 1977, and April, 1978. The hydrosoil was reduced by 70% and was no more than 12 cm deep in 1978. Aquatic plant cover was estimated from aerial photography before and after the drawdown:

	May 1976	July 1978
Open water	19	19
Floating-leaved aquatics	22	31
Floating Islands	29	23
Brasenia schreberi	30	27
	100	100

The reduction in the floating islands was thought to be caused by their becoming anchored to the lake bottom by roots growing through them during the drawdown. When the lake was refilled, the islands were held beneath the surface.

RESEARCH SUMMARY 48, continued.

The percent cover of the aquatic plants was determined in 60, meter-square quadrats spaced at 10-meter intervals along transect lines before and after the drawdown. The results were as follows:

	June 1976	June 1978
Open water	19	24
Nymphaea odorata	33	46
Brasenia schreberi	14	10
Decodon verticillatus, Panicum hemitomon, Cephalanthus occidentalis	10	6*
Utricularia purpurea	8	1
Cabomba caroliniana	8	0
Myriophyllum heterophyllum	3	2
Nuphar luteum	3	2
Limnobium spongia	1	3
Terrestrial annuals	1	5
Lemnaceae, Azolla caroliniana	-	1
	100	100

*Approximate because a floating island shifted in one transect.

RESEARCH SUMMARY 49. SEASON OF DISTURBANCE AND WEED FLORAS

33. Old Field Assemblages

Unpublished data of A. F. Clewell

Six 0.3 ha plots were established in 1969 in former corn fields at the Tall Timbers Research Station, northern Leon County. The plots were disked annually but each in a different month.

The soil was of fine sandy loam with a pH of 5.5-6.1.

The flora consisted of 132 species, including 11 non-indigenous introductions to northern Florida from other regions. They are distributed into the following life forms:

Annual herbs	42
Perennial herbs	41
Tree seedlings	10
Shrubs and woody vines	4
Biennial herbs	2
	100%

Density per m^2 is given below for the more important species. Each value represents data from 30, 0.25-m^2 quadrats in July, 1974. Annuals are designated by an asterisk (*).

Month of Disking:	Dec.	Feb.	Apr.	Jun.	Aug.	Oct.
Ambrosia artemisiifolia*	36	2	0	0	0	0
Andropogon virginicus	0	0	0	4	72	24
Rubus trivialis*	2	4	8	36	4	4
Bidens bipinnata*	0	40	0	0	0	0
Cassia obtusifolia*	0	8	24	0	0	0
Cenchrus echinatus*	0	32	4	0	0	0
Conyza canadensis*	8	0	0	12	8	0
Crotalaria spectabilis*	4	0	0	0	0	0
Cyperus rotundus	20	204	320	84	60	4
Desmodium tortuosum*	4	24	36	2	2	0
Digitaria sanguinalis*	4	48	40	0	16	0
Diodia teres*	16	16	44	0	0	4
Haplopappus divaricatus*	0	0	0	0	4	52
Heterotheca subaxillaris*	4	0	0	0	2	120
Richardia scabra*	20	472	808	4	96	2
Solidago canadensis	8	4	0	0	0	0

RESEARCH SUMMARY 49, continued.

In contrast to the weed floras on recently disturbed fields farther north, many species of stable communities colonized this field, including:

TREES

Carya glabra	Quercus falcata
Carya tomentosa	Quercus nigra
Diospyros virginianum	Quercus virginiana
Liquidambar styraciflua	Rhus copallina
Prunus serotina	Sassafras albidum

NON-ARBOREAL SPECIES

Acalypha gracilens	Ipomoea pandurata
Centrocema virginianum	Lespedeza stuevei
Cnidoscolus stimulosus	Rubus cuneifolius
Desmodium obtusifolium	Smilax bona-nox
Desmodium paniculatum	Sorghastrum nutans
Erianthus contortus	Tephrosia spicata
Eupatorium hyssopifolium	Tragia urens
Galactia macreei	

RESEARCH SUMMARY 50. TIMBERLANE FIELD

33. Old Field Assemblage

Unpublished data of A. F. Clewell

Northeast corner of junction U.S. 319 and S.R. 61, just north of I-10 north of Tallahassee, Leon County. Inventoried in 1968 by A. F. Clewell and 1977 by D. A. Rozar.

In 1968 the site was a field of *Andropogon virginicus* with an ample interspersion of *Rubus cuneifolius*. Sapling pines were up to 3 m tall. The taller ones were 8-12 years old. A local resident said that the site once had been used as a pasture. There was no evidence of fire or disturbance. In 1977 the pines had formed a nearly closed canopy with only a few openings. Some hardwoods were seen, a few of them nearly as tall as the pines.

All trees regardless of size were tallied in a 825 m^2 quadrat in 1968. In 1977 all trees at least 2 m tall were inventoried in a 400 m^2 quadrat; those trees less than 10 cm in dbh were considered saplings.

	1968	1977			
		TREES		SAPLINGS	
	Relative Density	Relative Basal Area	Relative Density	Relative Basal Area	Relative Density
Pinus taeda	47 (Pinus combined)	50	50	32	22
Pinus echinata		39	25	4	4
Pinus glabra		7	17	0	0
Liquidambar styraciflua	20	4	8	27	17
Malus angustifolius	0	0	0	11	13
Quercus hemisphaerica	0	0	0	9	19
Prunus serotina	7	0	0	7	4
Myrica cerifera	0	0	0	4	7
Diospyros virginiana	11	0	0	3	6
Rhus copallina	0	0	0	3	6
Ilex vomitoria	0	0	0	1	2
Sassafras albidum	7	0	0	0	0
Quercus virginiana	4	0	0	0	0
Basal Area (m^2/ha)		9.8		1.8	
Trees/ha	545		300		1325

Rhus copallina and *Myrica cerifera* were present in 1968 but not in the quadrat. *Quercus falcata*, *Q. nigra*, and *Vaccinium arboreum* were present in 1977 but not in the quadrat.

In 1968 the frequencies of the non-arboreal species were determined by interception in 110, 50 cm segments along a steel tape. The percentage of segments in which the more important species occurred were as follows:

RESEARCH SUMMARY 50, continued.

Andropogon virginicus	98
Rubus cuneifolius	82
Agalinus fasciculata	10
Oxalis dillenii	8
Eupatorium compositifolium	5

Other species present were Solidago canadensis, Gelsemium sempervirens, and Cnidoscolus stimulosus.

In 1977 nearly all of the herbaceous ground cover was absent, except in openings, and had been replaced by vines and litter. Species present included Parthenocissus quinquefolia and Asplenium platyneuron.

RESEARCH SUMMARY 51. FIRE ECOLOGY PLOTS

34. Pine-Oak Woods

Tall Timbers Research Station Bull. No. 2, 1962, and unpublished data of A. F. Clewell.

Permanent fire ecology demonstration plots at the Tall Timbers Research Station north of Lake Iamonia, Leon County. The inventories of 1971 and 1975 were made by E. Tobi, J. Wiese, and A. Clewell.

The plots occupied former cotton fields which had been lain fallow mostly before 1900. In 1959 they contained open stands of tall, mature shortleaf and loblolly pines. The sites had been annually winter-burned for decades. The undergrowth was dense with coppicing rootcrowns.

The half-acre plots were established in 1959 and the trees inventoried. The plots are burned at various scheduled intervals. Ten plots were selected for study, 5 of them not yet having been burned by 1975 and the other 5 having been burned 1-5 times since 1959. The plots were designated as follows: W2X, W3X, W4X, W5X, W20B, W35Y, W50Y, W75A, W75B, and WX7.

The number of trees per ha are presented below for all trees of at least 2.5 cm in dbh. The data show tree mortality and recruitment between sampling events.

	1959	- lost	+ gained	= 1971	- lost	+ gained	= 1975
Burned Plots							
Pines	159	20	24	163	8	81	236
Hardwoods	31	6	69	94	4	194	284
Unburned Plots							
Pines	98	12	337	423	21	168	570
Hardwoods	35	2	938	971	18	405	1358

Basal area data, both relative (%) and actual (m^2/ha), are given below for these same trees:

	1959	1971	1975
Burned Plots			
Pines (%)	95	90	82
Hardwoods (%)	5	10	18
Total (m^2/ha)	8.3	15.8	15.6
Unburned Plots			
Pines (%)	78	63	52
Hardwoods (%)	22	37	48
Total (m^2/ha)	11.3	19.9	26.1

RESEARCH SUMMARY 51, continued.

In the burned plots, the pines gained in density but lost in basal area from the loss of old-growth trees. The hardwoods gained in density and basal area as some sprouts from coppicing rootcrowns were able to survive the periodic fires and attain tree size.

In the unburned plots, the same trends were observed, but the hardwoods assumed a greater degree of dominance than in the burned plots.

Gains in hardwoods in 1971 and 1975 were mainly made by Quercus nigra, Liquidambar styraciflua, and Prunus serotina.

The trees in the plots were:

Pinus echinata
Pinus elliottii
Pinus palustris
Pinus taeda
Albizia julibrissin
Carya tomentosa
Cornus florida
Diospyros virginiana
Liquidambar styraciflua
Myrica cerifera
Nyssa sylvatica
Prunus serotina
Quercus alba
Quercus flacata
Quercus nigra
Quercus phellos
Quercus stellata
Quercus velutina
Quercus virginiana

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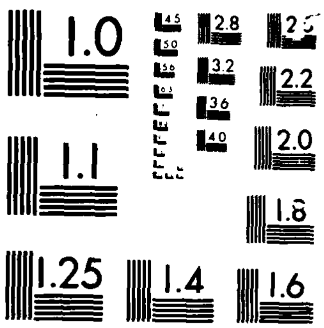

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RESEARCH SUMMARY 52. NB66.

34. Pine-Oak Woods

Unpublished data of A. F. Clewell and R. Komarek (from 1966), and

Tobi, E. R. 1977. Vegetational changes on formerly annually burned secondary pine-oak woods after ten fire-free years. Thesis, Fla. State Univ.

NB66 is a permanent plot located at the Tall Timbers Research Station between Lake Iamonia and the Georgia state line in northern Leon County. It once consisted of a collection of old agricultural fields (8.64 ha in all) mostly lain fallow from 1860-1920, few later. The fields were burned as soon as the sapling pines developing on them were about 2 m tall. The plot was annually winter-burned from 1935-1966. Fire has been excluded subsequently.

The soil was fine sandy loam, moist but well drained. The plot covered a hill 37 m tall from base to ridge.

In 1966 the flora consisted of 213 species: 9% trees, 7% shrubs, 5% woody vines, 62% perennial herbs, and 17% annual and biennial herbs. The annuals and biennials mostly grew in a small portion that was still harrowed in 1966.

Many arboreal species grew as coppicing sprouts from large root crowns. The sprouts were burned back to their crowns in the annual fires. These crowns tended to be clustered. Intervening grassy sites contained few crowns and were often dominated by *Andropogon virginicus* or *Sorghastrum nutans*.

Root crowns were inventoried in 791, 4-m^2 quadrats in 1966. One or more crowns were observed in 76% of the quadrats. The most frequent species were *Quercus nigra* 28%, *Sassafras albidum* 17%, *Diospyros virginiana* 15%, *Liquidambar styraciflua* 12%, and *Quercus phellos* 10%.

Since the exclusion of fire in 1967, the coppicing sprouts have formed a dense, thicket-like understory beneath the original overstory. The species composition has changed very little. Notable additions were seedlings of *Magnolia grandiflora* and *Ilex opaca*. A few grassy openings still persist with only a few seedlings of *Pinus echinata* or *Quercus nigra* in the centers. Root extensions from the thickets reached nearly to the centers and likely prevented the successful germination of tree seedlings. Twenty five m^2 trenched plots, installed in 1970, yielded data that substantiated the conclusion that root competition from existing coppicing hardwoods prevented seedling establishment.

All trees of at least 5 cm in dbh were tallied in 1966 and 1976, as follows:

RESEARCH SUMMARY 52, continued.

	Relative Basal Area		Relative Density	
	1966	1976	1966	1976
Acer rubrum	-	0	-	0
Carya glabra	-	-	-	-
Cornus florida	1	1	4	4
Diospyros virginiana	-	-	1	1
Liquidambar styraciflua	2	3	5	11
Malus angustifolius	-	-	-	-
Myrica cerifera	-	1	-	2
Nyssa sylvatica	-	-	1	-
Pinus echinata	38	36	42	12
Pinus elliottii	6	4	2	1
Pinus palustris	6	4	3	1
Pinus taeda	36	29	20	7
Quercus alba	-	-	-	1
Quercus falcata	1	1	3	2
Quercus hemisphaerica	-	1	1	1
Quercus nigra	3	11	10	43
Quercus phellos	-	1	1	4
Quercus stellata	-	1	-	-
Quercus virginiana	6	5	5	1
Prunus serotina	1	2	2	9
Sassafras albidum	0	0	-	-
	100	100	100	100

A dash (-) signifies a value less than 1.

Pine and hardwood recruitment and mortality were as follows:

	Trees/ha				Basal Area (m^2/ha)			
	1966	Added	Lost	1976	1976	Added	Lost	1976
Pines	72	99	2	169	8.9	2.9	0.1	11.7
Hardwoods	34	642	6	670	1.5	3.4	0.2	4.7
Total	106	741	8	839	10.4	6.3	0.3	16.4

RESEARCH SUMMARY 52, continued.

The non-arboreal species were sampled in 76, meter-square quadrats on the more maturely forested portions of NB66 in June, 1966. Sampling was repeated in November for fall-blooming species. The percentages of quadrats in which the species occurred were as follows:

Cassia fasciculata	99
Rubus cuneifolius	78
Dichanthelium acuminatum	65
Andropogon virginicus	61
Centrocema virginianum	50
Scleria pauciflora	47
Sorghastrum nutans	44
Pityopsis adenolepis	42
Aristida virgata	41
Tephrosia spicata	41
Rhus copallina	39
Gymnopogon ambiguus	31
Erianthus contortus	30
Galium pilosum	30
Desmodium obtusum	27
Lespedeza repens	24
Trichostema dichotomum	24
Solidago odora	23
Smilax bona-nox	22
Elephantopus elatus	22
Lespedeza procumbens	22
Ceanothus americanus	21
Schizachyrium tenerum	21
Ambrosia artemisiifolia	21
Solidago nemoralis	21
Helianthus angustifolius	20
Lespedeza stuevei	18
Eragrostis spectabilis	17
Crotalaria rotundifolia	16
Petalostemum caroliniense	16
Petalostemum albidus	15
Conoclinium coelestinum	15
Tridens flavus	13
Helianthemum carolinianum	12
Ipomoea pandurata	12
Vaccinium stamineum	11
Dichanthelium aciculare	11
Eupatorium hyssopifolium	11
56 species	<10

34. Pine-Oak Woods

Unpublished data of A. F. Clewell

Near the main laboratories of the Tall Timbers Research Station north of Lake Iamonia, Leon County, on a tract of land known as Beadel Course (section 15, T3N, R1E). Inventoried in November, 1974 by A. F. Clewell and D. Tober.

The woods developed on land that had lain fallow for at least a century following cultivation. The site had been annually burned for at least several decades.

All trees were inventoried in a quadrat of 0.2 ha. All but one tree exceeded 10 cm in dbh. Coppicing root crowns were tallied in a quadrat 100 m^2. There were 170 trees/ha with a collective basal area of 25.0 m^2/ha. There were 17,200 coppicing root crowns/ha. The trees and root crowns were distributed among the species as follows:

	TREES		ROOT CROWNS
	Relative Basal Area	Relative Density	Relative Density
Pinus taeda	68	53	0
Pinus echinata	18	29	0
Quercus nigra	9	12	68
Quercus virginiana	4	3	13
Pinus palustris	1	3	0
Liquidambar styraciflua	0	0	15
Prunus serotina	0	0	2
Diospyros virginiana	0	0	1
Nyssa sylvatica	0	0	1

Seventy three species of plants were observed on the site. The frequency of the non-arboreal species was determined in 30, meter-square quadrats. Species which occurred in at least 20% of the quadrats were:

Aristida lanosa	83	Trichostema dichotomum	37
Heterotheca adenolepis	83	Rubus cuneifolius	33
Andropogon virginicus	73	Andropogon ternarius	33
Ageratina jucunda	60	Galium pilosum	33
Cassia nictitans	60	Helianthus angustifolius	30
Dichanthelium spp.*	53	Gymnopogon ambiguus	27
Solidago odora	50	Eupatorium hyssopifolium	23
Rubus trivialis	43	Rhus copallina	23
Galactia aff. volubilis	40	Tridens flavus	23
Smilax bona-nox	37	Lespedeza procumbens	20

*including D. commutatum, D. consanguinium

RESEARCH SUMMARY 54. HORSESHOE PLANTATION COMPARISON

2. Longleaf Pine Savannahs
34. Pine-Oak Woods

Unpublished data of A. F. Clewell

Two mature, open, annually burned pinewoods were compared on either side of U.S. 319 north of Bradfordville, Leon County (sections 12, 14 of T2N, R1E). Inventoried in November 1974 by A. F. Clewell and D. Tober.

WEST SITE: Pine-oak woods 1.7 miles north of Bradfordville. The woods developed on an agricultural field that was lain fallow probably in the late 1800's. Trees were tallied in a quadrat of 0.2 ha. There were 100 trees/ha in the overstory. The percent composition was:

Pinus echinata	50
Pinus taeda	40
Quercus virginiana	10

The understory consisted of a few scattered trees of these species and of *Q. falcata*, *Q. nigra*, and *Q. stellata*.

EAST SITE: Longleaf pine savannahs 2.5 miles north of Bradfordville. The woods was of *Pinus palustris* formerly, but had been severely logged in the mid-1940's (Leon Neel, personal communication). An adjacent uncut stand of *P. palustris* was extant. Fatwood stumps with narrow growth rings strongly suggested that the harvested trees were of original growth. The few remaining trees included *Pinus palustris*, *P. echinata*, *Carya tomentosa*, *Quercus falcata*, and *Q. stellata*.

Coppicing root crowns were tallied in a 50 m^2 quadrat in each site. The relative densities were:

	West Site	East Site
Quercus nigra	52	3
Sassafras albidum	26	0
Quercus falcata	7	7
Quercus hemisphaerica	4	0
Quercus stellata	3	85
Quercus virginiana	3	0
Diospyros virginiana	3	2
Prunus serotina	2	0
Quercus incana	0	2
Carya tomentosa	0	1
SPROUTS/HA	21,800	19,200

RESEARCH SUMMARY 54, continued.

A careful search at both sites on the same day revealed 82 species at the west site and 100 species on the east site. At each site the species were tallied in 30, meter-square quadrats. Values in the tables below are the percentages of quadrats in which the species occurred.

SPECIES THAT WERE PRESENT ONLY AT THE WEST SITE

Acalypha gracilens	7	Galactia aff. macreei	17
Amphicarpa bracteata	20	Gnaphalium obtusifolium	0
Andropogon elliottii	3	Liatris elegans	0
Campsis radicans	0	Liquidambar styraciflua	0
Cassia nictitans	50	Monotropa uniflora	0
Cnidoscolus stimulosus	23	Nyssa sylvatica	0
Conyza canadensis	13	Quercus hemisphaerica	17
Desmodium cuspidatum	17	Rhynchosia reniformis	0
Desmodium lineatum	0	Sorghastrum elliottii	20
Eragrostis hirsuta	0	Seymeria cassioides	0
Erythrina herbacea	0	Tragia urens	3
Eupatorium hyssopifolium	0	Vitis aestivalis	0

SPECIES THAT WERE PRESENT ONLY AT THE EAST SITE

Aristolochia serpentaria	3	Paspalum floridanum	3
Asclepias tuberosa	0	Pinus palustris	0
Asimina longifolia	0	Pteridium aquilinum	87
Aster adnatus	3	Quercus incana	3
Aster dumosus	7	Quercus pumila	73
Carphephorus odoratissimus	0	Quercus margaretta	7
Castanea alnifolia	0	Salvia azurea	3
Chrysopsis mariana	3	Schizachyrium tenerum	0
Crataegus uniflora	7	Scutellaria sp.	0
Dyschoriste oblongifolia	80	Silphium simpsoni	0
Eupatorium album	13	Smilax auriculata	23
Eupatorium rotundifolium	0	Sporobolus junceus	17
Euphorbia pubentissima	7	Stylisma humistrata	10
Galactia regularis	3	Tephrosia virginiana	3
Gaylussacia dumosa	3	Trichostemon dichotomum	0
Gaylussacia frondosa	7	Vaccinium arboreum	7
Hedyotis procumbens	13	Vaccinium myrsinites	23
Hypericum stans	0	Verbesina aristata	3
Lechia minor	0	Vernonia angustifolia	7
Muhlenbergia capillaris	0	Viburnum rufidulum	3
Myrica cerifera	0	Vitis rotundifolia	0

RESEARCH SUMMARY 54, continued.

SPECIES THAT WERE PRESENT AT BOTH SITES

	West	East		West	East
Ageratina juncuda	23	10	Lespedeza procumbens	3	0
Andropogon ternarius	0	0	Lespedeza repens	10	7
Andropogon virginicus	73	80	Lespedeza stuevei	7	0
Aristida lanosa	7	7	Liatris graminifolia	0	0
Aristida virgata	17	0	Petalostemum albidus	3	27
Aster concolor	7	7	Pinus echinata	50	0
Aster tortifolius	0	17	Pinus taeda	3	0
Callicarpa americana	0	0	Prunus serotina	0	0
Carya tomentosa	0	3	Quercus falcata	20	37
Ceanothus americanus	10	27	Quercus nigra	63	3
Cornus florida	0	3	Quercus stellata	27	17
Crotalaria rotundifolia	7	13	Quercus virginiana	0	13
Cyperus retrofractus	7	0	Rhus copallina	57	27
Desmodium floridanum	13	20	Rhus toxicodendron	3	37
Desmodium obtusum	3	7	Rhynchosia tomentosa	7	3
Desmodium paniculatum	7	0	Rubus cuneifolius	40	17
Dichanthelium commutatum	77	63	Rubus trivialis	13	3
Diospyros virginiana	3	3	Sassafras albidum	50	13
Elephantopus elatus	40	13	Scleria sp.	13	20
Erianthus alopecuroides	33	7	Smilax bona-nox	40	47
Eupatorium compositifolium	3	0	Smilax glauca	23	67
Galium pilosum	0	3	Smilax smallii	10	10
Gelsemium sempervirens	0	7	Solidago odora	60	37
Gymnopogon ambiguus	13	10	Solidago stricta	0	0
Helianthus angustifolius	0	3	Sorghastrum nutans	7	7
Helianthus hirsutus	60	43	Sorghastrum secundum	23	40
Kuhnia eupatorioides	0	3	Tephrosia spicata	10	0
Lespedeza angustifolia	0	0	Tridens flavus	10	3
Lespedeza hirta	3	0	Vaccinium stamineum	7	37

The percentage distribution of the species into major groups was as follows:

	West	East
Trees	17	15
Shrubs and Woody Vines	15	24
Grasses	15	13
Composites	19	22
Legumes	24	14
Other Herbs	20	13
	100	101

The comparison between the two sites shows similarities in physiognomy, the distribution of species into major groups, and the total number of species. The comparison shows many dissimilarities in species composition and abundance. The second-growth community on the former fallow field does not seem to represent a seral stage in the development of the longleaf pine savannah community.

34. Pine-Oak Woods

Unpublished data of A. F. Clewell

The stand lies near the intersection of U.S. 319 and Raymond Diehl Road on the north edge of Tallahassee (n.e. section 8, T1N, R1E). The stand was inventoried in April, 1977 by A. F. Clewell and D. A. Rozar..

Trees of *Pinus echinata* were the oldest (43 years), tallest (19 m), and nearly the largest in diameter (32 cm). A tree of *Quercus falcata* was larger at 35 cm in dbh. A relatively large tree of *Liquidambar styraciflua* was 29 years old.

A faint trace of charred bark on a few trees revealed evidence of fire but not in recent years. There was no sign of logging, and the stand seems to have grown without significant disturbance, including fire. A resident said that the general region was in pasture before the woods developed.

Trees of at least 10 cm in dbh and all smaller trees (saplings) were inventoried in two quadrats totaling 880 m^2:

	TREES		SAPLINGS	
	Relative Basal Area	Relative Density	Relative Basal Area	Relative Density
Pinus echinata	58	43	4	2
Quercus falcata	14	11	5	3
Liquidambar styraciflua	13	19	16	14
Quercus nigra	9	19	29	34
Cornus florida	3	5	2	1
Carya tomentosa	1	1	4	8
Quercus stellata	1	1	6	3
Quercus virginiana	1	1	0	0
Prunus serotina	0	0	9	10
Quercus hemisphaerica	0	0	9	7
Malus angustifolius	0	0	6	7
Vaccinium arboreum	0	0	4	6
Nyssa sylvatica	0	0	1	1
Ilex vomitoria	0	0	1	1
Diospyros virginiana	0	0	1	1
Aralia spinosa	0	0	1	1
Crataegus sp.	0	0	1	1
Myrica cerifera	0	0	1	1
Basal Area (m^2/ha)	25.7		3.4	
Trees/ha		739		1659

Quercus velutina was rather common in the more mature woods of the area but was not recorded in the quadrats. *Magnolia grandiflora* was rare, even as saplings. *Quercus alba* was rare and *Fagus grandifolia* absent.

RESEARCH SUMMARY 55, continued.

Shrubs, vines, and herbs were scarce, and the sandy loam soil was covered with leaf litter. Species seen were Mitchella repens, Bignonia capreolata, Callicarpa americana, Gelsemium sempervirens, Vitis rotundifolia, Smilax bona-nox, S. glauca, S. pumila, S. walteri.

RESEARCH SUMMARY 56. GOODWOOD PLANTATION

34. Pine-Oak Woods

unpublished data of A. F. Clewell

The woods lies within the eastern city limits of Tallahassee along the north side of Miccosukee Road at the junction of Marys Drive. The stand was inventoried in November, 1967 by A. F. Clewell and D. Wise.

The site was a former agricultural field, and furrows were still visible. There was no sign of fire, logging, or other disturbance. A pine overstory was 21-23 m tall with about 75% canopy closure. The trees ranged from 13 to 46 cm in dbh. They were inventoried in quadrats totaling 2850 m^2. There were 274 trees/ha with a collective basal area of 19.9 m^2/ha.

A hardwood understory was up to 14-18 m tall. Trees of at least 2.5 (max. 21) cm in dbh were inventoried in quadrats totaling 458 m^2. There were 964 trees/ha with a collective basal area of 8.3 m^2/ha. The trees in the stand were distributed as follows:

	Relative Basal Area	Relative Density
OVERSTORY		
Pinus taeda	65	55
Pinus echinata	30	40
Pinus elliottii	3	3
Liquidambar styraciflua	1	1
Prunus serotina	1	1
	100	100
UNDERSTORY		
Liquidambar styraciflua	70	73
Prunus serotina	12	12
Cinnamomum camphora	8	4
Quercus hemisphaerica	7	4
Quercus nigra	3	7
	100	100

Increment borings revealed that 6 trees of *Pinus taeda* (30-45 cm in dbh) were 29-33 years old and that 2 trees of *Liquidambar styraciflua* (19, 22 cm) were 26 and 24 years old. The overstory pines were beginning to die out and were not being replaced by seedlings.

RESEARCH SUMMARY 56, continued.

Smaller saplings included:

Carya tomentosa
Cornus florida
Magnolia grandiflora
Myrica cerifera
Quercus falcata
Sassafras albidum
Asplenium platyneuron
Campsis radicans
Gelsemium sempervirens
Rhus toxicodendron
Smilax bona-nox
Vitis rotundifolia

Exotics which had escaped from cultivation were:

Cinnamomum camphora
Ardisia crenata
Wisteria sinensis

An old fence row was well marked by a row of several huge live oaks (*Quercus virginiana*). The top soil in the former field was 34 cm deep. In the fence row, the top soil was 100 cm deep.

RESEARCH SUMMARY 57. MILLPOND PLANTATION

34. Pine-Oak Woods

Blaisdell, R. S., J. W. Wooten, and R. K. Godfrey. 1974. The role of magnolia and beech in forest processes in the Tallahassee, Florida, Thomasville, Georgia area. Proc. Ann. Tall Timbers Fire Ecol. Confr. 13: 363-397.

Millpond Plantation lies on the southeastern edge of Thomasville, Thomas County, Georgia. Two stands were studied:

1) A loblolly pine stand which developed on a former field 100 years ago. This stand was burned regularly until 50 years ago and has been fire-free since then.

2) A longleaf pine stand on land never cultivated. The stand has been fire-free for 60 years.

The overstories are as follows:

	Relative Basal Area	Relative Density
LOBLOLLY PINE STAND		
Pinus taeda	77	60
Liquidambar styraciflua	9	17
Quercus hemisphaerica	5	8
Quercus nigra	5	7
Cornus florida	1	4
Carya glabra	1	3
Magnolia grandiflora	1	1
Quercus flacata	1	1
	100	101
LONGLEAF PINE STAND		
Pinus palustris	36	13
Liquidambar styraciflua	16	13
Pinus taeda	13	5
Oxydendrum arboreum	11	13
Magnolia grandiflora	7	23
Quercus alba	5	8
Quercus prinus	4	8
Quercus nigra	3	5
Quercus velutina	3	5
Cornus florida	1	5
Ilex opaca	1	3
Fagus grandifolia	1	3
	101	104

RESEARCH SUMMARY 57, continued.

Other woody species in the longleaf pine stand were:

Acer rubrum
Aralia spinosa
Callicarpa americana
Carya sp.
Cinnamomum camphora
Crataegus uniflora
Myrica cerifera
Osmanthus americana
Prunus caroliniana
Quercus hemisphaerica
Quercus stellata
Rhus copallina
Sassafras albidum
Symplocos tinctoria

RESEARCH SUMMARY 58. LIVE OAK HAMMOCK ALONG THE WAKULLA RIVER

34. Pine-Oak Woods

Unpublished data of A. F. Clewell

The site occupied the mesic slope bordering the river swamp along the west side of the Wakulla River, Wakulla County, just south of the "upper bridge", of S.R. 365 (n.e. section 2, T3S, R1W). Inventoried in 1977 by A. F. Clewell and M. N. Benavides.

All trees of at least 10 cm in dbh were sampled in a quadrat of 0.2 ha. There were 265 trees/ha with a collective basal area of 49.3 m^2/ha, distributed as follows:

	Relative Basal Area	Relative Density
Quercus virginiana	73	36
Quercus nigra	12	6
Pinus taeda	6	11
Quercus hemisphaerica	4	11
Liquidambar styraciflua	2	21
Pinus glabra	2	2
Nyssa sylvatica	1	4
Ilex opaca	-	7
Vaccinium arboreum	-	2
	100	100

The overstory was up to 26 m tall. Species not falling in the quadrat were Quercus prinus, Magnolia grandiflora, Carya glabra, Ostrya virginiana. Trees of Quercus virginiana reached 90 cm in dbh and had tall trunks with relatively narrow crowns.

The understory was dominated by Ilex opaca and Vaccinium stamineum. Lyonia fruticosa was common, some rather large. Incidental species were Fagus grandifolia, Hamamelisvirginiana, Ilex vomitoria, Myrica cerifera, Prunus caroliniana, Quercus stellata, Vaccinium arboreum, and V. aff. elliottii.

The undergrowth was characterized by Serenoa repens in dense patches. Other species were Bignonia capreolata, Callicarpa americana, Gelsemium sempervirens, Pteridium aquilinum, Smilax bona-nox, and Vitis rotundifolia. Epiphytes were Epidendrum conopseum and Tillandsia usneoides.

Adjacent to the site to the south was a hammock containing large trees mainly of Quercus hemisphaerica. Others were Q. nigra, Magnolia grandiflora, Nyssa sylvatica, Carya glabra, and Pinus glabra. The undergrowth was dense with Serenoa repens.

Ever farther south, the hammock consisted of Fagus grandifolia, Magnolia grandiflora, Quercus hemisphaerica, Q. alba, and scattered Cornus florida and Sabal palmetto. Serenoa repens grew in scattered patches.

The live oak hammock is listed as site 8 Wa 17 by the Florida Division of Archives, History, and Records Management. The site contains square nails, historical ceramics, pot sherds, and flint.

The site contains several evidences of occupation and former disturbance:

1. The square nails and ceramics suggest construction and occupation.

2. The site is bordered on the south and east sides by dense and extensive growths of saw-palmetto which end abruptly in straight lines. They appear to mark the extent of a former clearing.

3. A long low mound of earth which contains a bend at right angles is not natural and may have been associated with the foundation of a structure.

4. Top soil is absent, suggesting tillage or sheet erosion from a cleared area. Leaf litter and duff directly overlie white sand, peppered with organic matter.

5. Absence of mounds of soil which form as the soil clinging to the roots of wind-thrown trees accumulates. These mounds are common in the beech-magnolia-white oak-laurel oak hammock. Tillage would have eliminated any at the live oak hammock site.

6. Live oaks and the other common trees are all known to invade disturbed and abandoned sites.

7. The number of species is low, suggesting sterile soil and/or the elimination of species with disturbance.

8. The adjacent hammock of laurel oak suggests the harvest of beech and magnolia (fire wood?) and their replacement by laurel oak, which is an invader of open lands.

The evidence suggests a dwelling and large garden or pasture which were abandoned in the mid-19th century. The occupants may have run a ferry across the river.

Upon abandonment, there were no further disturbances. Fires, if any, have not affected the vegetation. The live oaks invaded, forming a dense forest. Because of the density of this young stand, the now-mature trees have tall trunks and restricted crowns.

RESEARCH SUMMARY 59. POPEVILLE TURPENTINE CAMP

34. Pine-Oak Woods

Unpublished data by A. F. Clewell

The site lies on the south side of S. R. 267, 3.5 miles east of junction S. R. 20 in the Apalachicola National Forest near Bloxham, Leon County (n.w. section 19, T1S, R3W). The site was inventoried in 1976.

The site is surrounded by pine flatwoods. Persistent pine stumps within the site are evidence that the site was once pine flatwoods. A local resident said that the site was a turpentine camp, called Popeville, which operated from about 1908 to 1918. Laborers grew vegetables in garden patches at the site. The entire region was clear-cut in the late 1920's. The oldest of 3 larger pines that were cored dated to 1931. Charred bark was evidence of subsequent fire, but heavy leaf litter showed that fires have been infrequent. The overstory and understory were inventoried in a quadrat of 1.6 ha.

The overstory, defined as trees at least 16 cm in dbh, was up to 24 m tall, and diameters ranged up to 39 cm. Pines were the largest trees. There were 231 trees/ha with a collective basal area of 16.8 m^2/ha.

The understory consisted of all trees and shrubs less than 16 cm in dbh and more than 1.5 m tall. There were 1113 trees and shrubs per ha in the understory.

	OVERSTORY		UNDERSTORY
	Relative Basal Area	Relative Density	Relative Density
Pinus elliottii	57	70	20
Pinus taeda	24	19	0
Pinus palustris	10	5	0
Quercus nigra	8	3	42
Quercus virginiana	1	3	5
Ilex glabra	0	0	10
Myrica cerifera	0	0	8
10 species	0	0	15

The 10 understory species were:

Cornus florida
Diospyros virginiana
Ilex opaca
Lyonia lucida
Magnolia virginica
Nyssa sylvatica
Quercus hemisphaerica
Rhus copallina
Vaccinium arboreum
Vaccinium stamineum

Gelsemium sempervirens exceeded 50% cover in the ground cover and was by far the most important species. Smilax glauca was commonly intermixed. Aristida stricta was scarcely present with a density of 19 plants per ha. There was a small patch of Serenoa repens and Quercus pumila. Notably absent was Vaccinium myrsinites. Plants representing species of Andropogon, Eupatorium, Dichanthelium, Pteridium, and Rubus were rare.

RESEARCH SUMMARY 60. BIRDSONG PASTURE

35. Pasture Assemblages

Unpublished data of A. F. Clewell

Birdsong Plantation is in Grady County, Georgia, near the Florida line north of Tallahassee. The inventory was made in 1974 by A. Clewell, R. Komarek, and the owner, E. V. Komarek.

The site was formerly a pine-oak-hickory woods primarily, with some long-leaf pine savannah and mesic hardwood hammock. The site was cleared in 1970 and planted with Paspalum notatum. This grass responded to lime and fertilizer and soon assumed a cover in excess of 90%. The pasture was grazed by cattle until 1966. Thereafter, cattle were permanently removed, and the pasture was annually winter-burned.

Within two years after release from grazing, Andropogon virginicus and A. ternarius, once scarce, became abundant. Subsequently, other native grasses invaded, sometimes in large, nearly pure patches. Paspalum notatum suffered a considerable reduction as these native grasses invaded.

The frequency of herbs and low shrubs (only Rubus cuneifolius) was determined by line interception in 100, meter-long segments. The number of segments in which plants of each species were intercepted were as follows; grasses are identified by an asterisk (*):

Andropogon virginicus*	86	Eupatorium hyssopifolium	4
Paspalum notatum*	66	Panicum anceps*	3
Rubus cuneifolius	55	Paspalum setacium*	3
Andropogon ternarius*	35	Sorghastrum nutans*	3
Eragrostis spectabilis*	33	Solidago canadensis	3
Aristida purpurascens*	20	Galium pilosum	3
Sporobolis indicus*	13	Tridens carolinianus*	2
Aster dumosus	13	Ruellia caroliniana	2
Galactia macreei	13	Digitaria villosa*	1
Elephantopus elatus	12	Verbesina aristata	1
Andropogon elliottii*	11	Hieracium gronovii	1
Desmodium obtusum	10	Lechea minor	1
Paspalum consanguinium*	4	Desmodium laevigatum	1
Schizachyrium tenerum*	4		

Other grasses present that were not intercepted were:

Andropogon gerardii
Andropogon aff. scoparius
Paspalum aff. difforme
Setaria geniculata

RESEARCH SUMMARY 61. MOORE LAKE PINE PLANTATION

36. Pine Plantations

Unpublished data of A. F. Clewell

The site lies slightly east of Forest Road 358A near Moore Lake in the Apalachicola National Forest, Leon County (n.w. section 23, T1S, R2W). The inventory was made in 1974 by W. Kenyon and B. Sabine.

The site was formerly a longleaf pine-xeric oak woods, which was the only native upland vegetation throughout the sandhills of the area. A field of 1.2 ha was cleared early in this century and was cultivated probably into the 1930's. The district forester said that the site was planted to Pinus elliottii without benefit of mechancial site preparation in 1943, thinned about 1961, and burned in 1970 and perhaps earlier as well.

The overstory consisted solely of planted pines. There were 506 pines per ha with a collective basal area of 19 m^2, as determined in a quadrat of 0.1 ha.

The understory was defined as all trees and shrubs under 11.5 cm in dbh and was inventoried in the same quadrat. There were 208 plants per ha with the following relative densities:

Pinus elliottii	58
Diospyros virginiana	16
Quercus virginiana	13
Rhus copallina	9
Vaccinium arboreum	2
Cornus florida	1
Quercus incana	1
	100

The density of plants/m^2 comprising the ground cover was determined in 20, 0.8 m^2 quadrats:

Pityopsis graminifolia	8
Licania michauxii	4
Vaccinium myrsinites	1
Dichanthelium aciculare	1
Andropogon sp.	-
Eupatorium compositifolium	-
Quercus minima	-
Quercus pumila	-
Rubus cuneifolius	-
Tragia urens	-

A dash (-) signifies a density less than 0.5/m^2.

RESEARCH SUMMARY 62. DOG LAKE PINE PLANTATION

36. Pine Plantations

Unpublished data by A. F. Clewell

The site lies at the n.e. corner of the junction of Forest Roads 358 and 358A near Dog Lake in the Apalachicola National Forest, Leon County (s.w. section 23, T1S, R2W).

The site was formerly a longleaf pine-xeric oak woods, which was the only native upland vegetation in the sandhills of this area. Fields were cleared early in this century and cultivated probably into the 1930's. The district forester said that Pinus elliottii was planted on the fallow field about 1956 without benefit of mechanical site preparation. The stand was thinned, but never burned. There was no understory and only a few, widely scattered herbaceous plants.

The pines were 16-19 m tall and mostly 13-27 cm in dbh. There were 1009 trees per ha and 400 stumps per ha (from thinning), as determined in a quadrat 1150 m^2 in 1976.

The density per m^2 of the only herbaceous species was determined in 30, m^2 quadrats:

Dichanthelium aff. aciculare	1.4
Andropogon aff. virginicus	0.3
Eupatorium compositifolium	0.3
Cassia fasciculata	0.1

A former fence-row bordered the plantation and at one point nearly bisected it. It was about 2 meters wide and contained mostly small trees of Quercus laevis. There were scattered plants of Q. incana, Q. margaretta, Q. pumila, Pteridium aquilinum, and where light was sufficient and the leaf litter not too deep, Aristida stricta. These plants did not occur in the adjacent former field, nor were they spreading by vegetative means from the fence-row into the former field. The margins of the fence-row were sharply defined by this native vegetation which apparently had persisted since before the time of cultivation.

RESEARCH SUMMARY 63. BRADFORD COUNTY PINE PLANTATIONS

36. Pine Plantations

Skoog, P. J. 1980. Utilization of pine plantations by white-tailed deer in north Florida. Thesis, Univ, Fla. 65 p.

Vicinity of Sampson Lake along S.R. 100, Bradford County. Commercial forests were machine-planted to seedling slash pines following site preparation which consisted of clear-cutting the natural second-growth flatwoods, ditching, chopping, burning, bedding. Fertilizer (P, N) was applied to a few stands up to 5 years old. Prescribed burning at invervals of at least 3 years was common in stands over 12 years old.

Average dry weights of the undergrowth were greatest at a stand age of 10 years (3014 kg/ha). The following data are the number of clip-plots (out of 10 in each age-group) in which a species attained a cover of at least 10%.

AGE GROUP (YEARS):	0-2	3-5	5-10	10-15	35
Eleocharis spp.	4				
Scleria sp.	1				
Xyris ambigua	1				
Hypericum spp.	1				
Aristida spiciformis	1				
Rhynchospora spp.	5	1			
Panicum, Dichanthelium spp.	5	4			
Andropogon capillipes	1	8	6		
Ilex glabra	6	5	7	7	7
Aristida stricta	1		2		1
Vaccinium myrsinites	1		2	2	
Serenoa repens	1		2	5	2
Andropogon virginicus		3			
Hypericum brachyphyllum		1			
Sorghastrum secundum		1			
Vaccinium arboreum			1	2	
Myrica cerifera			1		1
Gelsemium sempervirens				2	
Rubus spp.				1	
Lyonia lucida				2	2
Gordonia lasianthus				1	1
Ilex myrtifolia					1
Gaylussacia spp.					1
Nyssa biflora					1
Woodwardia virginica					1
Ilex cassine					1
Aronia arbutifolia					1

END

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