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Natural History and Phytogeography of the Loess Hills and Ravines, Lower Mississippi Embayment.

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NATURAL HISTORY AND PHYTOGEOGRAPHY OF THE LOESS HILLS AND RAVINES, LOWER MISSISSIPPI EMBAYMENT

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TABLE OF CONTENTS

VOLUME I

ACKNOWLEDGEMENTS ii

LIST OF FIGURES ix

ABSTRACT x

CHAPTER 1. INTRODUCTION: THE OVERLOOKED FORESTS 1
Purpose of the Study 7
Importance of the Study 8
Background Research 11

CHAPTER 2. METHODS AND FIELD PROCEDURE 21
Successional Characteristics of the Sampled Stands 25
Study Sites 28
Field Procedure 67
Stratification 69
Sampling Procedure and Plant Identification 74

CHAPTER 3. NATURAL SETTING 76
Physiography and the "Loess factor" 76
Loess as an Ecological Factor 92
Climate 98
Brief Summary and Conclusions 102

CHAPTER 4. THE ORIGINS AND PRE-ANTROPOGENIC EVOLUTION OF THE MIXED DECIDUOUS-EVERGREEN BEECH-MAGNOLIA FORESTS 104
Mesic Hardwood Forests in the Tertiary Period 104
The Pleistocene Cooling 113
The Pleistocene Refugium of the Temperate Forest 115
Forest Dynamics in the Early to Middle Holocene 122
The Questions of Endemism and Biodiversity 126

CHAPTER 5. THE HISTORY OF NATIVE SUBSISTENCE 132
Pre-Mississippian Time 133
Development of the Mississippian Pattern 149
Subsistence of the Early Historic Amerindians 160
Extent of Native Clearance 161
Techniques of Forest Clearance 168
Native Agroecosystems 175
Fire Management 179
Native Agroforestry 186
Implications for a Biogeographer 199
The Floristic "Irregularities" in the Modern Stands 202

CHAPTER 6. THE HISTORY OF THE EUROPEAN COLONIZATION, AGRICULTURAL DEVELOPMENT AND INDUSTRIAL LOGGING 208
The Early Historic Period of Colonization 208

The Ante-Bellum Period....216
The Civil War and the Post-Bellum Period....229
The Second Decline of the Cotton Agriculture....233
The Period of Industrial Timbering....235
The Post-Modern Period of Landscape Modification....241
Animal Husbandry and Its Influence on the Forest....249
Brief Summary and Conclusions....255

CHAPTER 7. THE STATE OF THE ORIGINAL AND MODERN FORESTS....257
Early Historic Accounts of the Original Forests....262
Species Composition of the Original Forests....265
The Concept of the Southern Mixed Hardwood Forest....269

CHAPTER 8. THE LATITUDINAL VARIATION IN THE CANOPY STRATUM....273
Patterns of Biogeographic Diversity and Heterogeneity....274
Latitudinal Variation among the Subtropical and Warm-Temperate Canopy Taxa....287
Forests of the Southern Fringe of the Loess Hills....293
Biogeographic Variation among the Cold-Resistant Temperate Deciduous Taxa....297
The Southern Limit of the Beech-Magnolia Forest and Beyond....303
Brief Summary and Conclusions....308

CHAPTER 9. THE GENERAL STRUCTURAL CHARACTERISTICS OF THE MATURE HARDWOOD FORESTS....315
The Role of the Light-Dependent Canopy Species....330
Brief Summary and Conclusions....344

VOLUME II

CHAPTER 10. THE VARIATION OF THE CANOPY ASSORTMENTS IN ACCORDANCE WITH PHYSIOGRAPHY, EDAPHIC CONDITIONS AND DISTURBANCE REGIMES....347
The Moist-Mesic to Mesic Forests of the Mississippi Bluff and Chicot Lake Area....353
Transition from the Deep-Loess Section to the Shallow and Thin-Loess Sections....397
Forest Types and Indicator Species as Determined by the Thinning of the Loess Mantle....405
The Dynamics of Potentially Dominant Species of the Shallow and Thin-Loess Sections....420
The Shallow-Loess Moist-Mesic Hardwood Forests on Terrace and Valley-Train Foundations....437
Brief Summary and Conclusions....440

CHAPTER 11. BIOGEOGRAPHIC VARIATION IN THE MIDSTORY STRATUM 446
Midstory Specialists 447
The Latitudinal Variation 463
Midstory Composition and Structure of the Moist-Mesic to Mesic Closed-Canopy Forests 476
Midstory Composition and Structure of the Physiographically-Disturbed Moist-Mesic Forests 487
The Biogeographic Transition with the Tninning of the Loess Mantle 500
The Shallow-Loess Midstory Assemblages 504
The Diversity Trends 510
Summary and Conclusions 515

CHAPTER 12. BIOGEOGRAPHIC VARIATION IN THE UNDERSTORY STRATUM 521
Latitudinal Variation of the Understory Specialists 525
Edaphic Preferences of the Understory Specialists 539
Light Preferences and Population Densities of the Understory Specialists 546
Species Diversity in the Understory Stratum 553
Brief Summary and Conclusions 555

CHAPTER 13. CONCLUSIONS 557
The Global Biogeographic Status of the Hardwood Forests of the Loess Hills 580

REFERENCES 596

APPENDIX A. LIST OF SPECIES AND FAMILIES REGISTERED IN SAMPLING SITES 621

APPENDIX B. LIST OF SPECIES WITH INDICATION OF THE SITES IN WHICH THEY WERE ENCOUNTERED 627

APPENDIX C. MAPS OF THE SAMPLING AREAS 637
Figure 5. The Steep Bluffs Area, Warren County, Mississippi 638
Figure 6. The Bluff Experimental Forest, Warren County, Mississippi 639
Figure 7. Magnolia Glen Preserve (the Tunica Hills Area), West Feliciana Parish, Louisiana 640
Figure 8. Audubon Memorial State Park (Oakley Plantation), West Feliciana, Parish Louisiana 641
Figure 9. Port Hudson Area, East Baton Rouge Parish, Louisiana 642
Figure 10. Burden Plantation, East Baton Rouge Parish, Louisiana 643
Figure 11. Forked Island Area, Vermillion Parish, Louisiana 644

Figure 12. Chicot State Park, Evangeline Parish, Louisiana 645
Figure 13. Louisiana State Arboretum, Evangeline Parish, Louisiana 646
Figure 14. Sicily Island Area, Catahoula Parish, Louisiana 647
Figure 15. Poverty Point Area, West Carroll Parish, Louisiana 648
Figure 16. Clear Springs Area, Homochito National Forest, Franklin County, Mississippi 649

VITA 650

LIST OF FIGURES

Figure		Page
1	Study Site Locations	23
2	The Physiographic and Edaphic Conditions of the Southern Loess Hills	80
3	The Forest Types of the Southern loess Hills as Determined by Latitude	289
4	The Forest Types of the Southern Loess Hills as Determined by the Physiographic and Edaphic Conditions	349

ABSTRACT

Although located near the middle of the Southeastern Coastal Plain, the hardwood forests of the Loess Hills of the Lower Mississippi Embayment have never been thoroughly studied or satisfactorily described in the literature.

This dissertation is a case study of the biogeographic variation in the species composition and structure of the mature ravine hardwood forests within the southern section of the Loess Hills, from Warren County, Mississippi, south to East Baton Rouge and Vermilion Parishes, Louisiana, as affected by latitude, physiography, edaphic conditions, and disturbance. A parallel goal is, on the basis of the current biogeographic conditions and successional dynamics, to make a reconstructive assessment of the original forests. The empirical findings of the study suggest that the effects imposed on the vegetation by the combined action of the different biogeographic factors are intricately interrelated, resulting in the complex, synergistic effect.

A very strong impact on the species composition, structure, and even the biogeographic variation is caused by the anthropogenic disturbance. During the Holocene, the forests of the Loess Hills evolved in the conditions of the persistent and growing anthropogenic pressure. This trend culminated during the 19th and 20th centuries when the

agricultural exploitation and industrial timbering. The anthropogenic disturbance appears to have influenced selectively different groups of species depending on latitude and depth of the loess mantle. It also seems to have caused an expansion of the understory and subcanopy species which may have played a lesser role in the original forests.

This study may contribute to the better understanding of the biogeographic variaton and successional dynamics of the the Coastal Plain forests in general and the Loess Hills forests in particular, as well as to the conservation and restoration of the latter.

CHAPTER 1

INTRODUCTION: THE OVERLOOKED FORESTS

This dissertation is a product of nearly seven years of travelling throughout the southern section of the Loess Hills belt and sampling the loessial forest. I became interested in these forests in 1992 – the year I came to Louisiana State University with the intention of studying the biogeography of the South American rainforests. Yet it was during a field trip in November of 1993 led by William Platt into the heart of Magnolia-Glen preserve, one of the last surviving pieces of the Tunica Hills' old growth, that the impressive beauty of the loessial forests captivated my attention.

I was surprised by the diversity and curious mixture of the southern and northern forms. Evergreen magnolias were towering in the splendid beauty of their shining xerophyllous foliage alongside a great variety of cool-temperate trees entangled by lianas and vines with southern and even tropical affinities. In the subcanopy, the elegant evergreen shrubs and small trees of subtropical and warm-temperate distributions such as Carolina laurel cherry, sweetleaf and American holly, shared the living space with their cold-adapted counterparts that are found as far north as the Saint-Lawrence Valley and Nova Scotia. The ubiquitous presence of yaupon (*Ilex vomitoria*), the sacred evergreen shrub of the Southeastern Indians, suggested the

strong maritime influence of the Gulf of Mexico. Abundance of spicebush in narrow ravine bottoms reminded me of the cool, swampy hardwoods of the northern Midwest. The steep ravine slopes beautified with fragrant groves of *Hydrangea quercifolia* gave the feeling of the Appalachian coves and gorges.

On the forest floor the tropical ferns of Caribbean descent prospered in a perfect harmony with their temperate relative, Christmas fern, and delicate mesophytic plants from the Appalachian forests. In some areas where the presence of the evergreen species was especially pronounced and where the subcanopy was abundantly decorated with elegant festoons of various vines and climbers of which many were equipped with the beard-like clumps of aerial roots, this rich assemblage had the look and feel of a subtropical forest. In other places where American beech reigned unchallenged and southern trees were only occasionally sprinkled among its ghostly-gray trunks, the forest matched the general look and feeling of the generically similar old-growth stands of southern Michigan and Adirondack. It was then and there that I decided to forego South America, and to study the Loess Hills. Since that fall day these forests became my focus for the next seven years.

Initially I was interested in studying large-scale latitudinal dynamics. The Mississippi Blufflands extend for

more than 500 miles from southern Louisiana to the southern tip of Illinois. They provide an excellent latitudinal transect which does not seem to be obscured by any essential changes in the edaphic conditions, soils, topography and underlying geology. No other comparable north-south transect can be found in the eastern United States. Soon, however, a bigger and more challenging research agenda began to emerge. The forests of the Loess Hills have never been thoroughly studied or satisfactorily described in the literature. Although located near the middle of the Gulf Coastal Plain, they have been routinely ignored or overlooked by most ecologists. The vast majority of the studies on the Coastal Plain hardwoods have been done in the relatively small hammocks of northern Florida, southwestern Georgia and southeastern Alabama, with the remainder being divided between eastern Texas and the Carolinas. Subsequently, nearly all generalizations about the structure and the species composition of the Coastal Plain forests were based on the results obtained from the forests developed on non-loessial surfaces.

There are several possible reasons for which the loessial forests became marginal to the mainstream research of the Coastal Plain hardwood forest ecology. Poor recognition of the Loess Region as a distinct biogeographic unit in part may have been caused by a set of subjective ideas about the geography of this portion of the American

South. The Lower Mississippi River Region is frequently visualized by outsiders, whether academics or laymen, as a domain of extensive alluvial landscapes. For those unaware of the striking relief contrasts of this region, the perception of the loessial forests well may be blurred by the more conventional images of the Mississippi Valley's bottomland forests. It appears that in the "mindscapes" of quite a few outside ecologists, the upland forests of the loessial hills flanking the Lower Mississippi Valley have existed in the "shadow" of the largest North American tract of the bottomland forest.

Of no less importance have been certain persistent biogeographic generalizations and misinterpretations. The notion of floristic affinity between the southern Blufflands and the Appalachian forests appears often in the literature, supported by extensive lists of the delicate herbacious mesophytes of Appalachian origins found in the Tunica Hills and other areas along the Loess Bluff (Braun, 1950; Brown, 1938; 1954; Brown and Correll, 1942/no; Kral, 1966; Delcourt, 1974; Delcourt and Delcourt, 1974). Braun (1950) who promoted the idea of antiquity of the Mixed Mesophytic Forest, placed the middle and northern section of the Blufflands into the Western Mesophytic Forest Region and identified the Loess Hills forests south of Vicksburg as "... a mixed mesophytic community modified chiefly by the presence of evergreen magnolia as one of the

dominants." It seems to contribute to the development of the general perception of these southern loessial forests as a mere extension of the Mixed Mesophytic Forest Region of the Appalachian region. These ideas became so deeply rooted that even the Delcourts (1974) (who made an attempt to reconstruct the species composition of the forests that developed in the southern end of the Loess Bluff and ended up with the association quite different from the south-Appalachian forests) still referred to it as "mixed mesophytic".

Political subdivision of the Loess Region may also have played a role. Separated by several state lines, the forests of the Loess Hills were subject of only few localized studies. Almost every state along the Loess Bluff tended to consider its own section of the loess belt as a unique region of its own — Tunica Hills in Louisiana, Mississippi Loess Hills in Mississippi, Cane Hills in Kentucky. Although the environmental similarity of the loessial lands was generally recognized by some naturalists such as Loughridge (1888) going back to the second half of the 19th century, it has not led to the development of a geographically holistic exploratory approach. Repeatedly I've been surprised by ecologists from one state not knowing about research, past or present, on loessial lands in adjacent states.

Southern ecology's close connections to commercial forestry and the timber industry have also retarded research on the loessial forests. The timber industry in Mississippi and especially Louisiana has done little to support research on identifying the vegetation zonation of the lands from which it profited. The same can be said for the fields of forestry and applied ecology. In Louisiana's case, the forest industry was particularly slow. Not until the 1930s, as a result of the Louisiana forest survey, did the state's foresters come to realize how much area was in hardwood forest. Moreover, the existence of the Loess Hills hardwoods was not acknowledged until then. Ironically, the laggardly pace in surveying these areas may account for why they are still there to be studied. Those few tracts of the late-successional forests that became subject of the present research have survived just because of the relatively late expansion of the timber industry into the loessial hardwood belt.

For the reasons mentioned, the call for the survey of the Loess Hills forests was never strong and loud. Located on the margins of all officially recognized forest regions of Eastern North America, in the land "in between", the Loess Hills forests turned out to be one of the very few and certainly the largest under-explored forest regions in eastern North America.

Purpose of the Study

This research project deals with the southern section of the Loess Region extending roughly from Vicksburg, Mississippi to Baton Rouge, Louisiana. It includes areas within two states: the southwestern portion of Mississippi and northeastern, mid-eastern, and southern sections of Louisiana. In this research project, I will examine the species composition and floral structure of the mature hardwood forests in the southern section of the Loess Hills in their biogeographic variation from the north to the south, from the deep-loess to the shallow-loess mantles, from the less-disturbed to the more disturbed community types.

The study has a dual research objective. The immediate goal is to explore variation patterns in the overstory, midstory, and understory of the present-day mature forests and work out the biogeographic zonation of the southern portion of the Loess Hills based on the distinct forest types. A parallel goal is, on the basis of the current successional dynamics, to make a reconstructive assessment of the original, early-historical forests. The project is strongly centered on the late-successional forests. In this work I apply the term "late-successional" to both the old-growth forests which were never subject to clearance and the second-growth forests at the advanced stages of the natural succession. The remnants of the old-growth forests

were, of course, the most desirable object of study. Such stands are likely to be the closest analogues of the original, prehistoric and early-historical forests. Unfortunately, the surviving old-growth patches are very few: a large-scale biogeographic study of the Loess Hills would be impossible with reliance only on this forest type. Because of this, the older secondary-growth forests with regenerated beech-magnolia overstory were also included in the survey.

The relatively young early-successional forests were likewise surveyed. But the space constraints do not allow me to discuss at length here their species composition, structure and variation patterns. However, the data from my early-successional sites will be used to fill gaps in my transect or for the analysis of successional patterns.

Importance of the Study

Several circumstances of the study of the Loess Hills forests are important. To begin with, these forests are biogeographically unique. One of the challenging aspects of the compositional profile of the loessial forests is that they do not fit readily into any major type recognized in Eastern North America. Moreover, it appears that the southern section of the Blufflands once had been a homeland for one of the most diverse (if not the richest) forest ecosystems in North America north of Mexico. My recent data from the old-growth forest in the highly dissected region

of Tunica Hills, southern Louisiana, for example, potentially suggests the highest biodiversity in the continental United States. Within 1 ha area of local ravines as many as 44 species of trees were found in the overstory and midstory alone, excluding the understory which is particularly species-rich. This is considerably more than the total number of trees which are likely to occur in areas of about one hectare in the forests of northern Florida which were suggested to contain the largest numbers of species of trees and shrubs per unite area in the continental United States. Platt (1985) refers to approximately 25-35 tree species per hectare in these northern Florida assemblages. To find comparably high indices of tree species diversity one has to move south into the neotropics.

Apart from the exceptionally high diversity, the historical Loess Hills forests are characterized by the extreme biogeographic heterogeneity with their striking mixture of northern and southern forms. The warm-loving evergreen taxa whose ranges are largely limited to the lower subtropical latitudes coexist here with a large assortment of the distinctively interior cool-adapted species many of which may well be relics of the Pleistocene glacial epoch.

Both the exceptionally high diversity and mixed heterogeneous nature of the Loess Hills hardwoods appear to

be related to the fact that the southern section of the Mississippi Blufflands have been the largest refugium area for the Eastern North American broadleaf flora during the Pleistocene glacial epoch. Much of the present-day hardwood forests of the eastern United States originated as a result spread of the mesic broadleaf tree flora, with associated floras of shrubs and herbs, from this refuge during the Holocene. Due to the relative antiquity and southern location of this portion of the North American land mass, the survived remnants of the Loess Hills forests are likely to date well into the Tertiary times (at least, into Pliocene-Miocene) and may represent true relict forests.

Never before has the need for practical results in biogeography and conservation geography been more urgent than it is now. The Loess Hills hardwoods one of the most threatened forest ecosystems in North America. Unfortunately, most of the original forests in the region were cut well before any systematic investigation of their species composition and floral structure could have even taken place. Today the last surviving tracts of the relatively mature forest are quickly disappearing under the ongoing industrial assault. The Nature Conservancy, state heritage programs and other conservationist organizations are unable to keep pace or compete financially with the powerful timber companies making profit out of the natural resources of the Bluffland belt. The next decade may well

be the last timespan during which we would be able to locate, study and possibly save some of the surviving pieces of the mature growth for the future generations.

Background Research

Surprisingly, no comprehensive large-scale biogeographic exploration of the Lower Mississippi River bluff forests has been ever done. Braun (1950:301), in her voluminous and otherwise very detailed book on the Eastern North American Deciduous Forests devoted only one page to the description of the Mississippi River bluff hardwoods and put this description in the extremely general terms, indicating that "... the forest changes somewhat from north to south, as more southern species enter, and more northern species drop out." She provided the data only for one site of the bluff forest located on ravine slopes cut in Montgomery Terrace north of Baton Rouge, southern Louisiana, accompanied with no information either about the size of the areas sampled or about the methods of the sampling. Given the relatively small number of species mentioned in her tables, particularly understory ones (14 species were reported from the first site and only 9 species - from the second), one can suggest that the sampled areas were too small and the ratio of the species was therefore somewhat non-representative. Since the more northern sites apparently were not even sampled, it is not surprising

that the lack of the data led Braun to classify the forests of the middle and northern section of the Blufflands as a part of the Western Mesophytic Forest Region, thus ignoring the presence of the Gulf-Atlantic taxa in their structure.

More recent studies of the Lower Mississippi River forests tend to be highly localized with a little, if any, coordination between the researchers and institutions in the different states. Apart from Braun's work, results of only few of these studies were published. Most of the existing publications known to the author are based on the surveys of the individual bluff sites in the state of Mississippi (McCook 1982, Johnson and Little 1985, Morris 1988). These were not preoccupied with distinguishing specifically late-successional sites and establishment of any biogeographic variation patterns but were focused mostly on the surveys of the local flora.

Somewhat more comparative local survey has been conducted in southwestern Mississippi by S. Rosso et al. (1994). It focused on Laurel Hill Plantation in Adams County characterized by the developed secondary forest but additionally covered 7 other privately owned well-preserved sites with the recovering magnolia-beech overstory. One of the deficiencies of this survey was that it was conducted in the relatively young

successional forests. Unfortunately, the survey was intended in a way that, based on its findings, few biogeographic generalization could have been made. To begin with, most of the surveyed sites were indicative of either the early stages of the forest succession with no or very little shade-tolerant trees being present in the overstory or very disturbed forests. Secondly, the authors made little account of a rather broad variation in the successional regimes and disturbance histories among the sites.

Judging by the remark that the authors did not have "a good explanation" for the absence of certain species, in particular American beech (*Fagus grandifolia*), on certain sites, it appears that very little biogeographic or ecological analysis was involved at the stage of site selection. The authors, for example, failed to recognize an important role of American beech as an indicator of the advanced stages of natural succession. Not surprisingly, in some cases (as it appears on the basis of the presented taxa lists), they sampled indiscriminately both early-successional and late-successional sections which brings unavoidable confusion to the results.

Earlier Caplenor and other workers (Caplenor 1968, Caplenor et al. 1968) conducted studies on the influence of loessal deposits of the species composition of the

bluff forests in the middle section of western Mississippi. Apart from the fact that this study has been done north of the beech-magnolia forest region, most of the assemblages sampled within this project were also indicative of the early stages of forest succession and highly disturbed forests.

Due to the strong distorting influence of the anthropogenic disturbance, sampling of the early-successional forests is probably not the best way to establish the nature of the biogeographic variation. Of even less sense is comparison of the forests on the widely different stages of the post-anthropogenic regeneration. From the methodological standpoint it is only correct to compare late-successional forests with late-successional forests and early-successional forests - with early-successional forests.

Little attention to the successional status of the sampled forests is one of the general flaws of most studies done in the Loess Hills. This probably reflects a poor understanding of, and lack of, agreement on the nature of the region's late-successional forests. Paradoxically, such theoretical uncertainty, in turn, rests on the lack of sampling and well-verified methodology: this is a vicious circle which could be broken only through the intensive fieldwork within the larger-scale projects accompanied by the substantial

increase of comparable data and accurate verification of the individual sites' histories.

The other aspect of the problem which all these studies remained share, is that they have little to say about the physiographic status of the forests sites they refer to. The pronounced edaphic variation along the slope gradient makes it necessary to consider ravine forests separately from those developed on the hilltops. Unfortunately, none of the above-mentioned studies refers to the section of edaphic gradient in which it was conducted.

Another general problem with most of these studies is variation in the size of the sampling plots and sampling techniques which makes the data from one site hardly comparable with the data from another. Even within one project, the sampling sites in many cases seems to have been much smaller than 1 ha (Braun 1950, Morris 1988, Rosso et al. 1994). According to Quigley (1994), this appears to be the minimum representative sampling size for the Eastern North American forests.

Recently Quigley himself made one of the most accurate and representative samplings in the old-growth forest in the southernmost end of the Mississippi River Bluff Ridge, in the region of Tunica Hills, southern Louisiana. But, unfortunately, it was the only site within the Mississippi River Bluff Region he sampled. It

is also important to refer to some limitations of Quigley's sampling techniques which render them inapplicable to the proposed study. For example, Quigley's stratum classification that identifies every tree above 2.5 m as a subcanopy tree (most canopy trees in Tunica Hills forest have heights between 24 and 32 meters) and any tree with unobstructed crown as a canopy tree may have contributed to some inappropriate generalizations about the species composition.

The data gathered in Laurel Hill Plantation and other 7 sites by Rosso et al. (1994) appears to be influenced by a similar problem. Here the list of the overstory species includes the common midstory species such as dogwood (*Cornus florida*) and even understory ones such as blackhaw (*Viburnum rufidulum*), American hornbeam (*Carpinus caroliniana*), red buckeye (*Aesculus pavia*) with the average dbh measures obviously too small (11-14 cm) to be considered as canopy trees. What happened probably was that either the portions of the midstory or small trees in the gaps were counted as the overstory individuals. As a result, the data concerning the overstory and midstory structure might have been somewhat distorted.

The sampling of the Southeastern forests, due to complicated structure and richness, requires not only a finer and more discrete classification of the forest

strata but also an avoidance of any limitations, particularly dbh limitations. Quigley (1994), for example, sampled in Tunica Hills woody plants with the dbh 1 cm. and above. The shrubs and treelets with the dbh below 1 cm. often may be 3 m. and higher. In the layer below 2 m. most of the individuals have dbh less than 1 cm. My sampling experience also shows that some species of the understory woody plants and lianas may not overstep the limit of 1 cm dbh within the sampling area of 1 ha. The list of these taxa may vary from one site to another but the fact remains that some (if not many) understory species and the significant part of the understory, in general, are likely to be excluded from the data if one chooses to apply the limitation strategy.

The lack of systematic sampling combined with the lack of the published and available data probably were among the most important factors that conditioned the highly controversial character of the present classifications of the Lower Mississippi River forests.

The status of the Lower Mississippi River section of the mesic Coastal Plain forests for a long time has been a subject of the classificational and terminological confusion in the American ecology. The roots of this confusion can be traced down to the classification scheme developed by Braun (1950). Braun classified the middle and northern portion of the Lower Mississippi River bluff

forests as a part of the Western Mesophytic Forest Region. North of Vicksburg *Magnolia grandiflora* and few other hardwood evergreen species supposedly drop from the forest structure but from southwestern Mississippi to southern Illinois the Bluff forests are still characterized by the dominance or significant presence of the deciduous and semi-evergreen (water oak) Coastal Plain species absent or nearly absent from the forests of the adjoining Western Mesophytic Region.

Biogeographically these forests seem to be closely related to the rest of the Coastal Plain forests and differ from the latter ones only in terms of their impoverished evergreen flora. Many ecologists today still follow Braun's lead and continue to consider the middle and northern portion of the Mississippi River Bluff as being a part of either the Western Mesophytic Forest Region or Oak-Hickory Forest Region (Kuchler 1964, Greller 1988, Bryant et al. 1993).

Greller (1988) modified the Braun classification system by including the sections of the Blufflands located in middle-eastern Mississippi, northeastern Louisisana and southeastern Arkanzas in zone of the Southeastern oak-pine forest. Loblolly pine (*Pinus taeda*), however, is not native to the bluff hardwood forests. Yet, the hardwood assemblage of the loblolly pine-hardwood ecosystem located east of the Mississippi

River Bluff Ridge is quite different from the assemblages of the primeval and secondary mesic bluff hardwoods (Platt and Schwartz 1990, Platt, personal communication, 1994).

Some of the workers did not recognize the Gulf-Atlantic floristic affinities of the even more southern deciduous—evergreen to evergreen-deciduous bluff ecosystems of Louisiana and southwestern Mississippi classified as magnolia-beech forests by Braun (1950), and as magnolia-beech-holly forests by the Delcourts (1974) and Platt (1994, personal communication). Kuchler (1964), as well as Ware, Frost, and Doerr (1993) who followed the Kuchler classification scheme excluded southern Blufflands from the Southern Mixed Forest Region (the former Braun's Southeastern Evergreen Forest Region). Whereas the similar hardwood forests east and west of the southernmost section of the Lower Mississippi River Region were still considered as a part of what was Braun's "Southeastern Evergreen Forest Region", the loessial hardwoods of southwestern Mississippi and southeastern Louisiana with their pronounced subtropical affinities were classified as the temperate oak-hickory forest all the way down to the Mississippi River Delta. Even taking into consideration the fact that almost all old-growth magnolia-beech-holly forests, except for the few miraculously saved islands, were cut, the secondary forests developed in their place

are still characterized by the strong dominance of the southeastern Coastal Plain taxa and significant presence of the evergreen components in the understory. The oak-hickory classification, therefore, hardly can be considered acceptable.

CHAPTER 2

METHODS AND FIELD PROCEDURE

This dissertation is focused on the late-successional forests. Throughout the southern Loess Hills, the destruction of the original forest by humans cover led to the development of the highly successional secondary forests (in fact, many of them are tertiary to quaternary in nature) which are structurally different from the original communities in being dominated by various light-demanding taxa, not by beech and magnolia. The pockets of the relatively mature forest dominated by American beech (*Fagus grandifolia*) and southern magnolia (*Magnolia grandiflora*) can be found today only in few isolated sites of the southern southern Loess Hills. These relict beech-magnolia tracts survived till the present times mostly owing to the heavily dissected relief of the Loess Hills.

The search for the surviving relic remnants of the original forests was a difficult and extremely time-consuming business. It involved the contacts with the Louisiana Office of State Parks, Louisiana Department of Wildlife and Fisheries, state heritage organizations of Louisiana and Mississippi, Nature Conservancy of Louisiana, Department of Plant Ecology of the Louisiana State University, Mississippi Museum of Natural History and the main office of the Anderson-Tully Company located in Vicksburg, Mississippi.

Except for Tunica Hills, where the degraded remnants of the older growth occur along the upper slopes and extend locally onto ridges, all discovered late-successional stands are associated with ravines which represent a serious physiographic impediment to the timber operations and agricultural cultivation. Survival of the last pockets of the beech-magnolia forest was later insured by the legal protection of this stands obtained under various fortuitous circumstances. Only in two cases out of eleven, the preservation efforts are focused on the conservation of the beech-magnolia forest as such. In five cases the remnants of the original forest cover are either located on the territories of the larger protected units which were set with more general (and sometimes unrelated) purposes or survived by mere luck.

To meet the goals of the intended research, eleven late-successional sites were selected in such a way that each would have reflected the latitudinal, physiographic and edaphic variation within the range of the loessial "beech-magnolia" forests (Figure 1). The sites flanked both sides of the Lower Mississippi Valley and formed a large-scale transect extending from northern Warren County, southwestern Mississippi to Eastern Baton Rouge and Vermilion Parishes, southern Louisiana.

East of the Mississippi River, upon the Mississippi Loess Bluff, the following late-successional forest sites

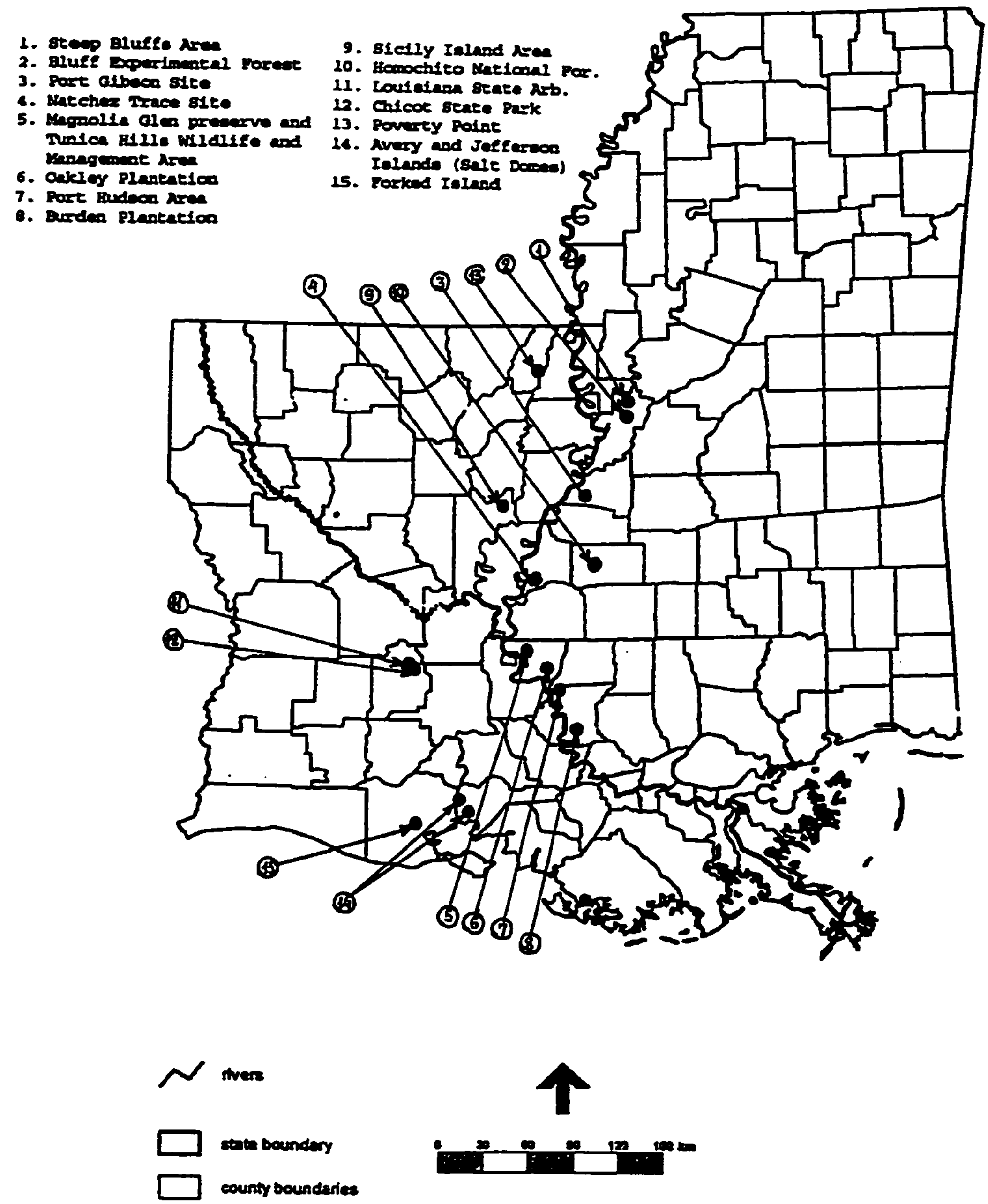

Figure 1. Study Site Locations

were sampled: the Steep Bluffs forest and the Bluff Experimental Forest, both in Warren County, southwestern Mississippi; the Port Gibson site, Claiborne County, southwestern Mississippi; Magnolia Glen preserve and the Tunica Hills Wildlife Management Area, both in the Tunica Hills area, West Feliciana Parish, southeastern Louisiana; the Port Hudson forest, extreme northwestern corner of East Baton Rouge Parish, southeastern Louisiana; the Burden Plantation Forest, southern section of East Baton Rouge Parish, southeastern Louisiana.

West of the Mississippi River, the sampled sites were: the Sicily Island forest, the Sicily Island Wildlife Management Area, Catahoula Parish, northern section of middle-eastern Louisiana; the Louisiana State Arboretum and Chicot State Park, eastern section of Evangeline Parish, northern part of south-central Louisiana; the Forked Island forest, Vermilion Parish, extreme south-central Louisiana. Of course, the distribution of the sites along this transect reflected the availability of the late-successional ("beech-magnolia") forests. The reason for which certain sections of this transect do not contain sites is that no old-successional forests were found in such areas. Such "gaps" are, for instance, between the Port Gibson and Tunica Hills areas east of the Mississippi River, and between Chicot State Park and Forked Island west of the River.

Essentially, I sampled all extant mature stands I found within the southern section of the Loess Hills Region. The only exception is 109-acre Mary Ann Brown preserve in the Tunica Hills now managed by the Nature Conservancy. I began and did most of my fieldwork in the time that this preserve was not yet created: consequently, I knew nothing of this area. Few other forest sites such Clark Creek Wildlife Management Area, northern Tunica Hills, Wilkinson County, extreme southwestern Mississippi and salt dome islands of Iberia Parish (Jefferson Island and Avery Island), extreme south-central Louisiana, were visited but not sampled.

Successional Characteristics of the Sampled Stands

The terms "old-growth forest", "late-successional forest", and "climax forest" are frequently used interchangeably, and so they require some clarification. Hunter (1989), as well as Batista and Platt (1997) defined an old-growth forest as a community that has not been recently cleared and whose dynamics are essentially the same as those that historically shaped the structure and species composition. Barbour et al. (1987) consider as "climax" only those communities which do not exhibit any directional, cumulative, non-random change in a period of 1-500 years. Climax communities are not static. Changes do occur but they are not cumulative and directional in their effect. Instead, the random, small changes merely result in

fluctuations about some long-term mean. As one can see, "climax" as defined by Barbour et al. (1987) in part overlaps with the definition of the "old-growth" proposed by Platt and Batista (1997). However, the requirement of minimum 500 years of the equilibrium state cannot be met by any of the Coastal Plain forests. Besides, "climax" is a "slippery" term for the Coastal Plain forests because of their very complex disturbance regime (Harcombe and Marks 1977, 1978, Marks and Harcombe 1981, Platt 1984, 1985, Glitzenstein et al. 1986, Platt and Hermann 1986, Platt and Schwartz 1990). For these reasons, this term is not used in this dissertation.

For the purposes of this research, I considered as old-growth forests only those stands which did not have any record of clearance and immediate signs of anthropogenic disturbance. Potentially, such forests date back to the early-historical and even prehistorical times. Only two such assemblages were found: the stand managed by Louisiana State Arboretum and ravine forest of Magnolia Glen Preserve in the Tunica Hills. Given the exceptional rarity of the true old-growth forests, this study could not have been accomplished based on the data obtained only from the old-growth assemblages. I had to adapt my study plan to the highly modified landscape of the Loess Hills and gather valuable statistical information from all mature stands I could find. The term "late-successional forest" which is

frequently used in this work identifies mature forests which were once or several times disturbed by humans but had time to recover and now approximate in major aspects the structure and species composition of the original old-growth forests. This term implies that these forests are now at the advanced stages of post-anthropogenic succession. It should be pointed out that, because of the floristic similarity between the old-growth and mature late-successional forests (most notably, the structural importance of the slowly-growing shade-tolerant species in the canopy stratum), these forests are typologically comparable. Both types of the mature forests are compositionally distinct from the younger early-successional forests which lack the shade-tolerant components in the canopy stratum

Initially the eight early-successional sites were also intended to be discussed in this dissertation but the lack of room in already expanded manuscript forced me to abandon the idea. Of these sites, only Crystall Springs (Homochito National Forest, Franklin County, southwestern Mississippi) will be discussed at length in this dissertation because no mature forest was found on the eastern periphery of the Mississippi Bluff. Brief references to two other early-successional sites - the Natchez Trace Forest located along the southern end of the Natchez Trace, Adams County, Mississippi, and the upland forest of Magnolia Glen

Preserve and Oakley Plantation, West Feliciana Parish, Louisiana - will be made when the data obtained from such stands is illustrative of some important trends. Of course, one should be aware of the reservations related to the early-successional nature of these stands. But in some cases, reasonable inferences of the presettlement species composition can be made based on the data obtained from these formations.

Study Sites

The following is a description of the study sites sampled in this research and discussed in this dissertation.

The Steep Bluffs Site

This site is the northernmost of all mature sites sampled within this research project. It is one located about 26 miles north of Vicksburg (Warren County, southwestern Mississippi), on the land owned by the Anderson-Tully Company. It is in a rather deserted area, largely devoid of any permanent human habitation. "Steep Bluffs" is a name which I had to give to the locality in the absence of any distinguishable toponyms. This site is situated on the escarpment of the Mississippi Bluff, in the heavily dissected area characterized by the deep, steep-slope ravines. Erosion of the loess mantle, very thick in this section of the Bluff, is a widespread phenomenon throughout the whole area. Large vertical faces of loess

and nearly vertical slopes are common physiographic features. High ridges and narrow gorges give this unique locality a scenic mountainous outlook.

Most of the Steep Bluffs area was originally old-growth forest but in 1997 a very large area bordering the sampling site was cleared by the Anderson-Tully Company. Although in August of 1998 when I visited the site, another part of the Steep Bluffs was still covered with the forest, the plans had been already made by that time to cut it down as well. After August of 1998 I did not visit the area again: perhaps, the forest I sampled is already gone. This remaining tract of Steep Bluffs ravine forest appeared to have been largely old-growth in origin. No records on previous clearings exist for this area (Glen Brown, Manager of Anderson-Tully Company, personal communication). The canopy of the ravine assemblage contained a broad array of tree sizes and was characterized by the relatively high frequency of the exceptionally large trees of different species. However, certain sections of this assemblage - those characterized by the higher densities of somewhat thinner and more even-aged trees - were likely to have been secondary in origin. These tended to descend from the hilltops down slope in strips which were not always possible to avoid in the sampling procedure. One hectare of the ravine forest was sampled in the Steep Bluffs;

approximately 10 to 15% of the sampled area fell on such questionable sections.

The Steep Bluff ravine forest is (or was) characterized by high diversity and somewhat exceptional heterogeneity of its canopy composition. Although American beech (*Fagus grandifolia*) was the most important canopy taxon, several light-dependent species were also abundant. Steep slopes and frequent land slides result in the somewhat irregularly structured overstory punctuated with gaps at different stages of the natural succession. The ridges and hilltops are dominated by the relatively old second-growth forest whose canopy is largely lacking shade-tolerant components.

The Bluff Experimental Forest

The Bluff Experimental Forest is a 450-acre late-successional stand managed by the Anderson-Tully Company and the Forest Service. This site is located 19 miles northeast of Vicksburg, in Warren County, southwestern Mississippi, within the section of thick loess deposits. The area is featured by the well-dissected relief with the deep ravines and rounded ridges. Slopes are moderately steep to gentle with almost no signs of erosion. This tract of forest was acquired in 1935 by the Anderson-Tully Company (one of the largest timber producer in the Blufflands) as a representive sample of the relatively old late-successional forest. In 1955 the land was leased to

the Forest Service for 99 years. Since that time until now the Bluff Experimental Forest has been used for experimental purposes by the Southern Hardwoods Laboratory of the Southern Forest Experiment Station which is a branch of the U.S. Forest Service.

The uplands and some of the gentle slopes of the Bluff Experimental Forest and surounding area were farmed from about 1835 to 1900 (Glen Brown, Manager of Anderson-Tully Company, 1998). Some time early in 20th century the land was abandoned and later, in 1935, acquired by the Anderson-Tully Company. Today ridgetops, upper slopes and some of the ravines adjacent to the main trail are covered with the old secondary forest of the early-successional nature: the dominant status here is assumed by large-sized southern oaks and winged elm, shade-tolerant components are largely lacking.

The late-successional growth is limited to ravines and characterized by the strong dominance of beech both in canopy and subcanopy. The area is characterized by the intermingling of the very mature secondary-growth and potentially old-growth stands. There is no exact information on when the original forests in these ravines were cut. Glen Brown, the manager of Anderson-Tully Company, pointed out (personal communication, 1998) that the Company did not undertake clearcut operations in the area. It is likely that such second-growth beech-dominated

sections originated as a result of the industrial clearings done by the previous land-owners back in the late 19th century or in the early 1900s.

The older, potentially old-growth sections are characterized by the prevalence of large to very large trees of both beech and the other species and less thick beech undergrowth. Most of such stands are located in the remote sections of the Forest away from the central trail. Among the beech trees present here not uncommon were those reaching 80-120 cm dbh.

After acquisition of the Bluff Experimental Forest by the Anderson-Tully Company, the stand underwent only limited selective cuttings. The last of them took place in 1945-46. However, these cuttings were done in the immediate vicinity from the available trails and did not extend too deep into the forest. Consequently, most of the areas where I laid out my transects were likely to have been only marginally affected.

The Port Gibson Site

This site is located on the Mississippi Bluff within the zone of deep loess deposits about 5 to 6 miles south of Port Gibson, Claiborne County, southwest Mississippi. The site is also a property of the Anderson-Tully Company. The forest covers slopes of the ridge which is currently surrounded by the vast deforested area. This is a small remnant of the recently more extensive beech-magnolia

forest which was clearcut by the Anderson-Tully in 1998. Because of the small size of the remaining forest area here only 0.25 ha was sampled. The history of this forest is obscure. Before 1998 this forest apparently was not much disturbed (the site was among the most recent purchases of the Anderson-Tully). No tree removal is known from this area before 1998. Some of the beech trees harvested in this forest by the Anderson-Tully Company were close or even more than 100 years old (Glen Brown, Manager of Anderson-Tully Company, personal communication, 1998). The stand is characterized by the well-developed beech-magnolia overstory. Yet the dbh sizes of the beech trees fluctuate largely between 40 and 60 cm (the maximum size was 68 cm) which may be indicative of the second-growth origins of the stand. By contrast, *Magnolia grandiflora* is represented by the range of sizes which, in fact, may indicate a more mature status of this stand. One of the magnolias registered in the site was 93 cm dbh. The diameters of the stumps in the clearcut area nearby (some exceed 80-90 cm dbh) suggest that at least some sections of this forest may have been old-growth in origin.

<u>The Natchez Trace Forest Site</u>

I gave this name to the forest which flanks the southern section of the Natchez Trace within Adams and Jefferson counties, southwestern Mississippi. The other names sometimes used both in the literature and general

parlor for the broader area around Natchez, Mississippi is the Natchez Bluff, the Natchez Forest or Natchez Bluff Forest. My sampling area in the Natchez Trace Forest flanked both sides of the southern end of the Natchez Trace It is located 7 to 9 miles north of Natchez, in the immediate vicinity from the Emerald Mound site, the former main town of the Natchez Indians.

Physiographically, the area I sampled can be qualified as an eastern section of the Bluff escarpment. This area is characterized by the strongly dissected topography with deep ravines and high narrow ridges. The section west of the Natchez Trace tends to be more dissected; east of the Trace ravine slopes are typically somewhat more gentle. The signs of erosion of the loess mantle are well pronounced throughout much of this area, although they somewhat less frequent than in the Tunica Hills. Within my sampling area I came across only one recent land slide.

The area along the southern end of the Natchez Trace has one of the longest histories of anthropogenic disturbance. Since the Mississipian epoch this area was cultivated by the Amerindian populations. The native fields were clustered in the area of Emerald Mound - precisely where my transects were laid out. Much of the Natchez Trace area was then cleared and cultivated during the Ante-Bellum Period and remained in the continuous cultivation during the rest of the 19th and much of the 20th centuries.

The present-day Natchez-Trace forest is an early-successional second-growth assemblage developed on the previously cleared and cultivated land. Throughout much of its southern margin this forest is limited to two relatively narrow strips, in some places less than 100 meters wide, extending along both sides of the Natchez Trace Parkway. It gradually expands north of Emerald Mound until it more or less merges with forest tracts extending toward Natchez Parkway from the Mississippi Bluff escarpment. The area of the Natchez Bluff was a very important section of my biogeographic transect because the beech-magnolia forest - if such was to be found in this area - would have exemplified a transitional link between the northern forests of Vicksburg-Port-Gibson area and southern forests of the Tunica Hills-Port Hudson area. I travelled extensively along the Natchez Parkway trying to locate the surviving pieces of the late-successional forest but my quest was unsuccessful. I managed to find only few steep-slope ravines where, in the middle of the early-successional forest, survived few canopy-sized beeches and magnolias. Together such spots did not make up even 0.05 hectares and so I had to lay out my transects in the early-successional forest. The first sampling plot was set about 1.5 miles of the entrance to the Natchez Parkway. From that point the transect proceeded north along the both sides of

the Parkway. In total, 1 hectare of the ravine Natchez Forest was sampled for the needs of this reserch.

This early-successional assemblage is characterized by the very diverse assortment of the canopy species largely lacking the shade-tolerant components. Its composition reflects a rather complex disturbance history. Over 67% of the sampled area were characterized by the extreme scarsity or absence of the important shade-tolerant components not only in the overstory but also in the subcanopy which is suggestive of the development of this assamblage on the previously cultivated land. About 30% of the sampled area, while being characterized by the early-successional overstory, had the populations of the shade-tolerant species in the subcanopy. This type of early successional forest was typically associated with the relatively steep slopes. In the past such slopes could have been cleared (and, perhaps, more than once), but they were less likely to have been cultivated for any prolonged period of time.

Finally, some precipitous slopes and coves difficult to access both for agriculturalist and timber industry harbor tiny pockets of the late successional community recognized by one or two canopy-size beeches or evergreen magnolias sill standing. Such patches may represent the true survived pieces of the old-growth forest or, what is more likely, they exemplify very old secondary beech-magnolia stands which began to develop after the Civil War

land abandonment and survived all hardships and uncertainties of the following 135 years. Whether or not some pieces of the old-growth forest survived along the Natchez Trace, it seems certain that some slopes of this heavily deforested area have survived the agricultural booms of the last two centuries and never were plowed.

The Clear Springs Area, Homochito National Forest

Located in Franklin County, southwestern Mississippi, within the southeastern section of Homochito National Forest, this forest site is a part of the physiographic region known as Southern Loessial Loam Hills (Evans et al. 1983). The area is located on the eastern periphery of the loess belt. Its gently rolling, hilly topography is dissected by relatively shallow ravines with gentle slopes and broad bottoms. This section of Homochito National Forest is underlaid with the relatively shallow loess mantle - about 1 meter thick or less. In some places loessial soils appear to be intermixed with older and coarser Citronelle deposits containing sand and gravel.

Most of Homochito National Forest, including the Clear Springs area, is strongly dominated by loblolly pine (*Pinus taeda*) which seems to be native to this area. The pine forest, with the admixture of the hardwood tree species occupies hilltops and most of the slope gradient. The hardwood forest, with admixture of pine, forms relatively narrow tongues associated with the ravine bottoms and lower

slopes. This hardwood forest is of early-successional nature: it is dominated by the light-dependent tree species and contains only little ammounts of beech and magnolia - largely limited to the understory and lower midstory. Most of it originated after extensive clearcuts back in the 1950s, although some small pockets - those marked with exceptionally large oaks - may, according to the forest managers, date back to 1920s or even early 1900s. Nevertheless, I took decision to sample 1 hectare of this forest because it was the only available assamblage representative of the marginal shallow-loess section east of the Mississippi River.

Magnolia Glen Forest, the Tunica Hills Area

The forests of the Tunica Hills of West Feliciana Parish, southeastern Louisiana, are represented by the ravine assemblage of the Magnolia Glen which originally was a Louisiana Nature Conservancy preserve but since 1996 has been owned and managed by the Louisiana Department of Wildlife and Fisheries. The site is located within the highest section of the Bluff escarpment immediately adjacent to the Mississppi Valley where the loessial mantle reaches its maximum depth forming the crest or "cap" of the loess ridge.

This area of the Tunica Hills is characterized by one of the most dramaticly dissected landscapes that can only be observed in the Loess Hills region. Small streams and

water courses cut in the loess mantle an extensive labyrinth of the deep, steep-sided ravines separated by narrow ridge tops. Nearly every ravine bottom harbors a sandy stream bed, either dry or partially filled with the rain water. After some exceptionally strong showers such beds become filled with short-living streams which disappear soon after the rain leaving behind small ponds of stagnant water.

Erosion of the loess mantle in Magnolia Glen is more pronounced than in any other Bluff site I visited during this research. Instability of the ravine slopes is caused by the highly dissected nature of the local terrain, as well as the erosive action of the intermittent bottom streams and strong subtropical showers. The moist microclimate of the deep narrow ravines contributes to the looseness of the loess deposits. The most widespread form of physiographic disturbance are small landslides associated with the fall of one or several trees. As many as 12 recent landslide-related gaps were encountered within the sampling area. The fresh evidence of the large-scale landslides - in the form of dramatic cliffs and spectacular canyon walls - is also present in the Magnolia Glen preserve but none of my transects ran through such disturbed areas.

The middle and lower slopes of the Magnolia Glen preserve are characterized by very heterogeneous and

exceptionally diverse old-growth forest with irregularly closed, gappy canopy perpetually disrupted by small-scale landslides and treefall. Together with LSA stand, it is the only contiguous tract of the old-growth forest in the southern Loess Hills that I am aware of. One hectare of this ravine forest was sampled for the needs of this research. Although American beech and evergreen magnolia are important components of the Magnolia Glen assemblage, they are not only members of the dominant association. This forest is also characterized by the high importance of many light-demanding and bottomland-centered species which typically have more modest population densities in the "conventional" beech-magnolia stands.

The uplands of Magnolia Glen preserve were cleared twice in this century - first in 1950s and secondly in the 1980s. At last time clearing was extended in some areas further down the slope (Platt, personal communication, 1994; Quigly, personal communication, 1994). As a result, today many hilltops here are dominated by degraded, low-stature woodlands and thickets which apparently have little capacity to further regeneration into the tall-timber forest. Such devastated areas are commonly found adjaicent to the old timber roads which extend along many ridgetops of Tunica Hills. However, the uplands of Magnolia Glen preserve also harbor the closed-canopy tall-timber forest associated with the upper sections of the slopes and

hilltop edges - it must be the successional growth untouched by the clearing operations of the 1980s. This upland assamblage is early-successional in nature: it is dominated by several species of Coastal Plain oaks (*Quercus pagoda, Q. nigra, Q. shumardii*), sweetgum, and tulip tree (Liriodendron tulipfera). The forest is also very rich and contains many other tree species.

The upland forest of Magnolia Glen preserve is the only tract of the upland forest sampled in this reseatch which contains small degraded remnants of the original upper-slope beech-magnolia forest. The population densities of the shade-tolerant species such as American beech, evergreen magnolia, and American holly in this assemblage are higher than in any other early-successional forest explored during this research.

I made the decision to sample one hectare of this unique upland forest. The sampling procedure the uplands of Tunica Hills was one of the most difficult tasks of this research — not only on account of extremely dissected terrain abounding with steep slopes and precipitous, nearly vertical walls, but also because of the devastation produced here by the timber operations. Where the recent timber operations extended from the ridgetops downslope, the more mature forest was interrupted by the tongues of the devastated tertiary regrowth which had to be dismissed from my study. To exclude such degraded sections from the

sampling area, I had no other way but to split some of our transects into smaller peaces.

The Tunica Hills Wildlife Management Area

The Area is located in the Tunica Hills, West Feliciana Parish, southeastern Louisiana and occupies 3,365 acres managed by the Department of Wildlife and Fisheries of the State of Louisiana. Sampled here was the small tract (0.1 hectare) of the potentially old-growth forest which occupied one of the relatively gentle slopes along the Old Tunica Road. This tract gives an idea of the potential look of the physiographically-undisturbed forests of the Tunica Hills. The area occupied by this late-successional forest was larger than 0.1 hectare but its lower section was damaged by Hurricane Andrew in 1992, and I had to exclude it from my sampling area.

The Oakley Plantation Site

This site is located at the southern foothills of the Tunica Hills area, about 2 miles from St. Francisville, West Feliciana Parish, southeastern Louisiana. It represents a rare example of the well-preserved middle-successional forest with the irregular canopy dominated by cherrybark oak, water oak, Shumard oak, loblolly pine, and sweetgum. The site has only one overstory magnolias (*Magnolia grandifolia*) and no canopy-sized beech. Before 1861 most of the land which is now occupied by this forest was under cotton fields. The origins of the present-day

forest date back to the end of the Civil War when Oakley Plantation was abandoned.

The Oakley forest provides a unique insight into the successional dynamics of the magnolia-beech community. The unique feature of this forest is its exceptionally well-developed midstory dominated by *Magnolia grandiflora*. It is one of the few sites - in fact, the only site I know - which developed from the well-documented stage of cotton field in 1863 into the tall-timber middle-successional forest with half-evergreen subcanopy in the late 1990s. The large share of magnolia in the present-day midstory layer is likely to indicative of the exceptionally high importance of this species in the future overstory in several decades from now when most of the modern light-dependent dominants will be replaced.

This forest originated at the same time as much of the ravine forest of the Port Hudson area which is characterized by the well-developed beech-magnolia overstory. The relatively slow recovery of the Oakley Plantation site is likely to be related to the fact that, unlike the Port Hudson assemblage, its forest originated in the place of the former cotton fields. Both the original vegetation and forest soil with its rich organic layer, therefore, were completely destroyed and the successional process in Oakley proceeded with much slower speed than that of Port Hudson.

The Oakley Plantation site is located on the extreme southern margin of the deep-loess section of the Mississippi Bluff and characterized by gently rolling relief of low hills alternating with shallow gullies and other depressions. Three habitats were distinguished and sampled within this forest: first, uplands and hilltops dominated by loblolly pine and oaks, especially cherrybark oak; second, the intermediate slopy terrain dominated by cherrybark oak, water oak, loblolly pine and sweetgum; third, the depressions and gullies dominated by water oak, sweetgum, and cherrybark oak. Of the upland terrain, an area of 0.25 hectare was sampled. Further I sampled one hectare of the slopy intermediate complex which occupies the major part of the Plantation territory and harbors its most representative forest type. Finally, I sampled 0.75 hectare of the forest which occupies the gullies and shallow depressions. The size of the latter sampling area was determined by the spatial limits of the ravine and low-lying terrain.

Port Hudson Site

The Port Hudson site is located in the extreme north of Eastern Baton Rouge Parish, on the territory of Port Hudson Commemorative Area which was created to preserve one of the important Civil War battlefields were in 1863 the Seige of Port Hudson was unfolding. In May-July of 1863, the Confederate Army took here a 48-day-long stand against

the advancing Federal troops aimed at Baton Rouge and New Orleans. The site occupies 899 acres and is managed by the Office of State Parks of Louisiana. It is located well south of the Tunica Hills and highest section of the Mississippi Bluff. The height of the bluff escarpment in the Port Hudson decreases almost three times compared to that of the Tunica Hills and makes up only about 70 feet from the Mississippi Floodplain to the escarpment top.

The area is dissected by the relatively shallow to moderately deep ravines, with broad bottoms and gentle slopes. No signs of physiographic disturbance was discovered in the general area of sampling. Most of the Commemorative Area, especially in the uplands, is covered with the early-successional forest and thinned park-like woodlands which are about 40 to 50 years old. The sections of the younger regrowth are scattered here and there throughout its upland portion.

Ravines of the Port Hudson Commemorative Area feature one of the most magnificent beech-magnolia forests left in Louisiana. This forest type do not form massive tracts but extends though the area with relatively narrow, sinuous "tongues" associated with ravine bottoms and their lower slopes. Some sections of this forest appear to be very well developed. It was here where my transects were laid out and the sampling procedure took place.

The site has a complex and rather unusual disturbance history. By the time of the Civil War most of the Port Hudson area was forested, although some more or less level upland areas were probably cleared for fields. The area is known for one of the important battles of the Civil War. Most of the original beech-magnolia forest here had been first time cut by the Confederate troops to errect barricades during the campain of the defence of Port Hudson in 1863 (Wright 1978, Edmonds 1984, Podds, personal communication 1998). Ravines filled with fallen trees formed a formidable line of defence which secured approaches to the Confederate positions on the tops of the adjacent bluffs and ridges. With nature and forest on their side, the defenders of Port Hudson were able, despite the lack of men and shortage of resources, to hold here the yankee troops for 48 days in succession inflicting heavy casualities on the enemy (Edmonds 1984).

It appears that much of the standing old-growth forest in the Port Hudson area was also shattered in pieces by the artillery during the siege. In many of the old photos exhibited in the Museum of the Port Hudson Commemorative Area one can see battlefields in the place of the devastated forest; in some of them lurking on the background, either lying or standing, are bitten trees of *Magnolia grandiflora* easily recognizable by their xerophyllous foliage.

Following the siege, the area was left alone and the beech-magnolia growth resprouted. The process of natural regeneration continued through the first decades of the 20th century. The late history is not so clear. The older parts recognizable by especially large beeches and magnolias may be the remnants of the old second-growth forest which resprouted in the ravines soon after the Civil War. Another part of the ravine beech-magnolia forest does not appear to fit into this category.

Gregory Podds, the Director of the Port Hudson Area, pointed out that another large-scale clearing was undertaken in the area in the 1930s. Cleared were mostly more or less level uplands but a large portion of the ravine timber was also taken out. After this most of the upland area and some slopes were under cotton fields but most of the cleared ravines were again allowed to become a forest fallow. Since ravines were abandoned and the soil, stumps, roots, and propagules remained largely untouched, beech and magnolia again regenerated and had time to develop into the third-growth beech-magnolia forest. About one third of the present-day ravine beech-magnolia association may be representative of this tertiary growth. Still another clearing took place in the area in 1960s: at this time the timber was taken exclusively for industrial purposes. Cleared were again significant portions of the upland forest and some sections of the ravine slopes and

bottoms. Fortunately, due to the comparatively recent nature of the disturbance, the results of clearcuts and selective logging in such areas are still well-visible and easy to avoid. Some few relatively small spots restricted to the relatively precipitous slopes located closed to the Bluff escarpment may harbor the remnants of the old-growth forests. In some sections with higher slopes, *Magnolia grandiflora* tends to stream upslope reaching the edge of the uplands, sometimes forming peculiar magnolia-white oak associations.

In the Port Hudson area I sampled one hectare of the ravine late-successional forest which was limited primarily to the ravine bottoms and lower slopes, and 0.25 hectare of the early-successional slope forest located well east of my beech-magnolia sites, along the U.S. 61. In the case of the early-successional forest, due to the lack of time, only the canopy stratum was sampled.

The Burden Plantation Site

This site harbors one of the unique examples of the survived "urban" forest. The forest is located in southern portion of Baton Rouge, on the property of Burden Plantation Museum. Once a part of the extensive hardwood mesophytic forests of the Baton Rouge area, today this tract of hardwood vegetation is completely surrounded by the urban structures of Louisiana's capital and has no connection with any other forest habitat.

The Burden Plantation forest exemplifies a relatively mature ecosystem. It could be qualified as middle-successional forest, with the canopy dominated by large-sized light-dependent trees such as Coastal Plain oaks (mostly *Quercus nigra* and *Q. pagoda*) and sweetgum but with the vigorous regeneration of *Magnolia grandiflora* in the midstory. The exact age of the Burden Plantation forest is unknown but some ideas can be suggested. According to Mr. Burden, the former owner of the site, the forest looked largely intact and mature in the early 1900s, since which time till now it suffered no anthropogenic disturbance. This suggests, perhaps, this urban assemblage originated as a result of the massive land abandonment after the Civil War. Since that time it was wisely preserved by the land owners, and since 1972 the preservation status of this unique urban forest was officially sealed in the agreement between Mr. Burden who donated his property to the City of Baton Rouge, and the municipal authorities.

Unfortunately this forest is strongly infested by exotic plant species, especially Chinese and Japanese privet (*Ligastrum sinense* and *L. japonicum*), as well as Japanese honey-suckle, which undoubtedly influenced its composition and the very course of the successional process. For a long time this forest was also exposed to feral pigs. One can only guess how much damage to the regenerating ecosystem was caused by these omnivores.

Still, despite the disturbance, the Burden Plantation assemblage represents a considerable interest. It is the most mature and extensive tract of the mesic hardwood forest in Baton Rouge area. Undoubtedly, it gives some insight into the structure and species composition of the mesic forests which once covered the extreme southern fringe of the Mississippi Bluff. Of special interest to me was the fact that the Burden Plantation forest also harbors small stands with large, canopy-size magnolias and beech trees. Such stands examplify a more advanced stage of the forest succession and may be representative either of very old secondary forest dating back well into Ante-Bellum period or even original old-growth forest. Unfortunately, some of these stands suffered some damage from Hurricane Andrew in 1992.

My sampling procedure in Burden Plantation forest was limited to such magnolia-rich communities. Unfortunately, the relatively small sizes of these successionally advanced stands did not allow me to sample the standard one hectare area and I had to limit myself to only 0.25 hectare.

The Forests of the Salt Dome Islands and Forked Island

Salt dome islands are relatively small isolated surfaces of upper ground in the coastal marshes of extreme southern Louisiana. Primary factors that conditioned the uplift of the salt domes was the relative difference between the rate of diapiric uplift and the rate of salt

dissolution. The result of this process was the development of the round, mound-shaped islands of upland terrain conspicuously rising above the marshy surface of the Mississippi Deltaic Plain (Autin et al. 1991). The surfaces of the salt-dome islands are dissected by ravines and resemble in many respects those of the mainland loessial surfaces. The salt domes are covered with loess mantles at least 1 m thick which overlay clays, silty colluvium and other late Plestocene deposits. Occasional exposures of coarse sand and gravels can be found in some of the salt domes such as Avery Island. The distribution of loess mantle at least on some of the salt-dome islands is rather uneven. In Avery Island, for instance, loess achieves maximum thickness on side slopes but thins toward ridgetops which suggests some erosion.

The forests developed on the salt-dome islands are quite different from the "conventional" beech-magnolia forests. These communities lack beech (*Fagus grandifolia*) and several other species of the cool-temperate deciduous trees. They are also characterized by the considerably increased importance of the evergreen components. Although salt domes do not have any endemic trees or shrubs, the local communities are truly relict in nature. Surrounded by extensive marshes, the salt-dome forests represent true refugia of the upland flora which developed in the relative isolation since some time in the Pleistocene. During the

fluvial epoch of the late Pleistocene-early Holocene these islands were likely to have remained above the level of the flood waters.

Today most of the salt-dome islands are privately owned, and one, Wicks Island, is used by the Federal Government as a strategic oil reserve. Due to their isolation and special status, the forests of salt domes are remarkably well preserved. Much of these forests, especially on Weeks, Cote Blanche and Belle islands, appear to represent genuine old-growth forests.

Because of the private ownership and strategic importance of the salt dome islands I had difficulty in obtaining permission for camping on any of them. But I visited Avery island and Jefferson Island and made observations of their vegetation cover. Avery Island is biogeographically the most modified of all salt dome islands. About half of its territory is stripped of its original vegetation. The large portion of the island is covered with gardens rich in the exotic species of trees and shrubs. There is no sharp boundary between the garden landscapes and remaining forests: throughout much of the Island the ornamental and native floras tend merge forming "garden forests" rich in exotic, primarily East-Asian species. Although Jefferson Island also has cleared areas, its forest is better preserved and characterized by essentially less numerous exotic populations.

To supplement for the absence of statistical data from the salt dome islands, I found floristically very similar tract of the old-growth mesic forest located about 20 to 25 miles west from Jefferson and Avery islands. The area which harbors this forest is known as Forked Island. It is located on extreme southern margin of the Prairie Complex (Saucier 1994) and represents an ornate mosaic of ancient alluvial ridges slightly elevated above the level of the flat surrounding landscape. Throughout the area ridges alternate with shallow depressions filled with the forest of more bottomland type. Forked Island is located closely to the western margin of the shallow-loess deposit zone (from 1 to 3 meters thick). This suggests that the thin layer of loess was likely to have been deposited throughout the area and mixed with the alluvium. Half a hectare of the ridge mesic forest was sampled here for the needs of this research.

Chicot Lake Site

The Chicot Lake Site was selected on the bluff slope of artificial Lake Chicot created in 1940s. It is located in the Chicot State Park which covers over 6,400 acres of rolling hilly terrain on the northeastern margin of Opelusas Ridge, in the eastern section of Evangeline Parish, northern part of the south-central Louisiana. The area of Chicot State Park exemplifies the complex physiographic transition from the alluvial surfaces of the

lower Red River Valley to the loess-capped uplands of the Opelousas Ridge. While throughout much of the area, the transition from the floodplains of the Red River Valley and the Atchafalaya Basin to the Opelousas Bluff is sharply pronounced, within the park the upland and lowland sections tend to fuse into one another forming a complex mosaic of edaphically segregated habitats. Physiographic and soil maps of Louisiana tend to disregard the presence of the upland loessial habitat in the immediate vicinity of Chicot Lake and identify the whole territory of the park as a part of the Red River Alluvial Valley. Although alluvial soils are present in the park, much of its territory, especially west of the Lake Chicot is occupied by comparatively low, gently rolling hills broken by shallow gullies and ravines. Here and there hilltops alternate with lower-lying upland "flats" underlaid by poorly permeable layers of clay. Loess seems to have been deposited over most of the upland terrain. The reddish surfaces of the loess deposits can be seen here and there in the Chicot hills. But the depth of the loess layer remains a question: most likely, it is relatively shallow (less than 1 meter thick) throughout most of the park as suggested by my observations on some eroded hillslopes.

The localized presence of a rather thick loess mantle is most likely on the steep bluff slope facing the western bank of Chicot Reservoir. In some places here loess forms

characteristic vertical faces similar to those found in the Tunica Hills and throughout the Mississippi Bluff. This slope appears to be one of the sections of the Opelousas Ridge escarpment for no comparable relief feature appears to be present on the east of the lake. The eastern section of the park is relatively low and flat: it indeed seems to belong more to the Red Valley than to the Opelousas bluff. The localization of the relatively thick (by the "western" standards) loess mantle on the central-eastern slope of Chicot Lake thus appears to be of no accident because, as the first considerable fold of relief on the way of the eastern winds, this slope was likely to have intercepted most of the Pleistocene loess dust.

The Chicot State Park harbors the largest tract of the mesic hardwood forest of the Opelousas Ridge. Most of the park is covered with very diverse early-successional forests characterized, due the complexity of the relief, by the unusual mixture of the upland and more bottomland forest flora.

Nearly the whole territory of Chicot State Park was clearcut in the 1920s and most of it was cultivated for one or two decades. Most of the logging roads that run through the park today were constructed at that time. Additional extensive cuttings took place in the 1930s and 1940s, just before Chicot dam was constructed. Almost all the forest was cut during this period. Some parts of the area were

cleared twice. The destruction of the original forest cover and associated forest soils determined the early-successional status of nearly all forest associations in the area. I sampled one hectare of the mixed early-successional forest of Chicot State Park but, due to its early-successional status and the lack of room, it will not be discussed in this dissertation.

The narrow strips of the second-growth beech and beech-magnolia stands were found to meander along some gullies and ravine creeks in the areas of more or less pronounced hilly relief. Few individual beech trees have also survived in some of the slopes and hilltops thus suggesting the predominance of the beech-magnolia or, at least, beech-rich forests throughout much of the upland area in the historical past. However, the only sizable strip of the late-successional forest was found on the western bluff slope facing Lake Chicot.

One hectare of this forest was sampled for the needs of this research. It can be qualified as one of the most magnificent examples of mature "beech-magnolia" type forest I came across in the Loess Region. Its survival was purely accidental and related to the rugged and complicated topography of the site. The steep and relatively high slope of the lake bluff was impossible to cultivate and difficult to extract timber from. It appears that most of the forest on the lake bluff was never cut. Here were found some of

the largest trees of *Magnolia grandiflora* (157 and 142 cm dbh) and *Quercus mischauxii* (105.8 cm dbh) registered within this research. Some other species such as *Liquidambar styraciflua*, *Carya ovata*, *Morus rubra*, and *Tilia americana* were also represented by the specimens of solid sizes. However, this supposedly old-growth forest was interrupted in some sections by somewhat pauperized, relatively even-aged strips dominated by *Quercus pagoda* which appeared to have indicated the areas where clearing operations extended down slope.

The structural characteristics of this forest were also considerably complicated by strong tornado which hit narrow strip of the lake bluff in 1995 leaving behind damaged canopies, broken trunks, tip-ups, and blockages of dead trees colonized by early-successional vegetation. Some sections of this forest were hardly accessible - both because of the piles of dead trunks and abundance of rattle snakes and cottonmouths which tended to favor such areas. The most devastated sections were avoided. Still, some more lighly damaged spots had to be sampled and these included two sections (74x10 meters total) where somewhat thinned canopy and abundant gaps resulted in the development of the extraordinally thick understory dominated by young treelets of *Carpinus caroliniana*.

Another type of disturbance which supposedly affected the whole lake-facing bluff slope was of hydrological

nature. The slope descended to the low and swampy margin of Lake Chicot colonized by the narrow band of cypress-dominated swamp forest. One of the likely signs of hydrological disturbance is the unusualy low importance of beech (*Fagus grandifolia*). The Chicot Lake forest is strongly dominated by magholia-sweetgum association.

The Louisiana State Arboretum

The deep dissection along the western margin of Lake Chicot reaches its culmination in the area managed by the Louisiana State Arboretum. This site is located about 1.5 to 2 miles northwest from my sampling area in Chicot State Park. The scenically dissected topography of the Arboretum rivals that of the Tunica Hills. The site is featured by the system of high and relatively steep terrace slopes falling into the waving strip of bottomlands centered along Ferguson's Gully. Essentially much of the site represents a giant sinuous gorge, with the bottomlands along Ferguson's Gully serving as a bottom. The dissection is deepest along the eastern margin of the gorge. The eastern bluff is slightly lower and somewhat more gentle. The area managed by the Arboretum also includes hilly upland terrain on the both sides of the bottomland divide.

The area managed by the Louisiana State Arboretum is located on the eastern margin of the loess-capped Prairie Formation. The depth of the loess deposits in the area is unknown but, given the fact that the territory of the

Arboretum is immediately exposed to the alluvial surfaces of the lower Red Valley from which some of the fluvial material had originated, it is not unlikely that some local sections may be underlaid by relatively deep mantles. Even if in average only the shallow veneer of loess was deposited throughout the Chicot Lake area, the high dissected slopes of Ferguson's Gully bluff, may have acted as a more efficient interceptor of the loess dust. Few vertical faces of loessial material occur sporadically within the slope section.

The ravines of the Louisiana State Arboretum harbor one of the most magnificent tracts of the beech-magnolia forest surviving in the Loess Hills Region. With no record of anthropogenic disturbance, the stand appears to represent a genuine old-growth forest - one of the only two found in the Loess Hills within this research. The canopy of the stand, however, was subsequently damaged in 1995 and 1998 by two highly localized tornados. As a result of these disturbances several trees in the old-growth forest was broken, crowns of many others were destroyed or beaten to various extent of many trees. Remarkably, the tornado was of highly localized nature. In both cases it rushed from the terrace ridge downslope and passed exactly through the middle of the old-growth section without causing much damage on the uplands.

The tornado of 1995 then made its way to the Chicot Lake bluff where it struck - again with surprising precision - the narrow band of predominantly old-growth forest along the reservoir. The magnitude of this atmospheric disturbance was awesome. The tornado proved fatal for some of the largest trees present in the Arboretum stand. The bottom of one of the ravines adjacent to Ferguson's Gully feature, for instance, the trunk of enormous beech trees of about 137 cm dbh which was slashed at the heihgt of 2.5 to 3 m above the ground. According to Jim Robinson, the Director of the Arboretum, nothing even remotedly similar was recorded in the history of the LSA before.

The tornados produced numerous gaps and small breaks in the canopy and stimulated the development of the large populations of several light-dependent subcanopy species such as paw-paw (*Asimina triloba*) and French mulberry (*Callicarpa americana*). As a result, the disrupted areas of this stand tend to have a thicker understory than the "typical" beech-magnolia forest. But the sections of the forest spared by the hurricanes still have a sparse subcanopy dominated by the shade-tolerant species.

The LSA area represented a very interesting object of study due to the pronounced physiographic gradient of the slope forest ranging from the hilltops down to the relatively broad accessory floodplain. The uplands adjacent

to the deep slopes of Ferguson's Gorge are covered with the relatively dry early-successional forest dominated by several species of oak (*Quercus* spp.) and hickories (*Carya* spp.). The relative abundance of beech and magnolia in the understory stratum indicate that this forest type originated in the place of the destroyed upland beech-magnolia forest. The floodplain forest bordering Ferguson's Gully is dominated by sweetgum and winged elm (*Ulmus alata*) with the admixture of the Coastal Plain oaks (*Q. nigra*, *Q. pagoda*, *Q. mischauxii*) and *Magnolia grandiflora*. This forest also appears to be of secondary in origin, although some large oak and magnolia trees here could be left-overs of the original old-growth forest.

Due to the physiographic and edaphic complexity of the site I took my time to sample three forest types: first, the middle to lower slope old-growth forest dominated by beech and magnolia (1 hectare); second, the early-successional upland "oak-hickory" forest (1 hectare); third, the old-growth forest developed on the footslope terrace flanking the bottom of Ferguson's Gully (0.25 hectare). The latter forest type examplifies the narrow transition zone between the mesic and bottomland hydrophytic forest.

<u>The Sicily Island Site</u>

This site is an isolated remnant of the upland terrain located between the Mississippi and Ouachita alluvial

valleys, the northern part of middle-eastern Louisiana, Catahoula Parish. From the geological standpoint, Sicily Island represents a relict fragment of the extensive sandy-graveliferous blanket of the Citronelle formation which was cut off and subsequently eroded by course changes of the ancestral Mississippi and Quachita rivers. It has survived the meandering action of these major watercourses as a relatively small, roughly circular outcrop of hilly terrain of about a 5 to 7 km in size. With the only exception of its northeastern section which is connected with the extreme southern tip of Macon Ridge, present-day Sicily Island is all surrounded by the extensive floodplain landscapes.

This upland area is characterized by the strongly dissected, rugged landscape of high hills and deep but relatively gentle-sloped ravines. The surface of the Island is covered with loess: an essentially thinner loess mantle than one formed on the Bluff Hills east of the Mississippi River. Nevertheless, this mantle appears to be at least 1 meter thick as indicated by the physiographic and soil maps. What maps do not say is that the thickness of the loess coat throughout the Island appears to be rather uneven. Its distribution of loess depends on topography: loess is very thin or absent on hilltops and thickest on lower side slopes. The loess material could have slipped downslope naturally but it is not unlikely that thinning of

loess on the hilltops and ridges was caused by the anthropogenic influences. Presently, gentle slopes of forested hills lack any signs of major erosion. By contrast, some of the recently cleared slopes are scared by freshly carved scenic gullies.

The rugged landscape of Sicily Island is dominated by a rather dry mixed forest which is made up largely by loblolly pine (*Pinus taeda*) and several species of oaks (*Quercus* spp.). Drought-adapted and xeromorphic oaks prevail. Some parts of the forest tend to be dominated by pines, others demonstrate the transition to the predominantly hardwood communities. Importance of loblolly pine tend to decrease from the hilltops downslope. Hilltops and ridges tend to be dominated by pine and xerophytic oaks. On the middle slopes xeric and dry-mesic oaks, with the subordinate amounts of few mesic species, increase in importance in relation to pine thus marking the transition to more hardwood forest. On the lower slopes and in the bottoms some decidedly mesic and moist-mesic species intermingle with xeric oaks and some pine. The understory of these hilltop and slope communities is characterized by the conspicuous abundance of several hawthorns (*Crataegus* spp.) admixed by deciduous holly (Ilex decidua) and rusty blackhaw (*Viburnum rufidulum*) - the species which are never abundant in the "typical" Loess Hills forests. The recently cleared upland patches are covered with the dense thickets

of these understory shrubs with smaller amounts of *Ostrya virginiana* and *Carpinus caroliniana*.

The pine oak communities of the hilltops and oak-pine communities of the slopes are early-successional in nature. They developed as a result of the clearcuts which most of the area underwent in the 1940s-1950s. It appears that much of the Sicily Island area was cleared at least twice: the first clearence took place early in the 20th century. The fact that in the historical past these uplands were likely to have belonged to the domain of the beech-magnolia forest is suggested by the occasional presence of large beech trees found here and there on the upper and middle slopes and, secondly, by the locally conspicuous presence of beech in the understory.

The late-successional forests of the "beech-magnolia" type survived as relatively narrow strips in the bottoms of some ravines. These relict assemblages are somewhat more heterogeneous than "typical" beech-magnolia forest. In particular, they represent the only late-successional community sampled in the Loess Region within this research that is characterized by co-occurence of the dominant shade-tolerant trees with loblolly pine. It appears that most of this forest has originated in the place of the cleared old-growth community back in the late 19th century or early 20th century. While most of the slopes and uplands were cleared yet another time, the forest in the ravine

bottoms escaped this misfortune and had a chance to enjoy a much longer period of uninterrupted succession which finally led to the re-establishment of somewhat modified beech-magnolia community. One hectare of this second-growth ravine-bottom beech-magnolia forest was sampled within this reserch. I also sampled one hectare of the canopy stratum of the early-successional slope forest but because of the lack of time and room it will not be discussed in this work.

The Poverty Point Site

The site is located in West Carroll Parish, northeastern Louisiana, on the eastern edge of Macon Ridge, an alluvial valley-train formation which was formed during the Wisconsin time. The Poverty Point site was acquired by the state for the preservation and exploration of the exceptionally large earthworks erected by the late Archaic Indians. It has the status of the State Commemorative Area and is operated by the Office of State Parks of Louisiana.

At Poverty Point, the surface of Macon Ridge is raised for approximately 20 feet above the Mississippi River floodplain forming a steep, highly eroded escarpment slope, which consists, to a large extent, of loess. Bayou Macon, a former channel of the Arkansas River flows southward at the very base of Macon Ridge forming a boundary between the upper ground and bottomland surfaces. With the exception of several Indian mounds, the Poverty Point area itself is

characterized by the slightly undulating, nearly flat landscape broken only by few shallow and narrow gullies meandering across the site in different directions. The local soils developed on the relatively thick - about 4 meters - loess mantle. Underlying the loess banket are valley-train deposits which form a base of Macon Ridge.

The site is largely deforested. The narrow bands of the early-successional forest flank the shallow gullies running through the site. The forest also covers the eastern slope of the Macon Ridge escarpment. Despite the early successional nature of the Poverty Point assemblage, it will be briefly considered in this work along with the late-successional stands because of the lack of the better sites on Macon Ridge. Macon Ridge is so badly deforested that to find any contiguous forest site in this region is difficult.

The Poverty Point site was the only one on Macon Ridge where I was certain to find at least some forest left and, secondly, it was the only site which had a relatively well recorded history of land use. All the area has been almost continuously cultivated since the late Ante-Bellum Period. The site was first cleared between 1840 and 1960. Another clearing of the remaining forests took place in the early 1960s. At this time much of the forest now present along the gullies and on the escarpment slope were cut. But some sections of the modern forest probably date back to at

least as early as 1930s. More than a half of the present-time Poverty Point site remained under agricultural fields before its acquisition by the state in 1968. Since that time, the forest along the gullies and on the escarpment slope finally had a chance to recover and slightly expand.

I sampled in total 0.25 ha of the forest both along the gullies and on the escarpment slope. The most mature tracts were selected. In terms in physiography and edaphic conditions all the forest in the area is undoubtedly representative of the upland type but it does not contain any beech and magnolia. This forest is characterized by the very diverse canopy stratum and a broad mixture of the bottomland and upland tree species.

Field Procedure

The optimum size of sampling area selected for this research was one hectare per site. In some sites, however, this size of sampling area was impossible to maintain - most notably due to the spatial limitations of the sampled habitats themselves. This is a reason why quarter-hectare and even one tenth-hectare sampling areas appeared in this research. In one case (Forked Island) the size of sampling area was limited due to my own time constraint. Less-than-one-hectare sampling areas give relatively good idea about the species composition and structure of a sampled forest site in terms of its dominant and structurally important

species but fail to give a representative sample of the site's biodiversity.

At each site one agregate sampling area consisted of randomly selected sampling plots 10m x 50m in size. The number of sampling plots depended on the size of sampling area: "typical" one hectare areas consisted of 20 sampling plots, 0.25 hectare areas were made up by 5 sampling plots etc. Sampling plots were selected along a transect which was established through representative forest, away from trails and recent anthropogenic disturbances. Sampling of the late-successional ravine forests was always undertaken consistently within middle and lower sections of the slope to avoid typically more disturbed upper-slope forests which developed in somewhat different edaphic regimes. When necessary, the mesic ravine bottoms were also sampled but the broad bottoms with floodplain vegetation were avoided or sampled separately from the slope forest.

The size and configuration of every transect depended strongly on size and configuration of the survived late-successional stands and local physiography. In localities where late-successional forest extended as long tongues in ravines, sampling plots were placed randomly within lower and middle sections of the right and left ravine slopes, parallel to the ravine bottom where the transect was established. In the areas where late-successional forests survived largely in ravine bottoms, like in Sicily Island,

the transect was again established through the middle of the bottom and the sampling plots were set alternatively in the right and left section of the bottom. In the late-successional stands which were more compact in size and shape and placed in the different physiographic framework, the sampling plots had to be established in somewhat different way. For instance, in the slope old-growth forest managed by the Louisiana State Arboretum, the sampling plots were run not parallel to the slope but from the middle section of the slope down to its footslope base. In this case the transect was established on top of the high ridge overlooking the slope.

Another option was impossible here because the slope facing Ferguson's Gully was broken by spur ridges some of which were culminated by walking paths. The similar strategy was applied in the Bluff Experimental Forest where half of the sampling plots also had to be established in "downslope" fashion because of very "spurry" slope relief. The small late-successional stand on the territory managed by the Department of Wildlife and Fisheries in the Tunica Hills, West Feliciana Parish was also sampled via two plots running down the slope, because of the spatial configuration of the site.

Stratification

The late-successional beech-magnolia forests are characterized by a rather complex vertical stratification.

Ecologists and biogeographers use latin word "stratum" (plural - "strata") to recognize in the structure of the forest certain important vertical sections. Of course, the vertical profile of forest ecosystem is lacking any sharp division lines. For this reason the vertical strata can not be unambiguously defined (Harcombe and Marks 1977). The designation of the vertical strata applied in this work is essentially an empirically correlated generalization based on a combined assessment of life forms, current and potential plant stature and species composition. Three major strata or layers based on the natural stratification of the mesic hardwood forests are recognized in this study: canopy, midstory or subcanopy, and understory. In addition, for the needs of this research the midstory and understory strata are subdivided into minor strata or sublayers. Total, seven vertical layers and sublayers were recognized during the sampling procedure.

In the present relict beech-magnolia forests the trees of the canopy stratum vary from very tall and tall to larger medium-sized averaging in height approximately from 30-32 m to 20 m. As a canopy tree, in this study was recognized any tree which had unobstructed crown and reached the height of 12 m and more.

In this research, all trees with obstructed canopies and all unobstructed trees which were less than 12 m tall are related to one of the several subcanopy strata. The

subcanopy life forms are represented in beech-magnolia forest by two major guilds of specialized taxa. The guild of midstory to understory specialists includes species of genetically small- to medium-sized trees which tend to congregate in the middle section of the forest continum. They also represent an important part of the understory but only rarely appear in the overstory.

Another large group is represented by the understory specialists. It includes shrubs and very small understory trees. These are limited almost exclusively to the lower stratum of the forest and only rarely sprinkle into its middle section. Intermingled in various proportions with the species of these two groups are immature individuals, juveniles and saplings of the canopy trees.

Based in part on the forest architecture and in part - on the prevalence of certain growth forms, beneath the forest canopy I recognized two major layers - the middle stratum or midstory (4 meters and above but below the canopy) and the lower stratum or understory (below 4 meters). The midstory stratum consists of the mixture of the midstory specialists and undergrowth of the canopy trees, with an occasional sprinkling of the exceptionally large shrubs in its lower section. The understory includes in various proportions understory specialists, undergrowth of the midstory specialists and saplings of canopy trees. The 4-meter division line applied to designate the midstory

from the understory is empirically conceived as an upper limit for shrubs and small understory trees. My field observations suggested that the diversity and frequency of occurence of the understory specialists drop abruptly above this limit.

Within the midstory I additionally differentiated a discontinuous layer of larger middle-size trees reaching anywhere between 10 and 20 m. in height whose crowns are placed immediately beneath those of canopy trees, and the lower sublayer which consists of small-sized and minor middle-sized trees reaching heights between 4 and 10 meters. The latter is characterized by much more abundant tree populations. In this work terms "midstory" and "subcanopy" are used interchangeably, whereas an additional term "immediate subcanopy" identifies specifically the upper section of the midstory stratum equivalent to the upper midstory.

The understory can be generally defined as a layer of shrubs and small trees. The density of the understory vegetation in the beech-magnolia forest may be very scarse in the section where the overstory is strongly dominated by beech and magnolia but can reach a rather considerable development in the less shady or gappy sections. The terms "shrubs" and "understory specialists" are frequently used interchangeably in this work in order to avoid repetitions. But it should be taken into consideration that these terms

are synonimous only in a broad sense - if one identifies certain woody life forms as "shrubs" based on their small size only. When it comes to the growth form, the situation becomes more complicated. In a narrow sense, shrubs are frequently defined as small-sized woody life forms with multiple stems. Such definition appear to be an oversimplification since among shrubs many are frequently represented by one-stem individuals and some species are predominantly monostemed.

Secondly, as it has been specified above, the understory flora also includes very small trees - with very short but singular and solid trunk. Such exceptionally small trees or treelets reach maturity in the lower section of the forest and only rarely reach into the midstory remaining throughout their lifespan well below the layer dominated by the typical midstory specialists such as American hornbeam, Eastern hophornbeam and flowering dogwood. Due to the mixture of plants exemplifying many life-forms and growth habits, understory is structurally the most complex stratum of the forest.

Within the understory stratum I identified the upper understory (2 meters and above but below 4 meters), the middle understory (1 meter and above but below 2 meters) and lower understory (25 centimeters and above but below 1 meter). Numbers of individuals and their dbh values were registered separately in each individual sublayer. Thus the

total midstory and understory values for every site are the agregate values of the related sublayers.

The subdivision of the subcanopy layers into more narrow sublayers was potentially important because it enabled me to recognize some intricate structural features of the beech-magnolia forests such as the variation of the life-forms and growth-sizes of certain species along the latitudinal gradient. Although not all expected variations of this kind were unambiguously validated in practice, this strategy proved helpful from yet another standpoint: it allowed me, when necessary, to analyze the data separately for every individual sublayer. When such detailed subdivision did not serve its purposes, it was always possible to transform "short" layers into broader, more inclusive strata.

All seedlings below 25 cm were included into the separate seedling stratum. The floras of ferns and lianas (among the latter only individuals reaching 2 meters and above in height were counted) were also quantified during this study. However, because of the lack of room, neither seedling populations, nor ferns and lianas will be discussed in this work.

Sampling Procedure and Plant Identification

Within each sampling area each plant was assigned a stratum category based on the height of the tallest stem. Stem diameters were measured for trees and shrubs in all

the strata and substrata mentioned above, except those which fit the category of seedlings (below 25 cm to the ground level). For trees and shrubs with the heights of 2 meters and above, diameter at breast height (hereafter, dbh) was measured at 1,7 m. For shrubs and small trees with the heights below 2 meters stem diameter was measured at the ground level (hereafter, dgl). The group of multiple stems coming from one point was considered as a single individual. For such plants dbh and dgl will be measured for all stems if the stems are within one strata. If the stems are distributed among 2 or several layers, only dbh or dgl values of the stem (or stems) belonging to the highest layer will be measured.

The absolute majority of trees and shrubs species were identified directly in the field. From those few that were not identified in the field, the samples were taken for identification in the Herbarium at Louisiana State University where I was given necessary help by Dr.Lowell Urbatsch and Dr. Tom Wendt. At the Department of Biology I was also given help by Dr. William Platt. Taxonomic nomenclature follows Radford et al. (1985); for the species of the Mississippi Embayment not found in the range covered by Radford et al. (1985), Clewell (1985) was consulted.

CHAPTER 3

NATURAL SETTING

Our perception of the lower Mississippi region is commonly restricted to the floodplain landscapes of the lower Mississippi Alluvial Valley, its extensive bottomland forests and somber swamps. However, the Mississippi River has also been an ultimate physiographic force that conditioned the development of the unique and some of the most striking upland landscapes of the Coastal Plain known as the Mississippi Blufflands.

Physiography and the "Loess Factor"

The Mississippi Blufflands are a narrow belt of the strongly dissected hilly land extending along the eastern margin of the lower Mississippi Valley for almost 800 miles, from Baton Rouge, southern Louisiana, to the southern tip of Illinois. The other name of this region, the "Mississippi Loess Hills" or simply the "Loess Hills", has reference to its most notable feature: the Blufflands are covered with a thick mantle of loess, a homogeneous, non-stratified, porous deposit consisting predominantly of yellowish brown eolian silt, with subordinate amounts of very fine sand and clay (Krinitzsky and Turnbull 1967). Loess was deposited on the hills bordering the escarpments of the Lower Mississippi Valley during the Pleistocene and early Holocene (Krinitzsky and Turbull 1967, Autin et al. 1991).

The origins of loess in the Lower Mississippi region are closely related to the Pleistocene glacial cycles and the resulting hydrocycles of the Mississippi. During the periods of the fluvial activity following each glacial stage, the Mississippi River and its tributaries carried an enormous amount of the organic and non-organic debris down stream. With return of the Mississippi drainage to the conditions of reduced flow, silt on the exposed surfaces dried up, and wind redeposited the resulted dry dust on the bluff escarpments.

Loess was deposited in a series of mantles following each of the Pleistocene glacial cycles. As many as three to four loess consecutive sheets such as the Marianna (the most ancient loess known only from Crowley's Ridge), the Crowley's Ridge Loess dated at 120,000 to 185,000 years B.P. by Johnson et al. (1984), the Sicily Island Loess which probably 75,000 to 90,000 years old (Johnson et al., 1984) and the Peoria or Vicksburg Loess were identified throughout the region (Wascher et al. 1948, Krinitzsky and Turnbull 1967, Snowden and Priddy 1968, West et al. 1980, Johnson et al. 1984, Miller et al. 1985a, 1985b, Rutledge et al. 1985). But only the most recent Peoria Loess associated with the last glacial cycle was more or less accurately mapped outside Louisiana (Krinitzsky and Turnbull 1967).

Loess was transported to the both sides of the Lower Mississippi River Valley but because of the predominantly eastward direction of the wind most of these eolian deposits were "intercepted" by the eastern escarpment. Over time the latter considerably outgrew its western counterpart. Throughout most of its range the Bluff Ridge rises abruptly like a wall above the flat landscape of the alluvial valley. It reaches up to 200 feet (66 meters) in height in the southern portion of the transect between Saint-Francisville, Louisiana, and Vicksburg, Mississippi.

Of course, not all of the Bluff has been built up with loess. Its base is formed by the predating ancient uplands which consist of coarse Tertiary sediments. However, the loess material makes up approximately as much as one third to one half of its total height. The loessial cap is especially thick in the section immediately adjacent to the Mississippi Valley where its average depth attains 15 meters. The maximum thickness of about 27 m is attained by the loessial mantle in the Natchez-Vicksburg area, southwestern Mississippi (Autin et al. 1991). The southernmost outcrops of loessial deposits extend from the southern suburbs of Baton Rouge to the southeast, in the general direction of lake Maurepas and eventuallly disappear in the extensive bottomlands of the Bayou Fountain and Amite River.

The Mississippi Loess Bluff is characterized by a rather complicated physiographic profile (Figure 1). The predominantly westerly winds that transported the dried silt from the alluvial surfaces of the Mississippi Valley deposited it in a way that the average depth of the loess mantle decreases logarithmically with a distance from the bluff escarpment. As a result, within the loess-capped area east of the Mississippi River one can distinguish two general divisions: a relatively narrow deep-loess section flanking the margin of the Lower Mississippi Valley and an essentially broader shallow-loess section further eastward. An abrupt and rather considerable thinning of the loess mantle in the close vicinity from the escarpment edge may serve as the natural physiographic boundary between these two sections.

A narrow section within which the depth of the loessial mantle decreases from 10 to 5 feet is characterized by a particularly sharp gradient of loess thinning. This is a "slope" of the Loess Bluff. The Geologic Map of Mississippi compiled by A. R. Bicker (1969) specified the upper boundary of the "slope" corresponding to a 10 feet limit as the eastern limit of the Loess Region. This compact western area of the eolian deposition will be considered in this work alternatively as the deep-loess section, the Mississippi Loess Bluff or the

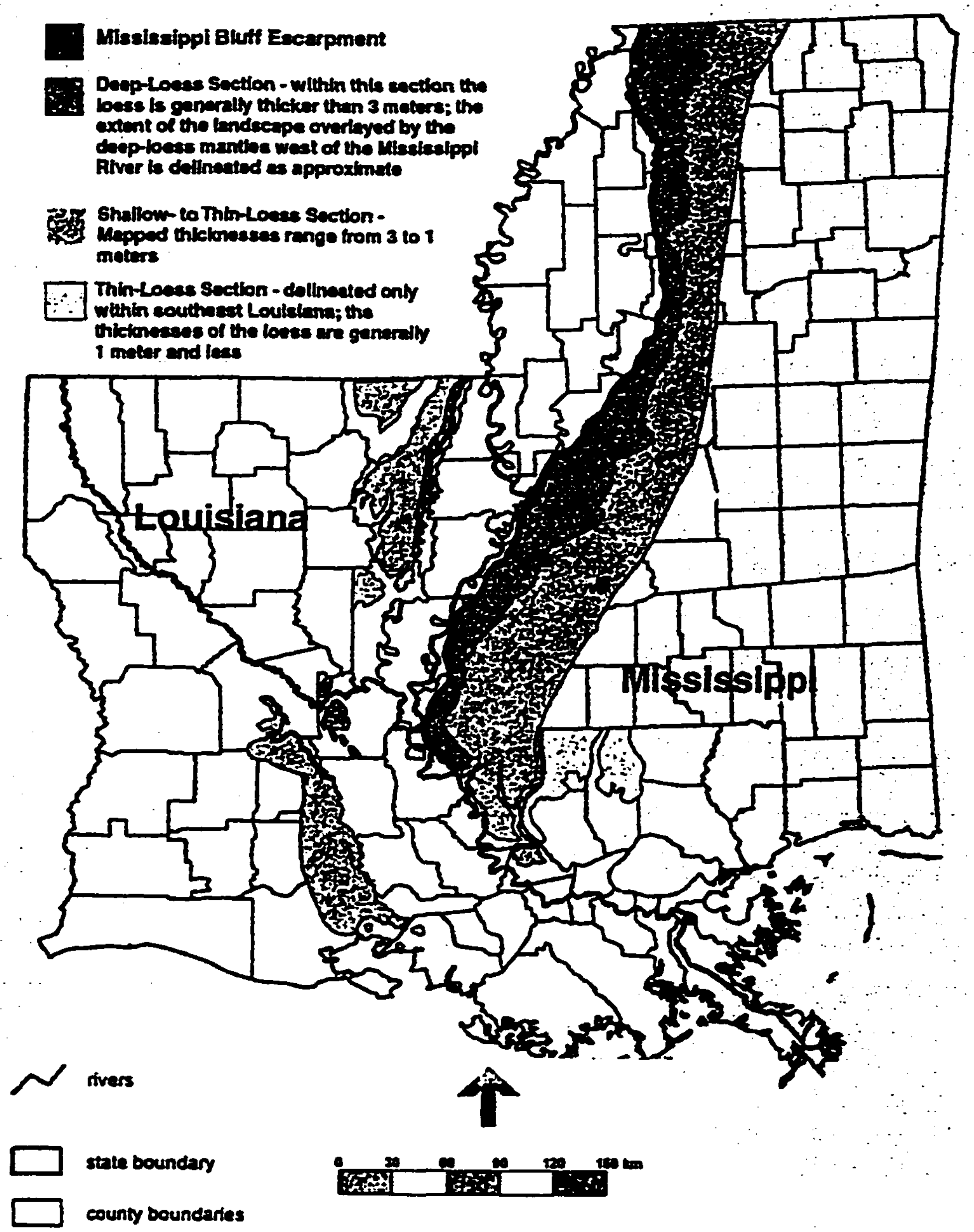

Figure 2. The Physiographic and Edaphic Conditions of the Southern Loess Hills

Sources: Biker A.R. 1969. Geologic Map of Mississippi, Scale 1:500,000; Braud, DeWitt. 1999. Louisiana GIS CD: A Digital Map of the State, Version 2.0

Blufflands *sensu strictu*. The deep-loess section was also recognized by Evans et al. (1983) as the Deep Loess Province or Deep Loess Hill and Bluff Region. This deeper section of the loessial belt within which the loess is generally thicker than 10 feet averages approximately from 12-14 to 35-40 km wide, with the extremes from 8 to 46 km.

East of the Bluff "slope", the average depth of the loess blanket decreases rather gradually, with a suggested average rate of thinning of about one feet (0,3 m) per mile with no regard to topography (Spicer 1969). Although the Geological Map of Mississippi indicated that "remnants of the mantle are present many miles farther east" of the 10 feet drop line, it essentially disregarded it as a part of the Loess Region. In this work this broad eastern margin of the Loess Hills will be considered as one of the subdivisions of the shallow-loess section. In southeast Louisiana, this shallow-loess belt was subdivided by Evans et al. (1983) into two subsections: Southern Loessial Loam Hills, Gentle Topography, characterized by a somewhat thicker loess mantle and Fragipan Loam Hills underlain by only a very thin layer of loess. Somewhere within Fragipan Loam Hills section the layer of loess gradually thins to the extent that its precise boundary with non-loessal surfaces becomes obscure and difficult to locate. The easternmost boundary of the shallow-loess section is

suggested to be Bogue Chitto River floodplain in Washington Parish.

Loess material consists primarily of quartz particles washed out from the Pleistocene glaciers and contains only small amounts of clay. Due to the humid climate of the Gulf Coastal Plain, the lack of clay particles makes loessial material highly susceptible to erosion. Since the time of deposition in the late Pleistiocene, the combined action of subtropical rains and innumerable small streams turned the loessial mantle of the Mississippi Bluff into a dense network of deep ravines divided by high, narrow hilltops and branching side slopes. Dissection is particularly pronounced along the western flank of the deep-loess section where the loess deposits achieve their maximum thickness forming a sort of a cap or crest over the remainder of the bluff ridge.

Thousands years of erosion created here a labyrinth of steep-slope loessial gorges with narrow meandering bottoms and towering, sharp-crested ridges. The main bottoms are entered under the different angles by the multitude of accessory ravines. Such ravines may range very deep into the ridge slope sometimes breaking through the hill into another drainage. Dissection of the Bluff escarpment was, in part, stimulated by the lateral movements of the Mississippi River. The ravine development was most intensive during the periods when the Mississippi shifted

eastward and, gradually eroding the basis of the Bluff edge, steepened the gradients of small tributary streams thus causing them to cut deeper into the loess mantle (Delcourt 1974). Today in the Tunica Hills this type of erosion slowed down because the Mississippi River deviated westward and the gradients of the tributary watercourses reduced. Many of them became smaller or more seasonal, other disappeared or nearly so. However, most of the ravine bottoms, especially the larger ones, still harbor narrow dry channels which become filled with water for a short time after strong showers. Such channels represent sandy-graveliferous beds which average from about three to six feet wide and deepened for about one, sometimes two or even more feet into the bottom of a ravine. These sands and gravels are washed out by streams from the underlying Citronelle deposits. Because of the humid microclimate, sand and gravel remain moist most of the time and dry only on the surface. Larger accessory stream beds may have small nearly permanent ponds which generally last from shower to shower. Some narrow stream beds with clayey bottom sections may also contain such ponds, particularly those hidden deep under the forest canopy.

Although the gradients of the tributary streams in the Tunica Hills and other escarpment areas decreased, erosion remains an important shaping factor of their physiographies. Exposed to erosive influence of strong

subtropical rains and temporary watercourses the steep slopes of the escarpment ravines are plagued by the perpetual physiographic disturbance in the form of frequent small landslides. The moist microclimate of this heavily dissected section per se is an equally important erosive factor because it conditions the constantly loose condition of the loess material and stimulates its self-imposed downsliding. Medium- and even large-size landslides, although relatively infrequent, also happen in the escarpment zone.

The intensive and perpetual erosion of the loess mantle in the escarpment zone results in the considerable diversity and complexity of relief forms. They range from narrow canyons and cliffs with near-vertical faces of loess to somewhat broader creek valleys and circular- to round-shaped coves developing between more or less gently-sloping spurs. Sometimes the massive sliding of the loess material immediately from the ravine slope results in the formation of the oval coves with narrow "neck", gently rising floor and nearly vertical walls. Over time such coves may evolve into a new accessory ravine. Landslides frequently result in the formation of vertical faces and walls of loess where it is exposed to weathering. Despite their seemingly fragile appearance, many of such exposed vertical surfaces are able to persist for years because of the carbonate and ferruginous cementation of their constituent silt particles

(Delcourt 1974). Conspicuously bright - from yellow-orange to red-orange - in color and highly variable in size, these vertical faces represent one of the remarkable physiographic components of the escarpment area landscapes. Medium- and large-size landslides typically produce high, strikingly scenic cliffs that may reach as much as 20-30 meters high and tens of meters in length along the base.

The shallow-loess zone east of the "fall line" is characterized by the landscape of gently rolling hills and relatively shallow and broad ravines with gentle/smoothly shaped slopes. No sign of erosion was registered in this section. The same topographic trend is characteristic for the southernmost end of the Mississippi Bluff south of Saint-Francisvilie. The height of the Bluff escarpment at Port Hudson has an average elevation of about 100 feet compared to about 200 feet in the Tunica Hills area. Consequently, the physiographic dissection of this area is essentially more shallow than that of the deep-loess section. The relatively small vertical faces of loess and shallow canyon-like ravine sections still occur in the the Vicinity of Port Hudson, particularly closer to the escarpment but they relatively uncharacteristic. Gently-sloping ravines predominate. As the Bluff decreases in height from Port Hudson southward to Baton Rouge, the topography grows increasingly more gentle, the density and

complexity of the drainage system diminishes and ravines become less numerous per an area unit.

On the other side of the lower Mississippi Valley loess formed a chain of fragments broken by the major tributary floodplains. It was deposited here on the surfaces of the different origins. Crowley's Ridge in north-eastern Arkansas and extreme south-eastern Missouri, as well as Sicily Island in the northern part of east-central Louisiana both are segregated portions of the western bluff which had been cut off from the upland surfaces by the meandering action of the ancestral Ohio and Mississippi rivers but survived its later meandering action. Being completely isolated from the other upland surfaces, Crowley's Ridge extends through the middle of Mississippi Valley for about 200 miles from Helena, eastern Arkansas north to near Commerce, Missouri. It rises to as much as 250 feet above the flat floodplain floor. The sedimentary rocks that compose the ridge are, in fact, of the same age as those of the bluff (Fenneman 1938). Both in Crowley's Ridge and Sicily Island the Pleistocene loess overlays the deeply eroded Tertiary strata (Bennet 1921, Autin et al. 1991).

The Marksville Prairie, the Marksville Prairie of central Louisiana and the Grand Prairie of Arkansas are the remnants of the Pleistocene fluvial terraces. The Western Lowlands and St. Fransis Basin in north-eastern Arkansas

and south-eastern Missouri as well as Macon Ridge in north-eastern Louisiana were formed during the fluvial periods of Wisconsin time as a result of the massive deposits of glacial outwash of the Mississippi and Ohio Rivers (Saucier 1964, 1967, Smith and Saucier 1971, Autin et al. 1991). Loess has been also deposited on the eastern edge of the Prairie Complex in south-central Louisiana which rises 12-15 meters above the floor of the Atchafalaya delta and Red River Valley (Daniels 1968, USDA 1974). This section is also known as Opelousas Ridge (Evans et al. 1983) and western (or southwestern) bluff. The southernmost loess-covered surfaces in Louisiana are salt domes located in the coastal section of the Atchafalaya Delta. These structures represent the islands of the upper ground surrounded by the vast expanses of the alluvial swamps and coastal marshes. Of six salt domes the largest are Avery Island, a nearly circular, dissected mound rising up to 48 meters above mean sea level, and Jefferson Island elevated for more than 23 meters (Autin et al. 1991).

Most of these western loess deposits were not even nearly as deep as those along the eastern margin of the lower Mississippi Valley. For example, the eastern edge of Macon Ridge is covered by the loessal mantle of no more than 4 m deep and this thins progressively further westward (Autin et al. 1991). This is quite "thick" by the western standards but seems to be marginal for the eastern bluff.

The single loess sheat overlying the easternmost section of Prairie and intermediate terraces in south-central Louisiana is also essentially more shallow than the loess mantle of the Mississippi Bluff and, like Macon Ridge loess, quickly thins in the western direction (Daniels 1968, Evans et al. 1983, Autin et al. 1991). One of the few notable counterparts of the Loess Bluff west is of the Mississippi River is Crowley's Ridge. The depth of the loess cap within the southern part of Crowley's Ridge are in some places 50 feet thick. The loess deposits of Sicily Island seem to be relatively shallow and, perhaps, patchy in nature. It appears that much of the loess material in Sicily Island has been washed from the hilltops to the ravines and lower slopes. The historical deforestation (once the Sicily Island was almost completely cleared) may have played an essential part in this process. Travelling throughout the area, one can observe locally the conspicuous signs of loess erosion and gullying on deforested slopes. However, unlike in the Tunica Hills, the erosion processes in Sicily Island immediately reveal its limitations due to the shallow nature of the loess mantle and its complete dependence on the anthropogenic disturbance.

It should be pointed out that the terminology applied by Louisiana geologists regarding the depth of the loess deposits on the state's maps (Lytle and Sturgis 1962, Braud

et al. 1999) is "less conservative" than that of their Mississippi collegues. In Louisiana all loess deposits with the depth of 1 meter or more are officially considered as "deep". It may be a confusing nuance for a reader because in this work I consider as "deep" only those deposits which are at least 3 meters thick. Terms "deep loess deposits" or "thick loess deposits" are also potentially confusing when applied without a reference to the actual depth in Louisiana-related literature. For instance, the loess-capped portions of Montgomery Formation and Prairie Terrace in south-central Louisiana are said to be blanketed by "thick loess deposits" (Touchet and Daniels 1970, USDA 1974), however, with no indication of how thick they are. It appears that the spatial dynamics of the loess distribution in these areas may be comparable to those observed in Macon Ridge. In other words, within the area of Opelousas Ridge, the depth of the loessial mantle may approach or slightly exceed 3 meters only in extreme eastern section which is immediately adjacent to the Atchfalaya floodplain. Consequently, only this narrow section and not the whole southwestern bluff is hypothesized to be a part of the deep-loess section on the basis of the classification system applied in this research. Still, what can be "thick" by the western standards but relatively marginal for the the eastern bluff. Thus, with the possible exception of the narrow

eastern strip of the southwestern bluff, extreme eastern margin of Macon Ridge and most of Crowley's Ridge, the western Loess Hills can be generally classified as representative of the shallow-loess section, although the concrete boundaries here are still difficult to draw due to the lamentable lack of the data.

The poor state of our knowledge on loessial distribution serves as an obstacle for the biogeographer. Not only the depth of loess deposits, but the very fact of their presence in a given area may represent an unanswered question. For instance, loess was overlooked in the narrow area around Chicot Lake (Lytle and Sturgis 1962). The failure to discover loess in this area is particularly surprising due to the fact that Chicot Lake is literally squeezed from nearly all sides by two large "deep-loess" regions - Montgomery Terrace and Opelousas Ridge. According to Lytle and Sturgis (1962) and Braud et al. (1999), "deep-loess" areas begin only 1.14 km east and 1.94 km south and 2-3 km west of the site. Although the depth of the loessial mantle around Lake Chicot is difficult to estimate, loess is undoubtedly present in the area. The small vertical faces of loess material can be observed here and there in Chicot State Park (especially along the lake-facing slope) and on the ravine slopes of Louisiana State Arboretum.

Only few of the western loessial "islands" such as Crowley's Ridge and Sicily Island, a relatively small hilly

area adjacent to the southern tip of Macon Ridge, have a pronounced relief. The extreme northeastern section of the western loess bluff in south-central Louisiana locally also has great variation in relief. The northern limit of the southwestern Loess Hills is made up by the eastern, loess-capped section of Montgomery Formation which occupies the northern part of Evangeline Parish in Louisiana. This generally gently rolling upland area has the greatest variation in relief in its northern and northeastern section immediately adjacent to the lower Red River Valley where it rises about 24 to 30 meters above the floodplain floor. The escarpment here is steep and highly dissected by ravines (USDA 1974).

The area of Chicot Lake adjacent to the Montgomery Terrace from the southeast is gently rolling but it also have locally pronounced variations in relief, especially around the lake. The topography of the land managed by the Louisiana State Arboretum is almost as dramatic as that of the Tunica Hills escarpment, although slopes here are not so steep and the dissection is far less complex. Further southward the altitude of the western loess bluff progressively decreases and so do the dissection and contrasts of the relief. Throughout most of the Opelusas Ridge, the loess-capped surface of the Prairie Formation is characterized by the level to nearly level (slightly

undulating) physiography (USDA 1974) which contrasts strongly with that of the eastern bluff.

Loess as an Ecological Factor

Once established, the loessial cap became a critical factor in the ecological history of this upland region. Most of the Coastal Plain uplands are underlaid with highly transmissable sandy, sandy-clayish and sandy-graveliferous substrates which are charaterized by low fertility and poor to very poor capacity to retain moisture. The rain water quickly percolates through these porous sediments to the depths where it is beyond the reach for the most moisture-loving species of hardwood trees and shrubs. Before the advent of the Europeans, the extensive upland watersheds of the Southeastern Coastal Plain were covered with the xeric conifer forests dominated by several species of southern pines which were better adapted to such harsh edaphic conditions.

The sandy-graveliferous deposits of the Citronelle and other formations which underlay the Mississippi Bluff are also excessively well-drained and poor in available nutrients. However, the thick mantle of loess overlying these coarse sediments causes a strong modifying influence on the local edaphic conditions. Since the loessal deposits consist largely of silt derived from organic-rich debris, the fertility of the Bluffland soils rivals that of the richest bottomland sites. Much of the Loess Hills Region is

underlain by silt loams, primarily gray-brown podzolics of the Alfisol soil group (Spicer 1969). The calcareous material, an important fertilizer dominant in the loess chemical structure, was of particular ecological significance for the development of these highly productive upland soils.

Fertility is not the only advantage of the soils developed on the deep-loess deposits. Loess also has a good capacity to keep moisture. Its fine silty texture prevents the fast loss of water through the downward percolation. On the other hand, the loessial deposits are still porous enough to provide a good drainage and soil airation which are typically complicated in the bottomland soils. The unique combination of the loess' properties made the edaphic conditions of the deep-loess region optimal for the development of some of the most magnificent and peculiar hardwood ecosystems of the southeastern United States. Throughout the deep-loess section the dominant formation is represented by well drained Memphis soils which have a dark grayish-brown silt loam surface and a dark brown silty clay loam to silt loam subsoil (Evans et al. 1983). The original soils of the "bluff plateau" were typically from four to seven feet deep. They were considered "first class upland" and contributed to the rise of the Bluffland region as one of the major foci of the southern plantation agriculture (Coles 1997).

Thinning of the loess mantle eastward from the Mississippi Bluff causes a "chain reaction" of the various edaphic factors which conditions a gradual but rather pronounced change of soil and environmental conditions (Spicer 1969). Increasing proximity of the sandy-graveliferous deposits of the Citronelle to the land surface along the gradient of loess thinning results in the progressively more well-drained and nutrient-deficient soils. The Citronelle deposits are especially poor in calcium. Consequently, in contrast to the calcium-rich soils of the Mississippi Bluff the soils of the shallow-loess section are typically calcium-deficient. The progressively faster drainage on the shallow-loess surfaces east of the Bluff leads to the increasingly more xeric conditions and leaching of carbonates from upper soil horizons. Finally, the combination of the calcium and carbonate defficiency with the high soil permeability contributes to the increase of both soil acidity and the extent of development of a fragipan layer (Spicer 1969, Evans et al. 1983).

Memphis soils are formed on the deposits which are more than 48 inches thick (Evans et al. 1983). In other words they underlay only the deep-loess deposits of the Mississippi Bluff area and the adjacent western part of Southern Loessial Loam Hills section. However, within the Memphis soil formation, there appears to be a transition

from fertile and better moisture-holding soils of the western section to more nutrient-defficient and permeable soils of the eastern section. With the further thinning of the loess mantle, Memphis soils are replaced by poorer Loring and Providence soils which occupy the eastern part of Southern Loessial Loam Hills. Loring soils have a brown silt loam surface and loam subsoil with a fragipan layer at about 23 inches in depth (Evans et al. 1983). They exemplify the transition between the rich soils of the Mississippi Bluff to the poor soils of the Providence group. The latter developed over the very thin veneer of the eolian deposits characteristic for the extreme eastern margins of the Loess Hills. These well-drained soils are characterized by a dark silt loam surface and a strong brown silty loam subsoil with a thick, compact, and brittle silt loam and loam fragipan at about 23 inches depth (Evans et al. 1983). The Providence soils range into Fragipan Loam Hills section where they co-occur with the Ruston and Lexington soils formed on the loess-free surfaces. The Ruston soils, for example, developed on Coastal Plain loams where thin deposits of loess were washed from from ravine slopes (Evans et al. 1983).

On the extreme southern margin of the Mississippi Bluff where the depth of the loess deposits is also decreasing, the soil conditions reveal a more complicated trend. South of Saint-Francisville, an abruptly decreased

depth of the loess blanket also results in the proximity of the porous Citronelle deposits to the land surface. The tongues of Citronelle under the more shallow mantle reach the area of Port Hudson (Durham et al. 1967). This may causes the partial edaphic similarity of this area with the eastern Bluff "slope" where the loess mantle is between 3 and 1.5 meters deep or with the transitional Loring soil subsection which is shifted somewhat further eastward.

The Port Hudson area is dominated by the soils of Olivier-Calhoun-Loring association (Soil Surveys Maps: East Baton Rouge and East Feliciana Parishes, September, 1968). Despite the gradual thinning of the loess mantle further southward, the permeability of the soils of the Baton Rouge Terrace is rather low. The dominant soil type here is represented by the Olivier soils, a somewhat poorly drained kind, which are also found in the flatwoods of southeastern Louisiana. Another component, the Calhoun soils, are characterized by even a poorer drainage. This soil type is predominant in the wet flatwoods of the southeastern Parishes. In Baton Rouge Terrace it is limited to the lower local elevations, whereas the higher elevations are dominated by the Olivier (Evans et al. 1983).

The reasons for the generally poor permeability of the Baton Rouge Terrace soils could be related to the

fact that southward, as pointed out by Delcourt (1974), the sediments of the Citronelle are characterized by the considerable increase in the relative percentage of silt and clay, and the progressive decrease in amounts and mean grain size of gravel and sand. According to Durham, et al. (1967), the Citronelle sediments, in fact, do not extend south of the Port Hudson area where they are replaced by the deposits of Port Hickney Terrace.

The soil associations of Macon Ridge are quite similar to those of the Baton Rouge Terrace. Predominant here are moderately well-drained Loring and Grenada soils in combination with poorly drained Calhoun soils and somewhat poorly drained soils of the Calloway formation. All of these formations, except the Calhoun, have a fragipan (Evans et al 1983). Of particular interest is absence in this region of the "classic" loessial soils of the Memphis group - despite the relatively deep loessial deposits in the eastern section of the ridge.

The marginally deep deposits of the extreme eastern edge of the Prairie Terraces of south-central Louisiana feature the transition from from Memphis soils on the marginally deep deposits in the section immediately adjacent to the bluff escarpment the to Loring soils in the more marginal shallow-loess section and then to the series of wet prairie soils - Coteau, Jeanerette, and Patoutville which also developed under thin loess cover

(Evans et al 1983). The moderately steep slopes around the Chicot Lake are generally dominated by McKamie-Dossman-Kenney association developed over shallow, pre-Prairie age loess (USDA 1974, Braud et al. 1999). These are loamy, well-drained soils characterized by moderately rapid to very slow permeability (USDA 1974). More gently sloping areas are dominated by the Wrightsville-Vidrine association which are relatively poorly drained and slowly permeable (USDA 1974).

The Sicily Island area is dominated by Memphis-Smithdale-Oula association which is related to Memphis-Calhoun-Loring series (Braud et al. 1999) developed over relatively shallow loess mantle. Some of the hilltops and slopes appear to be nearly devoid of the loess material due to erosion. On the other hand, the presence of the Memphis formation suggest that parts of this area are underlain by the loess mantle deeper than 1 meter.

Climate

The latitudinal extent of the Loess Hills accounts for a considerable thermoclimatic variation along its length. The southern and middle portions of the region from northern Tennessee gulfward were classified by Trewartha (1968) as humid subtropical. The northernmost part of the Loess Hills from northern section of Tennessee northward to southern Illinois is characterized by warm-temperate climate (Trewartha 1968). The

transition to cool-temperate climates starts north of the average January isotherm 0 C well above the northern limits of the Lower Mississippi River Bluff.

The climatic pattern in the Loess Hills is strongly influenced by the warm and moist tropical airmasses emanating from the Gulf of Mexico (Rumney 1968). In the summer time the tropical air floods all over the Lower Mississippi Valley and the variations in the average temperatures between the northern and southern portions of the region tend to be rather insignificant - ranging from +26 - +27 C at the Mississippi-Ohio confluence to +28 - +29 C in southern Louisiana (Wernstedt 1972, Quale and Presnell 1991). The summer months in southern Illinois and western Kentucky are almost as obsessively hot and sultry as they are in southern Louisiana and southwestern Mississippi.

In the winter time the warming influence of the Gulf air masses gradually decreases from the south to the north. As a result, the latitudinal variation in the average winter temperatures between the northern and southern ends of the Loess Hills is quite prominent. The average temperatures of January range from +2 C - +3 C in southern Illinois to +11 C - +12 C in southern Louisiana (Wernstedt 1972, Quale and Presnell 1991). The southern section of the Loess Hills which is subject to this research project represents the warmest part of the

region. The average temperature of January here fluctuates from +9.5 C in Vicksburg, Mississippi, to +11 and +12 C in Baton Rouge, Louisiana. One of the distinguishing features of the North American humid subtropics pointed out by Trewartha (1970) is that the relatively high average winter temperatures (which are, in fact, about three times higher than in the East Asia, a geographic counterpart of the Southeastern United States in the Old World) are accompanied here by anomalously low minima. For instance, New Orleans where the average January temperature is 55 F has an absolute minimum as low of 7 F has been recorded.

The variations in the precipitation are comparatively insignificant throughout the Loess Hills region ranging from 1600 mm in southern Louisiana to 1300 mm in southern Illinois (Wernstedt 1972, Quale and Presnell 1991). The variation is predominantly latitudinal in nature because considerable part of the rainfall, especially in the southern section, is associated with the circulation of the Gulf Airmass. In the southern section of the region, summer rain is normally associated with convectional thunderstorms, whereas winter rainfall is primarily a consequence of frontal cyclonic storms (Christensen 1988). The summer storms are mostly of local origin and typically of short duration. They develop as the humid tropical air masses

moving from the Gulf of Mexico contact with the heated land surfaces. The contact results in increasing instability due to warming at their bases and thus leads to convectional overturning (Trewartha 1968).

In the winter, the northward movement of the warm tropical air masses over the relatively cool land surface results in chilling of the air at their bases thus leading to high aerodynamical stability which prevents convection. Most of the winter precipitation comes with prolonged cyclonic rains accompanied by a persistent cloud cover over vast areas. Such rains, as a rule, are less intensive than the summer showers but, due to their persistent nature, may result in a higher daily or weekly rainfall. Gloomy, rainy weather with overcast skies may persist for days or even weaks during the winter.

Although the rainfall in the Loess Hills is distributed more or less evenly throughout the year, most of the region is characterized by the cool-season maximum. Only the extreme southern end of the Loess Hills is characterized by the warm-season maximum (Trewartha 1968, 1970). This has to do with the fact that the amount of convectional rainfall gradually decreases inland. Much of the convectional moisture tends to fall within the narrow coastal section which is characterized by the most frequent summer showers. As a result, some of those relatively short but intensive tropical thunderstorms

that are common in the area of Baton Rouge and Port Hudson from late June through September simply do not reach the Tunica Hills. As a matter of fact, nearly the whole area of the Loess Hills, with the exception of southern Illinois and northwestern Kentucky in the north and southern Louisiana south of the Tunica Hills where winter and spring have more or less equal rainfall amounts, lies within the zone of the winter maximum which reaches its peak in north-western Mississippi (here the winter rainfall makes up 120% of the spring rainfall). This rainfall pattern was considered by Trewartha (1970) as somewhat anomalous - due to the fact that the cold-season maximum was not registered in any other inland subtropical area on the leeward side of a great continent.

Brief Summary and Conclusions

The Loess Hills of the Mississippi Embayment form physiographicly, edaphically, and phytogeographically unique region of the Southeastern Coastal Plain. From the south to the north they make up a natural transect unobstructed by major changes in physiographic and edaphic conditions. The variation in the depth of the loess mantle provides another gradient of the biogeographic change - roughly east, south (south of the Tunica Hills, Louisiana), and west (across the Mississippi River) from the Mississippi Bluff Escarpment.

The combination of the bioclimatic and edaphic gradients creates a unique spectrum of biogeographic change unparallelled by any other region of the Coastal Plain.

CHAPTER 4

THE ORIGINS AND PRE-ANTHROPOGENIC EVOLUTION OF THE MIXED DECIDUOUS-EVERGREEN BEECH—MAGNOLIA FORESTS

The original forests of the southern and perhaps the middle section of the Loess Hills represented a relic fragment of one of the most ancient hardwood ecosystems in North America. Their antiquity is comparable to that of the tropical rainforests. Although these assemblages have experienced some rather pronounced climatic oscillations and compositional changes, their evolution has remained continuous since the early Tertiary times.

Mesic Hardwood Forests in the Tertiary Period

The history of the forests from which the present-day assemblages of the Loess Hills have originated can be traced back to the early Eocene, or some 40 millions years ago. At this time eastern North America was located in somewhat lower latitudes than it is now (Dietz and Holden 1970), the Rocky mountains did not exist and, as consequence, there was no dry shade effect which determines today the presence of the broad grassland belt extending across the middle United States. In the conditions of the equable early-Tertiary climate (Axelrod 1965, 1968) the distribution of the major forest zones in the southern and middle sections of North America was conditioned more by altitude than by latitude.

In the broad paleobiogeographic perspective, the modern beech-magnolia forests represent the product of the mutual diffusion of the Arcto-Tertiary and Madro-Tertiary geofloras both of which once formed more or less distinct forest types. The evergreen to evergreen-deciduous forest dominated by the sclerophyllous Madro-Tertiary geoflora extended in Eocene from the middle altitudes of Central America through the Mexican uplands and Sierra-Madre Occidental deep into North America. In the early to middle Eocene the northwestern extensions of this forest reached the present-day Colorado, Wyoming and Oregon, while their northeastern shoulder protruded well into the Appalachian region (Axelrod 1975).

The mixed Madro-Tertiary forest may have closely resembled - both physiognomically and compositionally - the present-day broadleaf evergreen forests of southern and southeastern China, southern Japan, and northern Taiwan. These are variously known as Subtropical Broadleaf Evergreen Forest (Wu 1983) and broad-leaved evergreen forests of the subtropical zone (Hou 1983). In the conditions of the highly equable Eocene climate they could have been locally enriched by some tropical taxa as it suggested by occurrence of *Cedrella*, *Cordia* and *Meliosma* in the Miocene deposits of Nebraska. The relict remnants of the Madro-Tertiary geoflora are represented in the present-day forests of the southern Loess Hills by their evergreen

and perhaps some semi-evergreen to deciduous subtropical components (Axelrod 1968, 1975).

The temperate to warm-temperate broadleaf forests dominated by deciduous Arcto-Tertiary geoflora probably occupied the northern parts of North America in early-Tertiary times (Axelrod 1983). These are now covered by the cool-temperate deciduous and boreal coniferous forests. It was the predominant vegetation type from the northern section of the present-day United States north to the Arctic Circle (Graham 1964). In Alaska, the Arcto-Tertiary geoflora ranged northward to latitude 67 degrees, with a boreal unit extending to within 8 degrees of the North Pole (Chaney 1947). These forests extended southward along the Appalachian mountains but appeared to have been limited there to relatively high altitudes (Axelrod 1965). Attenuated southern extension of the warm-temperate deciduous forest may have also existed within the higher altitudes of the Mexican uplands (Axelrod 1975).

The taxonomic composition of the Arcto-Tertiary deciduous communities is exemplified by the south-Appalachian assemblages from northern Alabama (the Claiborne flora) which contained in Eocene a rich assortment of the temperate genera (*Fagus, Quercus, Carya, Acer, Ulmus, Tilia, Celtis*, and *Ostrya-Carpinus*) (Gray 1960, Graham 1964). Although the deciduous Arcto-Tertiary forest apparently did not spread as a distinct vegetation

type much into the middle latitudes, the equable climate did favor, as mentioned above, the expansion of the temperate deciduous components from their native thermal zone in the higher latitudes southward and from the higher altitudes downslope into the zone dominated by the evergreen Madro-Tertian flora (Axelrod 1975).

The broad transitional ecotone of the evergreen-deciduous and deciduous-evergreen forests existed between the Madro-Tertiary and Arcto-Tertiary floristic provinces in the interior sections of eastern North America. Along the north-eastern maritime margin of North America this transitional belt extended well into high latitudes. The mixed, deciduous-evergreen warm-temperate to subtropical floras represented by *Juglans, Nyssa, Carya, Aristolochia, Sapindus* and *Cinnamomum* were reported, for instance, from the lignite deposit of Brandon, Vermont (Berry 1930).

Even richer (with nearly 300 species) mixed Eocene floras indicative of this transitional biotope were found close to the Arctic Circle in Greenland. The local assemblages contained *Fagus*, 5 species of *Acer*, 15 species of *Quercus*, 9 species of *Juglans, Castanea, Fraxinus, Ulmus, Nyssa, Cornus, Patanus, Populus, Salix, Ginkgo*, 7 species of *Lauraceae*, 5 species of *Andromeda*, 6 species of *Magnolia*, 2 species of *Palmaceae*, 27 conifers including *Taxodium* and *Sequoia* and numerous temperate to warm-temperate understory forms (Berry 1930).

Apart from intermingling with the evergreens in the belt dominated by the Tertio-Madrean flora, the deciduous components may well have infiltrated, at least later, in Miocene, even into some coastal tropical forests. This fact could be suggested by the presence of the pollen of such typical cool-temperate genera - if only this pollen was not transported from the adjacent mountains as suggested by Axelrod (1975) - as *Fagus, Juglans, Populus*, and *Alnus* in the middle Miocene Paraje Solo Formation on Veracruz's coast, eastern Mexico (Graham 1964).

Through the Eocene the lowland evergreen tropical forests extended from Central America along the eastern coast of Mexico north to the outer margins of the Mississippi Embayment (the latter was largely submerged at this time). The forests which covered the maritime seaward fringe of the Mississippi Embayment during this time, appear to have been located in the closest geographic vicinity to what later became the Mississippi Blufflands. These low-lying coastal environments supported diverse and mixed assemblages (the Wilcox flora) dominated by the tropical taxa such as *Cedrela, Nectandra, Coccoloba, Banksia, Ficus* (represented by many species), *Engelhardia, Artocarpus, Annona, Sterculia, Canna*, as well as *Sabalites* and *Persea* whose living relatives are today tropical to subtropical in distribution. Interestingly enough, the western section of the Mississippi Embayment exhibited more

floristic affinity to the Madro-Tertiary flora and modern floras of Mexico and Central America, while the eastern side was dominated by the flora derived largely from the Antillean region. Wilcox flora is one of the largest floras known in North America, with over 500 taxa listed (Berry 1930). Despite the general predominance of the tropical forms, its biogeographic status is difficult to define because the tropical taxa appeared to have coexisted in these maritime assemblages with numerous warm-temperate to subtropical components represented by *Magnolia, Ilex, Bumelia, Liquidambar, Taxodium, Nyssa, Aralia, Diospyros, Rhamnus, Myrica*, et cet. Moreover, many representatives of the currently temperate to cool-temperate, predominantly interior genera such as *Juglans, Carya, Fraxinus, Asimina, Cornus, Aralia, Cladrastis, Cercis* and others also occurred in these forests (Berry 1930, Graham 1964).

The possibility exists that some of the plant remains may have been transported to the maritime margins of the Mississippi Embayment from the adjacent highlands. However, once again, according to Axelrod (1958, 1966), the mixed nature of the Eocene vegetation may be better explained from the standpoint of the highly equable early-Tertiary climate which conditioned the narrower altitudinal zones and thus contributed to the greater mutual diffusion of the different floras. The confirmation of the possibility of such biogeographic scenario comes from some modern

communities. The closest present-day biogeographic analogues of the Wilcox maritime assemblages are the montane forests of eastern and southern Mexico, which are characterized by the striking mixture of the Neotropical evergreen and temperate to warm-temperate deciduous taxa (Rzedowski 1978).

The maritime Eocene floras of the Mississippi Embayment may be likewise indicative of the marginally tropical conditions. Later, in Miocene, the cool-temperate deciduous components may well have infiltrated even into some southern tropical forests. This fact could be suggested by the presence of the pollen of such typical cool-temperate genera (if only this pollen was not transported from the adjacent mountains) as *Fagus*, *Juglans*, *Populus*, and *Alnus* in the middle Miocene Paraje Solo Formation on Veracruz's coast, eastern Mexico (Graham, 1964). Interestingly enough, such typical Holarctic genera as *Fagus*, *Quercus*, *Populus*, and *Salix* were not yet represented in the Wilcox flora.

Throughout the Eocene, there appear to have been a steady progression toward more tropical conditions which culminated in the late Eocene and early Oligocene (Berry 1924). During the Eocene, the neotropical flora in the Mississippi Embayment extended as far north as latitude 37 degrees (Berry 1930). The coastal plain floras of these periods, marked with the presence of the tropical *Palmaceae*

appear to be most tropical of all known in the southeastern United States, as pointed out by Berry (1930). The trend toward cooler and more continental climate became pronounced at the end of the Oligocene and progressed during the late Tertiary (Axelrod 1975), as North America has been apparently shifting poleward (Wolfe 1986) and surrounding seas regressing (Graham 1964). This cooling trend resulted in a differential loss of warm-loving evergreen taxa from the interior Appalachian and the more seaward Coastal Plain forests.

Axelrod (1975) has suggested that most evergreen components were wiped out by increasingly colder winters from the Appalachian area as early as in the middle Oligocene. By the early Miocene the Madro-Tertiary flora is hypothesized to have become shifted from the interior to the Gulf coast and isolated from the similar forests of Mexico (Graham 1964, Wolfe 1985, 1986). These biogeographic changes were accompanied by the loss of some tropical components that had been previously present in the maritime environments of the Coastal Plain (Graham 1964, Wolfe 1985, 1986). By the end of the Tertiary, the Wilcox flora became restricted to latitude some 20 degrees south of its Eocene occurence in the Mississippi Embayment (Berry 1930). Finally, it was in the late Tertiary, as suggested by Axelrod (1975), that as a result of the increasingly drier conditions, the remaining Coastal Plain hardwood forests

became fragmented and limited to narrow strips along watercourses.

The velocity of the biogeographic changes and may well have been somewhat exaggerated, however. The presence of the evergreen oaks and even some tropical taxa such as *Cedrella, Meiosma* and *Cordia* in the late-Miocene assemblages of northwestern Nebraska, coupled with occurence of *Sabal* palms in the Pliocene of northern Texas indicate that some warm-loving components may have persisted in the interior throughout much of the late Tertiary and were perhaps eliminated only by the Pleistocene cooling. In the Southeast, many warm-temperate to subtropical taxa such as *Cercidiphyllum, Gingo, Trapa* and *Zelkova* were eliminated only by the close of the Tertiary epoch. The late Pliocene flora of the Citronelle formation of the Gulf coast closely resembled the modern Coastal Plain flora and yet even this one contained quite a few subtropical and warm-loving Asian components (Berry 1930).

Today the predominantly tropical families and genera are represented in eastern North America by only a few species which became adapted to the colder winters of the region. These include paw-paw (*Asimina triloba, Annonaceae*) and persimon *(Diospyros virginiana, Ebenaceae*) among the temperate and warm-temperate taxa, and *Bignonia capreolata* (*Bignoniaceae*), redbay (*Persea* spp.), bush palmetto

(*Sabal minor, Palmaceae*), and Southeastern coralbean (*Erythrina herbacea*) among the taxa which are presently subtropical (or tropical to subtropical - as the latter species) in distribution.

The Pleistocene Cooling

The Pleistocene cooling brought about a considerable environmental change throughout eastern North America. At the time of the last glacial maximum the temperate broadleaf deciduous forest was completely exterminated from the Appalachians and adjacent Low Interior Plateaus (Watts 1980, Delcourt and Delcourt 1983, Delcourt et al. 1983). During this period the broad section of the continent south of the Lawrentide Ice Sheet which included both the old topographies of the interior Highlands and the northern half of the Coastal Plain was covered with the various types of the boreal-like coniferous forest. The spruce forest, with some presence of jack pine (*Pinus banksiana*), was the predominant vegetation type west of the Mississippi River where it extended over much of the Great Plains region, with its northern lobe reaching into the southern section of Illinois (Watts 1980).

Most of the Southeast east of the Mississippi River was covered by the open woodlands where the dominant role belonged to the northern pines (Watts 1980, Delcourt 1983) such as jack pine (*P. banksiana*) or red pine (*P. resinosa*) (Whitehead 1965, Maxwell and Davis 1972).

Spruce (*Picea* spp.) was a secondary but omnipresent component of these boreal communities. As suggested by Watts (1980), all three common northern species, white spruce (*P. glauca*), red spruce (*P. rubens*) and black spruce (*P. marianna*) may have been involved. Spruce dominated the full-glacial assemblages of southeastern Virginia and by 14,000 B.P. began to increase in importance in the upper section of the Southeast (Watts 1970, Delcourt 1985). The northern boundary of the boreal-like communities is difficult to establish. 21,300 years ago *Picea glauca* was present at Pennington site located in the southwestern portion of Georgia (Watts 1971). The forests dominated by *Alnus*, of which one species, *A. rugosa*, is today cool-temperate to boreal in distribution, marked the southern limit of the spruce woodlands in the vicinity of the present-day Austin, east-central Texas (Bryant 1977).

It was generally suggested that the *Pinus banksiana-Picea* flora must have indicated the boreal or, at least, very northern cool-temperate climate much like that of modern Maine with its short growing period and long severe winters (Watts 1983). But intensity of the solar radiation in the Southeast clearly must have been higher than in the present-day boreal forests because of the lower latitude. This suggests, perhaps, the higher continentality and aridity of climate which appears to be validated by the

high importance of the xeric and heliophytic herbs and shrubs.

The extensive interstream watersheds throughout the lower section of the Coastal Plain supported xeric woodlands in which pines were mingled with few species of drought- and fire-resistant oaks and hickories. Even this southernmost belt of the late-Pleistocene vegetation was apparently dominated by northern pines for the climate of the whole region was too cold and dry for southern species to persist (Watts 1980).

The Pleistocene Refugium of the Temperate Forest

The Pleistocene glacial cycles, destructive as they were to the warm-loving broadleaf vegetation, evolved in the warmer Tertiary climates and contributed to the establishment of the major route for its retreat. At the time, loess was deposited on the previously dissected uplands of the Mississippi Bluff (Snowden and Priddy 1968), the region may have harbored some mesic forest. But before the Bluff became capped with a loess blanket, the hardwood forest probably had been limited to bottoms and slopes. Hilltops and watersheds were likely to have been dominated by the coniferous vegetation which is the case, for example, in the similarly dissected modern non-loessial bluffs of the Appalachicola River. With the establishment of the loess mantle the conditions grew more mesic which allowed the hardwood species to expand uphill and replace

the pine-dominated vegetation in the uplands. In this way a contiguous belt of the broadleaf mesophytic forest, as we know it today, may have established itself along the eastern flank of the lower Mississippi Valley.

It is difficult to say when exactly in the Pleistocene the deposition of loess started along the Mississippi River. But the initial stages of the loess accumulation can be traced well back into the shades of the middle-Pleistocene history. One of the older loess sheets, known as "Crowley's Ridge Loess" and found, respectively, on Crowley's Ridge in Arkansas and further gulfward along the Mississippi Bluff to as far south as Natchez, was dated by Johnson et al. (1984) at 120,000 to 185,000 years B.P. and considered to be Illinoian or Sangamon in origin. Yet the oldest loess, "Marianna" which predated "Crowley's Ridge loess" had been apparently deposited during even earlier middle-Pleistocene cycles (Autin, et al. 1991), perhaps during Yarmouthian stage.

During and after the deposition of loess, the Blufflands turned into the major long-term migration pathway for the eastern North American mesic flora. Under the stress of the Pleistocene glacial advances the temperate and warm-temperate broadleaf taxa with related herbaceous flora were pushed along the Mississippi Bluff gulfward, to the southern end of the Loess Hills. Eventually this floristic shift resulted in the

accumulation of diverse assemblages of mesophytic plants within the strongly dissected southern section of the Mississippi Loess Bluff, between present-day Vicksburg, southwest Mississippi and Baton Rouge, southeast Louisiana. The Delcourts (1974, 1977b) suggested that during the last glacial epoch this area was the major Pleistocene refugium for the temperate broadleaf mesophytic forest in North America. Similar southward expansions of the hardwood deciduous forest flora seem to have taken place at this time along the Apalachicola-Flint-Chattahoochee and Alabama-Tombigbee river systems (Delcourt and Delcourt 1974). However, with the establishment of the loess mantle, the Mississippi Bluff apparently became the only route along which the mesophytic hardwood forest expanded southward in a relatively broad front over the upland terrain.

The establishment of the mesophytic hardwood forest refugium at the time of the full glacial maximum was favored by the combination of the several factors – the low-latitude subtropical location of the southern Blufflands, their optimal edaphic conditions provided by loess, the deep dissection of the loess mantle and the cooling influence of the Mississippi River. As suggested by the Delcourts (1974), the late-Pleistocene mesophytic assemblages of the southern Blufflands developed in the regime of the persistent advection fogs. The moist and

foggy conditions resulted from contact of cold river water and associated cool air mass which funnelled down (southward) the Mississippi Valley with the warm air mass emanating from the Gulf of Mexico. Frequent or almost permanent fogs supplied the Loess Hills with abundant moisture and apparently heavy cloud cover. The moisture regime and summer temperatures of the southern Blufflands at that time may have closely resembled those of the present-day mountain cloud forests of eastern and southern Mexico. Thinning of the loess mantle and geographic limits of fog dispersion, the Delcourts hypothesized, have probably been the major impediments for migration and establishment of the mesophytic vegetation east of the Mississippi Bluff.

At the southern end of the Mississippi Bluff, in the Tunica Hills of southeast Louisiana, the Delcourts (1977) discovered fossil remains of a rich paleo-assemblage of the cold-resistant temperate deciduous species which they dated to approximately 12,740 yr B.P. The late-glacial forest of the Tunica Hills contained many temperate components, such as oaks (*Quercus*), beech (*Fagus*), hickory (*Carya*), elm (*Ulmus*), ash (*Fraxinus*), tulip tree (*Liriodendron tulipfera*) and hornbeam (*Ostrya/Cornus*), that remain common in the forests of this area today. The oak and hornbeam pollen in the sample from the Percy Bluff was particularly abundant. Some of the discovered taxa, such as white walnut

(*Junglans sinerea*), sugar maple (*Acer saccharum*), birch (*Betula*), and alder (*Alnus*) are limited now almost exclusively to the interior or northern forests. Modern populations of other local late-Pleistocene taxa, such as cucumber magnolia (*Magnolia acuminata*) and black walnut (*Junglans nigra*) only marginally extend onto the lower Coastal Plain.

One of the most extraordinary features of the late-glacial forest assemblages of the Tunica Hills was that they contained such typically boreal taxa as white spruce (*Picea glauca*) and tamarack (*Larix* spp.). By far, it is the southernmost site in the Coastal Plain where these boreal taxa were found. Abundant fossil remains of *Picea*, including twigs, needles and pollen, were discovered by the Delcourts in all three basal samples from the Fluviatile Terrace 1 in Tunica Bayou. From 40% to 50% of the pollen found in the basal sample from the second site, Persy Bluff, was also that of *Picea*. Abundant fossil remains of spruce, and the *Larix laricina* wood were reported earlier from the supposedly equivalent stratigraphic level of Persy Bluff deposits by Brown (1938).

It may appear that the late-Pleistocene Tunica Hills assemblage have borne some resemblance to the present-day mixed forests of the Great Lakes region. The Delcourts argued, however, that the northern conifer taxa and the temperate broadleaf trees did not intermingle uniformly

throughout the whole physiographic gradient of the Tunica Hills but formed rather distinct communities. While the temperate deciduous forest covered the the hill slopes, the boreal conifers tended to congregate in the ravine bottoms along the tributary streams where on sandy alluvial deposits the broadleaf trees were less competitive.

The question remains how the boreal taxa reached the Tunica Hills. It was hypothesized by the Delcourts (1977b) that white spruce and eastern tamarack migrated southward along the exposed alluvial sediments of the Lower Mississippi River floodplain and then expanded up into the southern Blufflands following tributary floodplains. The Delcourts specifically emphasized that the extended periods of extremely cold winter weather were not required for the survival of these two boreal conifers. Their persistence in these low subtropical latitudes can be explained by the cool and foggy microclimate that apparently prevailed in bottoms of Tunica Hills' deep ravines during the last glaciation.

Contrasting with spruce and tamarack was the presence of such explicit southern components as bamboo, *Arundinaria gigantea*, which apparently reached the best development, as it does now, in the bottoms and on the lower slopes of the ravine forest. Grape vines also gave a certain southern aspect to this otherwise cool-temperate forest. In some bottoms where bamboo and vines formed mixed assemblages

with spruce and tamarack, this extraordinary mixture of boreal and southern forms perhaps was physiognomically similar to the mixed communities that are present today in Hokkaido Island of northern Japan and in Sakhalin Island of the Russian Far East

The latitudinal extent of this unique cool-temperate cloud forest is not quite clear because so little paleobotanical research has been done in the Blufflands. Yet some conjectures can be made based on the data from the late—Pleistocene assemblage at Nonconnah Creek near Memphis, extreme southwestern Tennessee. The local full-glacial forest seems to have been strongly dominated by *Picea* (Delcourt et al. 1980). Spuce accounts for approximately 80% of the pollen in the alluvial sediments between 20,215 and 17,195 years B.P. and nearly all arboreal macrofossils found at the site. *Quercus* was represented in slightly more than 10% of the pollen. Small amounts the pollen were contributed by other broadleaf taxa such as beech (*Fagus grandyfolia*) and chestnut (*Castanea dentata*) which did not leave any macrofossil remains. Interestingly, the only two mesic taxa found in the macrofossil profile, *Ilex* and *Vitis*, today are both southern in distribution. The possibility exists, however, that Ilex, which was found at the base of the profile represents the small population that has been persisting in the area since the last interstadial from 73,000 to about

30,000-25,000 years ago. Since spruce tends to produce large amounts of pollen, its role in the assemblage of Nonconnah Creek can be easily overestimated. Nevertheless, it is evident that spruce was likely to have been at least twice as abundant in southwest Tennessee as in the Tunica Hills. Pockets of the broadleaf forest were present in Nonconnah Creek, and they covered, perhaps, a larger area than it may be suggested by the amount of the deciduous tree pollen found at the site. Yet the area appears to be at or close to the northern limit of the temperate deciduous forest at the time.

Forest Dynamics in the Early to Middle Holocene

The northward migrations of the temperate deciduous species along the Mississippi Bluff and their expansion from the Bluff into more interior regions seem have started during the very end of the Pleistocene as the warming trend gradually progressed. In this respect, the late-glacial assemblage of the the Tunica Hills represented, perhaps, an already somewhat modified community as compared to those that had existed here about 18,000 yr B.P., at the time of the last glacial maximum. The intensity of the plant migrations and biogeographic readjustments significantly increased between 12,000 B.P. and 10,000 B.P., when the early-Holocene warming led to the retreat of the Lawrentide ice sheet from essentially all of the northeastern United States and southern Canada (Watts 1980).

Reconstructed by Davis (1981) on the basis of the pollen records, the late-Pleistocene to early-Holocene reverse migration routes of some key components of the eastern North American flora such as beech (*Fagus grandifolia*), elms (*Ulmus* spp.) and chestnut (*Castanea* spp.) appear to have radiated from the general direction of the Loess Region which fact may indicate that the Blufflands were an ultimate center of these taxa's post-glacial diffusion and, perhaps, a critical refuge area for their survival. In the early Holocene, sweetgum (*Liquidambar styraciflua*) and blackgum (*Nyssa sylvatica*) were present as far in the interior as Anderson Pond in east-central Tennessee where they formed mixed assemblages with chestnut (Watts 1983). It is highly possible that these two species, like beech, elms and chestnut, also expanded into the western section of the south-Appalachian region from the loessial refugium of the Mississippi Bluff.

Between 12,000 B.P. and 10,000 B.P. the the whole vegetation complex of the Coastal Plain was in the state of the dynamic flux. One of the benchmarks of this period was the fast expansion of oaks (*Quercus* spp.) and hickories (*Carya* spp.). By 10,000 B.P. the oak-hickory forests became established over much of the Coastal Plain uplands (Watts 1980). Between 10,000 B.P. and 6,000 B.P., at which time the distributions center of *Carya* became generally located along the Mississippi drainage, the forests of the

Mississippi Bluff might have been characterized by greatly increased hickory populations. During this time span, the Blufflands seemed to have become the major pathway for hickories in their migration to the midwestern and the Great Lakes states.

The thermal conditions in the southern section of the Loess Region may have become close to those of the present time between 10,000 B.P. and 8,000 B.P. during which time the remnant of the Laurentide ice sheat became limited to the area surrounding Hudson Bay and apparently no longer caused much influence on the climate and environments of the Southeastern Coastal Plain. With the sea surface increased and general warming progressing, the evaporation rates increased and encouraged the northern shift of the hot and humid weather from the Caribbean characterized frequent thunderstorms and hurricanes. The thunderstorm activity in the Coastal Plain stimulated development of the regular fires which contributed to the replacement of the oak-hickory forests with pyrophytic pine forests and limited the hardwood vegetation to narrow strips along the watercourses and to other fire-protected areas. By 6000 yr. B.P., on the eve of the middle-Hollocene, only small remnants of Laurentide continental ice sheet remained present north of latitude 53 degrees in the sub-polar section of Labrador and these were no impediment for the

establishment of the modern biogeographic boundaries (Delcourt and Delcourt 1987).

Between 8500 and 4000 B.P., the warming trend culminated in the middle-Holocene Altithermal interval when the temperatures throughout the Southeast apparently reached its highest peak (Wright 1983, Watts 1980). This period can be illustrated by the middle-Holocene Percy Bluff assemblage from the Tunica Hills which was present at the site 5300 years B.P. (Delcourt and Delcourt 1977). This assemblage was characterized by the rich mixture of the temperate, warm-temperate and some subtropical taxa such as blackgum (*Nyssa sylvatica*), tulip tree (*Liriodendron tulipfera*), walnuts (*Juglans* spp.), hickory (*Carya* spp.), beech (*Fagus grandifolia*), elms (*Ulmus* spp.), ashes (Fraxinus spp.), sycamore (*Platanus occidentalis*), hornbeam (*Carpinus caroliniana*), hophornbeam (*Ostrya virginiana*), cherry (*Prunus* spp.), alder (*Alnus* spp.), sugarberry (*Celtis laevigata*), sweetgum (*Liquidambar styraciflua*), holly (*Ilex* spp.) water oak (*Quercus nigra*) and live oak (*Q. virginiana*), in association with bamboo (*Arundinaria gigantea*), grapevines (*Vitis* spp.) and Virginia creeper (*Parthenocissus quinquefolia*). The Delcourts identified this assortment as modern in nature but it should be noted that live oak today does not seem to extend naturally north of Baton Rouge, southern Louisiana. On the other hand, such an overwhemingly northern genus as *Alnus* also does not

appear to be represented in the present-day Tunica Hills flora. The same seems to be true for white walnut (*Juglans cinerea*) which was not recorded in Tunica Hills.

The Questions of Endemism and Biodiversity

The role of the Blufflands as a major Pleistocene pathway for the Eastern-American moisture-loving floras, as well as the impact of these plant migrations on the evolution of the Loess Hills' own flora are still poorly understood. Since the Pliocene, there appear to have been from 5 to 7 major continental advances of the Lawrentide Ice Shield in eastern North America separated by the relatively long and warm interglacials. At least two of these glacial epochs, Illinoian and Wisconsin, had three well-documented stadials separated by warmer interstadials. It implies that the Blufflands are likely to have funneled more than a dozen of the continental plant migrations of varied intensity. The Delcourts (1977b), for example, reported from the Tunica Hills a rich warm-temperate assemblage which is probably representative of the local flora during the Sangamon Interglacial. This contained such thermophyles as sweetgum (*Liquidambar styraciflua*), water tupelo (*Nyssa aquatica*), southern white cedar, holly (*Ilex*), corkwood (*Leitneria floridana*), snowbell (*Styrax*) and Virginia willow (*Itea virginica*).

The presence of the loessial pathway may, in fact, account for the extreme diversity and somewhat autonomous

nature of the circum-Mississippian flora. Many bottomland and upland species of trees and shrubs appear to be generally centered in or around the Mississippi Embayment. Some species such as swamp cottonwood (*Populus heterophylla*) and corkwood (*Leitneria floridana*) have remarkably disjunct distributions with one population being present in the Lower Mississippi Region, and another - in the eastern section of the Coastal Plain.

The presence of the long-term Pleistocene refugium in the southern section of the Loess Hills region may cast some light on the origins of the remarkably rich circum-Mississippian flora represented by Nuttall oak (*Quercus nuttallii*), bottomland post oak (*Q. similis*), pecan (*Carya illinoensis*), nutmeg hickory (*C. myristiciformis*), cedar elm (*Ulmus crassifolia*), water locust (*Gleditsia aquatica*), swamp privet (*Forestiera acuminata*), few plums (*Prunus* spp.), corkwood (*Leitneria floridana*), Kentucky coffeetree (*Gymnocladus dioicus*) and quite many other species of trees and shrubs.

The members of the circum-Mississippian flora are characterized by the conspicuously restricted distribution patterns: to the varied extent they are all centered either within the Lower Mississippi Valley or in the general area of the Mississippi Embayment. To my knowledge, there is no satisfactory explanation of this phenomenon. Therefore, it is reasonable to suggest that these species are the

Mississippian endemics which apparently became expelled from the other areas of the American South by the recurring Pleistocene coolings and survived only in the close proximity to what might have been their last refuge along the Lower Mississippi River.

The fact that most of the above-mentioned trees and shrubs are bottomland species, does not necessarily suggest that their refugium was located somewhere in the Lower Mississippi Alluvial Plain. In fact, it is doubtful that the Pleistocene Alluvial Plain with its alternating deluges and dry phases was as nearly as "convenient" for the survival of the numerous bottomland species as the ravines of the adjacent Loess Bluff. It may be inferred from the Delcourts' findings that during the full-glacial interval most of the Lower Mississippi Alluvial Plain, including its southernmost section was covered by the low-latitude Pleistocene analogue of the boreal forest dominated by spruce (*Picea* spp.) and, perhaps, tamarack (*Larix* spp.). The possibility should not be overlooked that many bottomland species may have limited to the moist and foggy Bluff ravines and only with the general warming and subsequent retreat of the boreal forest extended onto the Mississippi Floodplain.

This hypothesis is, in part, suggested by the fact that such distinctive bottomland species as corkwood (*Leitneria floridana*) and water tupelo (*Nyssa aquatica*)

were present in one of the Pleistocene assemblages reported from the Tunica Hills by Delcourt and Delcourt (1977b). To my knowledge, neither of these species was ever reported from the present-day assemblages of the Tunica Hills. Yet the fact that other bottomland species may still persist in the ravines of the Loess Region is proven by Quigly (1994) who reported from Tunica Hills such bottomlanders as Nuttal oak (*Quercus nuttallii*), willow oak (*Q. phellos*) and water elm (*Planera aquatica*). I also found many bottomlanders in these upland forests. Among are even the species of the alluvial swamp communities such as black willow (*Salix nigra*) and water hickory (*Carya aquatica*).

Finally, the highly disjunct distribution of some rather warm-loving interior trees and shrubs found in the southern Appalachians and mesic valleys of the Ozarks also poses some unanswered questions. It is well documented that the temperate broadleaf forest was completely expelled from the Appalachians and the Ozarks during the last glaciation (Watts 1971, 1980, Watts and Stuiver 1980, Delcourt 1980). Thus neither the Appalachians, nor the Ozarks have could supported during the Pleistocene glacial advances such relatively warm-loving interior species as umbrella magnolia (*Magnolia tripelata*), Fraser magnolia (*Magnolia frazeri*), and American smoketree (*Cotinus obovatus*). This implies that these species migrated in the Holocene to

areas of their present distribution from some southern refugia.

Given this, what could have been the migration pattern of the species with such remarkably disjunct distributions as umbrella magnolia, American smoketree, yellowwood (*Cladastris kentukea*) and others centered in the southern Appalachians and the Ozarks? Did they survive the Pleistocene in the similarly disjunct refugia east and west of the Mississippi River? While such possibility, naturally, can not be ruled out, the more reasonable explanation of the disjunct distributions may be suggested by the hypothesis that these taxa were likely to survive somewhere in between these two regions from where they expanded in the Holocene eastward and westward. It appears that the loess lands along the Mississippi River fit well such a scenario. In 1993, while making a reconnaissance trip in Tunica Hills, I found a specimen of American smoketree (*Cotinus obovatus*), an understory tree with remarkably limited distribution confined to the small limestone area in southern Appalachians, to the Ozarks and the Boston mountains. To my knowledge, it was the first representative of this taxon discovered in the Loess Hills. Besides I observed in the southern Blufflands other interior-centered plants such as white walnut (*Juglans cinerea*) and Kentucky coffeetree (*Gymnocladus dioicus*) which were thought to have been limited to the northern

margin of the Mississippi Embayment (Collingwood 1964, Duncan and Duncan 1988).

These findings fuel the inspiration and leave the hope that at least one of the botanical frontiers in North America remains open. The survived forests of the Mississippi Bluff pathway appear to represent an exceptionally rich reservoir of the temperate and warm-temperate flora on the continental scale. Enreached by the intrusion of definitely interior cool-temperate species from the north and warm-loving subtropical species from the south, the Mississippi Bluff may prove to harbor the vast majority of the deciduous arboreal plants now present in Eastern North America. Up to this time, the Loess Hills has remained some of the most poorly explored and least consistently sampled assemblages in the eastern United States. The possibility exists, that as the exploration and sampling continues, some species which are now thought to be absent from the Blufflands, will be found in these forests. The south-Appalachian and Ozarkian endemics, especially those with remarkably disjunst distributions, are perhaps among the first plants that will be discovered.

CHAPTER 5

THE HISTORY OF NATIVE SUBSISTENCE

Since their arrival at least ten millenia ago, native Amerindian populations have been an important biogeographic agent that modified - in different ways and with varied intensity - the species composition and the structure of the Loess Hills forests. Although the loessial forests have a long and continuous geological history, they developed into the ecosystem which we know today during the Holocene - under conditions of persistent and gradually increasing anthropogenic pressure. Recognition of this fact is very important because it gives a biogeographer a very different perspective and framework of study. The prehistoric forests preceeding the present-day anthropogenic landscape can no longer be considered "pristine". They developed with some - heavy or gentle, direct or indirect - involvement of human beings and their economic and cultural practices.

Consideration of Amerindian influence on the land is important because it gives an idea of the extent, velocity, and nature of the ecological and biogeographic evolution of the loessial landscapes during the pre-European period. Likewise, it may contribute to our better understanding of the composition and structure of the communities we call "original" or "old-growth" forests.

Pre-Mississippian Time

The first bands of Amerindian settlers colonized the northern part of the Lower Mississippi Valley some time between 13,000 and 8000 B.C. Hunting camps of the Paleoindian Stage have been found on Crowley's Ridge, which was shared by two distinct populations living on either side of the Ridge (Morse and Morse 1983). These Paleoindians relied heavily on hunting and fishing for subsistence. Apparently, they continued a nomadic lifestyle originally adapted to big-game hunting in the north and in the west (Meltzer and Smith 1986), but theirs was a more generalized and flexible economy. The contribution to the diet of plant foods and the industrial uses of plants have not been determined. Gradually the population became dispersed throughout the whole Lower Mississippi Valley and developed a set of more elaborate adaptations to the variety of environments and life zones present in the region. Subsequently, they became somewhat more settled.

The beginning of more intensive influence by the native population on forest communities probably began with the development of a sedentary or semi-sedentary settlement pattern in the Archaic Stage. Collecting wood material for fuel and shelter , the native people gradually modified the forest environments around their habitation sites. During the early and middle Archaic periods, Amerindian populations of the Southeast developed a subsistence

pattern which relied on a wide range of wild foods and employed an increased knowledge of seasonal availabilities (Byrd and Neuman 1978). In the late-Archaic period (4000-1000 B.C.) there was a growing trend toward utilization of plant resourses. At this point, the gathering of acorns, nuts, and fleshy fruits became an important part of the native diet. With the gradual expansion of the population and sophistication of their environmental knowledge, some Archaic groups seemed to have adopted a more sedentary way of life and developed a sharper sense of territoriality.

The development of a sedentary way of life during the Archaic Period contributed to the growth of cultural complexity and set the stage for the first anthropogenic transformations of the natural Mississippian landscape. The hardwood forests along the Mississippi River were subject to some of the earliest clearance practices in North America. The need for forest conversion came with developing ritualism of which very little is known. It can be suggested that the prehistoric indigenous people of southern Louisiana probably initiated forest clearing for their emerging mound sites as early as the middle and late Archaic Periods (6000-4000 and 4000-1000 years B.C.) - long before the beginning of any agricultural practices.

The Poverty Point Culture

The Poverty Point culture flourished from approximately 1300 to 1000 B.C. (Gibson 1994). The major

area of the Poverty Point culture was restricted to a 30 mile radius around Poverty Point, but its influence was much more widespread and included the western portion of the Achafalaya Delta, southeastern coastal Louisiana, middle and northern part of Louisiana's portion of the Mississippi Valley, southern Arkansas, as well as the Yazoo Basin in Mississippi, with the sites found both on the elevated sections of the alluvial floodplains and loess-capped uplands. Trading relations extended even further, as far as the Great Lakes and peninsular Florida. The culture is named for the famous Poverty Point Site in northeastern Louisiana, where the largest earthworks of the Archaic period were located.

The development of the Poverty Point site required an unprecedented clearing effort on the part of the prehistoric residents of the area. To have built up the enclosure only, would have required clearing 500 acres of the upland hardwood forest which once covered the loess-capped surface of Macon Ridge. This makes the Poverty Point one of the largest cleared prehistoric sites known from the Lower Mississippi River Region and probably the largest known Archaic site.

The presence of other earthworks and the borrow pits outside the main enclosure indicates that the surrounding area may also have been largely cleared. Dominating the Poverty Point site was a huge Bird Mound. Today it is about

21.3 m (70 feet) high and measures 640 X 710 feet at the base (Ford and Webb 1956). The overall cleared area of the Poverty Point site may have well approximated 900 acres.

The dimensions of Poverty Point are so impressive and unprecedented for the Archaic Period in North America that most archeologists assumed that it was built by an agricultural society. Nevertheless, no indication of agriculture has been found on the site. The subtropical portion of the Lower Mississippi Valley supported such rich and diverse biotic systems that with an economy based on ecotonal hunting, fishing, fowling, and gathering, the Poverty Point culture may have produced a significant food surplus without developing into an agricultural society.

Poverty Point was not even distantly paralleled by the other contemporaneous sites scattered throughout middle and northeastern Louisiana, the Yazoo River Basin, and eastern Arkansas (Webb 1977). Very few of these have small earthworks, and it generally appears that not much clearence was involved.

If, using a time machine, we transported ourselves to Poverty Point times and took a plane over the Lower Mississippi Valley, probably we would not have spotted much except for a few clearings here and there, tiny in size and far apart. And only had we flown over the eastern margin of Macon Ridge, the cyclopic clearing of Poverty Point would have immediately attracted our attention.

The period between 800 and 500 B.C. was marked by the decline of the Poverty Point culture pattern, the temporary decline of the earth building and an apparent decrease in population. The successors of the Poverty Point culture developed a new cultural pattern which lasted till approximately 1 A.D. Known as the Tchefuncte culture, this new pattern spread up the Mississippi River Valley as far north as central Arkansas. A coastal variant extended from eastern Texas to southeastern Mississippi. Along the coast, the Tchefuncte culture is known for its shell middens scattered in the present-day marshes of the Mississippi and Atchafalaya deltas. These shell middens, the only elevations in the now-subsided marshlands, are important landmarks of the modern deltaic landscape because they support communities of live oak (*Quercus virginiana*), sometimes with an understory of evergreen shrubs such as yaupon (*Ilex vomitoria*) and red-bay (*Persea borbonia*) in an otherwise featureless expanse of marshgrasses. However, the participants of the Tchefuncte culture are not known to have caused any long-term impact on more upland forest formations.

Hopewellian Influence (100 B.C.- A.D. 200)

A new epoch of mound-building in the Lower Mississippi River Region was stimulated by influences from the southern Midwest where by 150 B.C. the Hopewell culture had emerged. The rise of Hopewell in the Midwest may have been related

to some important shifts in the location of certain prehistoric northeastern tribes and their consequent advent to the Ohio and Illinois River Valleys where a new cultural pattern became crystallized. However, it would be inappropriate to restrict this cultural pattern to any kind of ethnic or even linguistic unity. Rather, it reflected a new way of life, a new ideology, and a new cultural style which began to spread among the different tribes of the southern Midwest in the very beginning of our era. The spread of Hopewellian traits into the Mississippi Valley was a gradual process of cultural diffussion.

The Hopewell culture developed new, sophisticated forms of religeous ceremonialism, mortuary practices and earthen architecture. Societies that participated in the Hopewellian ceremonial complex built more mounds than any preceding culture. Mound-building became the ultimate landscape manifestation of the Hopewellian way of life and thinking.

Development of mound-building ceremonialism during the Hopewell epoch was apparently related to the emergence of a new, particular type of leader known in archaeology under the names "Big Man" and "Big Woman" (Bense 1994). Such leaders were buried in log tombs and accompanied in their last journey by a vast array of ceremonial artifacts, many of which can be identified as Hopewellian prestige items (Brose and Greber 1979). Some archeologists have suggested

that Big Men and Big Women rose to such high positions in the social hierarchy by adopting key roles in the trade of these artifacts (Kehoe 1992, Bense 1994). According to Smith (1986), the location of the mound centers reflected critical points connecting Hopewellian raw material source areas.

The diffusion of the basic features of Hopewellian culture down the Mississippi River resulted in the development of the Marksville culture, which originated in the Lower Mississippi Valley at about A.D. 1 and lasted till A.D. 400 (Toth 1979). Although the Marksville complex shared some basic Hopewellian traits, it certainly was not identical to Midwestern Hopewell. It appears that the maximum development of the Marksville mortuary ritualism overlaps with the middle to late Hopewell transition in the Illinois Valley, i.e., within the timespan approximately between 100 B.C. and A.D. 200. After A.D. 200 the contacts seem to have ceased (Toth 1979).

Overall, 98 Marksville mounds sites of different sizes have been discovered in the Lower Mississippi River Region (Toth 1979). Of these, only comparatively few have been excavated. Undoubtedly, the region had considerably more mounds and moderately-sized mound centers than is suggested by archaeological records, for mounds were destroyed by the hundreds during Euro-American agricultural development in the Mississippi Valley (Toth 1979). Clusters of large mound

centers and major residential areas influenced to the different extent by the Hopewellian culture were located in central and east-central Louisiana (the Marksville, Troyville, and Crooks sites), in the southern Yazoo Basin-Vicksburg area (Grand Gulf, Point Lake, Anderson Landing, with many smaller sites on the Loess Bluff between Vicksburg and Natchez), in the northern Yazoo Basin-eastern Arkansas area (Twin Lakes, Dorr, Helena, Mound City), and, finally, in southwestern Tennesse (Pinson and Johnston).

The largest of all Southeastern Hopewellian sites, the Pinson mound center which was built upon the eastern slope of the Loess Bluff in southwestern Tennessee, covers an area of 400 acres and has at least 12 mounds, one large circular enclosure and several residential areas built up between 50 B.C. and A.D. 150 or 250. The Helena mound center is another site located in the zone of the loessial hardwood forests. It was built between 140 B.C. and A.D. 335 on the southern tip of Crowley's Ridge in eastern Arkansas - in the extreme northern margin of the Marksville culture area. One of the largest Hopewellian mound centers in Louisisana is the Marksville site, which was built upon the loessial outcrops of Marksville Prairie. The ceremonial area of the site includes three earthworks and ten mounds, all located on the western bank of a former Mississippi channel. The largest Marksville earthwork, a C-shaped

enclosure, covers an area of about 1500 feet in diameter and resembles the shape of the Poverty Point enclosure.

Development of the mound centers and, perhaps, even the larger-sized residential sites, probably required clearing relatively large tracts of virgin forest. Preliminary clearing was necessary, most likely, even for building of individual mounds unless these were erected right in the middle of the forest, among the forest trees. But even if we exclude individual mounds from consideration and chose to envision clearings associated with mound centers only, even then, the picture of hypothetical anthropogenic change would be rather remarkable. If an imagined surveyer could have viewed the early to middle Hopewellian landscape of the Lower Mississippi Valley and adjacent loess-capped uplands from the air, he would have discovered that the previously almost unbroken forest blanket had become dotted here and there with openings of various sizes and shapes. These were, of course, no more than small localized islands in the forest sea. But they signaled the beginning of a big change, for, based on the extent of mound building, one can suggest that the Marksville period was the first period in the history of the Lower Mississippi Valley when clearing forest for ceremonial purposes became a widespread activity throughout most of the region.

Opening the forest for the mortuary spots was, of course, an incredibly difficult task given the fact that the only tools available to Hopewellians were fire and stone axes. Clearing probably progressed gradually as more mounds were built and more open area was needed. The concentration of three large mound centers in east-central Louisiana (Marksville, Troyville, and Crooks) may be indicative of some of largest population concentrations in the Lower Mississippi River Region which, in turn, suggests some of the highest anthropogenic pressure experienced - in various forms by the contemporaneous forest communities.

Hopewellian forest clearing contributed to the expansion of pioneer species and early-successional growth. One may hypothesize that, as mound sites were abandoned, they were gradually reclaimed by forest through a sequence of successional stages. The spotty development of the early-successional vegetation phases probably culminated between A.D. 300 and A.D. 400 during which time mound building and mortuary practices in many mound centers ceased.

The Problem of Plant Cultivation

The history of native forest clearance in the Lower Mississippi Region is somewhat of a paradox. In the southern section of the region, an organized effort to clear forest was undertaken perhaps earlier than any other part of North America. The Poverty Point culture and the

mound-building cultures of the Hopewellian epoch were involved in some of the most extensive - by the measure of those early-prehistoric standards - forest-clearing operations in the extra-tropical part of the New World. And yet, the major factor of forest clearance - agriculture - was absent in the region until very late prehistoric times. Some archaeologists believe that Hopewellians practiced agriculture.

There is an ongoing debate on plant domestication and agriculture during the Hopewellian epoch and even earlier times. This discussion is important because it may indicate other incentives for disturbing the Mississippian forests. By around 1 A.D., throughout much of the Southeast, there appears to have been an important change in subsistence practices, reflected by a considerabe increase in the abundance of starchy seeds of several plant species on archeological sites. This assortment was dominated by four to five native starchy seed-bearing plants such as maygrass (*Phalaris caroliniana* Walt.), knotweed or smartweed (*Polygonum erectum*), giant ragweed (*Ambrosia trifida* L.), goosefoot (*Chenopodium*), and little barley (*Hordeum pussillum*) (Hudson, 1976, Asch and Asch 1983, Johannessen 1984, Crites 1984). A large-seeded variety of chenopodium has been found, suggesting that it may have been domesticated (Hudson, 1976). The second-order, indigenous oily seed annuals were sunflower (*Helianthus annuus* L.),

marsh elder, and sumpweed (*Iva annua*) (Hudson, 1976, Yarnell 1983, Ford 1985, Asch and Asch 1985). Some of these plants may have been domesticated remarkably early - and, interestingly enough, outside the Lower Mississippi Region. Smith (1992) hypothesizes that *Chenopodium* was domesticated in Kentucky roughly between 1450 and 1400 B.C.

Yarnell (1983), Ford (1985) and Asches and Asches (1985) suggest that the domestication of *Iva annua* "was underway" by about 2000 B.C. *Helianthus annuus*, as pointed out by the former two workers, may have been cultivated in eastern Tennesse about 850 B.C., although previously Yarnell (1978) had cautiously specified that sunflowers studied in the discussed site (Higgs) were in the relatively early stage of domestication. It was suggested that the starchy plants of the "riverine Hopewellian complex" were being gathered, although not necessarilly have been cultivated, during the late-Archaic period. Increasing sizes of the seeds of goosefoot, marsh elder and sunflower between 2000 B.C. and 1000 B.C. suggest deliberate selection and domestication (Asch and Asch 1985). However, it is evident now that the Lower Mississippi River Valley is not the area where these early forms of agriculture were practiced because local late-Archaic sites do not contain starchy seeds.

It is important to point out, however, that the nearly all references to the general increase of the starchy

plants in native diet are relevant only to the northern end of the Mississippi Embayment. Almost no evidence of utilizing seeds of strarchy plants came from the area of the Marksville Culture. Besides, even in the northern section of the Lower Mississippi River Valley, exploitation of some plants was likely to have involved a kind of "semi-cultivation." Most of the starchy seed-bearing plants which were part of the Hopewellian complex are characteristic colonizers of the abandoned fields in the bottomlands of the Mississippi Valley and some of them, such as *Iva annua*, are also successful colonizers of the upland loessial sites lacking forest vegetation. Their natural habitat in prehistoric time, when forest vegetation was omnipresent throughout the region, were newly exposed surfaces of the alluvial sediments and various wet, marshy areas with complicated drainage and soil aeration.

Throughout the whole Lower Mississippi River Valley and adjacent parts of the Midwestern bottomland landscapes maygrass, knotweed, giant ragweed, goosefoot, little barley, marshelder and sumpweed are important components in such marginal sites and in natural meadows devoid of the forest growth. They form thick, nearly monospecific or mixed-species communities. These are natural fields ready for exploitation - large quantities of seeds can be harvested here fast and without much effort. In such circumstances the prehistoric people of the Lower

Mississippi Valley were unlikely to have had much reason for burdening themselves with an arduous task of forest conversion. The early native management practices may have been limited only to plant propagation - perhaps, to favorite vacant spots located in the vicinity of the residential sites. Even primitive horticulture does not seem necessary given the ubiquitous nature of the plants and their high competitive abilities in the bottomlands.

During most of the Woodland Stage some agricultural clearance appears to have taken place on the northern and north-eastern margin of the Lower Mississippi Valley and outside the region - in the Mississippi Bottoms of southwestern Illinois and eastern Missouri, as well as in the river valleys of the McFarland culture region in the southern Appalachians. The latter may have been one of the first hardwood environments of the Southeast which underwent significant agricultural deforestation (Smith 1985a). These seem to have been the first areas in the eastern United States where the maize cultivation was initiated.

Baytown-Coles Creek Culture (A.D. 700-1200)

One of the hallmarks of the late Woodland period was a rather fast development of the full-blown maize agriculture in the southern section of the middle Mississippi Valley - in the American Bottom of southwestern Illinois and eastern Missouri, where maize made up 40% of the local diet as

early as by A.D. 700-800 (Bense 1994). Introduction of large-scale maize agriculture in this area triggered or, perhaps, itself became a consequence of, the cultural revolution which led to the establishment of the new forms of social organization, religion and mortuary practices. The societies of the American Bottom were some of the first in eastern North America to achieve the level of a more complex sociopolitical formation, a chiefdom, which was characterized by a unification of several communities under the centralized power of one kin or lineage group (Service 1971, Earle 1987).

The shift to a maize-centered economy in Illinois and Missouri caused important changes in the subsistence practices of the populations on the northern margins of the Loess Hills and Lower Mississippi Valley. The transition to the Mississippian way of subsistence in western Kentucky, for instance, appeared to be complete by A.D. 900 (Lewis 1990). In northeastern Arkansas, maize-centered agriculture became established some time after A.D. 800 (Kelly et al. 1984, Morse and Morse 1983, 1990, Smith 1990). The area of diffusion of maize-centered agriculture was, however, of limited extent. No direct evidence for agriculture was documented in the area of the Troyville culture in northwestern Mississippi and southeastern Arkansas (Fritz and Kidder 1993), let alone in more southern loess-capped

surfaces of the Mississippi Bluff and Macon Ridge (King 1982).

The Coles Creek cultural complex developed in the middle and southern part of the Lower Mississippi River Region by about A.D. 700 (Phillips 1970). Although Coles Creek settlement patterns include chiefdom-level settlement hierarchies characteristic of Mississippian settlement system, the societies of the Coles Creek period do not reveal any significant signs corn cultivation (Fritz and Kidder 1993, Kidder 1992, 1993). Forest clearance during the Coles Creek was largely conditioned by non-agricultural needs. The transition from the Marksville to Coles Creek in the Lower Mississippi River Region was marked by growing population densities. The number of the permanently habitated sites and mound centers increased. Lake George, which became one of the largest ceremonial centers of the Coles Creek period, developed from a small mound center of only local significance, as did the Osceola ceremonial mound center in the Tensas Basin. Throughout the Coles Creek culture region this trend resulted, as suggested by Fritz and Kidder (1993), in greater expanses of continually disturbed clearings.

It appears that during the Coles Creek period maize was cultivated as a ritual or high-rank "prestige" crop eaten by elite groups. It is not impossible to imagine that small corn gardens were created within the limits of mound

sites or residences of chiefly elites. If so, the corn cultivation involved little if any additional forest clearing.

The exploitation (or semi-cultivation) of riverine herbaceous communities remained one of the important forms of subsistence throughout the Cole Creek period. Yet, it should be pointed out that even native cultigens were neither abundant nor evenly distributed throughout the region. Coles Creek sites in eastern Louisiana, for instance, have failed to yield several important components of this complex, such as chenopod (*Chenopodium berlandieri* ssp. *jonesianum*), sumpweed (*Iva annua*) and sunflower (*Helianthus annuus*) (Fritz and Kidder 1993). Generally speaking, the populations of the middle and southern sections of the Lower Mississippi Valley appeared to be distinct from the societies of Illinois, Missouri and Arkansas "in that the seed crops either were not produced or were far less important." (Fritz and Kidder 1993:9).

Developement of the Mississippian Pattern

Although Philips initially dated the end of the Coles Creek complex by A.D. 1000, it is now evident that this cultural pattern persisted in the Lower Mississippi Valley to at least as late as A.D. 1200. It was only after this time that the full-blown Mississippian way of life became established throughout the region. In the beginning of the middle Mississippian period (A.D. 1200-1400), a maize-

centered subsistence pattern spread rather fast over about two thirds of the Lower Mississippi River Region, including most of the Yazoo Basin along with the associated section of the Loess Hills. There is plentiful evidence that "Mississippianized" societies of this area began to rely on corn cultivation soon after A.D. 1200 (Williams and Brain 1983, Brain 1989). In northwestern Mississippi (Wilsford site), maize agriculture was practiced by at least A.D. 1275 (Connaway 1984).

The major agricultural crops of the Mississippians were corn, beans, and squash, with corn being at the core of the subsistence pattern. In the prehistoric time, corn (*Zea maiz*) was represented largely by two varieties - tropical flint, which reached the eastern United States about 200 B.C., and eastern flint corn, which was adapted to a shorter growing season and thus more preferable for extratropical North America (Hudson 1976). Introduction of the common bean (*Phaseolus vulgaris*) into the Mississippian agricultural complex after A.D. 1200 generally coincided with expansion of the maize-centered agriculture into the Lower Mississippi River Region. It appears that the cultivation or intentional management of starchy seed-bearing plants remained an essential component of the Mississippian subsistence. As suggested by the evidence from the Kincaid site, in southern Illinois, sunflower,

ragweed, chenopod or goosefoot, and marsh elder also were a part of the Mississippian complex (Muller 1987).

The northernmost section of the Lower Mississippi River Region and adjacent parts of the Mississippi-Ohio confluence - in western Kentucky, southeastern Missouri, and the Cairo lowlands of extreme southern Illinois - give evidence of cultivation or management of erect knotweed, goosefoot, and maygrass (Edging and Dunavan 1986, Lewis 1990). Finally, the early-historical observations of Du Pratz (1972) in the Natchez Bluff area clearly indicate cultivation of some mysterious native grains locally called *Choupichoul* and *Widlogouil* - perhaps goosefoot (*Chenopodium berlandieri*) as supposed by Gilmore (1931) and Smith (1992), cockspur (*Echinochloa crusgalii*) as suggested by Swanton (1911, 1946), or maygrass (*Phalaris caroliniana*) as proposed by Yarnell (1972).

During the middle Mississippian Period (A.D. 1200-1400), all of Louisiana and southwestern Mississippi were a part of the Plaquemine Culture. This culture seems to have relied more on corn than the preceeding cultures of the Coles Creek period but appeared to have been less focused on maize than the "classic" Mississippian societies (Fritz and Kidder 1993). The Plaquemine period can be defined as a time of gradual diffusion of a corn-based economy and a slow modification of the previously largely non-agricultural societies. The full-blown maize agriculture

extended over most of the Lower Mississippi River Region only during the late Mississippian period (A.D. 1400-1500) and later, in the protohistoric period. During this time corn was recovered from Fatherland site and numerous Tunica and Natchez sites upon the Mississipi Bluff.

The Middle-Mississippian Environmental Change

The middle Mississippian period (A.D. 1200-1400) can be considered an important threshold in the environmental history of the region for it was the first time that the elevated alluvial terraces of the Mississippi Valley and upland surfaces of the Loess Bluff became disrupted by the relatively large-scale agricultural clearings. From what we know about the locations of the major mound centers and ethnogeography of the protohistorical and early-historical tribes, it appears that the major cleared agricultural areas were probably clustered in the Yazoo Basin and surrounding bluffs, upon the Vicksburg Bluff (Warren County, Mississippi), in eastern Arkansas and on Macon Ridge in northeastern to eastcentral Louisiana. Smaller and more broadly scattered agricultural clearings occurred throughout the southern section of the Lower Mississippi Valley and the Loess Hills, tending to form larger clusters in the vicinity of the Greenhouse site (east-central Louisiana) and the Medora site (west of Baton Rouge, southern Louisiana). In the north, the end of the middle Mississippian period was marked by the decline of Cahokia

culture by A.D. 1400, with the subsequent decrease in the number of farms and settlements and abandonment of many mound centers. As a result, extensive agricultural areas in the American Bottoms were claimed by the early-successional vegetation. But the situation in western Kentucky and southeastern Missouri during A.D. 1300-1500 (Medley Phase) does not appear to have changed much since the period of Cahokia florescence (Edging 1985, Lewis 1986, 1990 Sussenbach and Lewis 1987). This region continued support a rather dense population and cultivated agricultural clearings were probably abundant.

The expansion of maize-centered economies was synchronized with the essential increase in mound building in the Lower Mississippi River Region. Indeed, the majority of mound centers built in the Southeast were located along the Mississippi River (Bense 1994). This increase in mounds reflected new emphasis in the socio-political organization, in ritual, and in belief system. It may also indicate an increase in population densities. The hallmark of the middle Mississippian period was the development of the complex or paramount chiefdoms which are reflected in the elaborate ceremonialism known as the Southeastern Ceremonial Complex.

The general purpose of the Mississippian ceremonialism was to legitimize the hold on power of ruling elites through the ritualized reconfirmation of their divine

origins and abilities. Since succession of power in the Mississippian societies seems to have been hereditary, the ancesstral burial mounds were an extremely important part of their political-religious system (Brown 1985, Knight 1986).

Consequently, even though agricultural clearing was probably the major source of deforestation during the Middle and Late Mississippian Periods, the role of mound building and increasing population densities also should be acknowledged. In any event, more forest was cut in the Lower Mississippi Region due to the development of mound centers during this time than ever before, including the height of the Hopewellian period. This population growth implies increasing pressure on the natural environment caused by a broad range of occupational and subsistence activities, such as the clearing of residential sites, burning the woods, intensive hunting and gathering of plant foods.

Mississippian Warfare and its Ecological Consequences

The development of endemic warfare, reflected by the presence of fortifications around many sites, including Cahokia, was a characteristic feature of the middle Mississippian Period. This trend peaked during the late Mississippian stage (A.D. 1400-1500) at which time some towns and mound centers were either destroyed or relocated. In the extreme western margin of our region, in the

Arkansas Basin, late Mississippian turmoil culminated in the collapse of the complex chiefdoms in the basin, accompanied by the end of mound building. There was a major shift in the location of towns and mound centers in the Yazoo Basin and Natchez Bluff in favor of dissected upland sites that could be more easily defended. Abandoned and relocated to the Loess Bluff were some of the largest and oldest Mississippian mound centers that existed in the Yazoo Basin such as those along the Winterville River and Lake George. The smaller sizes of new mound centers and residential sites along with a reduced interest in mound building probably indicated the decline of the old socio-political structures, a decrease in population densities, and, perhaps, an increased instability of life that led to further frequent relocations.

De Soto's Expedition and Protohistorical Period

The upper boundary of the Mississippi Period is marked by De Soto's expedition. The interval between De Soto's *entrada* and the beginning of sustained European occupation in 1699 is termed the Protohistoric Period.

The passage of De Soto's party resulted in the disruption of the fragile socio-political and geopolitical ties that held together the remnants of complex Mississippian chiefdoms, and probably further stimulated warfare and socio-political decline. Some powerful chiefdoms survived the turmoil or managed to restructure

themselves by the beginning of the colonial epoch. Others did not and perished, having been shattered into small fragments and absorbed by large sociopolitical entities. Even more destructive was the introduction and spread of European diseases, against which the Indians had no immunity. This led to the collapse of many Indian populations and depopulation of large areas. One of the most unhappily famous areas which is known today as "Vacant or Empty Quarter" occupied the northermost section of the Lower Mississippi Valley and adjacent Loess Hills, much of the Central Mississippi Valley and the lower reaches of the Ohio and Tennessee Valleys.

Today it is somewhat difficult to say what was the primary reason for the depopulation - the late-Mississippian havoc of 15th and early 16th century or the passage of De Soto's party. Williams (1982, 1990) suggested that the Central Mississippi Valley was vacant as early as by A.D. 1500, i.e., before the arrival of the first Europeans. If so, depopulation may have been caused by endemic Mississippian warfare. Another point of view expressed, for instance by Phillips and his collegues (1951), as well as Dobyns (1983), held that the major depopulation of the "Vacant Quarter" occured during the 16th and 17th centuries as a result of epidemics of the Old-World diseases which carried away the lives of between 60 and 90% of the local Indians. Whatever the causes of the

depopulation of this area were, it certainly remained empty for two centuries or more(Swanton 1979).

Depopulation was not limited to the area of the Vacant Quarter. With varied intensity it struck other parts of the Lower Mississippi Valley as well. Southward along the Mississippi River, in eastern Arkansas and eastern Louisiana at the time of De Soto's passage there were, according to Swanton (1979), about 30 towns, villages and provinces that belonged most likely to the ancestors of the Tunica, Quapaw, Koroa, and Yazoo. In the very beginning of the 18th century, when the French started their exploration of the Lower Mississippi River Region, the population and population number of these peoples declined drastically - there were only four Quapaw towns in Arkansas, the three other tribes were also represented by only few settlements (Swanton 1979).

The late-Mississippian turbulence and the epidemics brought by De Soto's party obviously had important ecological consequencies. Although many Indian populations were decimated by diseases introduced by the Spanish, the cleared areas, in fact, probably increased because epidemics and socio-political instability stimulated migrations. The departure from the old residential areas in most cases implied abandonment of the old fields. To clear new forest plots and put fresh lands under cultivation was, of course, an exruciatingly difficult task given the fact

that fire and stone tools were the only means for such an undertaking. When possible, already cleared areas were selected for new fields and settlements but, obviously, such favorable sites were not always available. In fact, much of the tribal warfare during the protohistoric and early historic time was waged for gaining access to the old farmlands and residential places. Consequently, if a migrating tribe was not lucky enough to come across some vacant clearing or was unsuccessful in challenging a nation comfortably accommodated on its own old territory, it frequently faced the urgent necessity of establishing new fields and thus clearing new tracts of forest. As a result, the period of the political turmoil shortly after the passage of De Soto's party led to the general spread of various disturbed and early-successional anthropogenic plant communities.

The protohistoric period was characterized by the continuing shift of ecological pressures from the bottomland to the upland forests. Although there are no ecological data to support this, areas undergoing successional formations may have increased in the bottomlands as tribes migrated onto loess-capped uplands. Subsequently, between A.D. 1500 and 1700, freshly-cleared areas in the Loess Hills increased to an unprecidental extent. When De Soto and his expedition crossed the Loess Hills and the Mississippi River in 1541-43, large fractions

of some tribes, such as the Tunica and, perhaps, the Natchez still lived on the elevated surfaces of the Mississippi Valley. At the end of the 17th century, these tribes had become specialized upland farmers (Swanton 1979). At the beginning of the colonial period, upland areas along the Yazoo River were occupied by small tribes such as the Yazoo, Koroa, Tiou, Taposa, Ibitoupa, and Avoyel. These were the shattered fragments of the larger and more powerful tribes of the Mississippi Period (Swanton 1985).

Tribal migrations in the late 17th and 18th centuries were in part a lasting echo caused by the late Mississippian unrest and the devastating effects of De Soto's expedition. They were exacerbated by more regular European involvement in Indian affairs and the beginning of the rivalry between the European powers for zones of influence in the New World. The European-Amerindian contacts during this period also resulted in the quick diffusion of valuable European goods, among them iron axes. These trade goods made the Indian population dependent on the Europeans and, perhaps, more inclined to challenge primevel forests than ever before. Though the previously-cleared areas remained preferable to the migrating tribes, with iron axes the arduous task of clearing a virgin land became much easier.

Subsistence of the Early Historic Amerindians

The pronounced physiographic dichotomy of the Mississippi River Valley conditioned a rather conspicuous division of the early-historic residents of the region into two environmentally-specialized groups - the uplanders and the bottomlanders. Interestingly, the majority of the above mentioned Amerindian nations were predominantly upland dwellers and specialized hill farmers. The Natchez, Tunica and smaller tribes (some of them politically associated with the Natchez) such as the Ofo, Thioux, Grigras, and, perhaps, to a lesser extent, the Yazoo and Chakchiuma - cultivated the rich loessial soils of the Mississippi Bluff. Initially, the Houma also farmed the upland soils of the Tunica Hills area and only later positioned themselves on the alluvial terraces north of Bayou Goula (Iberville Parish, southern Louisiana) and later - further south in Terrebonne Parish. West of the Mississippi River, the Koroa occupied the elevated loess-capped surfaces of Macon Ridge in northeastern Louisiana, and the Opelousa resided on what is now known as the Opelousas Ridge. Historic immigrants into the area, the Choctaw and the Chickasaw were likewise highly specialized upland farmers. But these two nations moved into the Yazoo Basin only after the various smaller tribes along the river had been eliminated or reduced to fragments (Smith 1988).

Although all or nearly all above-mentioned Amerindian nations were heirs or cultural successors of the prehistoric Mississippian culture and thus relied on agriculture, the degrees of this reliance varied. All practiced a diversified subsistence pattern which, apart from agriculture, included hunting, gathering, and fishing. The maximum attention to corn agriculture was given by the Tunica, Koroa, the Natchezan tribes including the Taensa, Thioux, and Grigras, and Muskhogean peoples such as the Houma, Chickasaw, and Choctaw (Blitz 1985, Kniffen and Hilliard 1988, Hudson et al. 1990). Of these nations the most remarkable dependence on agriculture was demonstrated by the Tunica Indians and, perhaps, by their closest relatives, the Koroa. According to La Source (Shea 1902: 80-81), the Tunica did live "... entirely on Indian corn, they are employed solely on their fields; they do not hunt like the other Indians". According to Swanton (1911: 317), this is an overstatement. But it may indeed reflect a high degree of dependence on corn.

Extent of Native Clearance

As late as the 18th century, the Loess Hills were still being deforested in some areas by the native agriculturalists. The largest clusters of clearings appeared to have been centered around principal towns. One of the largest clusters was located northeast of Vicksburg, in the area of Haynes Bluff, facing the left bank of the

Yazoo River. This area was cultivated during protohistoric and early historic times by the Yazoo, Koroa, Tioux, Ofo, and Chakchiuma (Brain 1988, Brown 1990, Hoffman 1990). The towns, neighborhoods, and clearings of the Natchez Indians were scattered throughout a large area of some thirty-five square miles in the general vicinity of present-day Natchez (Natchez Bluff), almost exactly in the middle between Vicksburg and Baton Rouge. Most of the fields of the Tunica Nation were located on the relatively small escarpment area of the Tunica Hills Bluff by present-day Angola, in the northwestern corner of the West Feliciana Parish. The names "Tunica Fields" or "Old Tunica Fields" have been used since the 18th century to refer to this area. Other fields were located slightly southeast of Angola. The Trudeau site is the location of the principal village of the Tunica Indians in the middle 18th century (Brain 1979).

The environs of the main town of the Natchez probably were, with the possible exception of Haynes Bluff, the most deforested early historic native area of the southern Blufflands. Penicaut who visited this town with Bienville's expedition in 1704 refered to " many flower-adorned prairies, broken by little hills upon which there are thickets of all kinds of fragrant trees." (McWilliams 1988: 83). It appears that deforested areas had anthropogenic origins like those "illuminated grass fields" (Harper 1958: 248) not infrequently crossed by the members of De Soto's

expedition and later by William Bartram. This area of the Mississippi Bluff simply does not have any natural prairies. And if there indeed were some around the Fatherland site at this time, they had undoubtedly originated in the place of the cleared forests as a result of continuous burnings. Scattered surviving tree groves attached to the hilltops and, perhaps, slopes were indicative of the original forest vegetation of the area. "Prairies" were likely to have been nothing but abandoned fields.

And yet, deforested areas in the Blufflands appear to have been highly localized. Before the beginning of the cotton boom, the Blufflands were largely a timber country. In the late 18th-early 19th centur,y travellers such as William Bartram, John Dunbar, and Fortescue Cuming portrayed the southern Blufflands as a well-forested region without much evidence of abandoned or cultivated native fields. The predominant forest type appeared to have been beech-magnolia old growth. The Scottish-American naturalist William Dunbar, who travelled up the Mississippi River in 1775 and observed continuous forest almost all the way along (Rowland 1930).

Compared to the Blufflands, the valleys and bluffs of the smaller Coastal Plain, rivers were deforested to a much greater extent. In the eastern section of the Gulf Plain fertile soils suitable for agriculture were limited largely

to the relatively narrow valleys and alluvial terraces of the major rivers such as the Coosa, Tombigbee, Alabama, Chattahoochee, and Talapoosa. And so were the hardwood forests. Since the Indian populations generally avoided settling on extensive upland watersheds underlain with dry and infertile sands and sandy loams, the narrow strips of the hardwoods forests flanking the rivers of the densely-populated core of the Creek country in Georgia, Alabama and parts of of South Carolina and northern Florida were the primary targets of anthropogenic pressure. The combination of socio-political unrest, tribal wars, epidemics and the availability of European-made tools contributed to the early destruction of most hardwood forests in this area.

Important evidence on the state of riverine landscapes in the southeastern section of the Coastal Plain was left by William Bartram, who traveled though this region in 1775. Many of the riverine areas he observed were highly deforested, and the species composition of the surviving forests was indicative of the early-successional, post-anthropogenic nature of these formations. Bartram describes one of such deforested landscapes on the banks of the Oconee River where "...the high forests... projected into extensive green, open, level plain, consisting of the old Indian fields and plantations, being the rich low lands of the river, and stretching along its banks upward to a very great distance" (Harper 1958: 240). After crossing the

Oconee, Bartram again found "...sublime forest, contrasted by expansive illumined green fields, native meadows and cane breaks" (p. 241). Finally, he reaches the Oakmulge River where "...lie famous Oakmulge fields, where are yet conspicuous very wonderful remains of the power and grandeur of the ancient of this part of America, in the ruins of a capital town and settlement..." (p. 241). On the next day, before arriving "...at the banks of the Chata Uche [Chattahoochee] River opposite the Uche town", Bartram, once again, traversed "...almost endless grassy fields, detached groves and green lawns for the distance of nine or ten miles..." (p. 245). The Uche town itself "... has been situated on a peninsula formed by a doubling of the river, and indeed appears to have been a very famous capital by the artificial mounds and terraces and a very populous settlement from its extent and expansive old fields, stretching beyond the scope of the sight along the low grounds of the river." (p. 246).

In three days of westward journey to the town of Talasse, while descending southward along the banks of the Tallapoose River, Bartram was "...continually in sight of the Indian plantations and commons adjacent to their towns." The next stop was a town of Coolome: "Here are extensive old fields, the abandoned plantations and commons of the old town on the East side of the river..." (p. 251). Meticulously documenting his movement toward the

Mississippi River, Bartram left for us an amazing document. "Vast", "endless", "expansive" fields everywhere! More fields and cleared areas than forest! This was the landscape left in the riverine areas of the eastern Coastal Plain by generations of Mississippian agriculturalists and their early historic descendents. A very similar first-hand account was left to us by Benjamin Hawkins, who, in 1778, described cultivation of 50 towns along the Chattahoochee, Tallapoosa, and Coosa rivers. In his *Sketch of the Creek Country* there are a multitude of references to the level of agricultural deforestation in the region: one riverine area had fields extending "one mile and a half," another "four miles down the river, from one hundred to two hundred yards wide," and the third one covered "three thousand acres."

Bartram's and Hawkins' notes suggest at the anecdotal level that most of the hardwood forest cover in the river valleys and bluffs of the Creek country was gone well before the massive colonization of these old tribal areas by white settlers.

There are several reasons for the difference in the pace of deforestation. First, compared to the river valleys of the Choctaw-Creek heartland and northern Florida, the Mississippi Bluff appears to have been more sparsely populated during the protohistoric and early historic and periods. In the southern section of the region there was only one Indian nation whose population in early historic

times was comparable to the largest tribes of the Muskhogean stock and the Apalachee - the Natchez.

Second, the hardwood forests of the Loess Bluff and other loess-capped surfaces were much more extensive than forests flanking any river of the Coastal Plain. Consequently, the anthropogenic pressure per unit area of loessial forests was smaller. Even if the total area cleared by the natives along the Mississippi was roughly equal in size (which is unlikely) to those along the major watercourses of eastern Gulf Plain, this would have been effectively mitigated by the spatial extent of the loessial hardwoods.

Third, even though in prehistoric times the Blufflands may have supported an equal or even larger population than the riverine areas of the Gulf Plain, they had a relatively shallow history of deforestation compared to the other core areas of Mississippian culture because of the late transition to full-blown maize agriculture. The highly dissected relief of the Loess Hills and this region's fragile soils were, perhaps, among the other factors which did not contribute to rapid agricultural expansion.

Finally, the southern Blufflands lost most of their indigenous people quite early in the historic times. In response to the Natchez uprising of 1729, the French decimated a large portion of the Indian population and drove nearly all surviving native inhabitants away of the

Bluff. As a result, throughout most of the 18th century, the southern end of the Bluff remained almost vacant.

Techniques of Forest Clearance

The techniques of forest clearance used by the Southeastern Indian tribes in general and the nations of the Lower Mississippi River Region in particular can be identified as a particular type of the slash-and-burn system. Term "slash-and-burn," of course, immediately draws parallels with the type of agriculture practiced by the present-day cultures of the moist tropical forests but, in fact, the only similarity between the two systems is in their use of fire. The major difference between them stems from the fact that the Indians of the American Southeast practiced short fallow or even permanent plot agriculture, not the system of shifting cultivation applied by the present-day rainforest peoples. In the Southeast, native fields were cultivated sometimes for several generations. Benjamin Hawkins, who travelled through some riverine Creek areas in Alabama, noticed that fields on the Chattahoochee River had been "cultivated beyond the memory of the oldest man" (Williams 1990: 40). The descriptions of William Bartram also clearly indicate long-term agriculture.

The slash-and-burn shifting agriculture practiced in the humid tropics (otherwise known as "swidden" or "forest-fallow" agriculture) is almost nomadic in its nature. Given the fact that the soils in the rainforest ecosystems are

extremely infertile and almost all the nutrients are "locked" in the living tissues of the standing vegetation, the only way to release the organic matter and make it available for crops is to set them aflame and turn plant tissues into ash. Since the vegetation is the only possible source of nutrients in the rainforest, tropical slash-and-burn systems require that as much plant material as possible, in fact, all or almost all trees and brushes, must be burnt. For this reason, fire is a crucial factor of rainforest agriculture. Nevertheless, even abundantly fertilized with ash, such soils are subject to fast exaustion. In just a few years after the beginning of cultivation, rainforest farmers have to clear another forest plot. The alluvial or loessial soils farmed by the Indians of the Southeastern Coastal Plain were considerably richer in nutrients and organic matter than the almost sterile soils of the most tropical rainforests. Consequently, to most of the Coastal Plain Indians, fire was of a much less critical biochemical importance. It was applied chiefly for physical removal of forest vegetation.

Barking the trees or girdling, almost always in combination with burning the roots or stump bases, was applied broadly throughout the Coastal Plain. It was the only way to destroy large trees of the virgin forests, for chopping them down with a stone axe was practically impossible. Native girdling involved a removal of a belt of

bark all the way around the trunk. Clearing a new field spot was typically initiated in the first warm days of the early spring as the sap started rising in the trees. Using stone axes, the local Indians either simply bruised the bark near the base of the trunk or removed it on the tree trunks from the base to a height of three or four feet above the ground. With physiologically important fibers and sap channels in the interior layer of the bark cut, sap was drained out without reaching the canopy. This prevented the trees from sprouting new leaves and led to the gradual dying off of their above-ground sections.

Following girdling, the Indians did "scortch the roots with fire so that they grow no more" (Smith and Tyler 1907: 95-96). The next step was the destruction of the understory and smaller trees. To do this, the Indians initially separated their intended field from the remainder of the forest with a strip free of undergrowth which acted as a firebreak. They then uprooted all the underbrush inside the firebreak and set it aflame. When most of the canopy and undergrowth were irreversibly deadened and there was enough sunlight reaching the ground, and the ground itself was more or less free of weeds and sprouts, the Indians started planting crops. This usually took about one year, so that agriculture in the new plot started the next spring. In the humid and hot subtropical climate, the girdled trunks rotted away and fell under the pressure of storm winds

quite quickly. After this, their complete conversion into organic matter took just few years.

Since the soils were relatively rich in organic matter, establishing a new field did not require big inputs of ash and cutting all the trees at once was not worth the energy expended. Because of this, native agriculturalists throughout the Coastal Plain did not seem to care much about immediately taking all deadened trees out of their plots until the process of natural decay made such removal easy. Only occasionally, large trees were felled, before being overwhelmed by natural decomposition. This was done with stone axes. Corn and other crops were planted on the newly cleared plots with large trees and trunks left standing. In fact, the Indian farmers even benefited from the presence of the rotting trunks in their fields because the decomposing dead wood provided an additional supply of nutrients during the initial period of field cultivation. For those old trunks which preserved for some time an ability to sprout, "fire-scortching" operations accompanied by regular cutting out of the sprouts may have been applied repeatedly during the period of cultivation (Kniffen, et al. 1987).

In the Mississippi Loess Bluff, the use of fire by Amerindians had its own peculiar ecoregional features. Native burning techniques developed in the Blufflands were based on the fact that the understory of the local forests

had a vigorous growth of native bamboo, *Arundinaria gigantea*, known in the states of the Mississippi Embayment as "cane." According to Du Pratz, in preparation of "a plantation in woods, thick set with cane," the Natchez "begin with cutting down the canes" with hickory hoes "for a great extent of ground; the trees they peel two feet high quite round: this operation is performed in the beginning of March, as then the sap is in motion in that country: about fifteen days after, the canes, being dry, are set on fire: the sap of the trees are thereby made to descend, and the branches are burnt, which kills the trees." (Du Pratz 1972, pp. 164-165). With such a formidable natural fuel at hand, the Natchez understandably tended to have been more relient upon fire than the native residents of the areas where cane was absent or less abundant. But their girdling techniques appeared to have been very similar if not identical to those practiced on the other side of the Coastal Plain.

Even professional ecologists sometimes reject the idea that the hardwood forests as moist as those of the Loess Hills could have been readily burnt by the native Americans - even with with the help of cane. This disbelief is in part justified because the present-day forests have a much thinned and rarefied cane understory than their early-historical counterparts. The reproductive abilities of bamboo were undermined by nearly two centuries of

agricultural activities, industrial logging and livestock foraging. As a result of this anthropogenic pressure, *Arundinaria* appears to have deteriorated in size and abundance since the early historic period. Representative cane brakes survived only in a few well-preserved old-growth sites such as those in the Tunica Hills, however even there the brakes could have been routinely damaged by freely roaming livestock, especially feral pigs.

In the late 18th - early 19th century, before the beginning of the large-scale expansion of cotton agriculture, extensive and vigorous cane brakes still covered the Mississippi Bluff and were burnt occasionally by local white colonists and planters for their own needs. One such burning operation was witnessed in 1798 by the famous Scottish-American naturalist William Dunbar on the Bluff escarpment of the present-day Tunica Hills area (Dunbar Rowland 1930).

In Dunbar's description, the fire produced by burning slashed cane brakes appears to have been so powerful that it was likely to have immediately killed many of the large trees. Not only that, it could have also effectively scorched and destroyed all remaining shrubs and small trees of the subcanopy strata; if not turned completely into ashes, after burning they could have been easily pulled out. Consequently, "root-burning" might have played a less essential role in the forest-clearing practices of the

Natchez and other "bluff" tribes than among the Indians of other areas of the Coastal Plain. Although I know of no description of this particular type of forest clearance with reference to tribes other than the Natchez, I have little doubt that "cane burning" was also broadly applied by the Tunica, Houma, Yazoo and other specialized upland agriculturalists of the Loess Hills.

The periodic burning of certain portions of the forest was an important part of the Indian subsistence system in yet another sense. Periodic burning, Hudson (1976) hypothesized, triggered the growth of the plant communities on which deer and other animals fed upon. Burning also stimulated the development of meadows or open forests, which were also attractive for deer and turkey, as well as other game animals and birds. This was because it was easier for them to find acorns, nuts, and various fruits in such areas due to the absence of understory.

Indirect evidence that the Blufflands may have been routinely burnt by the Indians for various purposes other than agriculture is provided by Adam Hodgson, who traveled from Natchez through central Mississippi. He found that the forest was "delightful, open and interspersed with occasional small prairies and had the appearance of an English Park" (Williams 1990: 44). While some of the "small prairies" witnessed by Hodgson could have been old Indian fields, the generally open nature of the forest indicates

some form of periodical fire management. Direct or indirect evidence of forest burning by the Chickasaw, Natchez, and other nations is also present in the accounts of several early historic travelers such as Adair (Williams 1930), Du Pratz (1972), and Penicaut (McWilliams 1988).

Native Agroecosystems

The plant-cultivation practices of the early-historical Amerindian populations of the Loess Hills and the Lower Mississippi River Valley were probably similar to those applied by their Mississippian ancestors. The assortment of crops cultivated in the historic native fields derived largely from earlier Mississippian cultigens but the Indians of the historic period also came to rely on some adopted Old World plants. The variety of crops observed by European travelers and explorers in native fields was high, but the major cultigens, like in the prehistoric times, were corn, beans, and squash. James Adair refers to at least three varieties of corn (*Zea mays*) cultivated by the Indians of the Mississippian Region: a smaller sort of so called Indian corn, which usually ripened in two months and was called by the English the "six weeks corn," the "yellow and flinty" kind called "hommony-corn", and, finally, large and white soft-grained variety termed "bread-corn" (Williams 1930: 435-437). James Adair was acquainted with these kinds of corn largely through his observations of the cultivation practices among

the Chickasaw. But Du Pratz reports exactly the same varieties of corn from Louisiana (1972: 202-203).

Beans were represented by a great many varities such as red kidney, snap, navy, and pinto beans, as well as small variety known as peas or pease beans (Kniffen et al. 1987). Probably all these varieties derived from one common ancestor, the common bean (*Phaseolus vulgaris*). Other cultigens were squash, pumpkins sometimes refered to as "pompions" (*Cucurbito pepo*), gourd (*Lagenaria siceraria*), and a small kind of tobacco, probably *Nicotiana rustica*. Of the ancient starchy-seed cultigens, sunflower (*Helianthus annus*) and marsh elder (*Iva annua*) were broadly cultivated (Williams 1930, Du Pratz 1972, McWilliams 1988). Du Pratz (1972) also informs us about Choulpichoul, the mystery grain of the Natchez, which was cultivated on the exposed sand bars of the Mississippi. Bruce Smith (1992) suggests that it was goosefoot (*Chenopodium berlandieri*). Watermelons and peaches were grown from the Chickasaw country to southern Louisiana (Williams 1930, Du Pratz 1972, McWilliams 1988). Finally, rice was mentioned by Penicaut among the crops cultivated by the Natchez.

White travellers and explorers were frequently struck by the manner in which native fields were set and managed, because it was so different from the ways of a European farmer. The prevailing practice of plant management was intercropping, in which several species of crops were

cultivated together in the same field, forming complex agroecosystems. To an unaccustomed eye, Indian fields resembled a disordered mixture of random, heterogeneous elements rather than "agriculture" in the European sense of the word. Corn was planted together with beans, frequently of several kinds, with peas, and with squash. When corn shoots emerged, the Indians heaped the ground around them, producing small hills. Frequently they planted beans and other legumes together with corn in heaps so that the latter would subsequently grow using corn stalks for support (Hudson 1957). Among the heaps and along the margins of the field, there were planted squash, gourds, pumpkins, marsh-mallows, sunflowers and other plants of auxiliary importance (Williams 1930, Hudson 1957).

Among the Chickasaw, whose corn was typically planted in straight rows, beans were grown among the raws (Williams 1930). According to Adair (Williams 1930: 438), "different sorts of mellons," perhaps watermellons (an abundance of these was noted in southern Louisiana by Penicaut), as well pompions, were planted by the natives of West Florida parishes "in separate fields, at a considerable distance from the town." A small variety of tobacco and rice were two other cultigents which probably were grown in separate fields in southern Louisiana - at least we have no information about their cultivation in the agroecosystems. Corn monoculture was also practiced, but only in regard to

the large "bread-corn," which grew to the size of ten feet and ripened in about fourteen weeks (Hudson 1976).

What seemed strange to European eyes, i.e., the intermixture of different crops in one field, was, in fact, one of the effective techniques contributed to maintaining long-term fertility of the cultivated soil, specially in agriculture based primarily on corn. Corn cultivation tends to impoverish the land because corn absorbs much nitrogen from the soil. Without fertilization, the levels of nitrogen in the soil soon become too low for further corn cultivation (nutrient depletion due to corn cultivation is one of the most important reasons for the nomadic and semi-nomadic nature of slash-and-burn agriculture in the present-day tropics.) However, the combination of corn and beans in one field significantly improves the situation. Beans are legumes and, therefore, during their life cycle, they return nitrogen to the soil. By growing beans with corn, the soil nitrogen content is replenished, crop yields remain sufficient, and cleared areas can be cultivated for longer periods of time (Byrd & Neuman 1978).

In sum, Indian agroecosystems were ideally suited for fragile loessial soils. The thick, multilayered tangle of crops served as a good protective shield, preserving loose soil from being washed out by strong rains. The dense mass of roots in the upper layer of soil also prevent erosion. The practice of leaving trees standing in the fields also

played an important role in soil conservation (particularly on slopes) - both in terms of shielding the field from rain and in preventing downslope erosion.

Fire Management

Another technique which contributed to maintaining long-term soil fertility was to burn the old field vegetation from time to time and add potash to the soil. Indian fields, as a rule, contained more weeds and patches of scrubby vegetation than normally found in European fields. Many of these plants, particularly a number of the evergreens of subtropical origin such as palmetto (*Sabal minor*), greenbriers (*Smilax* spp.), wax myrtle (*Myrica* spp.), and marsh elder (*Iva annua*) were highly pyrophytic and probably played a very important part in Indian agroecosystems as major promoters of controlled burns. Each new season usually started with burning the weeds. Prolific cane, which tended to reclaim the fields during the period of rest, once again was of big help to the farmers. The Natchez country *Arundinaria* was such a prolific colonizer of resting fields that it served as a major fuel in such seasonal burnings (Du Pratz 1972).

Gathering dead wood material, bark, grass and cane from the adjacent forested area and burning it in the field was another sourse of potash. In this way the Indians also cleared the woods adjacent to their fields turning them into better hunting grounds. As mentioned previously, deer

and turkey were attracted to the open areas where fruits and nuts were more easily found on the ground (Hudson 1976).

What were the conditions of forest recovery on the abandoned fields? Some fields were used for many years in a row, and both the soil structure and its chemical qualities probably changed substantially during cultivation. By the end of the cultivation period, the soils were likely to have become compressed and depleted, which made them poor ground for forest regeneration. In addition, it probably took a fair amount of time for forest plants to colonize abandoned grounds in places where native fields merged into large treeless areas. What is more, in the absence of canopy cover and the thick layer of moist forest humus and mold to which most native trees are adapted, the dry edaphic conditions were a severe test for sprouting seedlings.

All of these factors made the process of forest recovery slow. In such conditions, various grasses frequently had the upper hand over trees in claiming the abandoned grounds. Once grasses became established, the regeneration of the forest became even more complicated because of the direct competition with the grass communities. In addition, grassland communities frequently harbor large populations of ants, some of which are avid consumers of seeds, particularly those of small sizes. The

combination of these factors provide a partial explanation for why many early-historical travellers and explorers observed "prairies", "meadows", and "grass fields" in the areas adjacent to old Indian towns. Such areas appeared to have been abandoned, and yet, they were not forested. Possibly some of the "prairies" and "meadows" were resting fields covered with weeds. But some of them indeed were covered by explicitly prairie-like vegetation.

Penicaut (McWilliams 1988: 83), who visited the Fatherland site (at that time a main town of the Natchez Nation) in 1704 wrote about "flower-adorned prairies, broken by little hills upon which there are thickets of all kinds of fragrant trees." Today it is hardly possible to imagine any natural prairie in this one-hundred-percent forested country with moist-subtropical climate and soils superb for tree growth. In the "prairies", Penicaut noticed "multitudes of strawberries as big as one's thumb and of exquisite flavor." (McWilliams 1988: 84). And so did James Adair (Williams 1930) during his travels in the Chickasaw country.

What could have been the species of strawberry that both Penicaut and Adair observed? It appears that we are dealing here with one of the strawberry kinds that also grows naturally in the pine woods. Samuel Cole Williams, Adair's editor, points out that "wild strawberry vines matted the earth where there were barrens" (1930: 439). He

cites F.A. Michaux (1803) who wrote that the ripe strawberries in such places "covered the ground as with a red cloth" (Williams 1930: 439). What is important to us from these observations and descriptions is that native strawberries grow in the barren, pine-dominated environments which are subject to frequent fires. Although I am not sure of the species, I also observed some strawberries in the longleaf pine forests of central Louisiana.

Of course, pine barrens did not exist on the deep-loess soils of the Mississippi Bluff escarpment where the capital of the Natchez nation was located. Adair is straight-forward about the fact that strawberries grew in the old Indian fields. Fire is likely to be the key to this ecological riddle. Beautiful and diverse flowers, "fragrant grass", and abundant strawberries were all attributable to the regular burnings which the Indians applied not only to their cultivated but also to their abandoned fields. The regular burnings of the old fields created an ecological regimes similar to that of the prairie. It is not surprising that the diversity of the herbaceous vegetation increased on such abandoned lands and some barren species also migrated there - or may have been propagated by the Indians. Perhaps, these grasslands also supported some typical prairie species. The abandoned fields of the Natchez and other Indians of the region were, indeed,

anthropogenic prairies created by humans on land which otherwise would have supported moist hardwood forests. These field-prairies were probably not forever abandoned. They were resting. In the meanwhile, the Natchez grew their crops in the other fields but they kept the resting grounds clear from woods in order to avoid a big investment of time and labor when these fallow fields were to be again turned to cultivation. This practice was, most likely, shared by the other Bluff tribes.

Regular burnings were probably the critical reason for which the "prairies", "meadows", and "illuminated grass fields" remained unforested long after the end of the cultivation. It was likely that the practice had a long history and was a part of the Mississippian agricultural cycle. Probably since at least A.D. 1200 when corn-based agriculture became widespread in the Lower Mississippi Region, relatively large areas of the Loess Hills were maintained as anthropogenic prairies. As we know from the turbulent history of the Mississippi period, some of these "prairies" were abandoned from time to time and gradually reclaimed by the forest. But other spots were cleared to replace them and gradually turned into similar anthropogenic "prairies." Of course, probably not all native fields were treated in the same way, but the majority probably were - and those were likely to have remained under the field-prairie cycle for decades.

In the early historic period, large field agglomerations in the Loess Hills were still under prairie-like vegetation. Judging by Penicaut's description, the area near the Fatherland site was more an anthropogenic prairie than a forest. This area and many smaller ones around present-day Natchez - within the radius of some thirty five miles - were gradually reclaimed by forest only after 1734, when the Natchez were defeated and dispersed by the French. Thus, much of the mature forest in the vicinity of Natchez, had it survived the major clearing operations of the 19th and 20th centuries, presently would be just 267 years old or even less, given the harsh conditions of regeneration. When the first European planters and farmers started their operations in the area, many of them faced the task of cutting a forest that was only 50-70 years old.

The same situation probably existed on the section of the Mississippi Bluff northeast of Vicksburg where much of the land was cleared and probably maintained under field-prairie rotation by the Yazoo and some other tribes which were ousted more or less simultaneously with the Natchez. Interestingly enough, the prairie-forest mosaic also existed in the area of present-day Baton Rouge when it was visited around 1700 by Penicaut. He and his companions even hunted bisons on the high banks of Mississippi. In many areas the native population maintained some of their "prairie-fields" much longer. For instance, the Tunica

abandoned their well-nurtured grounds on the Bluff Escarpment of the present-day Tunica Hills only in 1790. This is not to say that the anthropogenic prairies were the predominant type of vegetation in the early historic Blufflands. The forest was the overwhelmingly prevailing vegetation type. However, the anthropogenically modified, post-cultivation prairie landscape was characteristic for many areas where it can be hardly imagined now.

Of no less interest are frequent references of travellers to the apparently treeless spots covered by cane brakes. Such spots were sometimes called "cane fields" (Du Praz 1972: 25). It appears that such treeless "cane fields," found scattered throughout the Loess Bluff also were abandoned fields, for I do not know of any reasons for why forests would not grow on the same land that cane does. Today *Arundinaria* is commonly associated with forest vegetation. Perhaps, such cane brakes were the first stage of the natural regeneration following the "prairie stage." As soon as burnings were stopped, the anthropogenic "prairies" might have been first invaded by the native bamboo. This is not unlikely, because bamboo is very prolific - and it was, as we know, very abundant in the Blufflands. This means that sources of cane were always close to the fields. Bamboo would not have faced the same hardships as many other forest species in the colonization of Indian fields because it spreads with suckers which are

connected to the mother-colony. It also grows so fast that, in the absence of fires, it would not leave much chance for trees to recapture the abandoned spot first. Once *Arundinaria* became established, the colonization of the abandoned area by trees again becomes complicated and the forest regeneration is further retarded.

Native Agroforestry

Since the late 1960s there has been a great bed of literature published on native agroforestry in the Neotropics. Although there is no clear evidence that native agroforestry was also practiced in the American Southeast, observations of some European explorers give us rather strong grounds for such an assumption. It appears that the prehistoric and early historic farmers of the Coastal Plain and Lower Mississippi River Region not only cleared their forests but also established semi-cultivated, orchard-like tree communities on their cultivated and abandoned fields. These "forest-orchards" were the result of a long and sophisticated selection of useful plants by native Americans. The agroforestry techniques applied by native farmers in the river valleys of the Lower American South were very close to those practiced today by the traditional peoples in the neotropical rainforests. However, the agroforest ecosystems of the subtropical Southeast tended to have fewer arboreal species.

Agroforestry Practices throughout the Coastal Plain

A consideration of agroforestry practices outside of the Loess Hills is important because it may give a deeper insight into the situation in the Lower Mississippi Region. The earliest hints at native agroforestry in the Coastal Plain can be found in the account of the Gentleman from Elvas who in 1539 described the march of De Soto's military expedition through the territory of the Apalachee Indians, which then covered part of present-day northwestern Florida and the adjacent portion of southwestern Georgia. More than once Elvas noted that, along with corn, "dried plums" were one of the chief products stored in the Indian towns. In the town of Iniahica, "capital" of the Apalachee Country which was probably located on the northwestern edge of present-day Tallahassee, dried plums, together with maize, pumpkins, and beans, represented the main kind of stored food. And these were not the only fruits gathered and preserved by the Indians in large quantities. Near a town called Canasagua, De Soto's expedition was met by twenty Indians "each carrying his basket of mulberries which grow in abundance and good from Cutifachiqui thither and also on into other provinces, as well as wallnuts and plums" (Robertson 1993: 87). Could these fruits have been simply collected in natural habitats? I believe that gathering abundant stores of plums and mulberry in well-developed, closed-canopy woods would have been a difficult task, for

both mulberry and plum trees are not frequent components of mature forests. So here is a hint at some sort of direct or indirect promotion of certain arboreal species by the Indians. Indeed, Elvas informs us that these "trees grow wild in the fields without being planted or manured and are as large and as vigorous as if they were cultivated and irrigated in gardens" (Robertson 1993: 87).

Marching through Apalache territory, Elvas observed that "in the open fields were many plums, both those of Spain and those of the land" (Robertson 1993: 93). What were these "plums"? It appears that, apart from mulberry (most likely, red mulberry (*Morus rubra*), the traveller refers to at least several species. It is not impossible that some species of Old World fruit trees penetrated the southern Coastal Plain from Cuba and other Spanish colonies. But most likely, Gentleman's reference to plums "of Spain" is related to native fruit-bearing trees which could have been physiognomically and generically close to the species cultivated in southern Europe. In the American South there are several species of trees that have plum-like fruits. One of the most likely candidates is persimmon (*Diospyros virginiana*), the deciduous, warm-temperate representative of the tropical family *Ebenaceae*. The possibility is open for the native plums other than persimmon, however, Elvas seems to speak of at least several species.

Other possible candidates are several representatives of the genus *Prunus* such as Chickasaw plum (*P. angustifolia*), American plum (*P. americana*), hog plum (*P. umbellata*) or Mexican plum (*P. mexicana*). Yet one should take into consideration that, of all the native trees that have plum-like fruits, only the persimmon is a relatively common species in the South.

The observation of the Gentleman from Elvas is also in agreement with the fact persimmon is one of the several typical early-successional trees of the Southeast. In the late-successional forest, mature persimmon trees are relatively rare and restricted to old gaps. But, after the forest is cleared by humans, persimmons are among the first trees to colonize the land and initiate the processes of forest succession. The fact that persimmon was a dominant component of the early successional regrowth on the abandoned Indian fields is confirmed by the accounts of the early European explorers of the Coastal South. Not infrequently, it was listed among the most important tree species by William Bartram in his description of the early-successional forests that became established on the old fields in Creek country, especially those in the Savanna River Valley, where persimmon ranked first in the list of species (Harper 1958).

The major reason for the abundance of persimmon in old Indian fields may also be related to the fact that it most

likely was a promoted or semi-cultivated tree. Forest regeneration started shortly after the field was established. Apart from persimmon, the early-successional natural regrowth on the abandoned fields of the Coastal South included a number of other fast-growing, sun-loving colonists, such as several species of sumac (*Rhus* spp.), waxmyrtle (*Myrica cerifera*), yaupon holly (*Ilex vomitoria*), sassafras (*Sassafras albidum*), sycamore (*Platanus occidentalis*), tulip tree (*Liriodendron tulipfera*), sweetgum (*Liquidambar styraciflua*), elms (*Ulmus* spp.), and several oaks (*Quercus* spp.), particularly water oak (*Q. nigra*).

Because of the continuous, creeping invasion of forest pioneer species, fields must have been more or less regularly cleared manually or by fire. In these conditions it was up to the Indians to decide whether certain colonist species should have been left alone or removed. Selective weedings and burnings of the field by the native farmers during the whole period of its cultivation was likely to have been carried out in such a way as to leave the economically valuable trees unharmed. As suggested by Larson (1980), the removal of competitive brushes and trees would likely increase the productivity of persimmon. Apart from this, it must also have contributed to the establishment of the continuously growing populations of this species.

Due to the selective removal of its competitors, persimmon was one of the few arboreal species that were able to maintain a successful reproduction cycle on the Indian fields. It seems that in the course of time the increasing numbers of fostered persimmon trees provided an increase not only in fruit harvests, which greatly contributed to the native diet, but also in surviving seedlings. Since most of the Indian nations of the Coastal South practiced long-term sedentary agriculture, the selective management of forest regrowth on fields may have lasted for decades. As a result, in the course of the whole period of the field cultivation the share and absolute number of the economically important species of trees such as persimmon may have been continuously increasing. This may have led to the development of fruit groves and semi-cultivated gardens dominated by economically useful species. It seems likely that Indians started the promotion of useful species from the relatively early stages of field cultivation.

Observations of the Gentleman from Elvas indicate rather clearly that plums and other trees grew in fields (Robertson 1993). The very logic of persimmon harvesting also suggests this. If native farmers allowed persimmon to enter their fields only after the latter had been abandoned, they would have had to wait for the first harvest for at least 10 years, the age at which this

species begins bearing fruits. Moreover, for another 15 years they would probably have had only scarce harvests because persimmon has a reproductive peak between 25 and 50 years. The earlier trees could be established, the better. The observations of Elvas suggest that Indian cultivated lands most likely represented not just fields but rather orchards-fields in which persimmon trees composed an intermittent arboreal layer over the herbacious agrocommunities dominated by corn and beans. These artificial "agrosavannas" were maintained by fire and manual labor during the whole period of maize cultivation.

Although persimmon appears to have been the most widespread and common tree component of the native flora, Coastal Plain agroecosystems were probably characterized by quite large assortments of useful species. For instance, Bartram affirms the historic presence, at least in some areas, of heterogeneous garden fallows dominated by various fruit and nut trees (Harper 1958). One can suggest that, after the abandonment, these anthropogenically-shaped fallow ecosystems gradually turned into "garden forests". The species composition of such forests, due to the unusually high proportion of nut and fruit trees, was different not only from the original late-successional forests but also from the "natural" secondary formations which tend to replace the "old growth" in those areas that were not subject to continuous agroforestry management.

Travelling through the Southeastern Coastal Plain from South Carolina to southern Louisiana, Bartram provides abundant descriptions of the secondary formations with extraordinary high numbers of hickories and walnuts. Since many of the supposedly secondary forests depicted by Bartram were near areas of dense late prehistoric and early historic populations, there is a strong possiblity that some of these forests derived from previously managed agroecosystems.

Agroforestry in the Loess Hills and the Mississippi Valley

In the Lower Mississippi River Region we find a very similar picture. During early historic times, in terms abundance of various fleshy fruits, the southern part of the Lower Mississippi River Region appeared to have even exceeded other areas of the Coastal Plain. Natives gathered large quantities of persimmons (locally called "placminiers" by the French), plums, cherries and mulberries (Du Pratz 1972, McWilliams 1988). The importance of persimmons in the native subsistence of the region is suggestive of the anthropogenic nature of its propagation in a system similar to that observed among the Apalachee in Florida. Apart from persimmon, Du Pratz (1972: 210) mentions at least three other sorts of plum trees, "the best is that which bears violet-coloured plums, quite like ours", perhaps American or Mexican plum (*Prunus americana* or *P. mexicana*). According to Du Pratz (1972: 210), "The

other kind bears plums of the colour of an unripe cherry, and these are so tart that nobody can eat them; but I am of opinion they might be preserved like gooseberries; especially if pains were taken to cultivate them in open grounds." There were also "the small cherries, called the Indian cherry" that were "frequent in this country." The latter species almost undoubtedly was black cherry (*Prunus serotina*). Penicaut also mentions white and red plums collected in abundance by the Indians (McWilliams 1988). The Chickasaw likewise had "a large sort of plum" which, according to a legendary tradition presented by Adair, "their ancestors brought with them from South-America, and which are now become plenty among our colonies, called Chikkasah plums" (Williams 1930: 387). Perhaps, this was a species which is known under the name "Chickasaw plum" (*P. angustifolia*) by modern plant taxonomists. As for mulberries, "from the sea to the Arkansas" they were, according to Du Pratz (1972: 212-213), represented abundantly by at least three varieties valued by the Indians. The fruit which was called "Acimine" by the French, most likely paw-paw (*Asimina triloba*), also played an important part in the diet. Native apples (*Malus* spp.) were another economically-important group of trees.

Another strong piece of evidence in favor of arboreal gardening among the natives of the region was that they adopted peach trees and fig trees. Old-World pear trees,

apple trees, and pomegranates were also found on the Indian lands (Gray 1958). The presence of these economically important exotic species in the old native areas was routinely observed by early historic travellers in different parts of the Coastal Plain. Many exotic species were reported by Bartram (1940) from Florida and South Carolina. It is also known that on the Carolina cost, peaches were grown by the Indians in large quantities (Gray 1958).

On the basis of descriptions by Penicaut (McWilliams 1988), Le Page Du Pratz (1972), and Adair (Williams 1930), my impression is that in the southern portion of the Lower Mississippi Region, Old World arboreal cultigens were no less - and maybe more - abundant than they were in the eastern section of the lower Coastal Plain. They originated, most likely, from the Spanish, French or English plantations and were propagated by either the Indians themselves or by the European missionaries who chose to settle among them. Du Pratz (1972: 210-211) suggests that "the natives had doubtless got the peach-trees and fig-trees from the English colony of Carolina, before the French established themselves in Louisiana." The peaches were similar to the variety that was called "Alberges" by the French. Figs were of two varieties, "either blue or white" (Du Pratz 1972: 211).

Peaches were found in southern Louisiana by the French explorers as early as in 1699. Penicaut describes these peaches as "better and bigger" than those in France (McWilliams 1988, p. 18). Of the three varieties of mulberry mentioned by Du Pratz, two kinds of white mulberry were undoubtedly a product of an earlier import from the Old World. White mulberry (*Morus alba*) was for thousands of years cultivated in China for its leaves, which served as a food for silkworms. This species appeared to have been introduced in North America by Europeans around A.D.1600 in an unsuccessful attempt to establish a similar silk industry (Duncan and Duncan 1988). The fact that this exotic species was present among the natives indicates that it was also almost certainly cultivated.

The species composition of early historic forests in densely populated native areas also gives some important evidence for agroforestry. While visiting the village of the Natchez and its environs in 1704, Penicaut observed what could have been anthropogenically modified forests: "In their woods everywhere are many peach trees, plum trees, mulberries, and walnuts." He also noticed that "they have many cherries, which grow in bunches like our grapes in France:" this is undoubtedly a reference to black cherry (*Prunus serotina*) (McWilliams 1988: 84).

As already mentioned above, the mature and even the early-successional forests of the Loess Hills tend to have

relatively sparse populations of these fruit-bearing trees - none of the cherries, plums or mulberries are frequent enough in such forests to give impression of being "many" or "everywhere." But the strongest evidence of anthropogenic influence presented by Penicaut were peach trees growing in the forests. The forests visited by Penicaut were located in a relatively densely populated area where, apart from the main town, there were eight other villages. Here and there were numerous deforested patches called "prairies" by Penicaut - but which were most likely old abandoned fields of the Natchez Nation. It is not unlikely that at least some portions of the remaining forest in this highly modified environment were, in fact, second-growth "agroforests" which originated from the fallow or field orchards similar to those described by Gentleman from Elvas in Florida. Most telling is the fact that these fruit-rich forests were centered precisely around the main town of the Natchez Indians. "As for fruit, there is more than in any other place in Louisiana," wrote Penicaut of this location (McWilliams 1988: 84).

Nut trees were another exceptionally important part of the native subsistence throughout the Blufflands. Hickory nuts, walnuts, chestnuts, and hazelnuts were another critical components of native subsistence in the Lower Mississippi River Region. Penicaut mentions three kinds of hickory (*Carya* spp.) or walnut (*Junglans* spp.) which were

commonly gathered by the Natchez Indians but the most highly esteemed were pecan nuts (McWilliams, 1988). Pecan (*Carya illinoensis*) is strongly centered in the middle and western sections of the Mississippi Embayment and largely absent east of the Loess Hills except in one small locality in western Alabama where it was most likely brought by native migrants from the Mississippi Valley. Since Archaic times, pecans were one of the critical elements of the subsistence economy along the Mississippi River. For instance, it appears to have been among the major plant foods collected in the Poverty Point site by both participants of this culture and by their historical successors (Dennis LaBatt, Poverty Point Site, Manager, personal communication, 1998).

In terms of the hypothetical presence of the anthropogenic "nut forests," of interest is the evidence of Le Page Du Pratz who in 1719 bought a piece of land on the territory of the Natchez Nation. In the immediate vicinity of Du Pratz's residence there "was a forest of white walnuts (Hiccories) of nigh fifty acres, covered with grass knee deep." (Du Pratz 1972: 25)

Of special importance is the fact that the nut grove had a grass understory. This may be an indication that the hickory grove initially produceda rather sparse canopy which allowed enough light to pass through to the ground for grass to grow. In addition, it suggests that it was

likely to have been periodically managed by fire which kept it open and free from successional understory. Hickory-rich stands, let alone "nut forests," are not characteristic of the Natchez region and the Deep-Loess section of the Mississippi Bluff on the whole today.

Implications for a Biogeographer

The role of indigenous people in the evolution of mesic hardwood forests in the Coastal Plain has long been beyond the vision of most biogeographers and plant ecologists. In the recent anthropogeographic and ecohistorical literature (Silver 1990, Williams 1990, Delcourt et al. 1993) the Eastern-American Indians were typically given credit for their influence on the natural landscape but, except for the forest-prairie ecotone, the extent and nature of this biogeographic modification has not been appreciated or formally analyzed.

Loessial forests, as we know them today, are a Holocene phenomenon. Native Amerindian populations played an increasingly more important part in shaping the vegetation of the Loess Hills since at least the middle or late Archaic period (6000-4000 B.C. and 4000-1000 B.C.). Their modifying influence may have increased dramatically by the beginning of the Christian era with the diffusion of Hopewellian ceremonial and mortuary practices and culminated after A.D. 1200 with the adoption of large-scale, corn-centered agriculture. Along with climate,

relief, and edaphic conditions, subsistence and ceremonial activities of the native cultures must be appreciated as a "valid" biogeographic factor underlying species composition and structure of the modern forests.

My research into native subsistence practices influenced my whole approach toward exploration of the hardwood forests of the Loess Hills. Initially I was determined to find and sample only old-growth forests lacking any record of clearing or other forms of human intervention. However, my inquiry into the archaeological, historical, and ethnographic material on the subject, combined with the accounts of the early historic travellers and explorers caused a certain moderation of my initial old-growth zeal.

Indeed, the extent of Indian land clearing and cultivation suggested that even forests without any record of disturbance by the Europeans could have originated in old native fields. In fact, such forests were likely to be quite young, for the native population left the Blufflands only during 18th century. Besides, even if some of the surviving pieces of the supposedly "old-growth" forests were never cleared by the Indians, these forests may have evolved in a regime of regular seasonal burnings. These considerations pushed me toward the idea that, given the long anthropogenic history of these forests, my quest for the "ultimate" old-growth was not in accordance with the

history of the environmental situation of the Loess Region. This does not mean, of course, that all surviving pieces of supposedly pristine forests should be classified *a priori* as "anthropogenic." It simply means that early historic and, perhaps, prehistoric plant manipulation by native people cannot be excluded from the complex tangle of influences which have determined the structure and composition of surviving forests. The most difficult problem is, of course, to identify the evidence of such a factor. During the last two centuries, the Loess Region underwent such a drastic environmental change at the hands of Europeans and European Americans that signs of earlier successional responses of forest vegetation to native practices are today practically undiscernible.

But there was a slight chance that some "old-growth" forests could have preserved certain compositional particularities associated with native forms of forest management. This slim hope of mine rested on the assumption that native farmers were in the habit of changing forest composition by fostering economically important species. If such evidence only existed, I thought, it must have been present in some of the most mature stands that originated from Indian "agroforests" in the 18th century. One possible sign for early historic Indian forest management would be anomalously high frequencies of some economically important species. Such "anomalies were indeed found. However,

strangely enough, they were discovered not in the "old-growth" forests but in the early-successional forests.

The Floristic "Irregularities" in the Modern Stands

Some of the forest sites sampled within this research - interestingly enough, precisely those in the areas of the large prehistoric and early historic Amerindian centers - exemplify interesting phytogeographic anomalies.

Most of my transects in the early-successional forest along the southern end of the Natchez Trace was located in very close proximity (on the order of one mile or less) from the Emerald Mound site which had served as a primary center in the late Mississippi Period (ca. A.D. 1350-1600). Of particular surprise to me in the Natchez Trace forest was the fact that the understory of this assemblage was anomalously rich in Carolina buckthorn, or Indian cherry (*Rhamnus caroliniana*), a characteristic but usually very infrequent shrub of the beech-magnolia forest. In the late summer-early fall this species bears large quantities of coral-red to almost black, showy, berry-like fruits with sweet juicy pulp. These are highly attractive to birds and animals and edible for humans. Supposedly, the fruits have medicinal properties, they make good jam, and are still picked by local residents living along the Trace.

Another assemblage remarkable for its compositional deviations was that of the Poverty Point site in northeastern Louisiana. It was the second of only two

forest sites characterized by high popuation densities of Carolina buckthorn. Of no less interest was an extraordinarily high frequency of another, normally even rarer, understory specialist, Mexican plum (*Prunus mexicana*). No other site showed the high frequency of this species.

Carolina buckthorn was observed in the majority of my sites but its population densities everywhere, except the Natchez Trace and Poverty Point sites, were very low - averaging from 1 to 3 individuals per 1 hectare of forest. By contrast, in the understory of the Natchez Trace forest, I registered as many as 182 individuals of Carolina buckthorn on 1 hectare. The population densities of this species in the Poverty Point site appear to be essentialy lower; here I registered 12 individuals within an area of a quarter hectare. Still, these densities are remarkably higher than in any other site sampled. Mexican plum is an even rarer component of the loessial forests than the latter species. I found this small understory tree in only three of 16 sampled sites, and in two cases it was represented by just one specimen per 1 hectare. In the understory of the quarter-hectare sample of the Poverty Point assemblage, I registered 16 specimens of Mexican plum.

Four other species had larger populations along the Natchez Trace than in any other site. Black cherry (*Prunus*

serotina) and red mulberry (*Morus rubra*) had their largest understory and midstory populations along the Trace. Similarly, sugarberry (*Celtis llaevigata*) in the overstory strata of this site also occured more frequently than in any other site sampled. Of more interest is the relatively large population of pecan (*Carya illinoensis*), which typically is a rare component of the upland loessial forests. The number of mature pecan trees found in 1 hectare of the Natchez Trace forest is more than twice as high as in the 15 other sites sampled in this research combined!

Of course, environmental reasons for these phenomena may exist. They may be related to some peculiar qualities of the local soils. But the exclusive correlation of high population densities of at least two economically useful understory species, Carolina buckthorn and Mexican plum, with the old Indian sites is indeed remarkable and suspicious.

The forest along the Natchez Trace represents an early successional assemblage. A point may be made that large population densities of some species here may be determined by successional dynamics. This is likely to be true for black cherry, red mulberry, and sugarberry, which do indeed respond to anthropogenic disturbance. The population densities of these species, although reaching their peaks in certain layers of the Natchez Trace assemblage, are not

considerably higher than in other early-successional and even some late-successional sites.

The case of Carolina buckthorn and Mexican plum is different. First, these species appear to have remarkably high population peaks on the old Indian sites in contrast to their sparse distribution throughout the rest of the Loess Hills. Second, they do not seem to be much affected by anthropogenic disturbance - in fact, the population densities of Carolina buckthorn in the early-successional forests frequently appear to be lower than in mature stands. Thus, reference to anthropogenic disturbance does not explain their high frequencies on old Native American sites.

Still, another question may arise. How could any manifestation of early historic or, let alone, prehistoric native management have survived subsequent forest clearance and land cultivation by white farmers? Well, this is a difficult one, but some suggestions can be made. The Natchez Trace assemblage, although early-successional, harbors small spots of mature forest with large beeches and magnolias that survived in the steep, inaccessible ravines. This led me to think that, even during the period of the maximum extent of clearance and land cultivation in the area, there were always small pockets of uncut forests surviving in deep ravines here and there. Because of the steep slopes, these areas could not be easily plowed and

thus were unattractive to farmers. Even after some of these pockets were later harvested for timber, the original plant populations had a good chance for survival, for the ravines that supported them were likely to have been left for fallows. The scenario could have been, of course, even more complex.

From the history of European land use in the Blufflands, which will be discussed in the next chapter, we know that the region has undergone several periods of forest conversion and regeneration. During the periods of forest regeneration, some of which lasted for decades, the original plant populations may have extended from their local ravine refuges over larger areas, reached other potential refuges previously cleared, and survived there if these refuges remained untouched during the next period of conversion. Some of the original refuges of the old-growth stands may have been finally cleared and forest succession there could have been eventually interrupted, but the plant populations may have migrated from the primary into secondary refuges and thus lasted through time. The Natchez Trace forest represents a complex mosaic of micro-communities indicative of different levels of the successional process; this is suggestive of exactly this kind of environmental history. At the Poverty Point site, some plant populations may have survived in a similar way in some inaccessible pockets of terrain such as the steep

slopes of Bayou Macon and gully bottoms running through the generally flat surface of this part of Macon Ridge. The fact that at least some of these areas were never plowed (although they could have cleared once or twice) is indicated by the presence of undisturbed archeological sites.

The question of native land management is awaiting research and my reference to some of the compositional anomalies present in some loessial forests is only one of the initial insights into the problem which undoubtedly should be addressed in more detailed research. Whether or not the hypothesis of native forest management is relevant to the explanation of the compositional anomalies of the Natchez Trace and Poverty Point sites remains open. But the amount of historical evidence of Amerindian agroforestry is suggestive of the possibility that lasting signs of native forest management can be indeed found in the field - especially given the fair extent of the survivals of Loess Hills forests and the availability of highly dissected areas that may act as natural refuges of modified vegetation.

CHAPTER 6

THE HISTORY OF THE EUROPEAN COLONIZATION, AGRICULTURAL DEVELOPMENT AND INDUSTRIAL LOGGING

During the 1670s, the French colonists of Canada began to penetrate into more southern portions of the American interior and eventually "rediscovered" the Mississippi River from the north. Among these early explorers were two French Jesuits, Marquette and Joliet, who in 1673 descended the Mississippi River to its junction with the Arkansas River. In the spring of 1682, the Lower Mississippi River was explored with more precision by the French expedition of Rene Robert Cavelier, Sieur de La Salle, a resident of French Canada. The expedition descended the Mississippi River from Illinois to the Gulf of Mexico. Soon after La Salle expedition, in 1686, the Arkansas Post was built. It was the first effort to establish the European presence in the Lower Mississippi Valley and start exploitation of its rich natural resources.

The Early Historic Period of Colonization

To start the colonization project in earnest fell upon another Canadian Frenchman, Pierre le Moyene, Sieur de Iberville. His expedition of 1699 was the first to explore in some detail lakes Pontchartrain and Maurepas and essential parts of the Mississippi Delta including bayous Lafourche, Plaquemine, and Manchac. Penicaut, a member of Iberville's expedition, was one of the first European

explorers to make reference of "very high banks called ecorts" (McWilliams 1988: 25), which were the southern end of the Mississippi Bluff then called *Istrouma* by the Indians. Somewhat later this site became better known by its French name *Baton Rouge*. The Indian name referred to the red-painted post which marked here the boundary between the Bayogoula and the Houma Indians.

The French colonization of the region developed slowly. Biloxi, the first permanent settlement established by Iberville in 1699, was not on the Mississippi River itself but on the present-day Gulf coast of the state of Mississippi. By 1713 several hundred French colonists lived predominantly along the coastal line from the Mississippi River to Mobile Bay (Kniffen and Hilliard 1988). The Mississippi Valley and its loess bluffs in this time remained almost unsettled. During the period of the French occupation very little was done for the agricultural development of the region. Only in 1716 the French undertook a major attempt to establish their presence on the Mississippi Bluff by building Fort Rosalie, a predecessor of the later-day Natchez. Between 1716 and 1720 several hundred farmers with their families settled in the area, and first tracts of the loessial forests were cleared around Natchez (Moore 1958). However, the experiment was not a lasting one, for these immigrants were either killed or driven away by the uprising of the Natchez Indians in

1729. The uprising was suppressed to the almost complete destruction of the Natchez Nation but any ideas to rebuild Fort Rosalie were abandoned, and the French never resumed their colonization efforts in this area.

In 1718 Bienville, a brother of Iberville, founded a community on the natural levee between the Mississippi River and the Manchac swamp, known as the "Isle" of Orleans. This community was destined to develop into the largest city of the Mississippian frontier, New Orleans. As early as 1722 it became the capital of Louisiana and a major center of dispersal of the French and European population throughout the Lower Mississippi Valley. It should be pointed out, however, that during the French colonial occupation this dispersal was rather localized. It covered mostly the southernmost end of the Valley between the mouth of the Mississippi River and Pointe Coupee, natural levees along bayous Lafourche and Manchac, and, to a lesser extent, the lower reaches of the Red River Valley.

The elevated alluvial terraces along the Mississippi between New Orleans and Baton Rouge were the core area of the French colonial agriculture where the early plantation system emerged. Bienville made it obligatory for planters who acquired the land along this section of the Mississippi River to build levees which protected these rich bottomlands from floods. Due to the relatively fast hydrological improvement, this alluvial area became one of

the first targets of agricultural development and was completely deforested during 18th century. The cultivation of most commercially important crops had started in Louisiana during the French colonial rule. Cultivation of cotton began in 1740, and sugar cane was introduced by the Jesuits from Santo Domingo in 1751.

On the other hand, the French colonial agriculture only very marginally extended onto the upland loessial surfaces. Disturbance of the loessial forests was largely limited to the general vicinity of Baton Rouge and the Opelousas Ridge west of the Mississippi River. The primeval forests of the Mississippi bluffs and other loess-capped surfaces north of Baton Rouge Parish remained largely untouched by the white farmers, particularly after the destruction and abandonment of Fort Rosalie.

In 1763, as a result of Seven Year's War between France and Great Britain, France lost to the British all its possessions east of the Mississippi River, with the exception of the "Isle" of Orleans. Even earlier, in November of 1762, France had to cede the rest of Louisiana to Spain which largely meant the end of the French colonial experiment. When the British reached deserted Fort Rosalie site, they discovered here, apart from the ruins of the fort itself, only few modest clearings (Moore 1958). Either some of the fields were completely overgrown with forest or the French had not had much incentive to invest their time

and labor in agricultural cultivation. Whatever were the circumstances at Fort Rosalie, the limited interest the French showed in agricultural development throughout most of the greater Louisiana frontier was, no doubt, another side of their traditionally strong focus on fur trade.

From the very beginning of their colonial venture, the French tended to consider the Mississippi River mostly as a strategic route that would have provided the major fur-trade region north of the Mississippi-Ohio confluence with the easy access to the Gulf of Mexico and international markets. The eager development of the alluvial lands of southern Louisiana was a function of the geographic proximity of these areas to New Orleans which was developing from the very beginning as an important export outlet - the only one available to planters and farmers settled along the Mississippi. With increasing distance from the growing port, incentive for market-oriented agriculture faded, and the French settlers were easy to succumb to their more traditional and more trusted fur-trade adventure.

From the late 17th century through most of the 18th century the enormous forested wilderness between Illinois and large colonial outposts of southern Louisiana was roamed and explored largely by French hunters and traders. Many of these were *courer de bois*, or "runners of the woods", the name given to French frontier men who sought

the free life away from the colonial authorities and restrictions of the European civilization. The lifestyles of these adventurists were, in fact, even more "primitive" than those of the Indians for many of them did not even have a permanent residence and practiced no agriculture.

The population densities during most of the first French period of domination remained low. By 1762 only some 8000 to 12000 Europeans and Africans resided in whole of greater Louisiana (Kniffen and Hilliard 1988). The majority of colonists were concentrated within the Mississippi River Delta, especially in the New Orleans area, between New Orleans and Baton Rouge, along Bayou Lafourche, and, secondly, on the Opelousas Ridge, between Lafayette and Opelousas. West of the Mississippi River and north of Lafayette-Opelousas area the population was likewise very thin and colonization was extremely slow. Even as late as 1770 the European population of the Quachita Post region, which included most of Macon Ridge, numbered some 110 people broadly scattered throughout the area. In 1766-1768 the population of southern Louisiana considerably increased due to the arrival of Acadians from Nova Scotia. Most of these newcomers settled along the natural levees of the Atchafalaya Basin and along Bayou Lafourche, upon the Opelousas Ridge, and in the west prairies of southwestern Louisiana. However, the population densities in the Blufflands remained low. After the absorption of the

Mississippi Bluff by the British frontier in 1763, the British authorities took efforts to attract new settlers onto these virgin lands. But the recruits were few and population growth was very slow.

In 1779 the southern portion of the Mississippi Bluff and most of Louisiana were occupied by the Spanish. The northern boundary of their possessions was at the mouth of the Yazoo River. The Spanish faced the same problem as the British did - the sharp lack of settlers. In these conditions the Spanish authorities had to step back from their traditional policies of attracting exclusively Spanish colonists and welcomed the settlers from the protestant United States and the British subjects. Taking into consideration a little success of their British rivals, they granted land to new Anglo-American colonists on even more liberal terms than their predecessors. The idea was then to bind the developing enclave of Anglo-American frontier to New Orleans by the ambitious price-support program. Within this program, an essential part of the funds was allocated for purchasing tobacco grown in the Natchez District at prices higher than in the open market. As a result, tobacco cultivation experienced a short-term boom. The sharp decline of the tobacco market happened in 1790 when the Spanish authorities found it impossible to maintain the fund-consuming program. The prices fell, and

the industry was ruined. It was the first crisis of the one-crop system.

The Spanish colonial period set several important foundations for the further environmental history of the Loess Hills and southern Mississippi Valley. The Anglo-American population in the Natchez District and in the Felicianas indeed increased: this, in combination with the termination of the price-support program, eventually led to the shift of the de facto control over the Natchez District to the Americans in 1798. The growth of the Natchez colony got momentum. As it attracted rich planters from the East, capital began to flow into the area.

The influx of the Anglo-Americans was a turning point in the fate of the loessial forests for the attitude of these people toward the exploitation of the regional resources was quite different from that of the French. As for the crash of the tobacco enterprise, it was a serious blow but it could not stop the fly-wheel of the developing market agriculture. What is more, the crisis indirectly pointed out to the culture which appeared to show a great potential for becoming a good successor of tobacco. It was cotton, of course. Of all farmers and planters of the Bluffland region, only those involved in cultivation of cotton did not suffer much from the crisis because prices went down on everything except cotton. It was a dawn of the great era of "Lord Cotton".

The Ante-Bellum Period

The development of the plantation system based on cotton in the 18th century was slowed by the difficulty of separating cotton fiber from the seeds. Cotton cultivation remained relatively unimportant until Whitney's famous cotton gin was invented.

The saw gin produced a true technological revolution in Southern agriculture. In Louisiana and western Mississippi the large-scale cotton cultivation for export passed beyond the experimental stage in 1799 and continued to increase rapidly during the following decade (Moore 1958). The first experiments with cotton took place on the old plantations in the immediate vicinity of the Mississippi River especially on those in southern Louisiana. The development of the saw gin technology overlapped in time with some important geopolitical changes in the region.

In 1800 Spain ceded Louisiana back to France. In 1803 France signed the Louisiana Purchase treaty and ceded Louisiana to the United States. These political shifts were followed by an influx of American subjects into the new territory and gave another impulse to the development of the plantation system. The commercial plantation agriculture required significant tracts of the cleared land, and so the large-scale conversion of the local mesic forests has begun. Since about 1803 the planters had

started a more or less regular assault on the forests back of the Mississippi River (Gray, 1933; Williamson, 1940). It was the period when the forests of the Loess Hills became dotted with first extensive cotton fields.

The third impulse for the development of the cotton plantation system in the Blufflands was associated with decline of the older centers of the cotton cultivation located along the southeastern seaboard of the American South - in South Carolina and Georgia. By the second decade of the 19th century, the exaustion of the relatively poor soils of the Atlantic states had prompted the eastern planters to look for the fresher frontiers. The cotton front was slowly moving west through Georgia but new settlers were quick to understand that the productivity of the upland soils throughout most of the Gulf Plain was sadly poor. Another problem was the Indians.

Advancing westward in 1790-1810, white settlers came in immediate contact with the powerful Creek Confederation which became the major obstacle of the further European expansion. Attracted by the true and imaginory riches of the Lower Mississippi Valley, many white colonists migrated further west, to the banks of the Mississippi. Upon arrival, they discovered than most of the best land on the natural levees between Baton Rouge and New Orleans was already occupied. Brackenridge who visited Louisiana in 1810 that from New Orleans to Lafourche, about one hundred

miles distant, there was an unbroken sequence of plantations "laid off with great regularity and taste." (Parkins 1970: 108). On the other hand, the alluvial bottomlands of the Mississippi Valley, despite their fabuluos fertility, could not be considered for the commercial agriculture because of the extended hydroperiods of the Mississippi River. Within the floodplain, plantations could be set only on some of the most elevated levees but these were too small in acreage to accomodate many. Besides, even the highest of these natural levees were subject to some innundation in the years of big floods.

Located between the largely inaccessible bottomlands and poor uplands east of the Mississippi Valley, the Blufflands remained mostly vacant at the time. As many colonists soon discovered, this belt of hilly land combined the advantages of the bottomlands with those of the uplands. Fertility of the Loess Hills rivaled that of the alluvial bottomlands of the Mississippi Valley. On the other hand, settlers were free from the fear of destructive floods and somewhat distanced from the plagues and dangers of the low grounds associated with clouds of mosquitos and maladies they carried. Colonization of the southern Blufflands was also facilitated by the fact that this attractive land was free from the Indian claims. The only exception was the extreme eastern margin of the region

owned by the Choctaw. The only people whom the newcomers found on these virgin hills were the white planters and farmers who came here earlier.

From this early period, the Blufflands began to develop into one of the main foci of the agricultural development in the American South. Of 300.000 cotton planters who settled by 1821 along the Mississippi River in the territories of what is now the states of Louisiana and Mississippi, most established their farms and plantations in the Loess Hills region. The full-blown plantation system, based on cotton, had taken roots in Louisiana and southern half of Mississippi by 1830. From 1810 to the early 1830s, the Mississippi frontier moved from the Mississippi River eastward to the extent that the Choctaw and Chicasaw found themselves completely surrounded by cotton fields and rather densely populated white areas.

For a long time, since the first French colonial outposts had been established in the region till nearly the middle of the 19th century, the Lower Mississippi Region developed as a frontier enclave disconnected from the settled and colonized Anglo-American "mainland". With the Chicasaw Purchase such connection - via north - was finally established and this became one of the factors that pushed both the further settlement and the whole geoeconomic engine of the plantation system. Northwestern Mississippi was settled in part from the south but largely via western

Tennessee, particularly in the section immediately adjacent to Tennesse state line.

Much of the Lower Mississippi River - now not only in the south but also in the north was flanked by the European settlements with Baton Rouge, Natchez, Vicksburg and Memphis being the major foci of the white (and black) population, and New Orlean becoming the only sea port for this entire region. Now the Mississippi became the major commercial artery of Anglo-America which simplified the colonization of the few remaining retarded frontiers along its course and integrated the whole region into one market-oriented network. By 1850 all poorly populated or unsettled areas east of the Mississippi were finally colonized, except for the extensive tract of the impenetrable swamps and bottomland forests of the Yazoo delta. Closer to the middle of the 19th century, southern Louisiana (both the alluvial levees and the loessial lands), the loess hills of Mississippi, as well as western Tennessee and western Kentucky had some of the highest population densities in the Southeast - 18-45 men per square mile (Parkins 1970).

The colonization and development of the loessial surfaces west of the Mississippi River and north of the Opelousas Ridge was slower. The plantation system and slavery tended to be developed here on much smaller scale. Small land holdings prevailed and these were broadly scattered. During 1820s and 1830s most of Macon Ridge in

east-central and northeastern Louisiana were still covered by virgin hardwood forests which was broken here and there by small clearings for cabins and farm plots. Although deforestation gradually progressed, the situation did not change considerably even during the last two decades of the Ante-Bellum Period when the extent of clearing operations on the Mississippi Bluff and remaining alluvial levees along the Mississippi reached its apogee. Most of the plantations were set on the margins of Macon Ridge adjacent to the secondary waterways such as Bayou Macon, Bayou Lafourche, Boeuf Bayou, and Quachita River.

Much to the success of the cotton-based economy was the fact that in the first decades of the 19th century, the farmers of Mississippi developed a new strain of cotton which was created by crossing several varieties of the plant cultivated in the New World by the Spanish, French and British. The new variety ambiguously called "Mexican cotton of Mississippi" was so productive that in 1830 it was introduced into all cotton-growing states (Moore, 1958). It was, however, the cotton industry that inflicted upon the Loess Hills Region one of the worst form of land destruction in the whole American South (Bennett et al. 1928).

The Ecological Aspect of the Cotton Monoculture

Historically, the Loess Hills are an environmentally "unlucky" region. High fertility of the loessial soils has

contributed here to the establishment of some of the most destructive systems of land use in North America. Although fertile and well-suited to agriculture, the loessial soils, as well as the loessial material below them, are soft, loose and exceptionally fragile. The soil exaustion and erosion were known in the loess hills of Louisiana and Mississippi before 1780. During 18th century these problems were generated mostly by corn and tobacco culture. With the beginning of the intensive clearance and the development of the full-blown, market-oriented cotton monoculture during the early decades of the 19th century, erosion turned into a devastating environmental disaster.

Deforestation and erosion were integral parts of the vicious circle stimulated by human greed. Forest is the only defensive shield of the fragile loessial environments. Stripped of its vegetative coat, the loessial soils and the loessial mantle beneath inevitably become subject to physical deterioration. In the conditions of the humid subtropical climate of the Loess Hills Region, the major trigger of the erosion process is rain. In the context of the large-scale plantation monoculture, fields in cultivation were continuously denied the defensive cover of not only trees but also native shrubs and grasses. Not surprisingly, erosive processes started as soon as a new ground was cleared and topsoil was exposed to the washing effects of heavy rains. A certain amount of soil was washed

away by every shower. Soon the surfaces of previously rounded hills were scarred by webs of numerous small gullies which constantly grew in size. Some of them developed into large ravines within only a few years (Moore 1958). Erosion was aggravated by the natural dissection of the Loess Hills.

In the fertile deep-loess section, much if not the most, of the land surface was made up by slopes. In many areas slopes could not be avoided. Even if a farmer would have divided his fields into small segments and limited them to ridge tops, he would not have solved the problem because only a few degrees of hilltop slope would have ruined all his efforts. "A good Northern farmer would deem it a crying shame and sin to attempt to grow any crops upon such steep slopes, except grasses or shrubs which do not require tillage", wrote Frederick Law Olmsted (1907: 11) who travelled in Louisiana and Mississippi in the winter of 1853-54. For a southern farmer, however, both planter and small owner alike, these fragile, soft lands were the chance of a lifetime to make a fortune. No doubt, if capitalism and Nature put a northern farmer into the system with the same prospects and constraints, the result would have been the same.

In the country where any scar made by the plow on the surface of the land potentially meant a ravine, the life of a cultivated field was short. In three or four years the

soil and much of the loessial material were dumped into adjacent ravines or bottomlands, whereas the field itself was gullied beyond repair and abandoned. The native vegetation would reclaim the land. The question, however, is what kind of forest could have grown on such abused and distorted land.

It would be unfair to say that no efforts to improve the situation were undertaken. The destructiveness of erosion was early recognized in the Loess Region. The very need to cultivate - even for a short time - this erosive and sloppy terrain required some kind of primitive technique that would have prevented the immediate destruction of the soil layer. By the 1830s the system of horizontal rows first advocated by Thomas Jefferson and William Dunbar was almost universally applied on large plantation in the southern Blufflands. A primitive replica of terrace cultivation, this system prescribed plowing of rows running in horizontal circles around the contours of hills. The method was intended to eliminate an immediate danger of downslope soil washing. But it was of comparatively low efficiency. During strong showers, the water would collect in the furrows until it broke through the lowest point of a row, causing as much damage as on unterraced hills. Some refinements to this system were proposed. The most immediate adjustment was to lay out horizontal rows more accurately, with the use of measuring

instruments. Secondly, it was proposed to run the rows into drainage ditches. Finally, instead of putting few large ditches, some farmers gave a gentle incline to the whole system of rows thus turning each row into a small independent drainage ditch. Neither of these systems worked well. Contour row lines, whatever their design was, were easily overflowed after almost any strong shower. The ditches tended to turn into muddy torrents forming even larger gullies than those that eroded spontaneously. The fragile soils of the Loess Hills were simply unadapted to the extensive market-oriented monoculture. Finally, whatever were the advantages of the proposed systems, these improved techniques were applied, in fact, by few enthusiasts, whereas most of planters reduced themselves to the absolute minimum of effort.

This rather unique reluctance of a southern planter to take responsibility for a land stewardship was based on the rude economic realities of the southern frontier. The land on the southern frontier was cheap, whereas the prices for slave labor tended to be very high. This unfortunate combination meant destruction for both the land and the forest because, from the standpoint of a large landowner, there was no economic sense to invest time and effort in land and thus "waste" the labor. Instead - quite understandably - he prefered to waste the land.

The environmentally unfavorable set of economic conditions fueled by the relict American thirst "to get rich fast" contributed to the establishment of a unique cultivation practice which was truely nomadic in nature. Having been limited by the nature of the Loess Hills topography, climate and soil conditions to only few full agricultural cycles on one site, most of the plantations were constantly on the move, replacing the forest with the degraded, desert-like landscapes. Usually, as soon as the field was exausted, a new ground was cleared and brought under cultivation - sometimes nearby, in other cases fairly far away - depending on the availability of a vacant land. Many planters anticipated the decline in soil productivity well before they were forced to leave the worn-out area. While the old site was still in cultivation, they invested part of their profits in purchasing new tracts of land where then slaves and overseers were sent along with necessary tools. Typically, new sites were cleared from forest every winter which was a relatively "calm" season. This strategy gave the planters a relatively smooth transition from one area to another, with a "non-stop" production cycle. It is sadly ironic that clearing new ground in the language of cotton growers, was called an "improvement of the land" (Southern Planter 1842: 14). Rather it could be compared with the development of "...a

cancerous growth spreading death and desolation across the face of the land" (Southern Planter 1842: 14).

Many planters and farmers had exausted their lands in Mississippi and moved to Arkansas and Texas ready to start the vicious cycle again as early as in 1840s (Hurt, 1994).

Corn and tobacco which were important before the large-scale introduction of cotton retained their importance during the full-blown period of cotton cultivation although their importance in the Loess Hills decreased. Together with "King Cotton", they made up a triumvirate of major crops. Corn was produced on most plantations and farms as a major staple crop. Throughout the Loess Hills corn was especially important in the small-scale farms which did not use the slave labor. Small- and medium-scale farmers quickly recognized the advantages of their involvement in the cotton market. Like planters, they tried to enter this profitable business as soon as possible, sometimes exposing themselves to the extreme difficulties. Typically, on his newly cleared land, a new settler first set cotton production (Winters 1994). Only secondly he turned to cultivation of corn, grain and other crops that provided self-sufficiency (Winters 1994).

Corn, as cotton, was cultivated on farms of all sizes. But just as the large plantation put the greater emphasis on cotton, the smaller farms had to place emphasis on corn (Winters 1993). The importance of corn in the overall

agricultural production also tended to increase from the south to the north, as the climate grew cooler and the smaller farm units were becoming a predominant type of land holdings (Winters 1994). In southwestern Tennessee cotton was still a predominant crop but further north, from middle Tennessee to Kentucky the major crops were corn and tobacco (Winters 1994).

A small-scale farmer with limited financial resources was much less a threat to the environment than a rich, and for the most part wasteful, planter. After obtaining a farm, small farmers had to quickly turn to the task of constructing a humble family dwelling. Then much effort and time was invested in clearing of field plot and breaking the land. Frequently, due to the lack of resources and labor force, small farmers had to leave some of their trees in the field, with the intention to return to the laborious task of clearing under more favorable circumstances. As a result, because of the overshading effect of remaining trees, the first yields of their crops, weather cotton or corn, were somewhat reduced. Another difficulty was the presence of numerous tree stumps. These, after all, could have been ignored but working around them meant less precious planting space and thus a lower yield. For a small farmer, it normally took 5 to 6 years to clear the field (Waters 1994).

In the early 19th century the loessial forests of western Tennessee and Kentucky were dotted by a large number of small holdings. Many farmers who colonized these forests at the time were keen at observing and emulating the native techniques of forest clearance and land cultivation. In part it was related to the fact that they came here immediately from the east where they had lived - sometimes for several generations - almost side by side with the Indian farmers. Besides, in western Tennessee and Kentucky, as well as in northwestern Mississippi, the local Indian presence - especially that of the Chicasaw - was more noticeable than in the south where most of the Indians were driven from the loessial lands by the French. Leaving a few trees standing in the field was, for example, a typical Indian practice. It was particularly important in the Loess Hills with their steep, easily eroding slopes. Another characteristic Indian custom applied by the white farmers was burning tree stumps. This has been done in order to speed up the process of the land clearance and to add some ashes to the soil.

The Civil War and the Post-Bellum Period

The chaos and destruction of the Civil War supplemented by the effects of the sea blockade and the post-war crisis of the plantation system led to the temporary decline of the cotton industry and commercial agriculture on the whole. The immediate ecological

consequence of the War was the massive abandonment of previously cultivated areas. Most of such abandoned areas were reclaimed by forest. Given the extensive nature of the cotton agriculture in the Loess Hills, it appears that by the beginning of the Civil War most of the original growth had been already gone.

After the war, the forest regeneration in the Blufflands led to the establishment of the landscape which had more in common with the modern one than with that characteristic for the early 19th century. The Post-Bellum Blufflands were dominated by the forest regrowth which was composed of the highly successional light-dependent species, with beech and magnolia largely lacking. Surviving patches of the late-successional forest might have been associated with strongly dissected areas such as Tunica Hills or other physiographicly similar localities such as one mentioned by Mohr (1884) in the vicinity of Vicksburg, where "Beyond the Blackwater in the hilly region of the bluff formation, the great magnolia covers the hillsides". The life histories of some of the old secondary forests studied within this research project such as those sampled in Oakley Plantation and the Port Hudson area, can be traced back to the early Antebellum Period.

An essential reduction of the cultivated land took place during the war, as the land owners had to divert their main focus from cotton to food production. After the

war, the slow rate of recovery was related to the difficulties of reorganization of the plantation economy. The slow rate of the recovery is reflected by the crop dynamics. The harvest of 1866 was less than 2 million bales, i.e. less than half that of 1859 and a slightly more than the harvest of 1839 (Agelasto 1922). The cultivation of cotton on the loessal hills of Louisiana declined and eventually shifted to the northern and western portions of the state. The stabilization of the cotton production in Mississippi occured only in 1879. It was the first year when all southern states except Louisiana and Alabama produced more cotton than in 1859 (Agelasto 1922).

The total production of cotton in the United States doubled between 1879 and 1898 (Agelasto 1922). But the surplus came largely from newly plowed lands in Texas and Oklahoma and the more dynamically developing northern fringe of the cotton culture, especially in Arkansas. Although much of the land in the Blufflands was replowed during the Post-Bellum Reconstruction, many farmlands remained under forest through the remainder of the 19th century and some of them probably survived through the first decades of the next century. Since 1893, all increase of the cotton production was due to its expansion on the western frontier (Agelasto 1922).

The Post-Bellum Period, although a difficult for the people of the Loess Region, was a great period of the

forest recovery and land rest. It was the first time since the beginning of the cotton cultivation when the large areas of land in the Loess Belt were left alone and forest was allowed to grow back throughout much of the Mississippi Bluff. Such were the effects of the Civil War desolation that in some areas the recovering secondary growth did not attract attention of an agriculturalist for decades. The Civil War was an environmentally important treshold of Loess Hills history yet in another respect. Although between the end of the War and 1879, there was a slow increase of the cultivated area, this increase was largely a function of the gradual reclaiming of the former farmlands, not clearing the new ones. When so much abandoned land laid under the thin, young regrowth, there was not much reason in implementing the hard task of clearing the surviving sections of the old growth. The Civil War set back the whole extensive mechanism of southern agriculture and effectively suspended the destruction of the remaining tracts of the late-successional forest ecosystems.

The logic of the Post-Bellum development was not, however, similar for all the parts of the Loess Hills belt. The slow expansion of the cotton-based agriculture over the previously cultivated lands took place in Mississippi. In Louisiana cotton declined and was never restored to its former importance. On the northern margin of the cotton

production area, in western Tennessee, the situation was quite different. This area did not experience such a sharp post-war decline because the smaller-size Tennessean farms (many of them historically relied on free labor) adopted new ways faster than big holdings of Mississippi and Louisiana which had been highly specialized using slave labor. Consequently, after the war the cotton growers of this state did not appear to suspend their assault on the local forests to the extent it happened in the Lower South. On the contrary, the general Postbellum decline of the cotton agriculture was a chance for them to establish themselves with a more confidence on the recovering market.

The Second Decline of the Cotton Agriculture

The slow recovery of the cotton industry was interrupted by the invasion of the boll weevil. In 1891 the beetle entered Texas from Mexico and by 1901 spread throughout most the southern states (Hurt 1994). The Loess Hills Region was one of the first major cotton-growing areas struck by this new disaster. During 1920s the boll weevil completed its spread both eastward and northward and reached the northern margin of the loessial cotton-growing belt in Tennessee and Missouri (Rainwater 1952).

The beetle infestation grew into a big problem for southern cotton growers by 1901. Their losses especially increased after 1914 and peaked in 1921 (Agelasto 1922, Bennett and Chapline 1928, Hurt 1994). It was the second

big blow for the industry - the one from which it never quite recovered.

In a way, however, the boll weevil turned out to be a benefector of the southern agriculture for it finally eliminated a one-crop system and contributed to the agricultural diversification. The reduction in cotton acreage was in part compensated by increase in acreages of corn and legume hay. The ambiguous nature of this decline for the southern agriculture was expressed by W. J Spillman, with the USDA, who noted that "the boll weevil is really a blessing in disguise" because it began to destroy one-crop system in the South (Hurt 1994: 226).

The boll weevil infestation was of considerable importance for the ecological situation in the Blufflands. The ravage of the boll weevil resulted in the gradual decrease of the cultivated area throughout the South, especially in the old cotton regions such as were the Blufflands. Some structural changes began to occur after 1910, although cotton remained king for yet at least several years to come (Hurt 1994). The trend toward lower acreage became obvious in 1915, after the record crop of 1914. In 1917 the cotton acreage dropped considerably (Fite 1984). During the following dozen of years, the dynamics of the production decrease sharpened. The harvest of 1919 was only slightly larger than the harvest of 1909. The decline of the cotton industry culminated in the disasterous crop

of 1921 which was the shortest crop ever gathered since 1895 (Agelasto 1922). Throughout the 1920s cotton acreage remained stagnant. By 1929 the cotton industry of the Loess Hills, as throughout the South, was heavily beaten and exausted but the land was given another chance to recover.

The beetle infestation put the temporary end to the Post-Bellum agricultural expansion and allowed some forests to mature. On the other hand, one of the result of the boll weevil invasion was also an increased reliance on livestock. Compared to the 1870s, the number of cattle by the end of the boll weevil period doubled and the number of swine increased about 25% throughout the South (Agelasto 1922). This, in turn, increased the pressure on the remaining forest.

The Period of Industrial Timbering

The industrial timbering in the Loess Hills historically had a late start. The period between 1904 and 1913 which is sometimes referred as "the golden years" of forest industry in Louisiana and Mississippi was largely disassociated with the exploitation of the Loess Hills hardwood forests. The human pressure on the loessial hardwoods during this period was relatively mild. Some secondary forests developed on the abandoned fields during the Post-Bellum epoch were cleared again for the slowly recovering cotton culture but generally there was no considerable decrease in the forested area and the

remaining old-growth forests stayed largely intact. In 1905 only 3% of the total lumber cut were hardwoods (Kerr 1980).

In Louisiana's timber industry, the share of hardwoods increased in the early 1920s, and for 18 years - from 1923 to 1940 - this state led the nation in the hardwood lumber production (Kerr 1980). The understanding that Louisiana had the vast tracts of hardwood forest came comparatively late as a result of the state' survey that had begun in 1930. The result of the survey was somewhat shocking for foresters who, from the first years of Louisiana timber industry, relied heavily on pine (Kerr 1980). It turned out that by this time half the state's 16 million acres of forest land was made up of hardwood timber.

The third wave of hardwood conversion (in Louisiana it was largely stimulated by the above-mentioned survey) within the southern half of the Mississippi Bluff got momentum in the 1940 and picked up in the 1950s (Kerr 1958, 1980). In 1949 hardwoods made up 49% of Louisiana's lumber production. The fast growth of the state's timber industry is evident from the fact that only in two years, in 1951, hardwoods made up already 57% of all the timber cut in Louisiana which was 170 million feet more than pine (Kerr 1980).

By the early 1950s the hardwood forests of the loessial belt between Vicksburg and Baton Roge had been already quite depleted (Kerr 1958). The were two relatively

large blocks of forest remaining within this area - one in the general vicinity from Vicksburg, in Warren County, and another, the larger one, in the southern section of this transect, in Wilkinson County of extreme southwest Mississippi and West Feliciana Parish of Louisiana. The southern part of this area which included most of West Feliciana, narrow southwestern section of East Feliciana and southern section of Wilkinson County was locally known as the Tunica Hills. The forests of the Tunica Hills area were dotted by the numerous plantation sites but it appears that in this area the clearcut practices were rather localized and did not threaten the very existence of the forest as a whole.

One of the important thresholds in the history of the timber industry in the Loess Hills occurred in 1951 and 1952 when a severe drought struck Louisiana causing devastating fires all over the state (Kerr 1958). Both the dry pinelands and bottomland forests were threatened. The Loess Hills forests, too, were affected. As a result of the extensive fires, as much as 20 billion feet of timber were lost for three years after 1951 (Kerr 1951). In the single year of 1951 an estimated 200,000 acres of hardwood forest were burnt (Kerr 1980). An immediate response of the timber industry to the "fire period" of the early 1950s was an increased emphasis on the fire prevention and the reforestation programs. But in the more long-term

perspective, there was also a trend for the development of a "keep-a-close-eye" management approach, which made an emphasis on more active clearing practices. In the past Louisiana hardwood forests were "neglected". After the fire period of 1951-1953 no piece of timber was meant to escape the close attention of the timber industry. An increasing intensity of the clearcut practices and the regular thinning of hardwood forests now was considered to be a part of the closer managerial approach.

During the 1950s-1960s and the early 1970s the expansion of the timber industry in the Blufflands and adjacent alluvial bottomlands was coordinated with the expansion of the soy bean culture. During this period most of the mesic upland and the bottomland forests were initially cleared by the timber industry. Then farmers moved onto cleared areas and established soy bean fields. The soy bean boom grew out of the diversification trend initiated by the boll weevil invasion and further accentuated by the World War II. Understandably, this middle-twentieth-century's symbiosis of the industrial greed and agricultural rush with its middle-twentieth-century's technology and amplitude resulted in much more efficient deforestation of the Blufflands than the early nineteenth-century's drive for a single-crop commodity - cotton.

From the late 1940s to the early 1970s, most of the bottomland forests which remained relatively intact till the World War II were cleared. It was during this period that the timber industry eliminated nearly all surviving tracts of the late-successional beech-magnolia forests with the notable exception of the Magnolia Glen area in the Tunica Hills and some forests sites in the vicinity of Chicot Lake including one managed today by the Louisiana State Arboretum. The forest cover of Macon Ridge was reduced to nearly zero. Most of the secondary forests surviving from the Civil War and the earlier stages of industrial clearing were also destroyed. As a result, during the 1950s-1960s the Loess Hills turned out to be more deforested than they had ever been in the past.

By the middle 20th century, both major late-successional forest blocks which survived the Antebellum clearing rush became the subject to fast conversion. The Tunica Hill was cleared twice in this century - first in 1950s and secondly in the 1980s (Platt 1994, personal communication, Quigley 1994, personal communication). The uplands were cleared first but during the both episodes clearing operations were also extended down slope, especially in the areas were slopes were relatively gentle. I assume that most of the ravine forest in the area was also cut in the 1950s. This idea seems to find its

confirmation in the relatively mature nature of the secondary regrowth found in most ravines.

After the 1950s clearings, most of the cleared areas were allowed to be reclaimed by forest and some were replanted with pine plantations. Since that time, loblolly pine became a regular (albeit not a dominant) component in the structure of the upland forest. In the 1980s, some of the upland areas were recut but the second harvest of the ravine forests was rather limited. As a result of these activities, today many hilltops here are dominated by degraded, low-stature woodlands and thickets, which apparently have little capacity to further regeneration into the tall-timber forest. Such devastated areas are commonly found adjacent to the old timber roads, which extend along many ridgetops of Tunica Hills. But where the recent timber operations extended from the ridgetops downslope, this more mature forest was interrupted by the tongues of the devastated tertiary regrowth, which had to be dismissed from our study.

After the late 1960s agricultural development was no longer a primary reason for clearing the loessial forests. The area under cultivation was, in fact, decreasing. Many farmers in the Loess Hills, as throughout much of the South, consolidated their holdings and converted cotton fields into pastures. Farm sizes were increasing whereas the agricultural population was declining. Finally, during

the 1980s, many farmers remaining on the land began to experience serious financial difficulties because of the extensive investment in land and technology the federal government had encouraged (Hurt 1994). The collapse of soybean market in December of 1979 caused by President Carter's embargo of grain sales to the Soviet Union also played its important role in the decline of the agricultural dynamics in the Loess Region. Subsequently, since the early 1970s, the timber industry became almost the only factor that determined the acreage of the remaining forests.

The Post-Modern Period of Landscape Modification

In the absence of the agricultural activity, deforestation in the Loess Hills changed its pace and mode. Most of the lands cleared by the timber industry were not put under cultivation anymore, but left to fallow. This, of course, contributed to a faster and smoother forest regeneration. By doing so, the timber industry kept extending the areas under very young successional formations and continuously disrupted the successional process in recovering stands.

To evaluate the environmental changes which determine the state of the loessial forests today, it is useful to become acquainted with the strategies and practices that have been applied by the concrete timber companies during the 1990s and early 2000s. Some of the largest timber

companies currently present in the southern and middle Blufflands are "Soterra", "Anderson-Tully", and "Georgia-Pacific". These and smaller timber companies tend to harvest timber in rotation cycles gradually going through their lands. They also benefit from cutting the forest on the land owned by private individuals. Both the clearcut and selective-cut clearance have been traditionally practiced. Most of the timber companies have properties both in the loess-capped uplands of the Mississippi Bluff and in the alluvial lands of the Mississippi Valley. This determines a largely seasonal nature of their operations in the region. During the late summer, fall, and most of the winter when the alluvial soils are least saturated, the timber companies focus on harvesting the bottomland forests. With the beginning of the flood season in the late winter-early spring, they turn their attention to the upland forests and harvest their Bluff plots till the late summer when the bottomlands dry out.

Of special interest for ecologists are the practices applied by the Memphis-based Anderson-Tully Company. This company is distinguishable among others as a champion of sophisticated managerial approaches. They point to a trend that may become prevalent in the timber industry at the beginning of this new century. Invaluable help for understanding the nature of the Anderson-Tully system of forest management was given to me by the forest manager of

the company, Glen Brown in our conversations and joint field excursions in August of 1998.

For cutting its own woods, Anderson-Tully developed an ecologically-sound strategy that enables the company to avoid depletion of its resources. This strategy was first formulated and applied in 1967 when under John Tully's initiative a permanent system of growth plots was worked out. Today, under Anderson-Tully's complete forest management plan, the number and species to be annually cut, is dictated not by the needs and opportunities of the market, but by the degree of maturity and regenerative ability of the forest. As pointed out by Tony Parks, Anderson-Tully's vice president of land management, "What we cut is based on what we determine we can harvest in each species without exceeding its annual growth" (Stephano 1992: 64). Although clearcuts are sometimes applied by Anderson-Tully, the predominant practice on its own land are selective cuttings of various intensity which leave from one quarter to three quarters of the trees standing, depending on the individual conditions of each tract. This strategy provides good ecological conditions for fast and healthy regeneration - perhaps, even at the expense of the short-term profit. Unlike other timber companies which took effort in replanting the cleared areas in the Blufflands with the species alien to the region such as pines, Anderson-Tully literally allows nature to make the species

selection for each plot and then "...manages what she puts on those sites" (Stephano 1992: 64).

However, the managerial approach of Anderson-Tully to the state of its forests also has another aspect which should not be disregarded. Apart from selective logging of the commercially valuable timber on its plots, the company also does regular "sanitation" cuttings. The purpose of these operations is not only a removal of dying or unhealthy trees (tracts with the highest mortality and density, according to the company's strategy, are to be cut first), but also an extraction of commercially "non-valuable" species. Ironically, one such unwanted taxa is American beech (*Fagus grandifolia*), an indicator of the "old-growth" status or at least a longevity of a forest ecosystem in the Loess Hills. The reasons for low commercial status of beech are related to the tree's morphological and pathological characteristics.

To begin with, beech is a very "brushy" tree. Normally branch-free sections of beech trunks are relatively short, thus numerous knots in its wood. Secondly, beech trunks very often are hollow in the middle - due to the effect produced by heartwood eating fungus. The fungus disease does not seem to be lethal for beech. Many beech trees pick it up in comparatively young age and apparently are able to live with the pathogen and gradually rotting heart for centuries. But fungus certainly makes beech commercially

unattractive. As Glen Brown informed me, the industrial application of beech wood became limited nowadays largely to beer-brewing: chunks of beech wood have been currently added to Budweiser beer for aging. Evergreen magnolia (*Magnolia grandiflora*) also has a rather limited use in the timber industry, although its wood was appreciated and broadly used by pioneers and old-timers.

Since beech and magnolia achieve the dominant status only in the mature, late-successional stands, the purpose of the sanitation management can be otherwise considered as a deliberate removal of the remaining patches of the old-growth forest. The strategy of Anderson-Tully is literally to comb through their lands in the search of the remaining mature stands and put them to the saw. Few patches of the old beech-magnolia forests in Warren and Claiborne Counties were cut shortly before my arrival to this section of the Bluff in the summer of 1998. For instance, a solid stand of the relatively mature beech-magnolia forest was clearcut in the area of Port Gibson in 1997. I was lucky to sample a relatively small remnant of this stand, which survived because it was immediately adjacent to the local church. A large portion of the old-growth forest was harvested approximately at the same time at the Bluff escarpment about 11-12 miles north of Vicksburg, in the area to which I gave the name "Steep Bluffs". Again, I managed to sample

1 hectare of the remaining section of this forest but it is not likely that this tract would survive for long.

The logic of these forest management practices is clear: non-valuable and low-valuable shade-tolerant dominants occupy the living space where otherwise valuable species could have grown. Of the more or less frequent constituents of the mature beech-magnolia forest, the most commercially desirable species are white ash (*Fraxinus americana*) and oaks (*Quercus* spp.), especially cherrybark oak (*Q. pagoda*) and Shumard oak (*Q. shumardii*), and, to the less extent, - tulip tree (*Liriodendron tulipfera*) and black cherry (*Prunus serotina*). The repeated thinning of the timber applied by Anderson-Tully is intended "to improve" the loessial forests by deliberately promoting these species.

The Anderson-Tully Company currently owns about 90,000 acres of the Bluff forests and is aggressively buying new land at an average rate of about 1000 acres a year. The purpose is to establish a right balance of the company's harvesting capacity and available forest acreage. In the recent past it took 15-16 years of rotation period for Anderson-Tully to harvest and "screen" all its upland forests which is a somewhat short time span for the optimum regeneration.

On the other hand, such a rotation-period was rather long to solve the problem of the regeneration of the shade-

tolerant species (the ideal situation to which Anderson-Tully pushes itself hard and purposefully is to get rid of the "shade-tolerants"). The practical experience accumulated by the company's field forests indicates that 15-16 years is enough for the undergrowth of the shade-tolerant species to recapture a solid portion of understory and penetrate the midstory of the managed stands. To impose a more strict control on the regeneration of the shade-tolerant taxa, Anderson-Tully recently decided to reduce its rotation cycle to 10-12 years.

The implications for conservation ecologists are clear. Even though Anderson-Tully is sincerely committed to long-term forest preservation, the forest community it tends to promote is not quite one that biologists and conservation organizations would be glad to see and cherish. The company fosters the development of the truly anthropogenic forests whose species composition is being shaped and modified through repeated extraction of undesirable species toward the state determined by the ultimate commercial ideal. Due to the extension of Anderson-Tully forest management plan practices, an increasingly more extensive area of the loessial forests will be converted into such deliberately impoverished early-successional woodlands. Many of the last remaining patches of the rich and unique late-successional ecosystem

of which many are still unidentified and unexplored are facing destruction.

It would probably be rather irrelevant to have a grudge against the forest management system practiced by Anderson-Tully. After all, it is a commercial enterprise with commercial, not conservationist priorities. For a business-oriented organization, the company developed a remarkably ecologically-sound and wisely long-term program. It made it half of the way. What is really surprising is a rather passive and phlegmatic attitude to the problem of the preservation of the beech-magnolia forests noticeable among conservation biologists and managers of the environmental and heritage organizations. A program should be launched with the purpose of identification and exploration of the surviving old-growth forests in the Blufflands. The Loess Hills is a big region, so such efforts will not even necessarily interfere with the interests of the timber companies. Interestingly, conservation ecologists and companies such as Anderson-Tully may, in fact, develop cooperation in such exploration. If given a choice, the timber industry probably would not be interested in acquiring large tracts of pristine beech-magnolia forests because they require great investments of money, labor, and time for turning them into commercially valuable stands.

Second-growth stands dominated by the light-dependent species (today these are overwhelmingly predominant in the Loess Hills) can certainly be looked upon as more commercially valuable acquisitions. Luckily, the priorities of the conservationists are completely opposite. Interestingly enough, I got a general impression that the timber companies may not always be aware what kind of forest communities they have on their lands. I also noticed that foresters and ecologists are not always quite sure what exactly determines predominance of the light-dependent or shade-tolerant species in the loessial forests. Likewise, there is no clear understanding that forests rich in beech and magnolia are in fact not an omnipresent formation but rare relics of the advanced stages of the forest succession which are easy to avoid and lay apart for the conservation purposes. Working together in the areas of the perspective industrial purchases, conservation ecologists and industrial foresters may achieve a mutually beneficial goal: to save money for the companies and save the species-rich late-successional forests for the future generations.

Animal Husbandry and Its Influence on the Forest

One of the main sources of the environmental change in the Loess Hills was animal husbandry. Prehistoric Indians lacked the domestic animals that could have caused any important environmental change or damage to the region's

forest. The first large domestic animals such as cows, pigs, and horses stepped upon the soil of the southeastern North America with the first European exploration parties. De Soto's party marched through the Southeast accompanied by a large herd of swine guided by experienced pigmen from Galicia. In the course of the expedition, these domestic beasts in part ran away, in part were lost or left among the Indians. Later French colonists of Louisiana and southwestern Mississippi might have introduced cattle. One of the most surprising phenomena of the native subsistence in the Lower Mississsippi River Region was high reliance on livestock. James Adairs mentions that the Indian settlemnts of the Lower Mississippi Region, including those of the Chicasaw "abounded with hogs" (Adair 1930: 444). These animals, most likely, originated from the swine left behind by De Soto's party.

Cattle and pigs were a very important part of the Plantation System during the Antebellum Period. After the War - during the rest of the 19th and much of the 20th century - they remained one of the essential component of the local rural economy.

Since the early Ante-Bellum times, the farmers of the Cotton Belt gradually developed a unique system of animal husbandry by letting livestock to take care of itself. In the Loess Hills of Mississippi and Tennessee, livestock - both cattle and pigs - roamed loose and unfenced during

most of the year in the forests (Moore 1958, Winters 1994). For those travelling in the Southeast like, for instance, Solomon Robinson, it was surprising to see that the local livestock largely raised itself and resided in the woods independently of their owners (Kellar 1936). In the conditions of the mild subtropical climate and plentiful vegetation supply, the animals needed neither much care nor winter shelter.

Large plantations of the Old Natchez district often possessed as many as half-thousand head of cattle. Sometimes herds numbering as many as a thousand head roamed in the woods. The southern fields were typically perimetered by fenses and stockades which served the purpose of defending the crops from the encroachment of the omnipresent and voracious semi-wild grazers. Only in the fall, when the corn and other crops were harvested, the cattle were gathered and pigs were caught and both were put for a couple of months into the fields to graze upon the vegetable left-overs. It appears that this system of animal husbandry was borrowed by the European farmers from the local Indians: Adair (1930), for instance, refers to the Indian pigs as largely feral animals.

The major breed of cattle represented throughout much of the Loess Hills during 19th and most of the 20th century were so-called Atakapas and Opelousas, otherwise known as "scrub cattle" which proceeded from similarly named

districts of south-central and southwestern Louisiana. These cattle was considered "native" - in a sense that its ancestry did not have immediate European connections but emerged from the mists of the turbulent epoch of the Mississippian protohistory preceding the massive European colonization. They originated most likely from the very early European, presumably French, import that has been adjusted by several centuries of adaptive evolution. Atakapas and Opelousas were small, muscular beasts which produced an inferior grade beef which was hard and abounded with fibers. But they were hardy and well-adapted to the hot and sultry summers of this subtropical region.

The predominant breed of hogs were the famous "Arkansas Razorbacks", a small, highly mobile and again hardy race of swine which was likewise beyond any competition in terms of its adaptation to the hot subtropical climate. As it is indicated by the name, this breed originated in Arkansas and may have had genes of the swine that had escaped in 1539 from De Soto's expedition. A rarely seen race of feral pigs, the wild relatives of the Arkansas razorback, is nearly omnipresent in the modern forests of the Loess Hills.

Interest in breeding of scrub cattle and Arkansas razorbacks was, of course, conditioned by their hardiness and their abundance which stemmed from their remarkable ability to sustain themselves with the gifts of nature.

Moreover, their maintenance cost was next to nothing. George Washington Carver wrote in his paper "How to raise pigs with little money" wrote that hogs can be quickly and easily "raised with little or no cash outlay (1916: 3-4).

However, in our age of environmental thinking, it seems clear that the low costs and high profits of those involved in cattle- and hog-breeding economy was maintained at the expense of nature. In fact, cattle and pigs yielded in their ability to modify the forest ecosystems of the Loess Hills only to the semi-nomadic system of land use applied by the planters themselves. The Loess Hills were rich in various forms of scrubby plant growth that may have attracted the attention of the foraging livestock. But one feature of the region was especially pronounced. In the early-historical times the Loess Hills were exceptionally abundant in cane or native bamboo (*Arundinaria gigantea*) which had here the optimum conditions for its development. The Loess Hills forests were overgrown by this bamboo from the ravine bottoms where it treached the largest size to the hilltops where it assumed a more shrubby form. Nowadays *Arundinaria* is abundant only in the well-protected habitats. Many secondary forests are chatacterized by a rather sparse bamboo undergrowth. As suggested by Hilgard, most of this luxurious cane growth was destroyed by cattle by as early as 1860.

Destruction of the cane was not the only loss inflicted upon the Loess Hills forests by the feral animals. Cattle and pigs have also fed on shrubs and tree samplings, with a special taste for the evergreen and more succulent kinds. Thus during the Postbellum Period the foraging animals may have been an important factor that retarded the forest regeneration, or even made it impossible. The heavy impact of livestock grazing on the forest vegetation can be readily seen around the Oakley Plantation located near Saint-Francisville (Feliciana Parish, southeastern Louisiana). The understory and midstory of the middle-successional forest protected on the plantation site is for the most part very thick and abounds in various evergreen trees and shrubs, especially Carolina laurel-cherry (*Prunus caroliniana*) and southern magnolia (*Magnolia grandiflora*). It makes a sharp contrast with the thin and park-like surrounding woods which are now in private possession and throughout much of its history have been never denied the access of the livestock - as most of the forest in this area. The grazed woodlands like this one have almost no understory and are devoid of any evergreen life forms with the only exception of trifoliate orange (*Poncirus trifoliata*), an exceptionally prickly exotic shrub from subtropical China which is alone able to withstand grazing and even benefit from it.

Throughout much of the European part of its history large areas of the loessial forests were never closed to livestock. Moreover, after the decline of the agriculture throughout much of the Mississippi Bluff and enlargement of private holdings, many of the privately-owned woodlots were turned into pastures and grazing lands. The frontier days are gone and cattle do not roam across the forest landscape as freely as they did before. Protected areas are closed to the large herbivores but many decades of semi-wild animal foraging and the mentality of "grazing capitalism" that is very much akin to this kind of foraging certainly left its mark on the land. This should not be overlooked when it comes to the analysis of the species composition and structure of the present-day forests. One should also remember, the feral pigs - illusive and voracious, always avid and ready for acorns, beech nuts, magnolia cones and tree roots - they are still out there waiting for a new harvest.

Brief Summary and Conclusions

The major ecological and biogeographic change happened in the Loess Hills Region during the period of the European colonization and development. Most of the original forests of the Region were cleared during the Ante-Bellum Period for cotton monoculture. After the Civil War there were several decades of recovery but much of the recovered forest was then repeatedly cleared during the period from

approximately 1890 to 1920 when cotton expanded again. These period was not so destructive for the remaining late-successional forests because the clearance extended largely over the former farmlands. The third wave of deforestation began in 1940s, peaked in 1950-60s and declined in the early 1970s. It was related to the expansion of the soy beans culture and was characterized by the emphasis on the industrial clearing. It was a period of the hardwood timber boom and intensive development of the timber industry in the region. During this period the last substantial tracts of the survived late-successional forest and much of the second-growth forest were cleared.

Consequently, during the last two centuries most of the loessial forests were cleared 2-3 times. The intensive clearing practices contributed to the considerable biogeographic change in the Loess Hills. They stimulated the development of the essentially different forest type which was nearly lacking the shade-tolerant components in the canopy and was dominated by the expanded populations of the various light-dependent species, particularly sweetgum, southern oaks, and tulip tree which had the accessory status in the original early-historical forests.

CHAPTER 7

THE STATE OF THE ORIGINAL AND MODERN FORESTS

Extending for the full length of the loess deposits from the vicinity of Baton Rouge, south Louisiana, to extreme northern tip of the Coastal Plain in south Illinois, the Bluff hardwoods east of the Mississippi River originally formed a continuous belt of approximately 500 miles long and from roughly 7-10 to nearly 40-46 km wide. As such, it was the largest tract of the upland mesophytic forest in the Southeastern Coastal Plain. The other areas of the Coastal Plain where the similar forests were originally present, such the Tallahassee Red Hills, the Marianna Lowlands and the Apalachicola Bluff are considerably smaller in total acreage. The great south-north extent of the original Loess Hills forests suggests a latitudinal biogeographic variation which no other Coastal Plain forest could have matched. Given the relative continuity of the edaphic conditions, at least within the deepest section of the loess deposits, the Blufflands appear to offer a unique opportunity for large-scale biogeographic study little complicated by differencies in substrate and soils.

One of the noteworthy features of the Loess Hills hardwood forest is its relative isolation from other mesic forest regions. Edaphic conditions limit lateral expansion of this forest belt. Most of the species that make up the

mesophytic forest are intolerant of the saturated soils and poor drainage of the Mississippi floodplain. Thus, they drop out near the base of the western slope of the loess ridge. The eastern boundary of the mesic hardwood forest is determined by the thickness of the loess deposits. The species composition and the structure of the forest shifts where the loess blanket thins to approximately 6 feet (Delcourt and Delcourt 1974). The proximity of the sandy-graveliferous substrate to the land surface along the southeastern margin of the Loess Hills accounts for the transition to the more xeric and nutrient-deficient pine woodlands dominated by loblolly pine (*Pinus taeda*) (Spicer 1969). Similar conditions in the northern part of the Mississippi Embayment result in the strong predominance of the dry oak-hickory and shortleaf pine forests. This relatively broad belt of the drier environments separates the eastern Loess Hills hardwoods from the mesic forests of the Low Interior Plateaus which are part of the West Appalachian forest province. The only mesophytic forest region with which the Loess Hills hardwoods have a direct connection, the Ozark Hills of southern Illinois, is adjacent to the extreme northern tip of the Bluff.

The southern section of the Mississippi Bluff remains one of the most forested areas of the Coastal Plain. Two largest portions of the mesic hardwood forest survived here till the present time are associated with the Tunica Hills

area (West Feliciana Parish, southeastern Louisiana, and Wilkinson County, southwestern Mississippi) and Port Gibson to Vicksburg section of the Bluff which cover most of Claiborne and Warren counties in southwestern Mississippi. The section in between - in Adams and Jefferson counties - is also relatively well forested with the only exception of the area around Natchez where fields and pastures prevail over the forest. But throughout most of two-county section, the forest cover is broken by a mosaic of numerous clearings which make it less contiguous.

Needless to say, all this forest, with the exception of the small patches distinguished during this research, is early-successional in nature, with beech and magnolia largely lacking in the overstory. The best chances to find new late-successional stands are within the southernmost section of the Bluff Ridge, in the Greater Tunica Hills which includes most of West Feliciana Parish and adjacent Wilkinson County. Not only is this area heavily forested and poorly explored by biologists, it has also been historically located away from major roads which were the main routes of development in the Loess Hills.

After the Civil War this thinly populated region was only marginally involved in the agricultural development and some of its ravine forests may date back to the abandonment time. Travelling throughout the Tunica Hills on the both sides of the Louisiana-Mississippi state line,

I observed in the ravines of this area some of the best examples of regenerating magnolia and beech-magnolia growth. The chances of more or less extensive patches of the late-successional beech-magnolia forest are especially high in the area of the Bluff escarpment which has virtually no roads.

Apart from the eastern bluff ridge, the similar mesic forests were supported by somewhat thinner loess deposits along the western margin of the Lower Mississippi Valley, from southern Louisiana, through Arkansas into Missouri. Since the loess-capped surfaces west of the Mississippi River were segregated into fragments, the associated mesic forests also formed here a loose chain of islands. On the basis of the geomorphologic history of the region we can conclude that at least beginning from the early Holocene these insular mesic fragments had developed in relative isolation from the other southern mesophytic forests and from one another.

At least four to five major sections of these western forests on loess could be identified. A narrow mesic forest corridor must have existed in prehistoric and early-historical time between the coastal prairies of the southwest Louisiana and the Atchafalaya floodplain of south-central Louisiana. Edaphically it was associated with the loessial soils of the Opelousas Ridge and bluffs of the lower Red River Valley. Within this almost completely

deforested area by the present time, the only sizeable portion of this forest vegetation survives today in Chicot State Park. Unfortunately almost all this forest is of early-successional nature. From the Chicot State Park, in the northern section of this region, a few remaining small pockets of the mesophytic vegetation can be traced down to the loess-covered salt domes of coastal Louisiana where the state's most southern mesic forests are found. North of the lower Red River four isolated upland surfaces in Avoyelles Parish of central Louisiana (Lytle and Sturgis 1962) known as the Marksville Prairie probably also supported the mesophytic forest. Further northward two relatively large tracts of the mesic forest must have been associated with Macon Ridge and Crowley Ridge. Along with the Marksville Prairie, these two areas were completely isolated from mainland upland surfaces and from each other by the extensive floodplains of the Mississippi and its tributaries.

No original forests have survived on the loessial surfaces of the Marksville Prairie and Macon Ridge. Present-day Macon Ridge is so badly deforested that it is difficult today even to hypothesize on the nature of its early-historical forests. Allen (personal communication, 1998) suggested, for instance, that beech (*Fagus grandifolia*) was not present in the original forests of the region. He tended to relate the Macon Ridge's old-growth

forest to the bottomland forest type. Although I found this opinion difficult to accept, I also could not refute it since neither of those small patches of the early-successional forest that I came across in this largely deforested area contained any beech.

Early Historic Accounts of the Original Forests

As already mentioned, the original forest cover of the Loess Hills was either destroyed or strongly altered over nearly two centuries of agricultural exploitation and industrial timbering. One of the important sources of information about the early-historical vegetation of the Loess Hills are the accounts of the 18th and 19th century naturalists and travelers. Their observations were made when large tracks of the original growth were still in existence. Probably the most remarkable feature of these primeval forests was the structural importance of the evergreen taxa, particularly southern magnolia (*Magnolia grandiflora*).

Southern magnolia was of primary importance in a rich assortment of species observed by William Bartram in 1777 on the extreme southern margin of the loessal belt between the Amite River and Manchac, a small town on the banks of the Mississippi 15 miles south of Baton Rouge. William Dunbar, who traveled along the Loess Hills in 1798, has also mentioned magnolia first among the trees "peculiar to the high grounds" along the Mississippi in Louisiana and

referred to this tree in excitement as "One of the grandest and most admirable productions" of the Bluff (Rowland 1930: 94)

Passing through the area 20 miles north of Saint-Francisville on his way to Natchez in the winter of 1853-54 Frederick Law Olmsted observed "... frequent groves of magnolia grandiflora, large trees and every one in the glory of full blossom." It should be noted that such monodominant stands were apparently somewhat localized for Olmsted also provides us with an important ecological observation that "The magnolia does not, however, show well in masses, and those groves, not unfrequently met, were much finer where beech, elm and liquid amber formed the body and the magnolias stood singly out, magnificent chandeliers of fragrance (Olmsted 1907: 4-5).

Another largely evergreen forest area was witnessed by Mohr (1884) near Vicksburg, Mississippi, where "Beyond the Blackwater (Big Black River) in the hilly region of the (loess) bluff formation, the great magnolia covers the hill slides."

Cuming who traveled in 1809 in the southern Blufflands between Baton Rouge and Natchez described passing on horseback "... through a forest abounding with that beautiful and majestic evergreen, the magnolia or American laurel" (Thwaites 1904: 336). While recognizing the important role of magnolia and other evergreens in the

structure of the loess hills woods, he also noted the mixed and heterogeneous character of the local forests: "Some are evergreen with laurel and holly, and some, where oak, walnut, and poplar are the most predominant being wholly brown in winter" (Thwaites 1904: 350-353).

The pine forests which flank today the eastern margin of the Mississippi Bluff are apparently a genuine natural ecosystem which dominated this part of the Loess Hills in the early-historical times. Cuming who travelled in 1809 along the Mississippi Bluff from Baton Rouge to Natchez noticed that "...the pine woods... generally begin at from fifteen to twenty miles distance from the Mississippi river..." (Thwaites 1904: 353). Moreover, it is probably not quite well understood that these forests dominated by loblolly pine (*Pinus taeda*) also owe their existence to the loess deposits. On the large-scale biogeographic maps one can see that along the eastern margin of the Mississippi Bluff - in southwestern Mississippi and southeastern Louisiana - these forests extend deep into latitudes which throughout the rest of the Coastal Plain were originally dominated by the longleaf-pine forests. It appears that the major factors that contributed to the development of loblolly-pine (as opposed to longleaf-pine) forests in this section of the lower Coastal Plain was the lower frequency of fire regimes and, perhaps, the higher fertility of the local soils. Both factors were likely to have been

conditioned by moderating influence of loess which was not thick enough to prevent fires but whose presence promoted more mesic conditions than those that could accommodate longleaf forest.

Under less intensive fire regimes loblolly pine could maintain its competitive advantage over longleaf, and yet it was secure from the encroachment of the most mesophytic hardwood species.

Species Composition of the Original Forests

The species composition of the primeval forests of the southern Blufflands was reconstructed in 1974 by the Delcourts. Their research was based on the data of the forest survey conducted in 1821 by George Daugherty in the northwestern corner of southeastern Louisiana. This forest survey encompassed the whole territory of nowadays West Feliciana Parish and essentially covered the region known today as Tunica Hills. According to Delcourts' quantitative reconstruction, the early historical old-growth hardwood forests of Western Feliciana had been strongly dominated by the association composed of southern magnolia (*Magnolia grandiflora*), American beech (*Fagus grandifolia*), and American holly (*Ilex opaca*) In the ravine forests, where American holly seemed to have dominated over beech, the magnolia-holly-beech association made up 66.1% of the total forest structure. On ridge-tops, where beech somewhat prevailed over holly, the combined share of the three

species reached 49.5%. The remainder of the species composition was shared by the rich assemblage of the accessory, mostly deciduous, species among which Daugherty recorded black oak (*Quercus velutina*), red oak (*Q. rubra* or *Q.shumardii*), Spanish oak (*Q. falcata*), water oak (Q. nigra), white oak (*Q. alba*), ash (*Fraxinus* spp.), elm (*Ulmus* spp.), hickory (*Carya* spp.) sweetgum (*Liquidambar styraciflua*), black gum (*Nyssa sylvatica*), black locust (*Robinia pseudo-acacia*), black wallnut (*Juglans nigra*), box elder (*Acer negundo*), cherry (*Prunus* spp.), chinquepin (*Castanea pumila*) or *Quercus muhlenbergii*), linn (*Tilia americana*), maple (*Acer rubrum* or *A. saccharum*), sycamore (*Platanus occidentalis*), cowlick (*Halesia diptera*), mullberry (*Morus rubra*), sassafras (*Sassafras albidum*), dogwood (*Cornus florida*), hornbeam (*Carpinus caroliniana*), and ironwood (*Ostrya virginiana*).

The concept of magnolia-beech-holly association can be considered as a further development of the concept of the magnolia-beech climax which was initially proposed for the mesic sites of the lower Coastal Plain by Harper (1906, 1911) and later accepted by Gano (1917), Pessin (1933), Kurz (1944), Braun (1950), as well as Hubbel et al. (1956).

In the Coastal Plain such mesic sites corresponded to the narrow edaphic zones transitional between the periodically flooded alluvial bottomlands and the vast well-drained piney uplands. Thus, except for very few

regions such as Tallahassee Red Hills and the Marianna Lowlands, the distribution of the coastal plain forests dominated by magnolia-beech climax seems to have been restricted to the non-flooding outer margins of the river valleys — their alluvial terraces and bluffs, as pointed out by Braun (1950) and Delcourt and Delcourt (1974). The strips of mesic habitats which originally extended along the Coastal Plain rivers other than the Mississippi are so narrow that they can be hardly shown on large-scale vegetation maps. The remnants of such forests were described in 1777 by William Bartram during his travel across the Coastal Plain from South Carolina to Louisiana (Harper 1958).

The study of Delcourt and Delcourt (1974) was one of the first attempts to reconstruct the composition and structure of the early historical forests of the Coastal Plain. The methods and results appeared so persuasive that the Delcourts (1974) projected this model into all other edaphically suitable areas of the Coastal Plain such as the bluffs of the Apalachicola and the Savanna rivers the Marianna Lowlands and Talahassee Red Hills. However, the straight-forward application of the magnolia-beech-holly concept to the other regions of the Coastal Plain was complicated by some peculiar features of the reconstructed early-historical forests of West Feliciana.

One of the interesting particularities was, for example, the important role of American holly (*Ilex opaca*). To my knowledge, in the twentieth century holly was never reported to have achieved a status of the dominant species in the other areas of the Coastal Plain. The reconstruction of the presettlement magnolia-beech climax forest of the Apalachicola River Bluff later conducted by the Delcourts (1977) revealed that the relative importance of American holly in the early historical forests of this region was limited to only 5.9% compared to 13.5-20.3% in Louisiana's Tunica Hills. Another unique feature of the reconstructed magnolia-beech-holly forests was the outstandingly important role of the evergreen taxa in their structure in general.

Although only two species, southern magnolia (*Magnolia grandiflora*) and American holly (*Ilex opaca*) seem to have formed the bulk of the evergreens in Tunica Hills forest, their total share in the ravine association reached approximately 51.8% of the floral structure, with magnolia alone making up 31.5%. Thus, this "bottomland" forest was essentially an evergreen-deciduous formation. Although the share of the evergreens decreased to a total 38% of Tunica Hills' upland forests, it still was 15.9% higher than in the reconstructed presettlement magnolia-beech forest of the Apalachicola bluff in north-western Florida located approximately at the same latitude (Delcourt and Delcourt,

1977). On the other hand, such distinctive evergreen component of the mesic coastal plain forests as upland laurel oak (*Quercus hemisphaerica*) (Quarterman and Keever 1962, Greller 1980, Ware et al. 1993) was not present among the species mentioned by Daugherty.

The Concept of the Southern Mixed Hardwood Forest

Well before the Delcourts introduced their idea, the theory of the magnolia-beech climax had been already challenged by Quarterman and Keever (1962) who undertook a rather comprehensive study of the modern Coastal Plain forests and found that most of the relatively mature stands have been co-dominated by as many as five to nine major tree species.

As a result, Quarterman and Keever proposed the alternative concept of more heterogeneous Southern Mixed Hardwood Forest. The dominant status in the canopy of this association was shared by American beech (*Fagus grandifolia*), laurel oak (*Quercus haemispherica*), water oak (*Q. nigra*), southern red oak (*Q. falcata*), white oak (*Q. alba*), southern magnolia (*M. grandiflora*), sweetgum (*Liquidambar styraciflua*), mockernut hickory (*Carya tomentosa*), pignut hickory (*Carya glabra*), black gum (*Nyssa sylvatica*), and loblolly pine (*Pinus taeda*).

The concept became quickly accepted by many ecologists (Kuchler, 1964; Monk, 1965, 1966, 1968, Ware 1970, 1978, McLeod 1971, Murphy 1976, Harcombe and Marks 1977, Ware et

al. 1993) and generated, in my opinion, much confusion about the nature of the original and potential forest cover of the Coastal Plain which. Even the Delcourts who coined the term "magnolia-beech-holly" climax after 1977 were not so sure about the universal occurrence of beech-magnolia type forests on the mesic sites of the lower Coastal Plain. In their paper on the historical forests of the Apalachicola Bluff in Florida they (1977) made a suggestion that the modern forests of Coastal Plain do not appear to be converging into a beech-magnolia climax due to the action of the natural and anthropogenic disturbances which foster the reproduction of the shade-intolerant species.

With regard to eastern Texas, this point of view was further substantiated by Glitzenstein et al. (1986) who referred to a very complex disturbance regime of the local forests involving frequent canopy disruptions of varied intensity. Finally, Platt and Schartz (1990) keyed the natural middle- to large-scale disturbances such as those produced by hurricanes and fires, as a clue to the understanding of the dynamics, and composition of the Coastal Plain forests. According to this point of view, the successional replacement of the less shade-tolerant species with more shade-tolerant ones is "only a small part of forest dynamics in coastal plain hammocks" (1990: 227).

Given the lamentable lack of the field research in the Loess Region, the biogeographic status of the loessial

forests remains uncertain. Do these forests fit the paradigm of Southern Mixed Hardwood Forest proposed by Quaterman and Keever (1964) and further substantiated by Glitzenstein et al. (1986), as well as by Platt and Schwartz (1990) or they can be better understood and described in the context of "beech-magnolia" concept suggested by the earlier workers?

Is the Delcourts' model of magnolia-beech-holly climax indeed applicable to the southern portion of the Loess Hills? Do the present-day forests of the region contain any evidence that the magnolia-beech-holly climax - as opposed to the beech-magnolia - once was the prevailing forest type in the region? So far there were no field-verified answers to any of these questions. Amazingly, with all the controversy involved, none of the discussed models were ever attempted to be proved or disapproved in the field. The early-historical observations appear to indicate the structural importance of the shade-tolerant species, particularly evergreen magnolia, and yet these are subjective accounts which do not give a clear idea about the degree of dominance.

Although giving an important insight into the structure and species composition of the "primeval" forests, the Delcourts' model likewise cannot not be taken for granted - as it sometimes is - until it is confirmed empirically in the field. The reconstruction models based

on historical data are useful but they certainly cannot substitute for the "real-life" models based on the data collected in the living contemporary forests through consistent sampling techniques and purposeful methodology. I started this work with a firm conviction that the final assumptions on the compositional and structural nature of the original hardwood forests of the Loess Hills can only be made on the basis of the thorough and systematic sampling of the surviving late-successional stands. And so it became the main challenge of this research

CHAPTER 8

THE LATITUDINAL VARIATION IN THE CANOPY STRATUM

The species composition and the structure of the survived beech-magnolia forests are subject to biogeographic variation associated with the combined action of latitude, physiography, edaphic conditions and disturbance, both natural and anthropogenic. The spatial analysis of the community variation associated with these factors leads to the recognition of four major directions or *vectors* of biogeographic change. The latitudinal vector of the vegetation change is determined by increasingly cooler winter conditions as one progresses from the Gulf coast northward.

Although the whole former region of the beech-magnolia forest is located within the zone of the humid subtropical climates, as defined by Trewartha (1968), its southern and northern sections have slightly unsimilar winter conditions. The average temperature of January decreases by 2 C from Baton Rouge, southern Louisiana, to Vicksburg, southwestern Mississippi. This may not seem too much a difference but, in fact, the increasing latitude and decreasing winter temperatures account for a rather conspicuous change in the structure of the beech-magnolia forests associated with the decreasing importance of the subtropical and the increasing importance of the cold-adapted temperate components. Some subtropical components

drop at different points between Baton Rouge and Vicksburg, others extend all the way to Vicksburg but gradually decline in population densities.

Patterns of Biogeographic Diversity and Heterogeneity

The canopy stratum of the surviving beech-magnolia forests exemplifies one of the richest and most heterogeneous overstory types in North America. As many as 50 species of subtropical, warm-temperate and cold-adapted temperate trees were found in the canopy of the eleven late-successional ravine forest plots on the combined area of 8.1 ha. Two other tree species were found in the canopy of the 1 ha area sample of the Anderson-Tully forest site located north of the *Magnolia grandiflora*'s range. Beyond the latitudinal limits of the beech-magnolia forest, the biogeographic heterogeneity decreases. The more northern forests of the Mississippi Embayment are devoid of the canopy-size subtropical species and tend to be poor in the understory components of the subtropical origin. In contrast, the more southern forests located within the maritime section of the Gulf-Atlantic Coastal Plain and peninsular Florida are devoid of many cold-adapted temperate species which are present in the beech-magnolia forest region.

The mixed nature of the beech-magnolia forest manifests itself readily in its generic name. Two dominant overstory trees of the late-successional forests, *Fagus*

grandifolia and *Magnolia grandiflora*, are representative of the different biogeographic groups of the North American tree flora. Southern magnolia is an evergreen subtropical taxon restricted to the lower section of the Coastal Plain. In contrast, American beech is a highly frost-resistant temperate deciduous species with a broad range extending from southern Louisiana to as far north as southern Ontario and Saint-Lawrence Valley in southern Quebec. On this extreme northern fringe of its distribution beech is one of the key components of the northern hardwood-coniferous forest of the Great Lakes Region. Only in a comparatively narrow latitudinal belt extending for approximately 125 to 130 miles from the Gulf coast inland do these species come together to form one of the most peculiar and ecologically complex associations in Eastern North America.

Southern magnolia (*Magnolia grandiflora*) is the only structurally important canopy-size evergreen component of the Madro-Tertian flora surviving in forests of the Loess Hills Region. Undoubtedly, it is the most beautiful and conspicuous tree of the loessial forests. No other tree manifests the natural spirit and the splendid beauty of the southern Blufflands in more pronounced way than does evergreen magnolia. Likewise, no other tree found such a full expression in the local history, folklore, toponymy and cultural heratige as this one did. The name "magnolia" turned into one of the important toponyms of the southern

Loess Hills. Plantations, settlements and creeks were named in honour of southern magnolia which fact probably reflects outstanding importance of this tree in the original forests.

Both taxonomically and morphologically *Magnolia grandiflora* is a tree which stands quite by itself in the loessial forests. It belong to the largest section of American magnolias, *Theorhodon*, which includes some eighteen species. All of those are evergreen and all except *M. grandiflora* are tropical. The closest relative of southern magnolia is Schiede's magnolia (*Magnolia schiediana*) reaching the size of a large canopy tree in the montane forests of Mexico. These are the only two American magnolias with 114 chromosomes. Perhaps, *M. grandiflora* and *M. schiediana* originated from one common ancestor taxon and gradually evolved into the separate species after the forests of the American Southeast and Mexican highlands became separated from each other in the Miocene.

Apart from southern magnolia, three other species which are subtropical in distribution, namely pyramid magnolia (*Magnolia pyramidata*), hercules-club (*Zanthoxylum clava-herculis*), and Durand oak (*Quercus durandii*) may occasionally sprinkle in the canopy of the beech-magnolia forest. Of these, however, only the latter species can be considered as a genetically canopy-size tree. Secondly, the representatives of this group are remarkably rare - for

instance, the only specimen of Durand oak was registered in the vicinity of Port Gibson, while the whole population of hercules-club was largely shared between only two sampling areas one of which is associated with the lake-facing slope of the Chicot State Park. But the highest diversity and most impressive magnitude is reached by the rare subtropical trees in the ravines of Tunica Hills.

My sampling area in the Magnolia Glenn Preserve features an exceptionally tall, full-size canopy specimen of *Zanthoxylum* reaching 36.5 cm dbh. So far it is the largest individual of this species I found in the Blufflands. One of the individuals of pyramid magnolia, a midstory taxon registered exclusively in Tunica Hills, had dbh of 43.3 cm and likewise reached the height of a normal canopy tree. The finding of the canopy-size sweetleaf tree (*Symplocos tinctoria*) attaining about 15 m in height and 27.5 cm in dbh was another unique surprise of Tunica forest: elsewhere sweetleaf is an understory shrub or, less frequently, a relatively small midstory tree.

The exceptional diversity of the subtropical components in the canopy of Magnolia Glen old-growth appears to be function of not latitude but a highly dissected physiography and perpetual physiographic disturbance which allow some small and middle-sized species to reach the canopy stratum. Soils also may be involved

since one of the mentioned species, pyramid magnolia was nor registered anywhere outside the Tunica Hills.

On the mesic sites throughout most of the lower Coastal Plane, *Magnolia grandiflora* tends to co-occur with another canopy-size evergreen taxon, upland laurel oak (*Quercus hemisphaerica*). Interestingly, the forests developed on the deep-loess deposits of the Mississippi Bluff are conspicuously devoid of this species. Laurel oak appears only on the extreme margins of the Loess Hills Region (particularly east of the Mississippi Bluff) where the loess veneer thins and fertility of the soil decreases. In Homochito National Forest, southwest Mississippi, this taxon is a dominant component in the second-growth hardwood ravine assemblages. According to Ware (1988), upland laurel oak seems to prefer soils characterized by the high content of sand which seems to explain its absence within the deep-loess section of the Bluff.

Not unfrequently found in the literature are ideas about the floristic affinity of the southern Blufflands with the Appalachian forests supported by extensive list of the delicate herbacious mesophytes of the Appalachian origins found in the Tunica Hills and other areas along the Loess Bluff (Braun 1950, Brown 1938, 1954, Kral 1966, Delcourt and Delcourt 1974). Braun (1950) who promoted the idea of antiquity of the Mixed Mesophytic Forest, placed the middle and northern section of the Blufflands into the

Western Mesophytic Forest Region and identified the Loess Hills forests south of Vicksburg as nearly an extension of the Mixed Mesophytic Forest Region. A more comprehensive analysis of the species composition of the Loess Hills forests suggests that these assemblages by no means can be qualified as "... a mixed mesophytic community modified chiefly by the presence of evergreen magnolia as one of the dominants", as stated by Braun (1950).

Apart from the subtropical trees, the forests of the Loess Hills harbour a large assortment of the warm-temperate Coastal Plain species which are essentially absent from the more interior forests. The most widespread and abundant overstory representatives of the Coastal Plain flora are three species of southern oaks, water oak (*Quercus nigra*), cherrybark oak (*Q. pagoda*), and swamp chestnut oak or cow oak (*Q.michauxii*). Cherrybark oak (*Q. pagoda*) and swamp chestnut oak (*Q. michauxii*) are warm-loving deciduous species ranging from southern Louisiana north to the confluence of the Mississippi and Ohio rivers. The northern edge of the distribution of cow oak is associated with the Lower Ohio and Wabash river valleys in extreme southern and southwestern Indiana which harbor the northernmost extensions of the Coastal Plain bottomland flora.

Cherrybark oak is limited in its distribution by the extreme southern tip of Illinois. Water oak (*Q. nigra*)

terminates well south of the Mississippi-Ohio confluence - in northeastern Tennessee and extreme southeastern Missouri thus only slightly crossing the northern boundary of the subtropical belt as indicated by Trewartha (1968). Its affinity to the subtropical life zone is further accentuated by highly persistent xerophylous foliage. Leaffall of this tardy-deciduous to semi-evergreen species gradually progresses through December-January and terminates in February at which month canopies of large overstory trees are already covered with the bronze-yellowish haze of newly shooting leaf growth. East of the Mississippi River the warm-temperate oaks are accompanied by another Coastal Plain component, southern sugar maple (*Acer barbatum*). This species represents in the Loess Hills forests a substitute for more interior sugar maple (*Acer saccharum*) which is common in the Mixed Mesophytic Forest Region and further northward.

The assortment of the warm-temperate canopy taxa in the beech-magnolia forests is further diversified by the trees with the broader distributions which cover both the Coastal Plain and the geologically older upland surfaces south of the Ohio River. The most important and widespread of these species are sweetgum (*Liquidambar styraciflua*) and, to the less extent, winged elm (*Ulmus alata*). Almost every site except the drier stands on the periphery of the loessal cap is featured by the presence of sugarberry

(*Celtis laevigata*). Despite the generally broader distributions, these species are only marginally represented in the Mixed Mesophytic Forest Region and other interior forests.

Considering the species composition of the Mixed Mesophytic Forest, Braun (1950) refers to sweetgum and winged elm as "relics from the preceding developmental stages or accidentals from nearby unlike communities" (p. 54). *Celtis laevigata* is essentially absent from the Appalachian region and only marginally extends into the Low Interior Plateau of middle Tennessee. It is noteworthy that in the mature interior forests, probably with the only exception of the Nashville Basin in central Tennessee, both sweetgum and sugarberry are largely limited to the floodplain communities (Braun, 1950) while in the Loess Hills they keep high profile in the hillside mesic assamblages.

Four other deciduous species with warm-temperate distributions, southern red oak (*Quercus falcata*), post oak (*Q. stellata*), bigleaf magnolia (*Magnolia macrophylla*) and sourwood (*Oxydendrum arboreum*) represent edaphically marginal components which occur in the peripheral areas of the Loess Region underlain by more shallow loess deposits such as Sicily Island and Homochito National Forest. While the drought-resistant upland oaks are equally unimportant in the Mixed Mesophytic Forest Region and Low Interior

Plateaus where they are also limited to the xeric marginal habitats, bigleaf magnolia and sourwood exemplify well-profiled components of the south-Appalachian flora.

The opposite edaphic extreme of the warm-temperate Loess Hills flora is represented by pecan (*Carya illinoiensis*), a decidedly bottomland taxon which extends into the Mississippi Bluff from the floodplain forests of the Mississippi Valley. This tree is relatively widespread in the early-successional ravine forests of the Loess Ridge but only occasionally reveals its presence in the late-successional forests. The only late-successional site where I found pecan was the beech-dominated Anderson-Tully forest north of Vicksburg; earlier it was also reported from the old-growth ravine forest of the Tunica Hills by Quigly (1994).

Sugarberry, pecan and upland post oak can be of special interest to a biogeographer because of their distributional anomalies which may be related to some climatic or physiographic effects caused by the Mississippi River. The ranges of all three species are characterized by peculiar northern enclaves extending along the middle section of the Mississippi River up to western Illinois and even further north into southeastern Iowa - somewhat deeper into the middle-temperate latitudes than a typical southern species would probably go (Collingwood 1964, Duncan and Duncan 1988). In a broad biogeographic perspective, the

species with such distributions may exemplify the transitional link between the decidedly southern and temperate cold-adapted forms.

The cold-adapted temperate deciduous taxa are the most species-rich biogeographic group represented in the canopy of the Loess Hills forests. In the late Pleistocene most of these species formed the bulk of the local full-glacial assemblages. With the transition to the modern climatic conditions, the temperate broadleaf vegetation expanded northward but many of the cool-resistant temperate species have adapted to the subtropical climate of the southern Coastal Plain and remained present in the area of the former Pleistocene refugium.

"Cool-temperate" is a term frequently used in the American biogeographic and ecological literature without major distinction in reference to the great multitude of the cold-adapted temperate trees. This term, I assume, is more appropriate for those taxa which are limited to, or at least centered in the regions characterized by the cool-temperate climate. In contrast, the cold-adapted temperate taxa, while being tolerant enough to extend into the latitudes with cold winters, are not necessarily centered in these latitudes but range throughout much of the latitudinal extent of eastern North America. The modern canopy assemblages of southern Loess Hills include about 25 cold-adapted temperate tree species which extend from the

vicinity of the Gulf coast well into the northeastern states - many as far north as the Great Lakes region. American beech (*Fagus frandifolia*), white ash (*Fraxinus americana*), American basswood (*Tilia americana*), American and red elms (*Ulmus americana* and *U. rubra*), white oak (*Quercus alba*), bur oak (*Q. macrocarpa*), bitternut hickory (*C. cordiformis*) and black cherry (*Prunus serotina*) are perhaps the most cold-resistant taxa representative of this group. Their ranges extend into southern Ontario and the Saint-Lawrence River Valley in southern Quebec and cover most of the region occupied by the northern hardwood-coniferous forest.

The flora of the temperate deciduous forests located largely south of the Great Lakes is represented by tulip tree (*Liliodendron tulipfera*), Shumard oak (*Q. shumardii*), pignut chickory (*Carya glabra*), snagbark hickory (*C. ovata*), blackgum (*Nyssa sylvatica*), mockernut hickory (*C. tomentosa*), sycamore (*Platanus occidentalis*), red mullberry (*Morus rubra*), sassafrass (*Sassafrass albidum*), honey locust (*Gleditsia triacanthos*) and chinquapin oak (*Q. muehlenbergii*). These species terminate in the extreme southern tip of Ontario or, like somewhat more south-centered Shumard oak, in southern Michigan.

The overstory of nearly every site contains few large individuals of some temperate subcanopy trees such as hornbeam or blue beech (*Carpinus caroliniana*), American

hophornbeam (*Ostrya virginiana*) and, more rarely, flowering dogwood (*Cornus florida*) with the dbh sizes averaging between 24 and 40 cm. They are smaller in size than typical canopy trees (over 90% of overstory Carninus and Ostrya were 14-17 meters in height) but tall enough to keep their canopies unobstructed by other trees. In the marginal shallow-loess sites, the canopy may also contain large individuals of red maple (*Acer rubrum*) and sourwood (*Oxydendrum arboreum*). Along with American beech, white ash and elms, American hornbeam, Eastern hophornbeam and red maple represent the most hardy temperate components of the beech-magnolia overstory which could be found as far north as in the mixed hardwood-coniferous forests of the Great Lakes and Saint Lawrence Valley region. Dogwood is a slightly more southern species associated with the flora of the broadleaf deciduous forest.

Comparatively few of the cold-adapted temperate taxa are characterized by any strong deviations from the general distributional pattern which embraces most the Eastern Deciduous Forest Province as indicated by Braun (1950). Of these, one may refer to the distribution pattern of Shumard oak (*Q. shumardii*), a Coastal Plain-centered tree which extends further north through the silt-loam plains of Illinois and western Indiana into southern Michigan but is absent or marginal throughout most of the Appalachian region, as well as that of bur oak (*Q. macrocarpa*) which is

strongly centered in the regions west of the Mississippi and north of the Ohio rivers (Duncan and Duncan 1988).

Of special reference is the occurrence of a few predominantly interior and north-centered cool-temperate deciduous trees which only marginally extend onto the Southeastern Coastal Plain. It appears that they may have infiltrated into the southern Blufflands during the Pleistocene glacial advances and remained present in the area due to the microclimatic advantages provided by the deep dissection of the loessal mantle. One of the most conspicuous representatives of this group in the Loess Hills is cucumber magnolia (*Magnolia acuminata*), an interior-centered relict of the Appalachian flora which is only marginally extends into the Coastal Plain. The idea that the current population of cucumber magnolia in the Loess Hills may have originated as a result of the comparatively recent Pleistocene migration can, perhaps, be suggested by the fact that the taxon is represented in the Blufflands not by its marginal Coastal Plain variety (*M. acuminata* var. *cordata*) but by its more northern Appalachian form (*M. acuminata* var. *acuminata*) characteristic for the interior uplands.

The canopy stratum of the deep-loess ravine sites is not unfrequently featured by the presence of large individuals of boxelder maple (*Acer negundo*), a middle-size low-ground tree which occurs in the Mississippi Bluff on

the lower slopes and in the bottoms of the deep ravines – commonly along intermittent watercourses. This distinctly north-temperate tree has the highest frequencies in the Steep Bluffs and the Tunica Hills, two areas characterized by the heaviest dissection, and exceptionally deep and narrow ravines. Another conspicuously interior-centered tree present in the assemblages of the Mississippi Bluff is black walnut (*Juglans nigra*). Interestingly enough, within the beech-magnolia region the only three individuals of this taxon (one - in Tunica Hills and other two along the Natchez Trace) were also recorded in the exceptionally dissected areas, characterized by deep, steep-slope ravines. These facts suggest that some relief-related microclimatic effects, among the other factors, may play an important role on the southern edge of the distribution of both *Acer negundo* and *Juglans nigra*.

Latitudinal Variation among the Subtropical and Warm-Temperate Canopy Taxa

The latitudinal vector of the vegetation change is determined by the decreasing influence of the warm maritime airmass emanating from the Gulf of Mexico and increasing influence of cool airmasses and polar fronts northward in the winter time. As a result, although the whole former region of the beech-magnolia forest is located within the zone of the humid subtropical climates, as defined by Trewartha (1968), its southern and northern sections have slightly unsimilar winter conditions. The average

temperature of January decreases by 2 C from Baton Rouge, southern Louisiana, to Vicksburg, southwestern Mississippi.

The increasing latitude and decreasing winter temperatures account for a rather conspicuous change in the structure of the beech-magnolia forests associated with the decreasing importance of the subtropical and the increasing importance of the cold-adapted temperate components (Figure 3). As the only structurally important subtropical evergreen, southern magnolia (*Magnolia grandiflora*) is probably the most prominent indicator of the latitudinal change. The relative importance of magnolia decreases from 30% in the overstory of the Port Hudson site and 22% in the canopy of the old—growth stand managed by the Louisiana State Arboretum to 15,7% in the canopy of the Port Gibson site and 10.1% percent in the overstory of the Sicily Island site, which are both located within the northern section of the beech-magnolia forest region. Finally, it shrinks to 6.5% in the canopy of the Bluff Experimental Forest. Located 19 miles northeast of Vicksburg) this site features the northernmost "beech-magnolia" forest within my transect.

Further northward *Magnolia grandiflora* drops. It is completely absent from the potentially old growth forest site located 7 miles north from the Bluff Experimental Forest in the heavily wooded area owned by the Anderson-Tully Company. Consequently, I can suggest that the

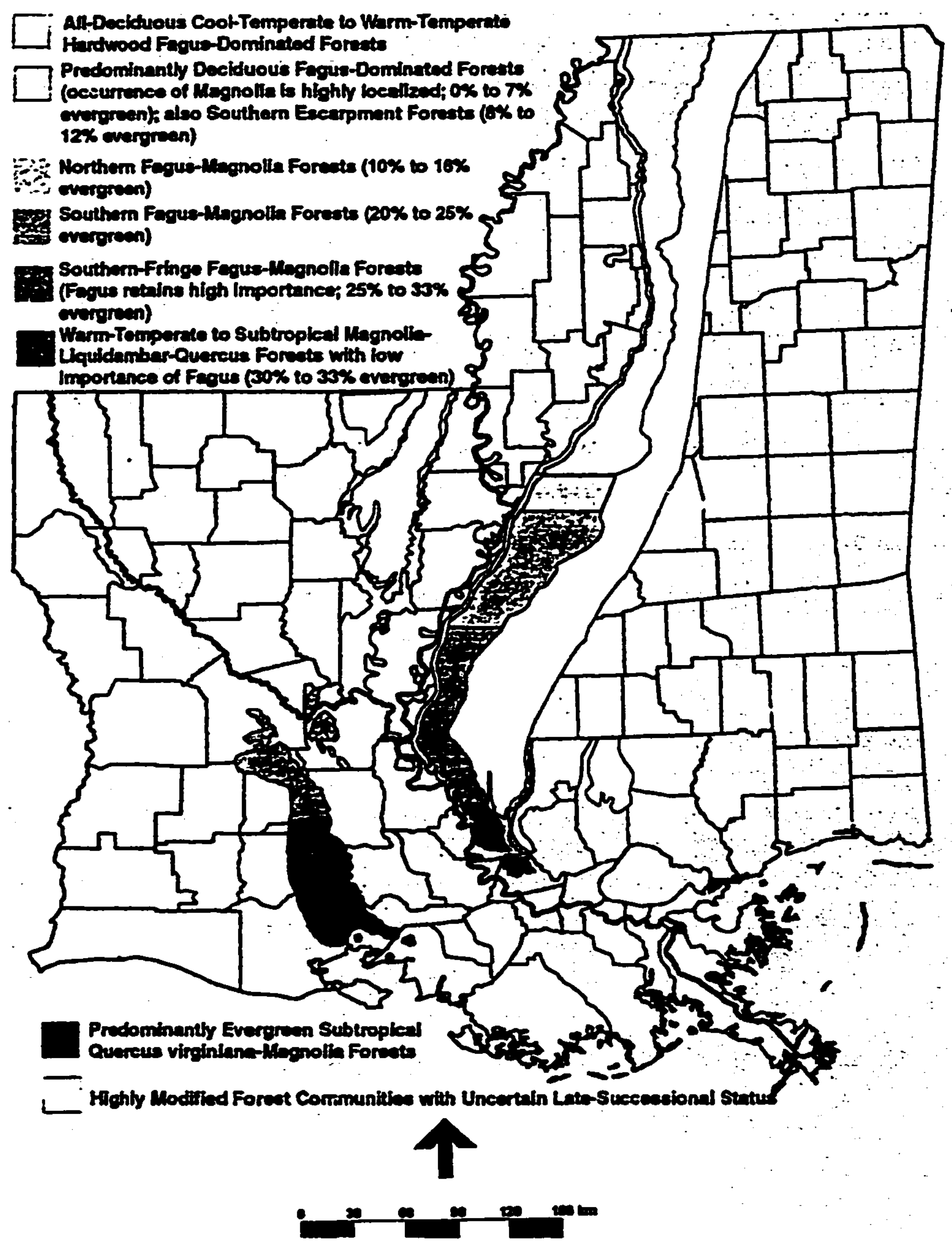

Figure 3. The Forest Types of the Southern loess Hills as Determined by Latitude

Sources: Biker A.R. 1969. Geologic Map of Mississippi, Scale 1:500,000; Brand, DeWitt. 1999. Louisiana GIS CD: A Digital Map of the State, Version 2.0

northern boundary of southern magnolia is located somewhere between 19 and 26 miles north of Vicksburg which is somewhat north from the limit suggested by Braun (1950) who hypothesized that Vicksburg was likely to be a northern terminal point of *Magnolia* range along the Bluff.

The name "beech-magnolia" is probably somewhat unprecise for the northern end of this forest type exemplified by the sites like Bluff Experimental Forest where *Magnolia grandiflora* still occurs but does not maintain its dominant status.

When considered alone, the relative values may give an impression of *Magnolia* populations decreasing gradually along the south-north transect. The real picture is somewhat more complicated. In fact, there is only an insignificant decrease of *Magnolia* population from the moderately southern sites such as the old growth-stand of the Louisiana State Arboretum where I registered 26 canopy-size trees to the moderately northern sites exemplified by the ravine forest of the Sicily Island area where 23 magnolias were found. The difference in the relative shares between these two sites is more accentuated because of the larger general tree population in the Sicily Island area.

The lake-facing slope of the Chicot Stake Park located in the vicinity of the Louisiana State Arboretum harbours, perhaps, a somewhat densier population of canopy magnolias per 1 ha sample than the LSA-managed stand does but, due to

the impenetrability of the internal section of this forest, I had to limit myself to sampling of only 0.7 ha of the slope area which resulted in recording 22 canopy trees. The variation in canopy populations of *Magnolia grandiflora* becomes more pronounced on the southern and northern fringes of the beech-magnolia forest. *Magnolia* populations increase dramatically on the extreme southern margin of the Loess Hills region: this trend is exemplified by the ravine forest of the Port Hudson area where I found as many as 67 canopy trees of *Magnolia grandiflora* on one hectare - three times more than in the Sicily Island area. On the opposite end of the beech-magnolia region, in the Bluff Experimental Forest, the overstory population of southern magnolia drops to only 14 canopy trees which is nearly five times less than in Port Hudson.

The pattern of the spatial distribution of *Magnolia grandiflora* throughout the forest also varies from the south to the north. Generally, magnolia becomes increasingly more patchy toward the northern limit of its range. On the northern sites it tends to gravitate strongly to the ecologically favorable expositions, sometimes clumping abundantly within relatively small areas. In one ha sample of the Bluff Experimental Forest, for instance, 10 out of 14 trees of *Magnolia grandiflora* were found within the last out of the twenty 10x50 m. transect. Thus the remainder 0.95 ha of the BEF site contained only four

canopy magnolias. Somewhat further south, in Sicily Island, the distribution of magnolia throughout the forest remains relatively patchy although the local contrasts are less sharp. Here only 7 transects out of 20 were lacking large magnolia trees, while the magnolia-rich spots seemed to have been less localized and less pronouced (overall, there were 3 10x50 m. transects with 3 canopy-size individuals within each). A conspicuously different pattern of nearly even distribution of magnolia was registered on our southernmost beech-magnolia site in the Port Hudson Commemorative Area. Here each of fifteen transects contained at least 3-4 canopy-size magnolias. Magnolia peaked to 5-7 individuals within 2 transects and decrease in frequency to 1-2 individuals within the other 3 transects. The similar pattern is demonstrated by magnolia on the Forked Island site in extreme south-central Louisiana which is located south of the beech range.

The warm-temperate deciduous taxa do not show any conspicuous north-south variation within the latitudinal range of the beech-magnolia forest. The notable exception, however, is exhibited by water oak (*Q. nigra*) which is nearly semi-evergreen and, strictly speaking, nearly subtropical in distribution. The relative and absolute decrease of this species' populations with latitude is not as conspicuous as that of southern magnolia but still relatively consistent. Its relative importance, for

instance, shrinks from 5.3% in Louisiana State Arboretum and 2.6% in the Port Hudson forest to 1.8% in the Port Gibson stand and 1.6% in the Bluff Experimental Forest. The Steep Bluffs area has higher population density of water oak than two latter northern sites but, due to the fact that water oak here appears to be promoted by perpetual disturbance of the loess mantle, it is correct to compare its population sizes in this area not with the closed canopy stands but with the similarly disturbed assemblage of Magnolia Glen preserve on the other end of the latitudinal range of the beech-magnolia forest.

The population of *Q. nigra* in Magnolia Glen site was almost two times higher than that of the Steep Bluffs area. My field observations also suggest that the semi-evergreen habit of water oak is also somewhat more pronounced in the area of the Tunica Hills and further south than in Vicksburg area and further north. In the loess hills of northwestern Mississippi and western Tennessee (beginning approximately from Tallahatchie to Panola Counties, Mississippi), water oak tends to lose almost all its folliage before the New Year eve, while in the southern section of Opelousas Ridge it can be qualified as a truely semi-evergreen tree.

Forests of the Southern Fringe of the Loess Hills

The southernmost forests of the beech-magnolia type did not survive to the present times. The persisting left-

overs of the mesic successional forests within East Baton Rouge Parish and Baton Rouge area are generally characterized by the increasing importance of the warm-temperate bottomland species such as pecan (*Carya illinoensis*), willow oak (*Quercus phellos*) and Nuttall oak (*Q. nuttallii*) which well could have occured in the original forests, too. The presence of these bottomlanders, however, seems to reflect the effect of the decreasing relief and change in edaphic conditions rather than result of the decreasing latitude. Unfortunately, it is hardly possible to trace any latitudinal dynamics of *Magnolia grandiflora* on this southernmost fringe, for almost all mesic forests surviving in Baton Rouge area and further south are of relatively recent origin.

Burden Plantation harbors the only more or less old mesic forest in Baton Rouge area, yet even this stand is dominated by the shade-intolerant species indicative of the early stages of natural succession. The forest patches that contain towering canopy-size magnolias and seem to bear the signs of the late-successional vegetation structure are too small to give a clear idea about the original look and structure of this assemblage. Generally speaking, the Burden Plantation stand appears to have been so strongly modified and disturbed for almost two centuries of the human presence (with some trees, perhaps, planted) that it

can be by no means considered as a representative sample of the original forests.

To envision the sublime pristine woods that once covered the area where is now Baton Rouge and extended further gulfward along the tongue-like extensions of the loess lands, one has to resort to the early-historical accounts. The original forests of this southernmost fringe of the Loess Bluff were almost certainly rich in magnolia. Southern magnolia was a tree of first importance in a diverse assortment of species observed by William Bartram in 1777 on the extreme southern margin of the loessal belt between the Amete River and Manchac, small town on the banks of the Mississippi 15 miles south of Baton Rouge.

Interestingly, among the trees "of the first order and magnitude" Bartram also mentioned "Laurus borbonia". If only Bartram did not confuse some other species for Persea which is unlikely for such an experienced naturalist, the trees he registered on the Amite River were almost certainly those of red bay (*Persea borbonia*), a warm-loving subtropical evergreen limited in its distribution to the narrow maritime strip along the Gulf coast (and outside it – to Florida and the Atlantic shore of Georgia and, to a less extent, the Carolinas).

Neither red bay nor its close relative, swamp bay (*Persea palustris*) were found in the loessial sites. The absence of swamp bay in the Loess Hills seems to be

determined exclusively by the edaphic factors for on non-loessial soils this species is present as far north as the southern part of Kisatchie National Forest in Louisiana. Within its more maritime range, red bay also seems to be an important component of the communities developed on the sandy, frequently acidic soils. But, unlike swamp bay, *P. borbonia* also occurs in the moist alluvial environments of the Mississippi Delta. In the light of this fact it does not seem unrealistic that red bay was also present in the subcanopy of the mesic forests on southernmost fringe of the loessial belt but did not extend far inland. Consequently, the southern fringe of the beech-magnolia forests, at least the section south of Baton Rouge, appeared to have exemplified a transition to more evergreen and more subtropical (both structurally and generically) forest type characterized by the increasing importance of trees with xerophylous, laurel-like leaves.

The question remains how far north *Persea* might have extended along the Bluff. In this regard, it should be pointed out that Bartram lists *Persea borbonia* among the major trees even as far north as in the vicinity of the Port Hudson area. Another problem is the size. We can only hypothesize if the forests of the extreme southern fringe of the Blufflands indeed harboured canopy- or nearly canopy-size trees of *Persea*. If Bartram was accurate in listing *Persea* among the "trees of the first order and

magnitude", the forests of the extreme southern Blufflands may have harbored canopy- or nearly canopy-size trees of *Persea*. This would have given these early-historical forests quite different physiognomy and outlook. In the modern non-loessial maritime forests where red bay today marks its presence, it is typically represented by relatively small, shrubby trees of the understory to low-midstory stature. Besides, it should be noted that I have never registered or observed *Persea* in any modern loessial forests, including maritime subtropical assemblages of the salt domes and Forked Island.

Biogeographic Variation among the Cold-Resistant Temperate Deciduous Taxa

Throughout the nearly whole latitudinal extent of the former beech-magnolia forest, deciduous trees of the cold-adapted temperate species represent the most important structural component in the canopy of the late-successional remnants of this ecosystem. Even on the southern sites such as Tunica Hills and Louisiana State Arboretum the cool-temperate taxa make up respectively 51.9% and 53.4% of the overstory structure. Further north their congregate shares increase to to 69.5% in Port Gibson and 74.3% in the Bluff Experimental Forest. The structural increase of the cold-adapted temperate species northward is associated first of all with the general increase of the canopy populations of such species as American beech, tulip tree, white ash, American basswood, sassfrass and cucumber magnolia. Certain

difficulties in the comparison of the southern and northern stands come from the fact that the northern beech-magnolia stands are predominantly second-growth in origin. It means that the higher population densities of some species in the northern forests may be caused or influenced by the successional factors. The possibility of such scenario is additionally suggested by the fact that the population densities of beech, tulip tree and white ash in the Port Hudson forest (which is likewise second-growth in origin) are also higher than in the old-growth formations of the Tunica Hills and the Louisiana State Arboretum.

The comparison among the second-growth sites only suggests that the populations of beech, tulip tree and white ash indeed tend to show a more vigorous response on disturbance in the northern section of the beech-magnolia forest, although an additional sampling is needed to verify this preliminary conclusion. For instance, the number of canopy beech trees increased from 53 individuals per hectare in Louisiana State Arboretum to 67 in Port Hudson but then to 84 in the Bluff Experimental Forest. The canopy populations of tulip tree increased from only 3 individuals per hectare in the Tunica Hills and the LSA stand to 12 in the Port Hudson area and then, respectively, to 20 individuals in the Bluff Experimental Forest and 24 individuals in the Sicily Island area. Likewise, white ash population densities ranged from only 1 and 3 canopy

specimens per hectar in the Tunica Hills and the LSA stands to 8 canopy trees in Port Hudson and then to 11 canopy trees per hectar in the Bluff Experimental Forest.

American basswood, boxelder maple, black wallnut, sassafrass, and cucumber magnolia exemplify a decidedly north-centered distribution pattern. These taxa (except for boxelder) have relatively sparse populations in all the (both old-growth and second-growth) southern beech-magnolia sites but become increasingly more important toward the northern end of the beech-magnolia region. The population density of American basswood, for instance, fluctuates from 1 canopy tree per hectar in the LSA stand and Chicot State Park to 2 canopy trees in Tunica Hills and Port-Hudson but increases to 5 trees per hectar in the canopy of the Bluff Experimental Forest and the Steep Bluffs assemblage. The presence of two canopy-size basswood trees within a 0.25 ha sample in the vicinity of Port Gibson suggests that the local beech-magnolia forest (now destroyed) also contained the relatively high population densities of *Tilia*.

While basswood can be found throughout the whole slope gradient of the deep-loess section, boxelder maple which is especially characteristic of the highly dissected escarpment area tends to congregate in narrow ravine bottoms and the lower section of the slope gradient. Like basswood, this taxon shows a stable increase in population densities northward - from 4 canopy individuals per hectar

in the Tunica Hills to 6 in the Steep Bluffs area and 7 in Bluff Experimental Forest. It is noteworthy that in the northern sites boxelder maple tends to expand further upslope than in the Tunica Hills and Clark Creek area.

Even more north-centered distribution pattern is characteristic for black walnut. Although being present in the deep ravines of the Mississippi Bluff escarpment at least as far south as the Tunica Hills, this tree becomes one of the relatively regular components of the canopy structure only north of Vicksburg, within more temperate beech-dominated forest type devoid of southern magnolia and other subtropical species. On 1 hectar sample plot in the Steep Bluff area I registered 3 overstory individuals of this species responsible for 1.4% % of the canopy structure. The only other specimen was found in the canopy of the Tunica Hills old growth forest. Black walnut is one of the most "classic" cool-temperate components of the loessial forests. From Warren County this taxon slowly increases in frequency northward along the whole latitudinal extent of the Loess Hills reaching its highest population densities only in the forests of the central Midwest.

Of all cold-adapted components of the loessial forests, the most pronounced latitudinal variations are shown by sassafrass and cucumber magnolia. Whereas in the southern late-successional sites (Tunica Hills, Port

Hudson, Chicot State Park) sassafras, for instance, is represented by only 1 canopy tree per 1 hectare, in the northern section of the beech-magnolia forest region its population densities increase to 4 canopy trees per hectar in Sicily Island, 13 trees per hectare in Bluff Experimental Forest and 15 in the Steep Bluffs area.

Cucumber magnolia is absent or extremely rare in the forests of the southern end of the Mississippi Bluff - at least, it was not recorded in the Port Hudson, the Tunica Hills, and the Clark Creek areas. Whereas the ephemeral signs of *M. acuminata* presence begin to emerge in the early-successional forests immediately north of Natchez, Mississippi, the southernmost canopy-size tree east of the Mississippi River was found only as far north as in the Port Gibson site. The fact that the latter specimen was registered within 0.25 ha sample indicates, perhaps, an increased population density of cucumber magnolia at this latitude. Interestingly, west of the Mississippi River, cucumber magnolia spreads somewhat further southward than it does along the Mississppi Bluff. For instance, both the Louisiana Arboretum stand and the survived section of the late-successional forest along Chicot Lake contain sparse canopy populations of this species (with the average density in the order of 1 tree per 1 hectar or slightly less). *Magnolia acuminata* considerably increases in importance only in the northern section of the beech-

magnolia forest. With a remarkably stable population density of 7 trees per hectare, it becomes one of the major accessory components in the late-successional assamblages of Sicily Island, Bluff Experimental Forest and Steep Bluffs area.

Because of the increased diversity and structural importance of the north-centered temperate trees, the plantscape of the northern beech-magnolia forests is physiognomically different from those of the southern end of the Loess Hills. The aggregate relative importance of the decidedly north-centered species in the northern section of the southern Loess Hills varies from 5.3% in Sicily Island to 12.8% in Bluff Experimental Forest and 14.7% in the Steep Bluffs area. By contrast, the respective values for the southern part of the beech-magnolia region vary from 1% in Port Hudson and 2.5% in Louisiana State Arboretum to 4.6% in the Tunica Hills. The populations of the north-centered species in any latitudinal division of the beech-magnolia region tend to be comparatively larger and more specious in the deep-loess section and peak in the area of the Bluff escarpment with its exceptionally deep and shady ravines.

The natural division between the "southern" and "northern" types of the beech-magnolia forest (the latter is poorer in evergreen magnolia and richer in the north-centered cool-temperate components) appears to cross the

Loess Hills region somewhere between Natchez and Port Gibson. My site located 7 miles south of Port Gibson seems to reflect the floral structure of the northern section. As suggested by my field observations, some of the cool-temperate species continue to increase further northward along the Mississippi Bluff beyond the natural range of southern magnolia. The forests of northwestern Mississippi and southwestern Tennessee are physiognomically richer in cucumber magnolia and black walnut. Northern red oak (*Quercus borealis*), a conspicuous component of the Appalachian forests is also present in those areas. Despite my extensive sampling, I did not manage to locate this taxon anywhere in the southern Loess Hills. Yet, it was reported from the Tunica Hills area (both West Feliciana Parish and Wilkinson County) by Brown (1938).

The Southern Limit of the Beech-Magnolia Forest and Beyond

The southern limits of the beech-magnolia forest are difficult to locate due to the poor preservation of the natural communities on the southernmost margins of the loessial lands. American beech extends at least as far south as Baton Rouge where it is present in the late-successional "spots" of the forest tract managed by Burden Plantation. However, here it does not seem structurally important. Most of the individuals found at Burden look somewhat surpressed, large trees are absent. Southern magnolia, on the other hand, reaches here a relatively

large size and frequently towers over ill-looking beaches. The general impression is that in Baton Rouge, beech approaches very closely to its southern limit. On the other hand, Platt (personal communication) pointed out that he observed beech on the outcrops of the loessial mantle well southeast of Baton Rouge - in the drainage system of the Manchac River.

It appears that on the extreme southern margins of the Loess Bluff south of Baton Rouge American beech may have been replaced by live oak (*Quercus virginiana*) but where and how this biogeographic transition occured remains an intriguing question to answer. Of particular interest is the question if there was a transitional section where beech and live oak naturally co-occured. In the present-day cultural and agricultural landscape of the loess-capped uplands live oak extends north to Vicksburg, Mississippi and Tallulah, north-east Louisiana gradually losing its importance to pecan and elm. The taxon seems to occur naturally south of Baton Rouge, in the lowland landscapes of the Mississippi Delta, where it is represented both in monospecific semi-wild groves and - as a component - in the survived tracts of the mixed bottomland hardwood forests. I found *Q. virginiana* scattered in low frequencies in the bottomland assemblages immediately south of Baton Rouge but it is difficult to say whether or not live oak was present in the southernmost outliers of the mesic loessial forests

located at the same latitude or even further southward. Bartram made no reference concerning the presence of live oak in the forests between the Amite river and Manchac. The young early-successional growth developed on the loessial outcrops in the southern surbubs of Baton Rouge do contain live oak but these may well be populations that have escaped from cultivation.

West of the Mississippi River, on the loess-capped surfaces of the terraces of south-central Louisiana adjacent to the Atchafalaya Delta the presence of live oak in the survived bottomland communities is better profiled. Here it appeared to have extended somewhat further north than east of the Mississippi River. Bill Fontenaut, a manager of *Q. virginiana*-dominated tract of the bottomland old-growth forest preserved by Lafayette City Park, suggested that live oak naturally ranged at least as far north as to Opelousas (personal communication, 1998).

The southern boundary of *Fagus* distribution west of the Mississippi River is located, according to Fontenaut, approximately 1 mile north of Opelousas. If the natural limits of beech and live oak indicated by Fontenaut are indeed correct, the latter taxon was present in the original mesic forests throughout the southern half of the Opelousas Ridge and did not co-occured with beech. Consequently, the southern section of the loess-capped surface of the Opelousas Ridge was covered by a

conspicuously different forest ecosystem in which two subtropical evergreens, southern magnolia and live oak, accounted for an essential part of the canopy structure. According to Fontenaut, some other temperate indicator species of the beech-magnolia forest such as tulip tree (*Liriodendron tulipfera*) also terminated approximately at the latitude of Opelousas. Consequently, these southernmost loessial forests may have had quite pauperized temperate deciduous flora. Unfortunately, only hypothetical reconstructions of their species composition and structure are possible, since no representative piece of more or less mature mesic forests survived in the western Blufflands south of Opelousas.

On the extreme southern margin of the Loess Region, the loess-capped salt-dome islands of coastal Louisiana harbour the remnants of the remarkable forests that are, perhaps, the close biogeographic analogue of the destroyed hardwoods of the Opelousas Ridge. The local assemblages are representative of a more evergreen forest type dominated by magnolia (*Magnolia grandiflora*) and live oak (*Quercus virginiana*); associated with them are several warm-temperate co-dominants of secondary importance such as cherrybark oak (*Quercus pagoda*), sweetgum (*Liquidamabar styraciflua*), sugarberry (*Celtis laevigata*) and water oak (*Q. nigra*). These forests are lacking beech and many other

cool-temperate deciduous components characteristic for the "classic" beech-magnolia forest.

The prolonged field work in the salt-dome islands is complicated by the fact that they are owned either by individuals or the Federal Government. Some of the islands contain strategic oil reserves or are being exploited for salt. Consequently, I had to limit myself to short-term excursions into salt-dome forests. I eventually found a substitute for salt dome islands, the mesic hardwood forest in the Forked Island area which I was able to sample. Forked Island is not a salt-dome but the forest vegetation developed on this "island" represents an identical biogeographic replic of the forests developed on the salt domes. With the aggregate importance of the overstory subtropical components reaching 46.4 %, the Fork Island forest structurally and floristically represents a close counterpart of the evergreen-deciduous hammocks of peninsular Florida and, perhaps, more than any other hardwood community of Louisiana deserves being termed "subtropical forest". In Asia its close structural counterpart is the Subtropical Evergreen Broadleaf Forest of southern China identified by Wu (1980), Hou (1983) and Ying (1983). As a matter of fact, the salt-dome forests and the Forked Island assemblage itself have even more evergreen appearance than it may be suggested by the share of the evergreen taxa because the significant portion of

their structurally important deciduous components such as sugarberry and sweetgum is represented by relatively young, slender-stemmed, middle-stature trees with small, frequenty ellongated crowns. Such trees grow in the old gaps and claim comparatively little canopy space; besides, it appears that only few individuals from these late-pioneer populations have chances to develop eventually into large canopy trees. On the contrary, the subtropical evergreens, especially live oaks, are represented by big, sometimes enormous individuas with large and broad canopies which control approximately 60-70 % of the overstory space. Water oak, making up 7.9 % of the canopy-tree growth and claiming about 12 to 14 % of the canopy space, also remains nearly evergreen of this low-latitude maritime forest.

Brief Summary and Conclusions

Given the relatively short distance between Warren County, Mississippi, and the Gulf Coast, the hardwood forests of the southern Loess Hills are characterized by a rather sharp latitudinal gradient. Forests of northern Warren County exemplify the middle-Bluffland type characterized by the intensive intermingling of the cool-temperate and warm-temperate components and considerable importance of the interior-centered cool-temperate species which are either absent in the southern Blufflands or represented there by low population densities. These are

all-deciduous forests lacking the subtropical and evergreen components in the canopy.

The forests of the "beech-magnolia" type begin some 19 to 26 miles north of Vicksburg and extend approximately to the middle East Baton Rouge Parish east of the Mississippi River and to Opelousas west of the River. Within most of this section, *Magnolia grandiflora* decreases rather gently from the south to the north. The sharp biogeographic changes occur only at the opposite ends of the "beech-magnolia" forest region. The population densities of *Magnolia* decrease abruptly at the northern fringe of its range in the vicinity of Vicksburg, Mississippi, and increase dramatically south of West Feliciana Parish in Louisiana. At the northern margin, the distribution of magnolia throughout the forest becomes very spotty. Throughout most of the beech-magnolia region, the population densities of *Magnolia* are considerably lower than those of *Fagus*. Only at the southern edge of this forest type, at Port Hudson, it achieves the equal population densities with beech.

Magnolia is not the only subtropical species which may be present in the canopy of the beech-magnolia forest. But other potentially overstory species - *Quercus durandii*, *Zanthoxylum clava-hercules*, and *Magnolia pyramidata* - are either very sparsely distributed or highly localized.

The latitudinal change is further accentuated by the northward decrease of the population densities of water oak (*Quercus nigra*) and the parallel increase of the population densities of a large assortment of broadly-ranging and interior-centered cool-temperate deciduous taxa such as beech (*Fagus grandifolia*), tulip tree (*Lirirodendron tulipfera*), white ash (*Fraxinus americana*), sassafras (*Sassafras albidum*), cucumber magnolia (*Magnolia acuminata*), black walnut (*Juglans nigra*), boxelder maple (*Acer negundo*), as well as southern sugar maple (*A. barbatum*).

The loessial forests of the "beech-magnolia" type can subdivided into four latitudinal sections: northern-fringe beech-magnolia forest, northern beech-magnolia forest, southern beech-magnolia forest, and southern-fringe beech-magnolia forest. The northernmost forest type was localized in the vicinity of Vicksburg and extended at least some 19 miles north of the present-time city limits. It was characterized by comparatively low importance and spotty distribution of *Magnolia gandiflora* and very high importance of American beech (*Fagus grandifolia*). Southern sugar maple (*Acer barbatum*) - a warm-temperate species - appears to have sharply increased in importance in this forest type and further north along the Bluff in response to the structural decline of evergreen magnolia and increasing importance of beech. Northern beech-magnolia

forest type extended approximately from southern Warren County to some point between Port Gibson and Natchez. West of the Mississippi River it included Sicily Island and southern section of Macon Ridge. The major structural difference between this forest and the northern-fringe forest type was in considerably increased *Magnolia* population densities. However, both forest types were characterized by very high - higher than in southern forests - importance of beech and low importance of water oak (*Quercus nigra*). The second-growth northern beech-magnolia stands are characterized by the higher importance of several cool-adapted temperate species - such as tulip tree (*Liriodendron tulipfera*) and white ash (*Fraxinus americana*). Another conspicuous feature of both forest types is a relatively high importance of the interior-centered cool-temperate trees such as sassafrass (*Sassafras albidum*), cucumber magnolia (*Magnolia acuminata*), and black walnut (*Juglans nigra*) which are either absent or poorly represented in the southern forests. Sassafras and black walnut further increase in importance in the middle-Bluffland forests.

The southern beech-magnolia forests are characterized by somewhat higher population densities of evergreen magnolia and slightly lower population densities of American beech than the forests of the northern type. But magnolia still has here essentially lower (about two times)

population densities than beech. The rare subtropical species are more likely to be found in these forests but the interior-centered cool-temperate species are either absent or characterized by very low population densities. Water oak, nearly semi-evergreen in these latitudes, is typically one of the most important accessory components after sweetgum in these southern forests.

The southern-fringe beech-magnolia forest type has surviving remnant only east of the Mississippi River, in the Port Hudson area. Historically it was probably limited to a very narrow segment of the Mississippi Bluff which extended from southernmost portion of West Feliciana Parish to northern East Baton Rouge Parish. This is the only beech-magnolia forest type where *Magnolia* achieves the equal population densities with *Fagus*.

The physiographicly disturbed forests of the Bluff Escarpment even in their southern section are characterized by essentially lower importance of the subtropical and evergreen components. On the other hand, these forests are likely to contain more species of subtropical and interior-centered cool-temperate trees per unit area than the closed-canopy beech-magnolia forests at the same latitude.

The transition to more southern than "beech-magnolia" forest types occurs in the middle and southern section of East Baton Rouge Parish where American beech seems to decrease in importance to the extent that it becomes a

species of the secondary importance. Live oak (*Quercus virginiana*) is still not a part of this community: it begins to sprinkle only in the bottomland forests south of Baton Rouge city limits. The original forests of East Baton Rouge Parish were probably strongly dominated by *Magnolia grandiflora* (which is evident from the exceptional importance of this taxon in the subcanopy of Burden Plantation forest). Sweetgum and water oak also seem to have been very important constituents of the original forests of this section and probably achieved the status of the second-order co-dominants.

The transition to a more evergreen and more subtropical forest type is more evident west of the Mississippi River, on Opelousas Ridge where beech declines approximately 1 mile north of Opelousas and live oak begins to sprinkle, gradually increasing in importance, in the mesic forests south of Opelousas.

The predominantly evergreen and subtropical forest type where live oak shares dominance with evergreen magnolia originally covered the southern third of Opelousas Ridge. The presence of the old-growth bottomland forest strongly dominated by live oak suggests that *Q.virginiana*-rich forest type originally extended at least as far north as Lafayette. Today live oak-magnolia forest type survived only in the immediate vicinity from the coast line on the salt-dome islands and Forked Island.

Consequently, based on the composition and structure of their canopy strata, the loessial forests of the southern Blufflands can be subdivided in three big units: the "interior" beech-magnolia forests characterized by the extremely mixed cool-temperate and warm-temperate flora, with the dominant role of one subtropical evergreen species, more subtropical and more evergreen sub-maritime magnolia-dominated type characteristic for the extreme southern margin of the Mississippi Bluff in East Baton Rouge Parish, and predominantly subtropical and evergreen forest type evolved under the maritime influnces in the southern section of Opelousas Ridge, on the salt-dome islands and on Forked Island.

CHAPTER 9

THE GENERAL STRUCTURAL CHARACTERISTICS OF THE MATURE HARDWOOD FORESTS

Throughout the southern section of the Loess Hills, American beech (*Fagus grandifolia*) and southern magnolia (*Magnolia grandiflora*) tend to achieve the dominant status in the old-growth or relatively old second-growth forests which developed on the soils that were not subject to plowing and agricultural cultivation. The structural importance of these two trees gives the present-day relict stands the general look and feel of the early-historical forests but such resemblance is of a rather superficial nature.

To begin with, the definition of magnolia-beech-holly forest provided by the Delcourts (1977) on the basis of the data from early-historical West Feliciana in general does not appear to be relevant to the most present-day mature forests of the southern Blufflands because of relative scarcity of American holly (*Ilex opaca*). Whether the low importance of holly is due to the one and a half century of anthropogenic influence or highly localized original distribution of the magnolia-beech-holly association specifically in West Feliciana parish of southeast Louisiana remains an intriguing question to answer.

Today the Tunica Hills seem to be the only area in the southern Blufflands where *Ilex opaca* may be locally abundant. Here I discovered a tiny remnant of what may be

potentially defined as a mature magnolia-beech-holly forest. American holly (*Ilex opaca*) forms here both the subcanopy and understory layers, with few trees reaching into openings in the canopy. This site is located on a gentle slope just next to the Old Tunica road opposite from the entrance to Magnolia Glenn old growth preserve. The abundance of small and medium-size *Ilex opaca* trees in much more disturbed upland forests is another remarkable feature of this preserve. Some of these trees exceed 40 cm in dbh and reach the overstory stratum. They may well be surviving remnants of the magnolia-holly-beech association (with magnolia and beech largely destroyed) witnessed by George Daugherty during his 1821 forest survey.

Secondly, in the present-day forest, it is beech, not magnolia, that most frequently ranks first both in relative importance and in absolute numbers. The assemblages of Magnolia Glenn preserve (Tunica Hills), Louisiana State Arboretum, Port Gibson site, in Sicily Island area and Bluff Experimental Forest all exemplify this trend. Only the extreme southern sites such as Port Hudson where each species was represented by the even number of canopy-size individuals (67) and the lake slope of Chicot State Park where beech ranked only third in importance after sweetgum and magnolia, represent the notable exception from this rule. The canopy structure of the two latter sites, particularly Port Hudson, may be in part influenced by low

latitude, which stimulates the development of the magnolia-rich forests. One can suggest, perhaps, that the scarcity of beech in the lake-margin assemblage of Chicot State Park could also be indicative of some latitudinal effects since this site is located very close to the southern limit of beech in south-central Louisiana. It should be pointed out, however, that the *Fagus* population shows no signs of depletion in other sites of this southern frontier - neither in the nearby stand managed by the Louisiana State Arboretum, nor in the shallow gullies of Chicot State Park itself where I additionally found two nearly monospecific beech stands.

Consequently, the "simple" latitudinal explanation does not "work". The relative scarcity of beech on the lake-facing slope of the Chicot State Park is more likely to be a result of the edaphic effects caused by the immediate proximity of this assemblage to the man-made Chicot Lake. Beech was also represented by fewer individuals than magnolia in the Tunica Hills' sample of the beech-magnolia-holly forest. However, the size of this site was too small to consider it as a representative piece of evidence.

The dominant status of beech and magnolia in the mature forests is determined by the morphological and ecological characteristics of these two species. Both beech and magnolia are long-living, relatively slowly-growing

and highly shade-tolerant trees known for their ability to produce dense shade under their own canopies (Gano 1917, Pessin 1933, Kurtz 1944, Braun 1950, Blaisdell et al 1973, Delcourt and Delcourt 1974, Ware et al. 1993). The light-deficient subcanopy environment of the mature beech-magnolia forest tends to supress the development of more sun-loving species and restrict their recruitment to gaps and various favorable expositions. It appears that no potential canopy species can reproduce itself under the mature *Magnolia* overstory. I observed in a number of instances that areas under the canopies of large magnolia trees were free from the undergrowth of any other overstory or subcanopy species. The dense shade produced by the large magnolias may be only a partial explanation for this phenomenon.

Blaisdell et all (1973) noticed that the leaf litter of *Magnolia grandiflora* may also cause some inhibitory effect on the reproduction of other species. In the Blufflands I observed that "sterile" spots under *Magnolia* trees are indeed commonly associated with accumulations of their fallen leaves which resist decay much longer than leaves of any deciduous tree. Inhibitory effects of a beech overstory are slightly less pronounced but still only very few species of canopy trees may reproduce themselves under its shade. The beech forest can perpetuate itself infinitely because *Fagus* readily germinates and develops

under its own overstory. Blaisdell and his co-workers. (1973: 386) indicated that beech reproduces "fairly well" even under canopy trees of magnolia but my observations suggest that this only can be true when the ground under magnolia trees is relatively free of *Magnolia* leaf fall. Magnolia in turn reproduces readily under a beech-dominated overstory but almost never germinates from seeds beneath canopy trees of its own species. On the other, large magnolias frequently sprout, sometimes in abundance, from their trunk bases and subterranean roots, and sprouting does not seem to the least degree to be inhibited either by shade or fallen leaves of the mother-tree.

Apart from beech and magnolia, one of the very few species that can reproduce more or less successfully under the beech canopy is southern sugar maple (*Acer barbatum*). Whereas undergrowth of *Magnolia* is never abundant in the areas strongly dominated by beech, southern sugar maple occasionally forms large, nearly monospecific subcanopy agglomerations in such spots. Its ability to maintain high subcanopy populations in the somber environment of the beech-dominated forest is especially pronounced in the Bluff Experimental Forest and beech coves of the Tunica Hills area. Like many other deciduous trees, southern sugar maple fails, however, to reproduce under magnolia.

Interestingly, despite its rather remarkable shade-tolerance and relatively high population densities in the

lower strata, southern sugar maple does not show any trend toward the dominance in the overstory. In most Bluff stands it is represented by only 1-2 canopy-size trees per one hectar. The only relatively large sample population - 8 canopy trees per one hectar - was registered in the Bluff Experimental Forest. Here sugar maple ranked eighth in frequency among the canopy trees and made up 2.8% of the overstory structure.

The case of the Bluff Experimental Forest suggests that there is a positive correlation between the high *Fagus* importance and high importance of southern sugar maple. Perhaps, beech - by arresting the reproduction of other species and limiting the competition - even promotes the development of large *Acer barbatum* populations. This assumption does not seem groundless in view of a fact that the physiographically-disturbed Tunica Hills forest which is characterized by the richest and most heterogeneous midstory of all sites has the lowest population density of southern sugar maple in the canopy (one specimen per one hectar).

The extent to which the beech-magnolia association dominates the mature forests of the Loess Hills depends primarily on the regime of disturbance. In the modern forests, the balance between the dominant association and the accessory species varies from site to site depending on the individual differences of disturbance regimes in each

area. The modern beech-magnolia forests of the Loess Region can be generally subdivided into three successional types: physiographically-undisturbed old-growth forests, old-growth forests developed in the regime of the permanent physiographic disturbance and physiographically-undisturbed second-growth beech-magnolia forests. In the mature, old-growth forest which has not subject to any major anthropogenic or physiographic disturbance, the successional process is maintained largely due to the death and fall of the individual canopy trees. When large, canopy-size beech or magnolia dies or falls, the resulting gap becomes a favorable habitat for the development of the light-dependent fast-growing species such as sweetgum, tulip tree, ash or some species of oak.

Eventually the opening is likely to be claimed, depending on its size, by one or a few of these colonizers which contribute, according to the definition given by Blaisdell, Wooten and Godfrey (1974: 380), to the "patchwork quilt kind of pattern" characteristic for the canopy of the mature beech-magnolia forest. The successional circle would be then completed by the undergrowth of beech or magnolia slowly developing under the canopy of the less shade-tolerant gap colonizer. With the natural death or breakage of the latter, subcanopy beech or magnolia (or, perhaps, both) would fill the gap and reestablish "the status quo". This type of successional

dynamics seems to lead to the development of the forest community characterized by a very high relative importance of the shade-tolerant components. In the present times the old-growth forests of this type represent probably the rarest and most threatened forest habitat of Louisiana and Mississippi.

The exceptionally well-preserved beech-magnolia stand managed by Louisiana State Arboretum is the only spatially representative site of this category that I managed to locate in the Loess Region. The relative importance of the beech-magnolia association in the canopy of this forest reaches 56.7%: this is the highest aggregate share of these two species I registered in the Loess Hills. The relic patch of the magnolia-beech-holly forest found on one of the gentle slopes along the Old Tunica Road, although very small to be considered as a representative sample, also appears to be related to this successional type. Here magnolia and beech together make up 51.2% of the canopy structure. With American holly, the aggregate canopy share of the shade-tolerant species in this site's overstory increases to 57.2%. These values are very close to those suggested for the early-historical forests of West Feliciana by the Delcourts (1974).

Much more complex successional dynamics are demonstrated by the forests which developed in the section of the Bluff escarpment where the loessial mantle reaches

its maximum depth and forms a cap dissected by extensive labyrinths of remarkably deep, steep-sloped ravines. Two sampling areas, Magnolia Glenn preserve in the Tunica Hills and the Anderson-Tully-owned Steep Bluffs area north of Vicksburg, are representative of this physiographic section. Both areas are characterized by instability of the ravine slopes. The highly dissected relief, ever-moist microclimate of the deep and narrow ravines and erosive action of the abundant subtropical rains and temporary streamcourses results in frequent landslides and associated treefall.

Physiographic disturbance is especially pronounced in the Tunica Hills. Only recent landslides and associated gaps in the ravines of the Magnolia Glenn preserve make up approximately 8 percent of one-hectare sampling area. As a random factor, landslides tend to affect first the dominant taxa. Although beech and magnolia generally retain the dominant status in the ravines Magnolia-Glenn, their aggregate sample canopy population in the local steep-slope forest was only 51 canopy trees per one hectar which is by 36.4% less than within the sample area of the same size in the old-growth forest of the Louisiana State Arboretum where as many as 79 canopy trees of these two species were registered. Respectively, in Magnolia Glen, beech and magnolia made up only 31.6% of the canopy structure which is by 25.1% less than in the canopy of the LSA-managed

stand. This value is also lower than in any other late-successional site.

Still another type of the successional dynamics and, consequently, the canopy structure is exemplified by the second-growth beech-magnolia forests. In the southern Loess Hills most of the survived remnants of the beech-magnolia growth such as ravine forests in the Port Hudson and Sicily Island areas, the Port Gibson stand and Bluff Experimental Forest belong to this category. These forests originated in the areas which were cleared at least once (some, perhaps, twice) within the last one and a half century. It is not unlikely that Sicily Island, Port-Hudson and especially Bluff Experimental Forest areas did contain some patches of the old-growth forest which were sampled along with the predominant second-growth matrix but these were small enough to be regarded as far as a general picture is concerned.

All four secondary-growth assemblages developed in physiographically more or less stable habitats with virtually no signs of ongoing erosion. Consequently, physiographic disturbance can be disregarded in the consideration of the above-mentioned stands. In this respect, they all are the duplicates of the physiographically-undisturbed gentle-slope old-growth forest type represented by the LSA stand. Life histories of the second-growth beech-magnolia forests appear to have

been never interrupted by the periods of the agricultural cultivation. They developed as a result of the successional process that started immediately following the destruction of the original overstory. This means that they sprouted from the soil which was never ploughed and thus preserved its litter and humus layers with most propagules, roots, stumps and other living matter largely untouched.

After such a clearcut, the development of a new forest starts with the regeneration of the surviving remnants of the understory which contains saplings and seedlings of both shade-tolerant and accessory taxa. Soon these will be joined by fresh shoots coming out of roots and surviving stumps, as well as new sprouts germinating from propagules. Unlike beech and magnolia which are slowly-growing trees, most of the accessory species are moderately to highly fast-growing. Thus under the even start conditions, the faster-growing accessory species have an obvious advantage over the climax species. Released from the supression of the shade-tolerant dominants, the accessory species fill the upper layers of the early-successional regrowth and later form the canopy of the young secondary forest.

The beech-magnolia association slowly develops under the canopy dominated by the successional taxa until it forms more or less closed subcanopy which complicates the further reproduction of the light-dependent trees. Beginning from this point, the last stage of forest

succession starts: In part replacing trees of more successional kinds, in part intermingling with them, the larger representatives of beech and magnolia gradually reach into the overstory to form what can be considered as the second-growth beech-magnolia forest. The latter is still not a quite "classic" beech-magnolia forest: despite the predominance of beech and magnolia in the upper layers, the canopy of such secondary forest remains more mixed than that of the old-growth forest. Thus the successional process will proceed to the point when anessential part of the remaining light-dependednt overstory trees would be replaced. Based on the difference in the population sizes and relative shares of the shade-tolerant and light-dependent species, I would suggest that the studied samples of the second-growth beech-magnolia forests represent, perhaps, the different series of this last successional stage. Each of these samples includes, however, also a certain number of the old-growth trees which remained spared during the clearcut operations thus contributing to a rather uneven, mixed-age nature of these stands.

The second-growth forests are characterized by essentially higher densities of canopy trees than the old-growth forests. One-hectare samples of the old-growth forest in the Tunica Hills and Louisiana State Arboretum contained 156 and 150 trees respectively. By contrast, the exemplary areas of the same size sampled in the second-

growth forests of the Port Hudson area, Sicily Island area and the Bluff Experimental Forest each gave 271, 227 and 238 canopy trees. The lower densities of the canopy trees in the old-growth forests as compared to the secondary-growth ones seems to be a result of the supressive effect caused by the beech-magnolia overstory.

The destruction of the original beech-magnolia overstory in the areas which are now under second-growth beech-magnolia forests has temporarily released the undergrowth and propagules of the canopy trees from the light supression and resulted in the development of the new overstory characterized by the higher tree densities. The general increase of the canopy tree densities in the second-growth forests is a product of the successional phenomenon which I term a "post-clearance syndrome" - a chain reaction of the different groups of species on the short-term and large-scale anthropogenic disturbance associated with the clearcut and immediate abandonment. The disturbance of this type seems to lead to the increase of the canopy populations of most of the tree species present in the beech-magnolia forest including the shade-tolerant ones. But the positive response on disturbance from the different groups of species seem to come in "waves" associated with the different stages of the forest recovery.

Many light-demanding species such as oaks, sweetgum, tulip tree would probably start building up their populations immediately after clearcut and slow down as soon as more or less close canopy is formed. The moderately light—demanding taxa such as hickories, white ash and winged elm which are able to develop under the closed canopy formed by shade-intolerant trees would probably maintain the relatively high recruitement rates for a somewhat longer period. Finally, the shade-tolerant species begin build up their populations at a somewhat more advanced stage of the forest regeneration.

Although initially swamped by the developing populations of the light-demanding species and suffering from the mechanical damage and change of the microclimatic conditions, the recovering beech—magnolia growth would eventually find itself in more favorable environmental situation under the closed overstory formed by the trees of successional kinds than under the original canopy of the old-growth forest. The population increase of the light-demanding species in the canopy of the second-growth beech-magnolia forests is more pronounced than that of the shade-tolerant ones. Consequently, the sampled secondary-growth forests were characterized by the lower relative importance of the beech-magnolia association than physiographically-stable old-growth forests — this is despite the fact that total numbers of the shade-tolerant trees on one ha of

every secondary-growth plot were higher than in the area of the same size of the old-growth forest managed by Louisiana State Arboretum. The aggregate relative importance of beech and magnolia in the secondary forests is subject to a rather broad variation ranging from 36.4% in the Sicily Island to 41.5% in the Bluff Experimental Forest and 44.8% in Port-Gibson and reaching its maximum, 51.3%, in the canopy of the second-growth ravine forest of the Port-Hudson area.

In this sense, the structure of the Port-Hudson assemblage is very close to those exemplified by the gentle-slope old-growth assemblages. The interesting fact about the Port-Hudson site is that the one-hectare sample area of its ravine forest contained an extraordinary high aggregate population of beech and magnolia far exceeding that of any other site, both primary and secondary. As many as 134 canopy trees of both species were registered here, half of them being represented by *Magnolia grandiflora* which seemed to have been a main contributor to the large population pool of the shade—tolerant species for the beech densities, although high as they were, more or less fit the general pattern. An unusually high density of magnolia in Port-Hudson area has been already briefly discussed: my guess is that it is a combination of the latitudinal and successional effects, rather than the latitudinal effect alone, that produced such magnolia-rich assemblage. The

turbulent history of the Port-Hudson ravine forest, most of which has been cut or severely disturbed at least twice for the last 150 years, is strongly suggestive of this standpoint.

The Role of the Light-Dependent Canopy Species

Beech and magnolia are not the only dominant species that may be present in the canopy of the modern beech-magnolia forests. Due to the disturbed nature of the present-day late-successional stands, some five to six light-dependent tree species which seem to have occupied the marginal niches in the early-historical assemblages, today are also found to approach the frequencies of the dominant taxa - although not all in one site. The list of the potential second-rank co-dominants includes sweetgum (*Liquidambar styraciflua*) tulip tree (*Liriodendron tulipfera*), water oak (*Quercus nigra*), white oak (*Q. alba*), loblolly pine (*Pinus taeda*), white ash (*Fraxinus americana*), sassafras (*Sassafras albidum*) and few other species but their concrete site by site composition varies rather strongly from one section to another depending on the edaphic conditions and nature of disturbance.

The aggregate population sizes of the light-dependent accessory component (unlike those of many individual accessory species) in the canopy of the modern beech-magnolia forests vary depending predominantly on the nature and intensity of the disturbance regimes. The aggregate

sample population of the accessory taxa was lowest in the closed-canopy old-growth beech-magnolia forest of the Louisiana State Arboretum: there I found only 71 light-dependent canopy trees on 1 hectar. In the steep-slope, physiographically-disturbed assemblage of Magnolia Glenn preserve in Tunica Hills the total population of the light-dependent species increased to 105 individuals per one hectar. Finally, the canopy of the second-growth beech-magnolia assemblages of the Port Hudson area, Sicily Island area, and the Bluff Experimental Forest contained respectively 137, 144 and 140 individuals of the accessory light-dependent taxa per 1 hectar.

The peak of the light-dependent tree populations in the second-growth forests exemplifies the fact that the anthropogenic disturbance in general seems to be the strongest stimulating factor for the accessory component of the beech-magnolia forest. Evidently, the development of the large numbers of the light-dependent successional trees in the old-growth forests is inhibited by the dense shade of the beech-magnolia overstory which appears to be the major reason for the generally smaller number of canopy trees in the Tunica Hills and Louisiana State Arboretum. However, in terms of the relative population densities, the intensive small-scale gap dynamics caused by physiographic disturbance appear to be a very "efficient" way of

recruitment of several light-demanding trees into the canopy.

The Role of Sweetgum

One of the most conspicuous and rather universal features of the modern beech-magnolia forests is the relatively high importance of sweetgum (*Liquidambar styraciflua*). Sweetgum had been mentioned by Daugherty among the trees present in the early historical forest of the Tunica Hills area. However, Delcourt listed it among 21-23 most sparcely distributed canopy species whose total relative frequency was only 22.6 %. This fact suggests that the individual frequency of sweetgum in the early-historical forests of West Feliciana may have been of the order of 1-2% or only slightly more unless some kind of mistake was comitted during either calculation of its potential importance or the original sampling. By contrast, the average share of *Liquidambar* in the canopy structure of the modern beech-magnolia stands aproximates 12.0%. Along with beech and magnolia, sweetgum is currently a codominant species in at least 5 out of 9 surveyed ravine forests and very important accessory canopy taxon in the remainder of the sampled stands. It ranks second after beech in the old-growth forests of the Tunica Hills and Louisiana State Arboretum and assumes the status the first-rank dominant species on the slopes facing the Chicot Lake in south-central Louisiana.

Successional characteristics of sweetgum seems to be essentially different from those of beech and magnolia. To begin with, sweetgum is a relatively fast-growing tree, especially in the initial period of its life cycle. Blaisdell et al. (1973) who observed the reproduction of sweetgum in five beech-magnolia stands in Talahassee Red Hills, north Florida, emphasized its dependence on gaps. In a number of cases I observed that sweetgum is nearly absent from the understory of the closed-canopy stands, especially if the overstory of such stands is dominated by the shade-tolerant taxa. Generally, the reproduction of this species in the mesic beech-magnolia forest is strongly centered in the various openings whether they are associated with treefall or landslides.

If one assumes that the original early-historical forests seemed to have been relatively poor in sweetgum, its importance in the canopy of the second-growth forests can be interpreted as a result of the extensive anthropogenic impact associated with the large-scale forest clearence and establishment of more successional regimes. The comparatively recent nature of *Liquidambar* expansion in most beech-magnolia stands could possibly be validated by the fact that the majority of canopy-size sweetgum trees are represented by relatively small dbh classes which are well below the average dbhs of such overstory trees as beech, magnolia and oaks.

On the other hand, the steady trend of this taxon toward the dominance in the present-day assemblages sets a stage for an interesting biogeographic question. Can we readily assume that sweetgum was that unimportant in the pre-cultivation forests as it is suggested by the Delcourts' model? Apparently, not so. It should be pointed out in this regard that two forest sites where sweetgum achieved the dominant status - one on the territory of Magnolia Glen preserve and another - in the Louisiana State Arboretum - were the old-growth assemblages. This fact indicates that high importance of sweetgum in their canopy strata seems to reflect the original structure and be determined by natural, non-anthropogenic causes.

The Case of the Escarpment Forests. It appears that sweetgum was historically one of the major dominant species in the heavilly dissected section of the Mississippi Bluff Escarpment. In the deep, steep-slope ravines of Magnolia Glen preserve in the Tunica Hills and the Steep Bluffs area north of Vicksburg, the high population densities of sweetgum seem to be promoted by the intensive erosion of the loess mantle resulting in frequent landslides and associated treefall. As a fast-growing and highly-specialized gap-colonizer, sweetgum is one of the first species which benefit from the perpetual physiographic disturbance. The highest relative importance among the old-growth sites - 18.5% - was achieved by

sweetgum in the canopy of the Tunica Hills assamblage. In the Steep Bluffs it was slightly lower - 14.0%. But this site had its own record - the largest number of *Liquidambar* canopy trees per 1 hectar sample

The "clear-and-abandon" type of anthropogenic disturbance which led through time to the development of the second-growth beech-magnolia forests seems to be far less "efficient" means of sweetgum recruitment into the canopy than the natural physiographic disturbance. Unlike in the highly eroded section of the Bluff escarpment, sweetgum populations in the physiographically-undisturbed secondary forests could have expanded only during relatively limited period of time following clearence, i.e. once or twice for the last 150 years. With the regeneration of the beech-magnolia subcanopy, the reproductive ability of sweetgum in such forests was likely to have decreased to the level comparable to that of the mature beech-magnolia forest. As a result, the physiographically-undisturbed second-growth forests tend to have smaller sweetgum population than permanently-disturbed old-growth stands. Within the deep-loess section, the relative importance of sweetgum in the canopy stratum fluctuates from 6.6% in the exceptionally beech-rich assemblage of the Bluff Experimental Forest to 10.6% in the Port Gibson site.

The edaphic variation throughout the Loess Hills region is, perhaps, of no less importance for sweetgum than

the variation in intensity of disturbance regimes. Unlike beech and magnolia which do not stand any innundation and thus are absent or nearly so from the floodplains, sweetgum is one of the key components of the southern bottomland forest (Braun, 1950; Harcombe and Marks, 1983; Monette and Ware, 1983; Sharitz and Mitsch, 1993). The edaphic optimum of this species appears to be centered on the ridges and elevated margins of the alluvial river valleys (Sharitz and Mitsch, 1993) from where it extends upslope into more mesic habitats.

The edaphic preferences of sweetgum are evident from the essential difference in its distribution patterns between the forests of the bluff ridge and those on the peryphery of the Loess Hills. Loughridge (1888) was one of the first naturalists who observed that, because of the high water-retention capacity of the thick loess deposits, sweetgum and other bottomland-centered species are important components of the local upland forests. In the present-day early-successional forests of the deep loess section of the Mississippi Bluff, sweetgum tends to be abundant throughout the slope gradient from the ravine bottoms to the hilltops. However, the uplands, due to the higher fluctuations of the soil moisture, are usually less prefered.

In the areas where ravines are occupied by the closed-canopy beech-magnolia forest, the situation may be, in fact

reverse, and the population densities of sweetgum are higher on the upper slopes and ridgetops where the shade-tolerant species are largely lacking in the canopy. In the Tunica Hills where the old-growth forest evolved in the conditions of the intensive slope erosion, the positive and negative factors are effectively counter-balanced and the distribution of sweetgum along the slope gradient is nearly even - ranging from 29 canopy-size sweetgum trees per 1 hectar in the lower-slope old-growth forest to 26 canopy-size trees per hectar in the early-successional upland forest in the immediate vicinity of the ridgetops.

On the better drained surfaces east of the bluff ridge and west of the Mississippi River where only a thin layer of loess overlies the sandy loams of the Citronelle Formation, the vast majority of the canopy-size sweetgum trees tend to congregate in the ravine bottoms even if these are dominated by the late-successional assemblages. The bottomland-centered nature of the sweetgum distribution is especially evident in such marginal areas of the Loess Region as the Homochito National Forest and Sicily Island.

The Case of the LSA Stand. The case of the old-growth forest managed by Louisiana State Arboretum is of particular interest to us because it illustrates the potential ability of sweetgum to achieve high importance even in the exceptionally well-developed, closed-canopy beech-magnolia forest without any record of historical

clearing or signs of ongoing physiographic disturbance. With the population density almost as high (27 *vers* 29 individuals per 1 hectar) as in the Tunica Hills, sweetgum ranks here second among the canopy trees in relative frequency (18.0%) and third in relative importance (15.9%).

To comprehend the *Liquidambar* dynamics in this relict old-growth assemblage, one should pay a closer attention to the nature of its spatial distribution and reproductive strategies along the edaphic gradient. First of all, in the Arboretum assemblage sweetgum increases in importance rather dramatically from the upper slopes to the bottoms so that about 70% of the canopy trees were registered within the lower section of the slope gradient. Secondly, the slopes of Louisiana State Arboretum are descending toward a relatively broad accessory floodplain which is covered by the bottomland forest where sweetgum is an absolute dominant. The pronounced trend toward the dominance within the lower-slope mesic forest zone, may be in part stimulated by the pressure from this large "back-up" population pool.

Most of the reproductive success of sweetgum in the lower section of the slope gradient appears to be related to its increased ability to sprout from subterranean roots. Because of this, the lower section of the Arboretum assemblage is characterized by an essentially more vigorous subcanopy reproduction of sweetgum than any other closed-

canopy beech-magnolia stand. Different interpretations of this strategy can be suggested. Sprouting may be a general ecological response of sweetgum to the favorable edaphic conditions, namely the high moisture content on the lower-slope soil and the proximity of the water table to the land surface. It can also be interpreted as an endemic adaptational response to the closed-canopy conditions within the edaphically favorable section of the slope gradient.

In the middle to upper section of the slope sprouting ability sharply decreased and was only of the marginal importance. The key point here is that in the lower section of the slope gradient sprouts (as well as seedlings and saplings) of sweetgum were not necessarily associated with gaps. In the conditions of plentiful moisture supply, sprouting strategy appears to give sweetgum additional stamina for persistence and slow development even under nearly closed overstory.

Within the lower-slope section, the midstory stratum of the LSA stand was packed with the advanced thin-stemmed sprouts developing, for the most part, under light-deficient conditions. The decrease in population density upslope, both in the canopy and midstory, was a function of a change in the reproductive strategies which in turn seems to reflect the decreasing moisture availability. The reproduction of sweetgum in the middle and upper sections

of the slope depended largely on seedlings and saplings. Secondly, these were not distributed here as randomly as in the lower portions of slope but tended to be strongly associated with gaps.

The Case of the Chicot Bluff. As an additional confirmation of the considerable importance of the edaphic conditions for the population dynamics of *Liquidambar* I can refer to a very high (21.9%) frequency of this taxon on the slopes facing Chicot Lake. This is the only slope "beech-magnolia" forest where sweetgum achieves the status of the first-rank dominant species. In some sections of this site clearing operations of the 1940s extended downslope which suggests that the anthropogenic disturbance should not be dismissed as a partial explanation for its exceptionally high importance. However, in this site, sweetgum is abundant not only in such disturbed areas but also in physiognomically much more mature pockets with large beeches and magnolias.

The Chicot site has probably the greater number of the large-size sweetgum trees than any other site. Such "old-looking" sweetgum-rich stands may be indicative of the original, old-growth canopy structure. Indeed, before the construction of the dam, the present-day lake-facing slope was a bayou slope - not unlike that of the Louisiana State Arboretum. The original mesic forest on this slope may have developed in the conditions of the moist microclimate in

the immediate vicinity to the more hydrophytic forest which occupied the bayou bottom. On the other hand, the canopy and subcanopy of the present-day lake-slope forest is also characterized by a conspicuously vigorous growth of younger and slender sweetgum trees. I have already refered to the hydrological disturbance as a primary possible reason for the unusual structure of the Chicot lake-slope community. The construction of the reservoir may have resulted in the rise of the water table, which in turn could have triggered a complex chain of ecological changes throughout most of the slope gradient. The hydrological disturbance undermined the beech reproduction and thus affected the recruitment of the new beech trees to the canopy of the lake-slope community. The increased content of soil moisture, combined with the decrease of the shading effect produced by beech overstory must have been an important pre-condition for the development of the large sweetgum population in this area. The lake margin to which the slope is immediately adjacent today is dominated by the cypress-tupelo swamp forest which probably originated as a result of the drastic change in edaphic conditions after the construction of the dam.

Beech-Magnolia-Sweetgum Association. Both the assemblage of the Magnolia Glen preserve and the old-growth stand of the Louisiana State Arboretum - each one in its own peculiar way - exemplify the natural transition from the "conventional" beech-magnolia forest to the

successionally more complex beech-magnolia-sweetgum association. I suggest that within the highest section of the Loess Ridge facing the Mississippi Valley, in such heavily dissected, erosion-prone areas as Magnolia Glen, sweetgum was historically one of the major dominant species. This conclusion seems to be also supported by the high importance of sweetgum in the canopy of the similarly eroded Steep Bluffs forest site north of Vicksburg. The Tunica Hills and other deeply dissected escarpment areas around Vicksburg have also featured the more conventional beech-magnolia or magnolia-beech-holly forests like those statistically reconstructed by the Delcourts (1974) but these forests apparently prevailed on more gentle, undisturbed slopes.

The case of the LSA old-growth stand suggests that the beech-magnolia-sweetgum or beech-sweetgum-magnolia association was likely to have been an original climax not only in eroded steep-slope localities but also in some portions of the lower section of the beech-magnolia slope gradient, especially in the areas where ravines were immediately adjacent to the Mississippi Alluvial Valley or smaller accessory floodplains. The Delcourts (1974) do not mention sweetgum among the primary trees of their magnolia-beech-holly bottomland association but a point should be made that the term "bottomland forest" was likely to have been used by them to imply ravine forests in their whole

integrity, with slopes and ravine bottoms combined, rather than its original denotation suggesting exclusively ravine bottoms.

The upper and middle slopes of the original ravine or forests may have indeed been not very rich in sweetgum. What is more, the only way to positively identify sweetgum-rich section of the beech-magnolia forest is to run a transect along the ravine slope. Most of the loessial ravines are quite narrow. Consequently, if the transect is crossing ravines rather than following their course, the narrow tongues of beech-magnolia-sweetgum association on the lower slopes and ravine bottoms may simply drop below the level of statistical visibility.

If this was the design of Daugherty's inventory, it may have easily failed to document some important features of the micro-biogeographic variation along the vertical slope gradient even if his transect did cross some sweetgum-rich sections. Besides, as it has been already stated, the sweetgum-rich forests were most likely to occupy a narrow western margin of the Mississippi Bluff. On a larger-scale perspective, the statistical data from the Escarpment Area could have been easily obscured by the data from the broader middle to eastern section of the Bluff with more gentle slopes and largely away from broad accessory floodplains. This portion of the Bluff was likely

to have been covered by the closed-canopy beech-magnolia forests which may have been relatively poor in sweetgum.

Brief Summary and Conclusions

American beech (*Fagus grandifolia*) and southern magnolia (*Magnolia grandiflora*) are the dominant species in all mature forests surviving in the southern Loess Hills. The dominant status of these species is determined by their shade-tolerance and their ability to produce dense under their canopies. Only a very few potentially canopy tree species, including beech, magnolia, American holly (*Ilex opaca*) and southern sugar maple (*Acer barbatum*) may reproduce and develop under *Fagus* and none, including magnolia itself, can reproduce and develop from seeds under *Magnolia*.

The extent to which beech and magnolia dominate the late-successional forests depends on the regime of disturbance. In the conditions of a disturbed forest, beech and magnolia tend to lose competition to the faster growing light-dependent species; consequently, the disturbed forests are generally characterized by the lower structural importance of beech and magnolia and higher structural importance of the light-dependent species.

The importance of the dominant shade-tolerant species tend to be higher in the old-growth closed-canopy forests developed on stable slopes with no or little physiographic disturbance. The recruitment of the light-dependent species

in the canopy stratum of such forests is largely limited to gaps which are formed as a result of the death and fall of the individual canopy trees.

The second-growth closed-canopy beech-magnolia forests developed on stable slopes replicate the general structure of the closed-canopy forests but they are typically characterized by essentially larger populations of canopy trees per unit area and somewhat higher aggregate relative importance of the light-dependent species as compared to the old-growth closed-canopy beech-magnolia forests. The larger populations of the light-dependent species are indicative of the earlier successional phases of these regenerated communities

The aggregate share of both shade-tolerant species is lowest in the canopy stratum of the forests developed in the exceptionally deep, steep-slope ravines of the Bluff Escarpment. These forests evolved in the conditions of the perpetual physiographic disturbance associated with the small-scale landslides which frequently open the canopy and contribute to a much more intensive recruitment, as well as higher importance and diversity of the light-dependent species than the closed-canopy forests.

The modern beech-magnolia forests are somewhat different from those reconstructed by Delcourt and Delcourt (1974) on the basis of Daugherty survey. First of all, most of the present-day forests do not contain American holly

(Ilex opaca) in the canopy stratum and tend to have rather low midstory population densities. The only evidence of beech-magnolia-holly forest postulated by the Delcourts (1974) comes from the Tunica Hills where this forest type was limited to the ridgetops and gently-sloping ravines. This is the only forest type where American holly seems to have been relatively important in the overstory stratum. Secondly, in the vast majority of the modern beech-magnolia stands, including most of the southern forests, it is beech, not magnolia, that is the first-rank dominant species. Only in the extreme southern fringe of the beech-magnolia forest does *Magnolia grandiflora* achieve the equal population density with beech. Thirdly, beech and magnolia are not the only species that may be present in the canopy of the modern beech-magnolia forests. Some five to six species which seem to have occupied the marginal niches in the early-successional forests are found today under different situations to approach the status of the dominant species. The most conspicuous feature of all modern beech-magnolia forests is the high importance of sweetgum which either the part of the dominant association or occupies the niche of the first-rank accessory species.

NATURAL HISTORY AND PHYTOGEOGRAPHY OF THE LOESS HILLS AND RAVINES, LOWER MISSISSIPPI EMBAYMENT

VOLUME II

A Dissertation

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in

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CHAPTER 10

THE VARIATION OF THE CANOPY ASSORTMENTS IN ACCORDANCE WITH PHYSIOGRAPHY, EDAPHIC CONDITIONS AND DISTURBANCE REGIMES

Initially I planned to discuss the aspects of the biogeographic variation mentioned in this title in two separate chapters. In practice, such an approach turned out to be difficult to implement. Effects imposed on the vegetation by the combined action of the edaphic conditions, physiography and disturbance in most cases are so intricately interrelated that the proper comprehension of their biogeographic significance can be only achieved if all three factors are taken into account and discussed together. Anthropogenic disturbance, for example, tends to produce essentially different biogeographic effects depending on the variation in depth of the loessial deposits. Besides, the nature of disturbance regime itself may be, to a large extent, determined by the depth of the loess mantle. In this chapter, the biogeographic significance of disturbance will be analyzed on the basis of the pre-existing physiographic and edaphic conditions.

The forests of the Loess Hills can be roughly subdivided into five biogeographic types or sections, of which two are associated with the deep-loess section of the Mississippi Bluff, and three others - with the periphery of the Loess Region underlain by the shallow and thin loess mantles (Figure 4). Because beech and magnolia in most

cases do not seem to be influenced by the variation in edaphic conditions related to the thinning of the loess mantle, the segregation of these five forests types is based on essentially distinct assortments of the accessory species.

The pronounced physiographic dissection of the Mississippi Bluff combined with the high water-retention capacity of the thick loess deposits fostered the development of forests rich in moisture-loving mesic and bottomland-centered trees. These communities are representative of the forest subdivision which, on the basis of its environmental and floristic characteristics, will be defined in this research as moist-mesic or, in a broader and more transitional term, moist-mesic to mesic. Included under this definition are at least two forest types: first, the relatively narrow (even on the scale of the Loess Hills belt) section of the steep-slope broken-canopy forests of the Bluff escarpment which are subject to perpetual physiographic disturbance; secondly, the broader section of the physiographically-undisturbed, relatively closed-canopy forests developed on stable, gentle to moderately-steep slopes. Both sections are characterized by very similar edaphic conditions: their biogeographic segregation is enforced largely by physiographic factors. In the Escarpment Section, the most dramatically dissected

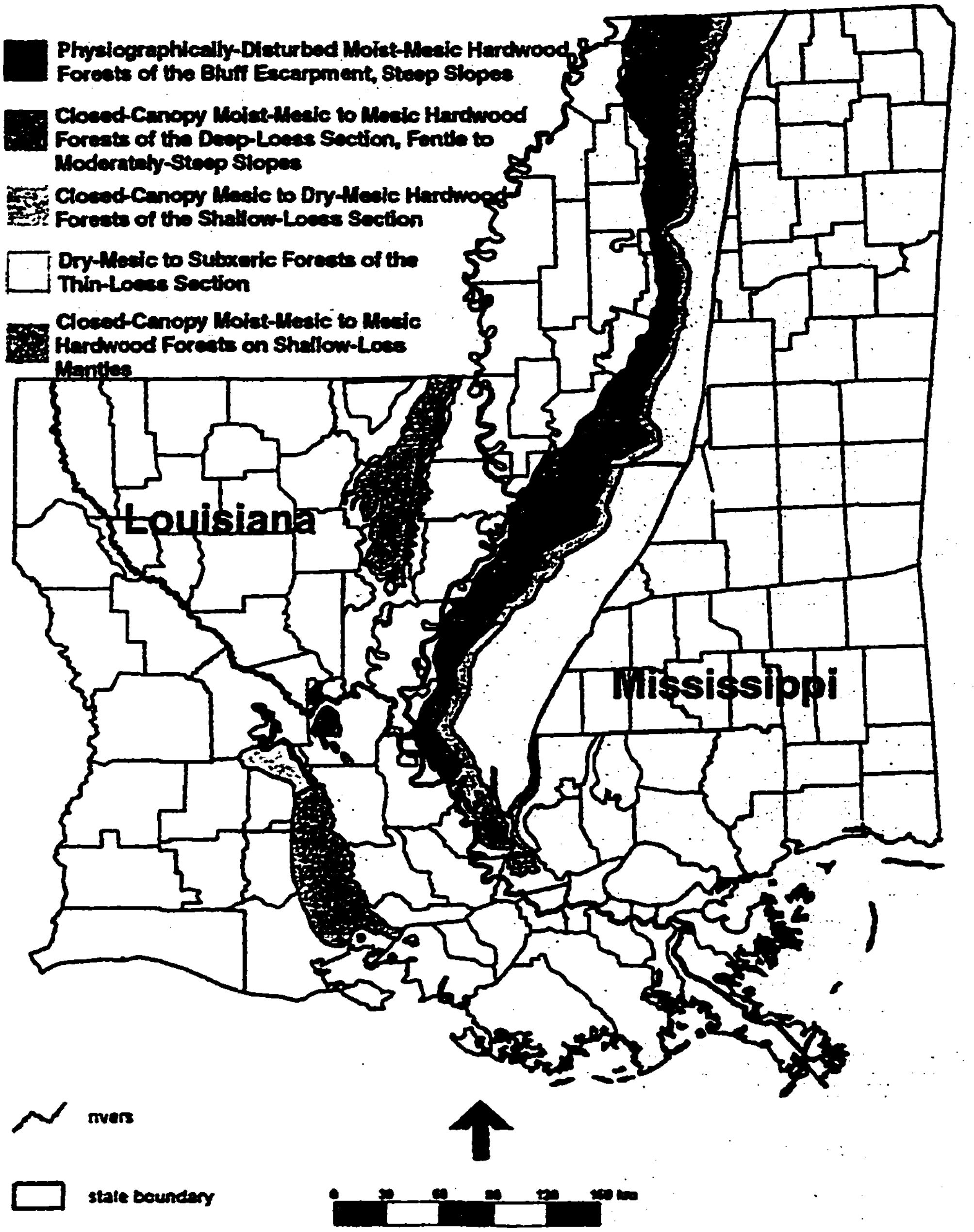

Figure 4. The Forest Types of the Southern Loess Hills As Determined by the Physiographic and Edaphic Conditions

Sources: Biker A.R. 1969. Geologic Map of Mississippi, Scale 1:500,000; Braud, DeWitt. 1999. Louisiana GIS CD: A Digital Map of the State, Version 2.0

area of the Bluff, the structure and species composition of the forest communities are greatly affected by ongoing erosion of the loess mantle. Frequent small-scale landslides on slopes result in perpetual tree fall and canopy disruption. An intensive regime of successional dynamics accounts for much of the floristic difference between the assemblages of the escarpment area and those evolved on more stable slopes further eastward. Besides, serving as effective natural reservoirs of exceptionally moist and relatively cool microclimate, the narrow and deep ravines of the Escarpment section can be readily distinguished by the rich assortments of the bottomland and cool-temperate species - generally more diverse here than throughout the rest of the Mississippi Bluff.

The marginal and somewhat transitional type of the moist-mesic to mesic forests was found west of the Mississippi River where it forms the small segregated fragments in the Chicot Lake area. Here it was associated with the localities characterized by the pronounced relief and obvious signs of loess deposition such as the lake-facing slope of the Chicot State Park and deeply dissected area managed by the Louisiana State Arboretum. In their major aspects (the structural importance of the moisture-loving species) the local forests represent the impoverished replicas of the Bluff assemblages. Yet the lack of several "deep-loess indicators" and presence

(especially in Chicot State Park) of few "shallow-loess specialists" suggest that they are not completely identical to those of the Bluff and should be considered as, perhaps, a marginal variation of the latter or as a transition to the edaphically drier forest types.

The hardwood communities developed within the deep-loess section of the Mississippi Bluff and in the deep ravines in the vicinity of Lake Chicot are environmentally and biogeographically different from somewhat more xeric forest types developed on the periphery of the Loess Region. The biogeographic segregation between these divisions is caused largely by the difference in edaphic regimes which increases with the thinning of the loess mantle. The forest types developed on the shallow and thin loess mantles will be classified in this work in a broad sense as mesic to dry mesic.

Along the gradient of loess thinning in these forests there is an increasing representation of species adapted to greater fluctuations of available soil moisture, more xeric conditions, and poorer, more acidic soils. The Port-Hudson area, the Sicily Island area, and Homochito National Forest are all, to a different extent, indicative of this mesic to dry-mesic transition trend. However, the exact boundary between the "moister" and "drier" beech-magnolia forests is not easy to establish: both types tend to fuse one into another forming a series of transitional seres with either

one or another set of features being predominant. For instance, although the Port Hudson assemblage has floristically much in common with the forests of the mesic to dry-mesic division – most likely because of the considerable drop in depth of the loess mantle south of the Saint Francisville - it also shares certain important floristic features with the forests developed on the deep-loess deposits throughout the rest of the Mississippi Bluff. To establish this boundary, as well as the one between the "shallow-loess" and "thin-loess" forest types, the distribution and dynamics patterns of certain edaphic indicators will be discussed and analyzed in this Chapter.

The fifth forest type developed on the marginally deep (4 meters or less) or shallow loess mantles underlain by the terrace and valley-train alluvial deposits and overlaid by slowly drained soils. It was found mostly south from the Port Hudson area in Baton Rouge and Ascencion Parishes of southeastern Louisiana. It appears that the same forest type covered most of Macon Ridge in northeastern Louisiana as it is suggested by the species composition of the tiny remnants of the early-successional growth sprinkling here and there on the surface of this generally deforested area. Unlike other shallow-loess forest types, this one is characterized by high importance of moisture-loving and bottomland species. It contains not only those bottomland-centered species which are typical in the deep-loess

section but also some others which are uncommon for or absent from the high portion of the Mississippi Bluff.

The reason for the high importance of the moisture-loving components in this forest type seems to be related to the fact that the terrace and alluvial deposits, which underlay the loess in these areas are rich in silt and clay. Thus thinning of the loess mantle over such deposits does not result in the establishment of the increasingly more xeric and nutrient-deficient edaphic regimes as it the case in the areas underlain by the Citronelle but instead leads to the development of more clayey and slowly permeable soils whose structure and properties emulate to some extent those of the bottomland and flatwoods formations.

The Moist-Mesic to Mesic Forests of the Mississippi Bluff and Chicot Lake Area

Apart from the shade-tolerant dominants, the canopy stratum of mesic to moist-mesic forests is found to contain 42 accessory tree species. This is a total number of species from the aggregate sample area of 5.35 ha which included the 7 late-successional assemblages of the Loess Bluff (excluding the Port-Hudson area). The beech-magnolia stand managed by the Louisiana State Arboretum and the lake-slope assemblage from the Chicot State Park, although standing somewhat apart, are also related to this category because they more closely match the basic features of the Bluff forests than those of any other loessial forest type.

Among all the light-dependent tree species, sweetgum (*Liquidambar styraciflua*) is worth of special reference as one of the key, "formational" components of the moist-mesic to mesic forest type. It achieves the dominant status in three out of five late-successional stands of the deep-loess section of the Mississippi Bluff and in the both stands of the Chicot Lake area. After sweetgum, the most widespread and frequent accessory associates throughout the mesic to moist-mesic section of the Loess Hills region are water oak (*Quercus nigra*), cherrybark oak (*Q. pagoda*), bottomland chestnut oak (*Q. michauxii*), Shumard oak (*Q. shumardii*), tulip tree (*Liliodendron tulipfera*), white ash (*Fraxinus americana*), bitternut hickory (*Carya cordiformis*), pignut hickory (*C. glabra*) and, more locally, winged elm (*Ulmus alata*). Throughout the moist-mesic to mesic section of the Loess Hills Region these nine "core" species, aggregately coined in this work as Group 1, form the bulk of the accessory growth responsible for about a quarter of the canopy structure, with the lowest extreme in the LSA stand (22.3%) and a peak in the Chicot lake-facing slope forest (34.6%).

Another group of accessory species of the moist-mesic to mesic beech-magnolia forest (coined hereafter aggregately as Group 2) such basswood (*Tilia americana*), white oak (*Q. alba*), black cherry (*Prunus serotina*), sassafras (*Sassafrass albidum*), cucumber magnolia

(*Magnolia acuminata*), sycomore (*Platanus occidentalis*), sugarberry (*Celtis laevigata*), southern sugar maple (*Acer barbatum*) and boxelder maple (*A. negundo*), red mulberry (*Morus rubra*), red elm (*Ulmus rubra*), and American elm (*U. americana*) are recognized by more sparse distribution habit. These taxa are generally present in the majority of 1 ha samples but in most cases their frequencies are somewhat or essentially lower than those of the "core" accessory species. Few typically midstory specialists as American hornbeam (*Carpinus caroliniana*) and Eastern hophornbeam (*Ostrya virginiana*) which are present in small numbers in the canopy stratum of almost every 1 ha site can also be related to this category.

The aggregate shares of the Group 2 taxa range greatly between sites east and west of the Mississippi River - from 17.8% to 18,7% in the Mississippi Bluff to 5.0% - 5.5% in Chicot Lake area. This reflects a rather impoverished nature of the western moist-mesic assemblages in terms of species numbers and population densities of the Group 2 components. This does not come as surprise since Group 2 includes many moisture-loving species which appear to depend - in part or in a rather strong way - on the depth of the loess deposits thus exhibiting a rather pronounced Bluff-centric pattern of distribution.

About 13 to 15 species of trees found in the canopy of the moist-mesic to mesic forests can be qualified as rare,

scarsely distributed or highly localized taxa, otherwise coined here collectively as Group 3. Related to this Group were tree species registered in the canopy of one or few but in any case in less than a half of the surveyed sites such as honey locust (*Gleditsia triacanthos*), pyramide magnolia (*Magnolia pyramidata*), bigleaf magnolia (*M. macrophylla*), hercules-club (*Zanthoxylum clava-herculis*), Durand oak (*Quercus durandii*), chinquapin oak (*Q. muehlenberggi*), black wallnut (*Juglans nigra*), blackgum (*Nyssa sylvatica*), black willow (*Salix nigra*), pecan (*Carya illinoensis*), mockernut hickory (*C. tomentosa*), snagbark hickory (*C. ovata*), and persimon (*Diospyros virginiana*). All but one species (snagbark hickory) were registered in the deep-loess, moist-mesic forests of the Mississippi Bluff. Two very common understory to midstory trees, sugarleaf (*Simplocos tinctoria*), and flowering dogwood (*Cornus florida*), can be also, technically speaking, included in the category of rare canopy trees because they are known reach the overstory stratum only in one or two of the Bluff Escarpment sites.

The scarcity of these species involves a broad spectrum of reasons. Pyramid magnolia (*Magnolia pyramidata*), hercules-club (*Zanthoxillum clava-hercules*) and Durand oak (*Q. durandii*) are genuinely rare components of the Coastal flora. The sparse distribution of such species may be based on their genetic inability to build up

large populations combined with their high vulnerability to competition. Most of the other species, however, can be called "rare" only in a restricted sense which implies that the Loess Hills are but peripheral area of their distribution. Such species marginally extend into the Loess Hills from the other habitats or regions where they are typically more common or may be even structurally important. Some cases may involve a bioclimatic explanation. As stated above, black walnut (*Juglans nigra*), for instance, is a north-centered species with only marginal populations in the forests of the subtropical latitudes. Some species infiltrate to the Loess Hills from the different geological regions. One of such "marginals" is, for instance, chinquapin oak (*Q. muehlenbergii*) which is centered in the forests developed on the highly calcareous substrates of the Interior Plateaus (Braun 1950; Bryant et al. 1993).

The vast majority of the species which tend to be "rare" in the loessial forests are centered in the edaphically unsimilar habitats and forest types. Such components as pecan (*Carya illinoensis*), green ash (*Fraxinus pensylvanica*) and black willow (*Salix nigra*) represent the "rearguard" populations of the hydrophytic flora which extends into ravines of the Mississippi Bluff from the adjacent bottomland habitats. Other relatively rare trees of the moist-mesic section are ecologically

linked with the various dry upland habitats or non-loessial mesic forests developed on the well-drained sandy substrates throughout the rest of the Coastal Plain. Within the Loess Region the species of this subgroup tend to have the highest diversity in the peripheral areas underlain by the relatively thin loess deposits. Only some of them such as blackgum (*Nyssa sylvatica*), mockernut hickory (*Carya tomentosa*), snagbark hickory (*C. ovata*), and bigleaf magnolia (*Magnolia macrophyla*) were found in the late-successional ravine forests in the Mississippi Bluff. Few other moderately drought-resistant species such as southern red oak (*Q. falcata*) and loblolly pine (*Pinus taeda*) also occur in the thick-loess deposits of the Bluff region but – apparently because of their high dependence on sunlight - they are limited here exclusively to the early-successional (especially upland) forests devoid of the beech-magnolia overstory.

The relatively sparse distribution of most of the mentioned species may be, at least in part, explained by their dependence on disturbance. The absolute majority of the "rare" canopy trees reach the highest diversity in the physiographically-disturbed forests of the Bluff escarpment – i. e. in the assemblages characterized by the irregular, broken overstories with the diminished importance of the shade-tolerant taxa. The analysis of the combination of the disturbance regimes and edaphic conditions may explain much

in the distribution of the rare and localized species throughout the Loess Region.

<u>The Closed-Canopy Old-Growth Forests of the Moist-Mesic to Mesic Section</u>

The assemblage of the Louisiana State Arboretum - the only survived representative patch of the physiographically undisturbed old-growth forest — seems to be by far our only clue into the general structural pattern of the early-historical "primeval" forests of the Loess Hills. It is noteworthy that this assemblage indeed appears to be relatively close in structure to the early-historical forests reconstructed for West Feliciana by the Delcourts (1974) — in general features, not in details. The major deviation from the canopy structure of the "conventional" beech-magnolia or beech-magnolia-holly community described by the Delcourts (1974) is, of course, the absence of American holly from the canopy stratum the high population density of sweetgum which ranks here second among the canopy trees in relative frequency (18.0%) and third in relative importance (15.9%).

If to set aside the abundance of sweetgum, other differences will be reduced to the inconspicuous details. The ratio of the dominant and accessory species in the canopy of this forest represents a relatively close match to the early-historical forests described by the Delcourts (1974). Sixteen species of the accessory light-dependent tree species (excluding sweetgum) make up 27.4% of the

Louisiana Arboretum forest's canopy structure. The most frequent accessory associates in the LSA stand are water oak (*Quercus nigra*), tulip tree (*Liliodendron tulipfera*), cherrybark oak (*Q. pagoda*), and winged elm (*Ulmus alata*), with four other species - bottomland chestnut oak (*Q. michauxii*), white ash (*Fraxinus americana*), bitternut hickory (*Carya cordiformis*), and pignut hickory (*C. glabra*) - being represented by slightly lower population densities. The general assortment of the major accessory taxa (Group 1) registered in the LSA stand is characteristic for the late-successional assemblages throughout most of the deep-loess section. But their aggregate relative importance (22.3%) in the Arboretum assemblage is lower than in any other sizable late-successional stand sampled within this research project.

The species of the second and third groups are represented in the LSA stand by a conspicuously impoverished, compared to the Bluff stands, assortment which includes sassafrass (*Sassafrass albidum*), basswood (*Tilia americana*), red elm (*Ulmus rubra*), white oak (*Quercus alba*), sugarberry (*Celtis laevigata*), red mulberry (*Morus rubra*) and mockernut hickory (*Carya tomentosa*). With the exception of sassafrass, every of these associates is represented in one-hectare sample of the LSA stand by only a single canopy-size individual. This leaves for the species of the second and third group only 5.7% of the

canopy structure - the value that is also lower than in any other mature forest sampled within this research in the Loess Hills. An exceptionally mature state of this old-growth forest might be one of the possible explanations for the low importance and unit diversity of the light-dependent accessory species. Indeed, missing in this assemblage are many species of highly light-demanding canopy trees that are normally present in more disturbed stands. With only 19 species of canopy trees registered within 1 hectare sample, the Arboretum stand exemplifies the beech-magnolia site with the lowest diversity of the overstory stratum of all those surveyed in this research.

A somewhat impoverished nature of the LSA accessory assortment can be also interpreted from the standpoint of a broader biogeographic perspective. The comparative analysis of the eastern and western late-successional assemblages indicates the general biogeographic fact that the mesic slope forests on the loessial lands west of the Mississippi River, both disturbed and relatively undisturbed alike, tend to lack several second-order accessory associates and most "rare" trees found in the forests of the Mississippi Bluff. In this regard the Arboretum assemblage is, perhaps, not quite identical to the "classical" Bluff communities reconstructed by the Delcourts on the other side of the Mississippi River, in West Feliciana Parish.

On the other hand, the importance of the moisture-loving edaphic indicators represented by sweetgum (*Liquidambar styraciflua*), water oak (*Quercus nigra*) and bottomland chestnut oak (*Q. mischauxii*), along with the presence of other bottomland-centered taxa such as red elm (*Ulmus rubra*), sugarberry (*Celtis laevigata*) and red mulberry (*Morus rubra*), make the assemblage of the Louisiana State Arboretum remarkably close to the moist-mesic forests developed within the deep-loess section of the Mississippi Bluff. This similarity is further augmented by the absence of the most edaphic indicators characteristic for the excessively well-drained soils formed on the shallow loess mantles. Of these, only mockernut is present in the canopy of the LSA stand. But this species was also found in some assemblages of the Mississippi Bluff and thus should not necessarily be considered as an exclusive indicator of xeric and subxeric forests.

The relatively modest share of the light-dependent accessory species in the LSA stand's canopy structure seemed to be indicative of the slow rate of natural disturbance associated, perhaps, with the predominantly "death-and-fall" nature of the gap dynamics of this physiographically-stable, never-cut forest. The recent tornadoes created favorable conditions for the reproduction of the light-demanding accessory species but the result of

this disturbance will affect the canopy stratum of the LSA stand only in few decades from now when some of the currently established saplings turn into adult trees and reach the overstory. The size of the sample population of any of these accessory species is separated from that of any of three dominant species by a big quantitative gap. For instance, the relative importance of water oak (*Quercus nigra*), - the most important accessory tree in the canopy of the Arboretum assemblage which ranks forth in the species list - is only 5.3%, i. e. by 10.6% less than that of sweetgum which ranks third and by 13.2% less than that of magnolia which ranks second. Consequently, the sample population of the most important accessory species in the LSA stand is 3 times smaller than that of the least important dominant species - either sweetgum or magnolia.

The big statistical break in the population densities between the dominant and accessory taxa is also indicated in the model of the early-historical forests reconstructed by the Delcourts (1974). Apparently, this structural phenomenon is a general feature of all closed-canopy old-growth forests. With the exception of the Port Hudson site, it is not generally the case for the more disturbed stands where the transition from the dominant to the accessory status tends to be relatively gentle and gradual.

The Second-Growth Closed-Canopy Late-Successional Forests

Related to this category are the late-successional assemblages of the Bluff Experimental Forest and Port Gibson site, and - in part - a predominantly old-growth assemblage developed on the lake-facing slope of the Chicot State Park - because it includes relatively large sections (from 20 to 30% of the sampled area) of the secondary forest. Effects of anthropogenic disturbance are statistically "visible" in some sections of this site. Although this part of the discussion is centered around moist-mesic to mesic late-successional forests, some comments should be made about the Port Hudson assemblage - because of its considerable floristic similarity with the other moist-mesic to mesic Bluff sites.

Most of the secondary-growth beech-magnolia forests found throughout the Loess Hills Region are typologically similar to the LSU stand in a sense that they originated in the place of the closed-canopy physiographically-undisturbed old-growth forests. However, one of the important distinctive features of the second-growth late-successional forests is that, although being dominated by beech and magnolia, they are also characterized by the increased population densities of certain light-dependent species indicative of the former anthropogenic disturbance. Their populations in the second-growth beech-magnolia forests represent left-overs of the early-successional

populations which regenerated on the cleared areas following destruction of the original forest cover. Throughout the deep-loess section the most vigorous response to the historical clearing practices is shown by sweetgum (*Liquidambar styraciflua*) and six "core" accessory species (Group 1) - water oak (*Quercus nigra*), cherrybark oak (*Q. pagoda*), Shumard oak (*Q. shumardii*), tulip tree (*Liliodendron tulipfera*), white ash (*Fraxinus americana*), and winged elm (*Ulmus alata*) which is indicated by the essentially higher population densities of these trees in the early-successional forests and secondary beech-magnolia forests.

This group of species can be subdivided into three categories: the species which tend to increase in population densities in the early-successional forests but show no increase from the old-growth to the second-growth beech-magnolia forests; the species which show a well-profiled two-step increase from the old-growth to the second-growth beech-magnolia forests and from the latter - to the early-successional forests; the species whose population densities increase from the old-growth to the second-growth beech-magnolia forests but show no or little increase from the second-growth forests to the early-successional forests.

The first category is represented by sweetgum and water oak. In the early-successional forests throughout the

southern section of the Mississippi Bluff these two species demonstrate some of the most "enthusiastic" responses to the anthropogenic disturbance, particularly in the ravines. The pattern typical of the early-successional ravine forest is exemplified by the assemblage sampled along the southern end of the Natchez Trace. Here sweetgum and water oak are represented, respectively, by 67 and 41 canopy-sized individuals per 1 hectare and make up 23.4% and 14.8% of the canopy structure. In the upland forests of the Mississippi Bluff these two species retain the dominant role but typically rank second and third after cherrybark oak. A good illustration of this trend comes from the upper-slope to hilltop assemblage of Magnolia Glen preserve in the Tunica Hills where water oak and sweetgum were represented by 29 and 26 trees per 1 hectare and made up respectively 12.0% and 10.8% of the canopy structure.

On the other hand, sweetgum and water oak show no increase in the second-growth closed-canopy beech-magnolia forests as compared to the available old-growth stands. In the Bluff Experimental Forest and Port Hudson area where sweetgum makes up respectively 6.6% and 5.9% of the canopy stratum, which are some of the lowest population densities of all sites sampled in this research. Port Gibson is about the only closed-canopy beech-magnolia site where *Liquidambar* makes up 10.6% of the canopy structure, approaches the status of the co-dominant canopy taxon. The

lake-facing slope of Chicot State Park has, of course, the second largest *Liquidambar* canopy population but the success of sweetgum in this forest can be only partially explained by anthropogenic disturbance since it has high importance not only in the formerly clearcut sections but also in seemingly old-growth areas.

In fact, the second-growth beech-magnolia stands tended to even have lower population densities of sweetgum (both in absolute numbers and relative values) than the only two available fully old-growth forests. This was particularly true for water oak which decreased in relative importance from 5.3% in the LSA stand to 2.6% in Port Hudson and Chicot State Park, 1.8% in Port Gibson and 1.6% in the Bluff Experimental Forest. The general impression is that both species somewhat stagnate (especially water oak) in the second-growth closed-canopy communities. Probably more sampling is needed to rationalize these dynamics for the observed variation may be random in nature. For instance, the forest managed by the Louisiana State Arboretum is likely to represent (first of all, due to the abundance of sweetgum) an old-growth stand with somewhat "anomalous" structure.

Nevertheless, some explanations may be presented. For water oak the decrease in population densities was suggested along the latitudinal gradient from Port Hudson to Vicksburg. This, however, does not explain why two

southern second-growth (or partially second-growth) sites, Port Hudson and Chicot State Park also had somewhat smaller *Q. nigra* populations than the southern old-growth sites. As for sweetgum, it does not show any latitudinal variation in the southern Loess Hills. The most reasonable "successional" explanation of the sharp decrease of the overstory population densities of sweetgum and water oak from the early-successional to the second-growth beech-magnolia forests could be related to the high mortality rates of the canopy trees of these species at the early stages of the successional process - soon after both *Liquidambar* and *Quercus nigra* reach the dominant status in the canopy. Finally, one should not overlook the fact that the exceptionally large populations of sweetgum and water oak tend to exist in the early-successional forests developed on the formerly cultivated lands such as Natchez Trace Forest.

The successful establishment of these trees in such environmentally modified areas is probably related to the fact that here they could avoid an early checking influence of the shade-tolerant species and, perhaps, some other competitors. By contrast, all second-growth beech-magnolia forests originated in places where cleared areas were left for fallow after clearcuts and the ability of the shade-tolerant species to self-regeneration was not undermined by long cultivation episodes. Perhaps, the early start of the

regenerating beech-magnolia growth in such areas may have impeded the reproduction of some light-dependent species such as sweetgum and water oak which otherwise would have the dominant components of the early-successional overstory. The latter scenario, however, does not address the question why many other accessory species, some of them apparently even more light-dependent than swetgum and water oak, tend to show higher population densities in the second-growth than in the old-growth forests.

Two other species - cherrybark oak and Shumard oak tend to demonstrate two-step increase. They have moderately higher population densities in the second-growth beech-magnolia forests as compared to the old-growth ones. Their relative importance increases, for instance, from respectively 2.5% and 1.7% in the LSA stand to 8.6% and 3.1% on Chicot Lake Bluff slope, as well as 3.9% and 3.5% in the Bluff Experimental Forest. The population densities of cherrybark oak then sharply increase in the early-successional forests reaching 15.3% in the uplands of the Tunica Hills and 14.7% in the ravine forests along the southern end of the Natchez Trace. The population densities of Shumard oak increase rather abruptly only in the upland early-successional forests reaching 9.0% in the Tunica Hills.

Finally, the broad assortment of light-dependent species such as tulip tree, white ash, and, to the lesser

extent, winged elm and black cherry tend increase in importance in the second-growth beech-magnolia forests as compared to the old-growth ones but demonstrate essentially no or very little increase in population densities from the second-growth beech-magnolia forests to the early-successional assemblages.

The "Anthropogenic" Species. Five "core" accessory taxa such as cherrybark oak, Shumard oak, tulip tree, white ash, and winged elm are dependent on the anthropogenic disturbance to the extent that they are more than any other species of the beech-magnolia forest deserve to be termed "anthropogenic". On the other hand, they do not seem to show any response to the perpetual small-scale natural disturbance such as the erosion of the loess mantle. The old-growth forests, both closed-canopy and physiographically-disturbed ones, are characterized by the low to modest aggregate sample population sizes of these taxa - ranging from 10 individuals per 1 hectare in the Tunica Hills to 18 in the Louisiana State Arboretum site. In the second-growth beech-magnolia forests their aggregate canopy populations considerably expand - to 35 individuals per 1 hectare in the Port Hudson assemblage and 48 individuals per 1 hectare in the Bluff Experimental Forest. The shares of the individual species vary depending on site but usually the largest populations are formed by tulip tree which "expands" from 5 canopy trees per 1 hectare on

both old-growth sites to 12 in Port Hudson and 20 in the Bluff Experimental Forest where it makes one of the second-rank dominant species. Tulip tree is followed in the Bluff Experimental Forest and Port Hudson site by white ash and, secondly, cherrybark oak. By constrast, on the lake-facing slope of the Chicot State Park, cherrybark oak and, secondly, Shumard oak, winged elm and bitternut hickory were more important than other accessory species, while tulip tree, surprisingly enough, was absent.

In the Tunica Hills old-growth forest, the relative scarsity of *Quercus pagoda*, *Q. shumardii*, *Fraxinus americana*, and *Ulmus alata*, along with relatively modest frequency of *Liliodendron tulipfera* contrast strongly with the abundance of these species on the upper slopes and hilltops which have been clearcut in the 1950s. Their aggregate canopy population on 1 ha exemplary plot of the upper-slope to hilltop secondary formation was eight times higher than in the sample area of the same size within the old-growth section of the slope gradient. Cherrybark oak, Shumard oak, and tulip tree - along with water oak and sweetgum - today reach the status of the dominant species in the Tunica Hills uplands.

Hickory Dynamics. Among the major accessory species, hickories - pignut (*Carya glabra*) and bitternut (*C. cordiformis*) - are perhaps subject to more pronounced local variation in population densities than any other taxon.

Typically, they shows very moderate response to disturbance. Within the moist-mesic to mesic section, the population densities of both *Carya* species may vary anywhere from 1 canopy specimen per 1 ha (the Bluff Experimental Forest) to 11 specimens per 1 ha (Chicot Lake Bluff).

In overall, it appears that the variation in *Carya* densities in the modern secondary-growth stands depends, to a large extent, on the combination of the edaphic conditions and disturbance regimes. Depending on the nature of the edaphic situation, anthropogenic disturbance may (or may not) contribute to the increase of the population densities of one or another *Carya* species. Throughout the deep-loess section bitternut hickory generally tends to have higher population densities than pignut. It has a highest relative importance (8.6%) in the second-growth beech-magnolia stand in the vicinity of Port-Gibson which is the only site within the moist-mesic to mesic section of the edaphic gradient where one of the hickories approaches the status of the dominant species. Importance of *C. glabra* seems to increase with the thinning of the loess mantle south of Saint-Francisville and reaches its peak in the beech-magnolia forest of the Port Hudson area where this taxon largely replaces *C. cordiformis*.

The variation in edaphic conditions and disturbance regimes does not seem to explain satisfactory all the

variation in *Carya* population densities. Some areas of the beech-magnolia region appear to be - for whatever reason - poorer in hickories than the others. The very low importance (0.4%) of hickories in the canopy stratum of the Bluff Experimental Forest, for instance, may be indicative of their low importance in the original old-growth forests or, perhaps, the selective cuttings in the early 20th century.

Dynamics of Swamp Chestnut Oak. The last component of the Group 1, bottomland chestnut oak (*Quercus michauxii*), in general, appears to be the most "conservative" of all major accessory species. It shows a relatively moderate positive response on the anthropogenic disturbance illustrated by a rather gentle increase from 3 canopy specimens per 1 ha (1.5%) in the closed-canopy old-growth LSA stand to 7-9 specimens per 1 ha (2.9%-3.6%) in the secondary-growth beech—magnolia forests. The highest relative importance is achieved by *Q. michauxii* in the assemblage of Chicot State Park (6.3%) where it is likely to be stimulated by the hydrological disturbance.

Interestingly enough, bottomland chestnut oak appears to be a very marginal contributor to the most early-successional stands with the only exception of the upper-slope to hilltop assemblage of the Tunica Hills. Many early-successional forests of the Mississippi Bluff tend to have far lower densities of this oak than the late-

successional forests. The early-successional Natchez Trace assemblage, for example, featured only 1 canopy tree of *Q. mischauxii* per 1 hectare. Given its relatively sluggish response to disturbance, general dissociation with the most early-successional assemblages and moderate shade-tolerance, bottomland chestnut oak appears to exemplify one of the indicator species of the late-successional loessial forests.

Dynamics of the Species of Group 2. The canopy populations of a large portion of the more sparsely distributed accessory species which belong to the Group 2 such as *Morus rubra, Celtis laevigata, Ulmus rubra*, and *Platanus occidentalis* do not increase or increase only a little in the second-growth beech-magnolia forests. Consequently, their relative importance in the second-growth forests (due to the general increase of the canopy tree numbers), in fact, tends to be even lower than in the closed-canopy old-growth forests. Some species such as cucumber magnolia (*Magnolia acuminata*), American basswood (*Tilia americana*), sassafras (*Sassafras albidum*), boxelder maple (*Acer negundo*) do have larger population densities in the northern second-growth beech-magnolia forests but this seems to be more a result of the latitudinal effects (see discussion in the Chapter 7).

Among the second-order accessory trees, black cherry (*Prunus serotina*) is, perhaps, the only species which

appears to show a rather strong positive response to the anthropogenic disturbance. Its population densities tend to increase from 1-2 canopy trees per 1 ha in the old-growth forests to 6-7 overstory specimens in the second-growth beech-magnolia assemblages.

Rare and Sparsely Distributed Species. The species of the Group 3 are regularly found in the canopy of the second-growth closed-canopy forests but their diversity per one-hectare unit area is low. Typically, they are represented by 1-2 species per site - by chinquapin oak (*Quercus muehlenbergii*) and exceptionally tall persimmon (*Diospyros virginiana*) in the Bluff Experimental Forest, Durand oak (*Quercus durandii*) in the Port Gibson site, and snagbark hickory (*Carya ovata*) and hercules-club (*Zanthoxylum clava-herculis*) on the lake-facing slope of Chicot State Park. The relatively low diversity of the rare and sparsely distributed species in the second-growth closed-canopy assemblages is probably indicative of their relatively low population densities in the predating old-growth forests. It is noteworthy, however, that none of the above-mentioned species was found in more than one second-growth closed-canopy stand. This probably suggests that closed-canopy beech-magnolia forests are, in fact, rich in locally rare tree species but high diversity of such taxa can be discerned only within much larger-scale units.

The Physiographicly-Disturbed Forests of the Bluff Escarpment

The assemblages developed under the influence of the perpetual small-scale gap dynamics in the highly eroded steep-slope ravines of the Bluff escarpment are quite different from any type of closed-canopy beech-magnolia forests which are not subject to such disturbance. The relatively low relative importance of the shade-tolerant components (36.0%) in old-growth assemblage of Magnolia Glenn preserve exemplifies the fact, mentioned already, that the physiographically-disturbed late-successional forests tend to have more sparse populations of the shade-tolerant dominant species and the more mixed composition of the canopy stratum. The same trend, in reference to beech only, is also displayed by the heavily eroded steep-slope forest in the Anderson-Tully site north of the biogeographic limit of southern magnolia. Consequently, the Tunica Hills old growth and, to the lesser extent, the Steep Bluffs forest represent, perhaps, the two most heterogeneous late-successional assemblages observed in the Loess Region.

The Dominant Association. The ravine assemblage of Magnolia Glenn preserve is dominated by beech-sweetgum-magnolia-water oak association which aggregately makes up 59.8% of its canopy structure. The structural heterogeneity of this old-growth forest is maintained through the perpetual disruption of the canopy stratum by landslides.

The physiographic disturbance leads to a very complex disturbance picture which represents a mosaic of the successional plots at the different stages of the successional process. In this dynamically changing forest landscape, some sections, especially on the relatively gentle slopes, may escape physiographic damage for decades or, perhaps, hundreds of years, whereas other areas and spots may be affected by erosion repeatedly within relatively short periods of time.

Between these two poles, there is a sequence of sites and spots once affected by land sides, where the natural successions continues uninterrupted for many years. In such sites, the upper stratum is initially claimed by the successional light-demanding species. Later on, because they are more tolerant of shade, beech and magnolia tend to enter the understory and midstory under the successional trees. In few decades from now, in the absence of repeated disturbance, this trend leads to the development of the mixed overstory in which the shade-tolerant trees are gradually replacing the shade-intolerant ones.

In these peculiar conditions the overall dominant role of the "conventional" shade-tolerant taxa (beech and magnolia), understandably, decreases in favor of those successional taxa that are able to use the space and time in the most efficient way, i. e. are capable of winning the competition in most of the gaps and grow fast. The dominant

status of sweetgum and water oak in the Tunica Hills old growth is maintained via the quite unsimilar successional strategies. In the moist conditions of the Magnolia Glen ravines, like in the LSA stand, much of the reproductive success of sweetgum can be explained by its ability to resprout from the base stumps or roots. It suggests why, with the relatively insignificant understory population compared to the other species, such as water oak, beech or magnolia, sweetgum is able to maintain high midstory and overstory populations and efficiently recapture space in the newly formed gaps. With the population density of 29 canopy trees per 1 hectare and the relative importance of 18.5%, sweetgum is the second most important species in the overstory of Magnolia Glen.

An argument could be advanced suggesting the general similarity of the Louisiana State Arboretum and Magnolia Glen assemblages in terms of *Liquidamabar* population sizes. If compared, the absolute and relative values can indeed look like a close match, but there is a rather remarkable difference in spatial distribution. Unlike in the assemblage of the Louisiana State Arboretum where most the of sweetgum trees were found to have been centered within the lower section of the slope gradient, the sweetgum population in Magnolia Glen preserve tended to have been distributed relatively evenly along the slope gradient, from the ravine bottoms to the hilltops.

Reproductive success of the water oak, on the other hand, may be in part related to the fact that this species is able to give very large harvests of acorns exceeding in this respect any other oak species which occur in the Blufflands. Besides, acorns of water oak may germinate and develop into small saplings even under closed-canopy conditions (except under beech and magnolia trees). It appears that both seedlings and saplings of water oak are able to persist for some time in the understory or at the ground level waiting for some kind of disturbance event to take place and make a break in the canopy. Both the high reproductive activity and modest shade-tolerance, at least at the initial stage of its life, enable water oak to accumulate relatively large understory populations and thus acquire some advantage over more sparcely- or more spotty-distributed species wherever and whenever the canopy stratum becomes subject to some disruption.

In the conditions of the permanent small-scale disturbance, this strategy proves efficient. The old-growth forest of the Magnolia Glenn Preserve is the only late-successional community studied within this project where water oaks attains the status of the third-order dominant species. One-hectare sample of this forest can boast 14 canopy individuals of *Q. nigra* responsible for 9.7% of the overstory structure. By contrast, the 1 ha sample of beech population in this forest (36 canopy-size individuals) is

by 32% smaller than that of the Louisiana State Arboretum stand and from 1.8 to 2.2 times smaller than 1 ha sample populations from any of the second-growth beech-magnolia assemblages.

Of particular interest is the surprisingly low (9.2%) importance of evergreen magnolia. The Tunica Hills area is located in the southern section of magnolia range, so the relative scarcity of this tree in Magnolia Glenn has nothing to do with latitudinal variation. Initially I supposed that this phenomenon could be explained by some features of the Tunica Hills microclimate. In the winter time, I thought, the exceptionally deep and narrow ravines of this area could have acted as reservoirs of the cool stagnant air that would have complicated the reproduction of *Magnolia grandiflora*. However, the structure of the subcanopy strata of Magnolia Glen assemblage shows no sign of such suppression. In fact, the understory of the Tunica Hills old growth is charaterized by some of the most dense populations of the magnolia in the Loess Hills. This led me to the conclusion that the relatively sparse population of Magnolia in Magnolia Glen old growth forest is maintained through the physical removal of the large-size *Magnolia* trees by the physiographic disturbance.

The Role of the Bottomland Components. The physiographically-disturbed assemblages of the Mississippi escarpment are characterized by a remarkably high

importance of the bottomland-centered components which typically play a rather marginal role in the "conventional", closed-canopy beech-magnolia forests. In the moist ravines of the Tunica Hills 7 species of the bottomland-centered trees such as sycomore (*Platanus occidentalis*), sugarberry (*Celtis laevigata*), boxelder maple (*Acer negundo*), American elm (*Ulmus americana*), red elm (*U. rubra*) and red mulberry (*Morus rubra*) make up aggregately 14.2% of the canopy structure as opposed to 2.0% in the Arboretum assemblage and 4.9% in the Bluff Experimental Forest.

In the physiographically-stable beech-magnolia forests the frequencies of these taxa (with the exception of boxelder maple which could be relatively important in the moist ravines) are commonly not higher than 1-2 specimens per 1 hectare - apparently because of their dependence on sunlight which is deficient in the closed-canopy assemblages. But the moist, eroded ravines of the Tunica Hills and Steep Bluffs areas appear to offer an essentially more favorable scenario. Each of these two site samples feature, for instance, 7 canopy-size individuals of sycamore and 4 individuals of sugarberry (with 13 subcanopy *Celtis* specimens being about ready to enter the overstory in the Tunica Hills). These are rather remarkable population sizes because the population densities of sycamore and sugarberry in the closed-canopy forests - due,

perhaps, to their strong dependence on sunlight - normally do not exceed one specimen per one hectar.

In the ravines of the Tunica Hills Escarpment, sycamore makes up 5.2% of the canopy stratum and ranks fifth in the list of the overstory species thus being the most frequent accessory component. The bottomland-centered elms (*Ulmus rubra* and *U. americana*) likewise peak in the steep-slope forest of Magnolia Glen preserve where they are represented by 5 canopy-size individuals responsible for 2.7% of the overstory structure. Red mulberry is represented by 2 canopy-size individuals in both Magnolia Glen and Bluff Experimental Forest assemblage samples but the number of the subcanopy specimens of *Morus rubra* that are about to enter the overstory in the disturbed sites in the Tinica Hills and Steep Bluffs forest sample is higher than in any other late-successional site.

The Role of Rare Tree Species. The important sign of the increased heterogeneity of the physiographically-disturbed forests is the large assortment of the rare, sparsely distributed and highly localized canopy trees species. In the canopy of 1 ha sample of the Tunica Hills old growth I found 5 rare tree species - honey-locust (*Gleditsia triacanthos*), mockernut hickory (*Carya tomentosa*), pyramid magnolia (*Magnolia pyramidata*), hercules-club (*Zanthoxylum clava-herculis*), black walnut (*Juglans nigra*), and black willow (*Salix nigra*). Black

willow was not registered in the sample plots but twice was found just next to them growing alongside with the typical mesic species. The trunk diameter of one of such willows reached 49 cm, and it developed a rather unusual for this species round, somewhat umbrella-like crown, a notable adaptation to the conditions of the old-growth mesophytic forest.

The remarkable heterogeneity of the Tunica Hills forest was further accentuated by the fact that its lower strata additionally contained four potentially canopy species that were not found in the overstory - chinquapin oak (*Quercus muehlenbergii*), overcup oak (*Q. lyrata*), and green ash (*Fraxinus pennsylvanica*) in the midstory and white oak (*Q. alba*) and willow oak (*Q. phellos*) in the understory. The canopy of the Steep Bluffs assemblage also contained 5 localized and rare overstory species - bigleaf magnolia (*Magnolia macrophylla*), blackgum (*Nyssa sylvatica*), pecan (*Carya illinoensis*) and, again, chinquapin oak and black walnut.

I have already made a special reference to the possibility that the presence of some of these species in the Tunica Hills and Steep Bluffs area may be in part a function of the special qualities of the local soils or microclimatic conditions. The endemic occurrence in Tunica Hills of such edaphic indicators as chalk maple (*Acer leucoderme*) and American smoketree (*Cotinus obovatus*)

suggests, for example, that the local soils might be especially rich in calcium. This, in turn, could, perhaps, explain the ocurrence in the Tunica Hills of such rare local endemic as pyramid magnolia which was not found anywhere else in the Loess Region. The unique occurence of bigleaf magnolia in the Steep Bluffs may similarly give a hint at some specific qualities of the local soils that could accomodate this typically "non-loessial" species.

Six species came to the escarpment forests from the edaphicly marginal habitats - either from the alluvial bottomlands of the Mississippi River Valley or from the xeric upland forests east of the Loess Region. On the other hand, nearly all rare and localized species on both sites were found in old gaps and various favorable expositions which suggests that it is the perpetual disturbance that seems, after all, to play a role of the common denominator.

Of the mentioned 12 rare and localized canopy species registered in the overstory and midstory, 9 species (except mockernut hickory and chinquapin oak) were found only in physiographically-disturbed late-successional forests. Interestingly, all cited bottomland species (pecan, green ash, black willow, overcup oak, and willow oak) were confined exclusively to the late-successional mesic forests with disturbed canopies. One of the components of this assortment, pecan, is a regular component of the early-successional ravine forests throughout much of the

Mississippi Bluff but the Steep Bluffs is the only late-successional assemblage in which it appears at the level of 1 ha site visibility.

Extra-Sized Midstory Specialists. The canopy strata of the physiographically-disturbed escarpment sites are also characterized by the largest assortments of the extra-sized midstory specialists. Steep slopes, uneven, broken nature of the canopy and frequent gap formation create here a multitude of favorable expositions in which midstory trees may compete with the overstory taxa more effectively than in the closed-canopy forests. Exceptionally large individuas of *Carpinus* and *Ostrya* generally tend to more frequent in eroded, steep-slope ravines of the Magnolia Glenn preserve and Steep Bluffs area than in the relatively gentle-slope, closed canopy forest sites. Apart from these two species, the sample of the Tunica Hills forest also features exceptionally large individuals of *Cornus florida*, *Simplocos tinctoria* and *Ilex opaca* which were not found in the more "conventional" beech-magnolia forests. Finally, two other components of the canopy stratum in Magnolia Glen preserve, *Magnolia pyramidata* and *Z. clava-herculis*, could also be related to the midstory specialists although they are representative, perhaps, of a somewhat larger size class that the above-mentioned species. In overall, 6 species of extra-sized subcanopy trees were represented in the canopy of 1 hectare

sample the Tunica Hills ravine forest - compared to only 1-2 species occasionally reaching the overstory in the areas of the same size in the closed-canopy assemblages.

The oversized midstory specialists were typically found in the old gaps, on the steep loessial cliffs or in the ravine bottoms where disturbance and physiography make them more competitive. Most of them did not rival in size the tallest canopy trees but, for the middle-stature trees, they reached conspicuously large sizes. Although most heights were distributed between 14 and 18 meters, some of these components such as hercules-club, pyramid magnolia and hophornbeam attained in the Tunica Hills the size class of full-stature canopy trees rivaling in height the adjacent overstory beeches and sweetgums. The dbh classes of the largest midstory trees found in the Tunica Hills old growth are also worth of reference. Virtually all canopy-sized subcanopy specialists were represented here by the record sizes. The largest American holly was represented here by dbh of 42.2 sm, the largest dogwood - 41.0 cm, the largest hophornbeam - 39.0 cm, the largest hornbeam - 38.1 cm, the largest sweetleaf - 27.5 cm.

Interestingly, with the exception of sweetgum and water oak, most of the "key" accessory mesophytic species do not show any population increase in the physiographically-disturbed forests. For instance, tulip tree and hickories (*Carya cordiformis* and *C. glabra*), which

make up, respectively, 3.5% and 3.9% of the canopy structure in Magnolia Glen old growth, are represented here by the same sample population sizes as they are in the physiographically-stable and largely undisturbed (until recently) assemblage of Louisiana Arboretum. Remarkably, the eroded ravine forest of Magnolia Glen, in fact, proved to have some of the lowest frequencies of cherrybark oak, Shumard oak, white ash and winged elm in the Loess Hills: with the exception of cherrybark, each of these taxa was represented here by only one canopy tree per 1 hectare. Consequently, the aggregate relative importance of the four above-mentioned species accounted for only 3.6% of Magnolia-Glen's canopy structure - constrasting with 8.0% in the canopy of the Arboretum stand. The canopy sample of the Steep Bluffs area has higher population densities of Shumard oak, white ash and, particularly, tulip tree but nearly all this increase comes from the sections which are now under the secondary growth.

This trend indicates that the intensity of the small-scale disturbance regime in the Tunica Hills causes no essential positive influence on the recruitment rates of many "core" accessory trees into the canopy stratum. My hint is that under intensive small-scale disturbance in the moist deep ravines of the Bluff escarpment, tulip tree and four to six other above-mentioned mesophytic trees lose competition in gaps to more moisture-loving and bottomland-

centered species such as sweetgum, water oak, sycamore, sugarberry and boxelder maple.

The larger-scale natural disturbances (caused by hurricanes or fires) would, perhaps, also help some of these species to capture some extra living space even in the old-growth forests but, unlike in Florida hammocks, no such disturbance is known to occur in the Loess Hills communities on a regular basis. Consequently, expansion of their populations is necessarily associated with the human intervention. Only large- to middle-scale clearance of the forest community or colonization of the previously deforested lands may lead to the development of the communities rich in these taxa.

Discussion on the Variation of the Dominant Association in the Moist-Mesic to Mesic Section

Can the ideas of Quarterman and Keever (1962) about the highly mixed and undifferentiated nature of their Southern Mixed Hardwood Forest be confirmed by the data from the forests of the deep-loess section of the Mississippi Bluff and other moist-mesic to mesic sites of the Loess Region? Let us consider their arguments point by point. To begin with, Quarterman and Keever (1962) specifically emphasized the fact that any of their list of 12 potentially dominant species could achieve dominance in any stand with no correlation with any measured environmental factor. This is clearly untrue for the forests of the Loess Region where, as this research

suggests there is a well pronounced subdivision into several forest types based on physiography, edaphic conditions and disturbance.

At least 6 species from Quarterman and Keever's list such as loblolly pine, white oak, red oak, laurel oak, blackgum, and mockernut hickory are absent or unimportant within the deep-loess section of the Mississippi Bluff and generally within the moist-mesic to mesic section of the edaphic gradient. Loblolly pine is about the only one of the above-mentioned species that can be relatively important in some sections of the Mississippi Bluff - but exclusively in the early-successional forests. There are enough statistical data to suggest that two other canopy tree species - water oak and pignut hickory, although being omnipresent and relatively important in the forests of the deep-loess section, do not appear to be stimulated by the "death-and fall" gap dynamics in the closed-canopy late-successional forests to the extent as to even closely approach the population densities of the dominant species. Strangely, Quaterman and Keever did not mention among their "core" species such widespread and characteristic accessory tree species of the Mississippi Bluff as tulip tree, cherrybark oak, bottomland chestnut oak, white ash, bitternut hickory, and winged elm. But these taxa also do not reach the dominant status in the closed-canopy old-growth forests. The intensive gap dynamics of the Bluff

Escarpment section likewise do not affect the population densities of the absolute majority of the "core" accessory species.

It is true that many of the "core" light-dependent species (most of them are not even in Quaterman and Keever's list) such as tulip tree (*Liriodendron tulipfera*), cherrybark oak (*Quercus pagoda*), white ash (*Fraxinus americana*), sweetgum (outside the Escarpment section), and even sassafras (*Sassafras albidum*), which is a species of Group 2, do demonstrate ability to reach or approach the status of the second-order dominant species in the canopy of some late-successional forests within the moist-mesic to mesic section of the Loess Hills Region. But this does not seem confirm the concept of the historical or putative future climax suggested by Quarterman and Keever (1962) because all the forests, in which these taxa shared the dominant status with beech and magnolia, were secondary in origin. The fact that the high importance of these and many other light-dependent species in the canopy of some second-growth beech-magnolia assemblages is a post-clearence phenomenon is strongly suggested by the comparative analysis of their structure with that of the survived old-growth forests, both closed-canopy and physiographicly-disturbed alike, where they are represented in typically modest or relatively low population densities.

The poor ability of nearly all "core" species either to reproduce or maintain high recruitment rates in the modern beech-magnolia forests suggests against the possibility that they could have claimed the status of the dominant species in the early-historical assemblages or will claim it in the putative future climax. Throughout the region, some second-growth late-successional assemblages characterized by somewhat higher importance of certain light-dependent species have already reached the stage at which point the reproduction of these species became suppressed by the regenerated shade-tolerant overstory. If secured from the repeated anthropogenic disturbance, such late-successional stands as those of Port Hudson and Bluff Experimental Forest areas such second-growth formation tend replicate the structure of the original old-growth assemblages in several decades from now. Thus most of the Mississippi Bluff was originally covered undoubtedly by beech-magnolia, not the mixed polydominant forests as suggested by Quarterman and Keever (1962). The SMHF concept must be consequently considered as largely untenable for the forests developed on the deep loess mantles.

Of ten light-dependent "core" species mentioned by Quaterman and Keever, only sweetgum appears to have been potentially capable of reaching the co-dominant status in the undisturbed late-successional forests of the Mississippi Bluff. This gives us an idea of beech-magnolia-

sweetgum association which was not considered by the Delcourts (1974). Still, even in the deep-loess section of the Bluff sweetgum may have achieved the dominant status only within very limited range of habitats, and - most notably - exclusively within the moist-mesic end of the edaphic gradient.

First of all, it appears that sweetgum was, as it continues to be, a very important co-dominant taxon (more important than *Magnolia grandiflora*) in the moist-mesic deep-ravine communities of the Bluff escarpment where intensive erosion of the loess mantle leads to the frequent disruption of the forest canopy by landslides. Secondly, the beech-magnolia-sweetgum association probably occupied the bottoms and perhaps the lower slopes of some deep, ever-moist ravines which were, like ravines of Chicot Lake area, immediately adjacent to more or less broad floodplains of tributary streams and small river that cut through the Blufflands. In such areas, the expansion of sweetgum upslope could have been supported by its relatively large bottomland populations. However, while somewhat different from beech-magnolia or magnolia-beech-holly associations suggested by earlier workers, beech-magnolia-sweetgum association still is a long shot from the "Southern Mixed Hardwood Forest" for no other "core" species seems to be able to show a comparable environmental plasticity.

Throughout the broader interior section of the Mississippi Bluff, away from Escarpment and accessory floodplains, on more gentle slopes sweetgum was unlikely to have maintained the dominant status due to the closed-canopy nature of the late-successional forests and strong development of the shade-tolerant species. I suggest that throughout much of this section the dominant association indeed contained only two species, American beech (*Fagus grandifolia*) and southern magnolia (*Magnolia grandiflora*). American holly (*Ilex opaca*) was likely to have been a co-dominant species only in the forests of the Tunica Hills, West Feliciana Parish, where its importance in the old-growth forests was probably stimulated by some endemic properties of the local soils. Forests dominated by beech-magnolia-holly association occupied only gentle slopes. Intensive erosion of the loess mantle appears to cause a negative effect on recruitment of *Ilex opaca* into the overstory stratum. Holly probably developed especially large populations and was more likely to have participated in the canopy structure on the upper slopes and ridgetops. Ravine bottoms probably harbored essentially smaller populations. It appears that holly-rich forests did not extended much north of West Feliciana Parish. The forests of adjacent Wilkinson County including those of Clark Creek's Area, for example, do not contain any conspicuous evidence of the former abundance of *Ilex opaca*.

As the dominance of *Magnolia grandiflora* decreased northward, its niche in the late-successional forests was gradually recaptured by *Fagus grandifolia*. In Vicksburg area, on the northern fringe of *Magnolia* distribution, where the population densities of American beech seems to have been several times that of magnolia, the original forest structure was not quite like that of the "conventional" beech-magnolia forest. The marginal formation of this type can be identified as *Fagus*-dominated forest with the presence of *Magnolia* as one of the major accessory species. Nevertheless, despite the considerable difference in relative importance between the two taxa, magnolia may have still been here the second-rank species following beech. The gentle-slope forests north of *Magnolia* termination line located somewhere between 19 to 26 miles north of Vicksburg, were very strongly *Fagus*-dominated.

Although these forests contained diverse assortments of accessory taxa, American beech here appears to have been the only dominant taxon. Of special importance in these forests (although unlikely approaching the status of the co-dominant species), may have been southern sugar maple (*Acer barbatum*). This is one of the very few canopy taxa which is able to develop under closed beech overstory. At the same time, southern sugar maple does not develop well under magnolias and in the spots covered with *Magnolia* leaf litter. Thus, as it suggested by the importance of

Acer barbatum in the Bluff Experimental Forest, it may have expanded in response to the structural decrease and subsequent drop of southern magnolia out of the species.

The most heterogeneous and diverse late-successional forests were supported by the Mississippi Bluff Escarpment. this forest type was quite unlike "typical" beech-magnolia forest. Because of the perpetual physiographic disturbance, it contained the smaller amounts of the shade-tolerant trees and was dominated by the most heterogeneous association which included four species: American beech (22.4%), sweetgum (18.5%), southern magnolia (9.2%), and water oak (9.7%). The mixed and heterogeneous forests of the Bluff Escarpment superficially appear to fit the concept of the Southern Mixed Hardwood Forest more than any loessial forest type but, in fact, only two light-dependedent species of Quarterman and Keever's list do reach here the dominant status. Many other "core" species are represented in this formation in rather modest or even low densities. And vice versa, many tree species with typically very sparse populations in the closed-canopy beech-magnolia forests such as sycamore (*Platanus occidentalis*), sugarberry (*Celtis laevigata*), black cherry (*Prunus serotina*), American and red elms (*Ulmus americana* and *U. rubra*), and red mulberry (*Morus rubra*) achieved relatively high (or at least, higher than in average) population densities in this forest. Boxelder maple (*Acer*

negundo) was also conspicuously important in the ravines of this section.

North of the *Magnolia* range, where the structural importance of water oak (*Q. nigra*) also decreased, the original escarpment forests were likely to have been dominated by beech-sweetgum association, with diverse assortment of other characteristic species such as sassafras (*Sassafras albidum*), white oak (*Quercus alba*), cucumber magnolia (*Magnolia acuminata*), bigleaf magnolia (*Magnolia macrophylla*), and black wallnut (*Juglans nigra*) reaching the status of major accessory components.

As it has been already briefly mentioned above, the structure of the second-growth beech-magnolia forests is characterized by somewhat higher heterogeneity and smooth, gradual transition from the dominant association to the accessory tree assortments. The massive amount of data accumulated during this research suggests that high population densities of such species as tulip tree, cherrybark oak, Shumard oak, white ash, winged elm, sassafrass, black cherry, and, perhaps, hickories (although not every one of these components can be abundant in same stand) represent a rather consistent feature of the anthropogenically-disturbed beech-magnolia forests. In the northern stands, the dominant association is made up by beech, which is always a first-rank dominant tree, and

several second-rank dominant species whose importance is gradually decreasing to the level of accessory components.

Transition from the Deep-Loess Section to the Shallow and Thin-Loess Sections

The most extensive and peculiar biogeographic transitions within the Loess Region are those among the forests developed on the deep-loess, shallow-loess, and thin-loess mantles deposited over the Citronelle formation. The biogeographic change progresses along with the thinning of the loess mantle as the bottomland-centered and many important mesic species drop out or decrease in importance, and more drought-adapted species enter or increase in abundance. Among the key accessory species, the most conspicuous variation along the gradient of diminishing soil moisture is demonstrated by sweetgum and Coastal Plain oaks.

Dynamics of the Bluff-Centered Species

The first, rather mild signs of the biogeographic change associated with the structural decrease of the moisture-loving bottomland and mesic species appear in the Port Hudson assemblage where the relative importance of sweetgum drops to 5.9% which is the lowest value of all sites along the Mississippi Bluff. It should mentioned, however, that the powerful development of the beech-magnolia overstory may have also contributed the relatively low importance of sweetgum in this site. In many aspects, the Port Hudson assemblage still retains the basic features

of the deep-loess Bluff forests: the Coastal Plain oaks, for instance, remain relatively important in this site making up together 7.9% of the canopy structure. From this area located on the southern "slope" of the Loess Bluff, the vegetation change continues to progress toward the margins of the Loess Hills Region exemplified by the assemblages of Sicily Island and Homochito National Forest, where the Citronelle formation comes closer to the surface.

Remarkably, both Sicily Island and Homochito National Forest represent considerably disturbed sites. The perpetual disturbance of the canopy stratum throughout much of the sampled area in the ravines of Sicily Island is comparative to that of the physiographically-disturbed old-growth forest of the Tunica Hills. And yet the canopy population densities of sweetgum range considerably between these two sites - from 29 trees per a hectare on the slopes of Magnolia Glen preserve to only 12 in in the ravine bottoms of Sicily Island. This trend is illustrative of the fact that, as a moisture-loving species, sweetgum tends to expand more readily on disturbed sites characterized by thick loess deposits and relatively high levels of soil moisture than on drier, more permeable sites underlain by more shallow loess deposits.

The same number of canopy sweetgum trees per 1 hectare as in Sicily Island was found in the ravines of Homochito National Forest - this is despite the fact that this

assemblage has a light, early-successional overstory partially made up by loose pine crowns. Although accommodating from the successional standpoint, the HNF forest (as well as that of Sicily Island) has more sparse canopy sweetgum population than any of the closed-canopy beech-magnolia stands within the moister section of edaphic gradient including even such "somber", shady stands as those of the Bluff Experimental Forest and Port Hudson area. Remarkable edaphic importance of the "loess factor" can be illustrated by the comparison of the HNF assemblage with the early-successional ravine forest along the Natchez Trace where the sample population of sweetgum in the canopy stratum was six times higher than in Homochito.

The warm-temperate Coastal Plain oaks (*Quercus nigra, Q. pagoda, Q. michauxii*) are also sensitive to the thinning of the loess mantle. Their aggregate shares decrease from 14.8 % in the Tunica Hills and 8.4 % in the Bluff Experimental Forest to 2.6 % in the Sicily Island and 2.8 % in the Homochito National Forest. Bottomland chestnut oak (*Q. michauxii*) is typically lacking from the canopy of the two latter marginal sites.

The ravine forests of the Deep Loess Section are also characterized by the presense in their canopy of a wide variety of the bottomland-centered and moisture-loving mesic species such as sycamore, boxelder maple, sugarberry, red and American elms, basswood, southern sugar maple and

red mulberry which are absent from the canopy of the ravine forests in Sicily Island and Homochito National Forest. Some of the "bottomlanders" such as sycamore, American elm and boxelder maple were found to extend upslope into the mesic section of edaphic gradient of the beech-magnolia forests only within the deep-loess section of the Mississippi Bluff.

West of the Mississippi River and east of the Bluff they were limited predominantly to the floodplain habitats and did not contribute to the mesic assemblages of the upper grounds. This trend is well expressed in the area managed by the Louisiana State Arboretum which exhibits one of the best slope gradients in the Loess Region. Here sycomore and boxelder maple reach the highest ground of their local distribution on the slightly elevated margins of the floodplain and prove nowhere to be found on the slopes. *Acer barbatum* was found exclusively on the deep-loess deposits east of the Mississippi River where it extended at least as far south as the Port Hudson area.

Overall, the moist-mesic forests of the Mississippi Bluff feature 4 relatively common canopy species which do not occur in the slope beech-magnolia forests of Chicot Lake area and 9 relatively common species which do not occur or untypical for the ravine hardwood assemblages developed on the eastern and western margins of the of the Loess Hills - in Homochito National Forest and Sicily

Island. Apart from these, there are additionally 6 to 7 species of rare canopy trees which were registered in the forests of the Mississippi Bluff, especially within the Escarpment section, but appeared to have been untypical for the forests on more shallow-loess deposits. Such species as black wallnut, pecan, Durand oak, honey-locust, chinquapin oak, and pyramid magnolia were registered exclusively in in the deep-loess section - either in the Tunica Hills or further north along the Bluff but not south of Saint-Francisville from which point the depth of the loessial mantle begins to decrease. Hercules-club was registered only in one site outside the Mississippi Bluff - the lake-facing slope of Chicot State Park - and was, consequently, also missing from all dry-mesic assemblages. The overall canopy importance of the species which are limited to the forests of the Mississippi Bluff was 10.8 % for the Tunica Hills, 10.6% for the Port Gibson site, and 6.8 % for the Bluff Experimental Forest.

The marginal populations of other species biogeographically-centered in the forests of the Mississippi Bluff, such as basswood, sugarberry, red elm and canopy-sized red mulberry, were found in the mesic forests west of the Mississippi River - but only in the pockets of the edaphically and environmentally similar slope habitats in the vicinity of Chicot Lake. Each of these four species, for example, was represented by one

canopy specimen per one hectare in the ravine forest of the Louisiana State Arboretum and two of them - red mulberry and basswood - were also represented by the single individuals on the lake-slope of Chicot State Park. Two bottomland-centered species, red elm and sugarberry, were, in fact, represented by larger-than-average canopy populations (3 specimens per 1 hectare each) for a closed-canopy beech-magnolia forest.

Judging by burgeoning subcanopy populations they were expanding - perhaps, due to the favorable change of hydrological conditions and subsequent decline of beech population. The presence of bottomland chestnut oak was another factor that made forests of Chicot Lake area similar to those of the Mississippi Bluff and different from the shallow-loess peripheral assemblages of Sicily Island and Homochito where this was species totally lacking from the canopy. The structural importance of swamp chestnut oak on the lake-facing slope of Chicot State Park may be a result of the hydrological disturbance.

In general, surviving forests of Chicot Lake area make a rather strong contrast with the marginal shallow loess sites and, with some reservations, can be qualified as an impoverished replicas of the moist-mesic to mesic forests of the Mississippi Bluff. The aggregate share of all moisture-loving mesic and bottomland-centered species which are present in the late-successional ravine the Mississippi

Bluff and Chicot Lake area but absent from the marginal dry-mesic sites such as Sicily Island and Homochito National Forest, range from 23.2% in the Tunica Hills, 14-15% in the Port Gibson area and Bluff Experimental Forest to 11.8% in Chicot State Park and 4.5% in Louisiana State Arboretum.

<u>The Dynamics of White Oak and Blackgum on the Deep Loess Mantles</u>

The deep-loess section and generally all moist-mesic sites are characterized by comparatively low, although variable, population densities of two omnipresent and structurally important components of the forests developed on shallow loess mantles and generally drier sites, white oak (*Quercus alba*) and blackgum (*Nyssa sylvatica*).

White oak is relatively unimportant within the Deep Loess Section east of the Mississippi River and north of Saint Francisville. It is conspicuously absent (or nearly so) from the canopy of both ravine and ridgetop forests of western Tunica Hills. Within 1 ha sample area of the moist ravine forest in Magnolia Glen preserve I found only one small sapling of this species. White oak is also very sparse in the deep-loess section of Wilkinson, Adams, and most or all of Jefferson counties is southwestern Mississippi. No response to disturbance is shown by this species within this section: for instance, the highly successional forest along the Natchez Trace, an association characterized by conspicuously increased populations of

many accessory components of the beech-magnolia forest, contained only one canopy specimen of *Q. alba*.

The tree becomes somewhat more important in the northern fringe of beech-magnolia forest where 5 and 7 canopy specimens of white oak per 1 hectare were found respectively in the canopy of the Bluff Experimental Forest and the assemblage of the Steep Bluffs area, making up, respectively, from 2.3% to 3.8% of the canopy structure. The first area on my way north along the Bluff where I noticed some structural increase of white oak was southern Claiborne County. My quarter-hectare sampling site south of Port Gibson featured, for instance, already 2 canopy specimens of *Q. alba* which suggested the ultimate population density comparable to that of the Bluff Experimental Forest. Whether this variation is of latitudinal nature or it is indicative of some special properties of the local soils, remains a rather interesting problem to attend.

Blackgum is generally even more untypical for the deep-loess section than white oak. Of all deep-loess sites of the Mississippi Bluff only one contained blackgum in the canopy stratum - and it was again the Steep Bluff area. The increase of the population densities of *Q. alba* and *N. sylvatica* toward the northern margin of the beech-magnolia forest, quasi-latitudinal as it may seem, could be, perhaps, related to the presence of Chicasawhay limestone

beneath the loess mantle in Warren County where both sites are located. The edaphic, rather than bioclimatic explanation of this phenomenon is additionally suggested by the fact that the Steep Bluff area also features another species highly uncharacteristic for loessial soils, bigleaf magnolia (*Magnolia macrophylla*).

The moist-mesic to mesic sites of Chicot Lake area showed the biogeographic "solidarity" with the deep-loess section of the Mississippi Bluff. The Arboretum stand featured only 1 canopy white oak per 1 hectare and no blackgum (although few specimens were found in the lower midstory and understory). The lake-facing slope of Chicot State Park had 2 canopy blackgums per 1 hectare but no white oak. However, these slope sites are bordered with early-successional upland forests which, unlike those of the Mississippi Bluff, were relatively rich in white oak and characterized by a regular occurrence of blackgum. This fact suggested a rather marginal, "frontier" nature of these surviving moist-mesic beech-magnolia stands.

Forest Types and Indicator Species as Determined by the Thinning of the Loess Mantle

Thinning of the loess mantle east, west and south of the Mississippi Bluff results in the partial replacement of the moisture-loving species with those better adapted to the faster drainage regimes and poorer soils of the edaphic margins of the Loess Hills region. This group includes both mesic and xeric, to a different extent "loess-phobic"

species many of which are shared by this peripheral, shallow-loess forests with the mesic hardwood forests developed on sandy and sandy-graveliferous substrates common for the rest of the Coastal Plain. The preference of these taxa to non-loessial or shallow-loess soils may be related to some specific properties these soils possess such as better drainage and aeration or higher acidity.

The number of the species adapted to xeric conditions and fast water percolation tends to increase with the loess thinning, although not as fast as to substitute for the loss of the bottomland-centered and moisture-loving mesic species. Apart from such edaphically specialized taxa, a large group of mesic species such as tulip tree, white ash, Shumard oak, pignut hickory, winged elm, black cherry, sassafras, cucumber magnolia appear to show no particular preference for deep-loess or shallow-loess soils or, at least, demonstrate no decrease.

The Shallow-Loess "Slope" Section

The eastern and southern "slopes" of the Mississippi Bluff which are underlain with shallower loess mantles and characterized therefore by somewhat poorer, more percolative and acidic soils than those of deep-loess section are not yet fully xeric. This transitional section is still a domain of the hardwood forest but the local communities are characterized by the decreasing importance of the warm-temperate Coastal Plain oaks and sweetgum.

Sweetgum does retain the status of the major accessory species in the mesic ravines of this section but here it is essentially less important than in the deep-loess section. Thinner sweetgum populations tend to congregate in the ravine bottoms where the underground moisture is more readily accessible. The indicator trees of the Bluff "slope" are white oak (*Quercus alba*) and blackgum (*Nyssa sylvatica*). With some variation, these two trees tend to maintain their structural importance throughout the whole edaphic spectrum of shallow-loess sites, from the Bluff "slope" further outward. On the shallow loess mantles white oak commonly replaces sweetgum as a second-order dominant species reaching as much as 10.3 % in the Port Hudson area, 9,2 % in the Sicily Island, and 10.5 % in the ravines of the Homochito National Forest. Blackgum which is typically either absent or only ephemerally present in the forests on deep loess mantles becomes a major accessory species only in the "slope section".

The Port Hudson assemblage is one of the few if not the only representative example of the shallow-loess hardwood forest of the "slope" phase. It is located on the southern "slope" of the Bluff, within the narrow section almost exactly in the middle between the Tunica Hills and Baton Rouge where the depth of the loess mantle sharply decreases and sandy-graveliferous deposits of the Intermediate Complex come closer to the surface forming

mosaic with the younger Terrace deposits. This area exemplifies a unique floristic transition between the moister any drier section of the edaphic gradient.

To begin with, the assemblage of Port Hudson retains many components of the deep-loess forests such as bottomland chestnut oak, American basswood, southern sugar maple, and sycomore, although only *Q. michauxii* is structurally important making up 3.6% of the canopy structure. The two latter species do not occur in the moist-mesic slope forests west of the Mississippi River, and neither of the species mentioned was found was found in the canopy strata of either Sicily Island or Homochito assemblages. The aggregate share of all the moisture-loving components present in the canopy of the Port Hudson forest but absent from the dry-mesic sites on the peryphery of the Loess Belt was 4.8%. Water and chewrrybark oaks were also relatively important on the site, and, unlike in the marginal dry-mesic sites, Coastal Plain oaks aggregately formed a rather large segment - 7.9% - of the overstory stratum.. Evidently, this forest seems to reflect conditions of the moister section of the shallow-loess gradient.

On the other hand, the Port Hudson formation is remarkably different from the deep-loess moist-mesic forests of the Tunica Hills area further north in that it is characterized by high population densities of two above-

mentioned indicators of shallow loess mantles, *Quercus alba* and *Nyssa sylvatica*. Of special interest are comparative population dynamics of these taxa. The beech-magnolia forest of Port Hudson area features the largest canopy population of white oak among the late-successional sites of the mesic to dry-mesic section - 27 specimens per 1 hectare. Despite the more successionally favorable situation in the ravine stands of Sicily Island and Homochito National Forest, their respective assemblages were characterized by gently but consistently decreasing canopy populations of this taxon (to 21 trees in Sicily Island and 19 trees in Homochito).

This trend may be suggestive of the fact that white oak tends to achieve its edaphic optimum within the "slope" section and then slowly diminishes in importance with the further thinning of the loess mantle. Blackgum shows the opposite trend: after abruptly marking its presence in the "slope" section (in Port Hudson it makes up 2.5% of the canopy structure), this taxon then gradually increases in importance with the thinning of the loess mantle and reaches its maximum on the margins of the Loess Region. The subcanopy of the Port Hudson assemblage, as those of all mesic to dry-mesic sites on shallow and thin loess mantles, is characterized by high importance of sourwood (*Oxydendrum arboreum*) and red maple (*Acer rubrum*) which tend to sprinkle into the overstory stratum in gaps. But, compared

to the other two sites, the successional conditions of the the Port Hudson assemblage with its exceptionally well-developed and relatively closed beech-magnolia overstory appear to be less favorable for the infiltration of these subcanopy components into the overstory. Consequently, sourwood has very low canopy density in the site (1 overstory tree per 1 ha), and red maple was not even registered within 1 ha overstory sample.

The Port Hudson assemblage is also known for its largest, of all sites, aggregate hickory (*Carya* spp.) population numbering 22 overstory trees per 1 ha and accounting for 7.9% of the canopy structure. This area shows, in particular, an abrupt peak - 18 canopy trees per 1 hectare - of pignut hickory (*C. glabra*). Nowhere else either in the deep-loess or shallow-less section this taxon achieves a comparable sample population size. Sicily Island, which appears to be the "next" site along the gradient of loess thinning, is relatively poor in hickories: here only 2 pignuts were registered on 1 ha. The maximum canopy population size achieved by this this species within the deep-loess section of the Mississippi Bluff also does not exceed 2 specimens per 1 ha.

While more or less exclusively shallow-loess components (blackgum and sourwood) aggregately made up 2.8% of the Port Hudson overstory, the aggregate share of all the species which were either almost lacking within the

deep-loess section or considerably expanded compared to the Bluff sites made up as much as 19.5% of its overstory.

<u>The Thin-Loess Peryphery of the Loess Region</u>

On the broad eastern margin of the Loess Region and on some segregated sections of the bluff west of the Mississippi River where the loess deposits are very thin and locally intermixed with sand, the uplands are dominated by loblolly pine (*Pinus taeda*). This is not mixed hardwood-pine or white oak-pine community as indicated by Braun (1950) and the Delcourts (1974) but a predominantly pine forest. But the ravine bottoms and lower slopes of this section harbor predominantly hardwood forest. Related to this section is a predominantly hardwood ravine assemblages of Sicily Island area and Homochito National Forest developed in the upland matrix of strongly mixed pine-oak or predominantly pine forests.

The boundary between the shallow-loess or "slope" and marginal thin-loess forest types where the hardwood section rich in white oak and blackgum fuses into the predominantly pine forests, is a major biogeographic division within the Loess Hills Region as it serves as an outer boundary of the whole belt of the moist-mesic and meso-mesic hardwood forests, the "loessial" forests in narrow sense. East and west of the Mississippi River this boundary today is strongly obscured by expanded populations of loblolly pine

which does not appear to be native for the shallow-loess "white oak-blackgum" hardwood section.

The "shallow-loess specialists" common for Sicily Island and Homochito Forest are supplemented in the latter assemblage by two other important indicator species, upland laurel oak (*Quercus hemisphaerica*) and bigleaf magnolia (*Magnolia macrophylla*). Neither upland laurel oak, nor bigleaf magnolia occur in Sicily Island area, and, although to a different extent, these species should be qualified as uncharacteristic for the western margin of the Loess Belt. In the ravine assemblages of the Homochito National Forest upland laurel oak is one of the major dominant species making up as much as 11.8% of the canopy structure and ranking second only after blackgum. The distribution of laurel oak is positively correlated with high sand content of soil (Ware 1988). While being a typical component of the hardwood assamblages throughout much of the lower Coastal Plain, this species seems to avoid areas underlaid with the thick-loess deposists. The western edge of *Q. hemisphaerica* distribution east of the Mississippi River overlaps relatively well with that of loblolly pine.

In the areas east of the Mississippi Bluff where loblolly pine begins to prevail over the hardwoods in the uplands, laurel oak becomes a regular component of the forest structure in the ravines. The hardwood assemblages of the Mississippi Bluff, including the "slope" forests are

distinctively lacking this species. Among the western forest sites laurel oak is represented in rather minor quantities only in the canopy of the upland early-successional forest of Chicot State Park.

The exceptionally high importance of laurel oak in the Homochito National Forest and its spotty presence in the upland assemblage of the Chicot State Park may be also related to the early-successional status of these two communities. It is noteworthy that the both *Q. hemisphaerica*-rich assemblages are nearly devoid of the shade-tolerant components, which could complicate reproduction of laurel oak in these stands. By contrast, the assemblage of the lake-facing slope in the Chicot State Park features a single subcanopy individual of laurel oak which is, in fact, the only *Q. hemisphaerica* specimen found during this research in the late-successional forest. The dearth of upland laurel population on Chicot Bluff can be, however, also explained by the difference of its edaphic and soil regimes from the rest of Chicot State Park.

Bigleaf magnolia is characteristic specifically of the eastern edge of the Loess Hills Region where it occurs not only in the ravine assemblages of Homochito National Forest but also in the adjacent sections of south-central Mississippi and southeastern Louisiana. It was not found anywhere west of the Mississippi River. The distribution of this taxon in the Coastal Plain also seems to reflect its

preference for the well-drained soils developed on sands and sandy-graveliferous deposits. Its typical habitat are the narrow strips of hardwood forest bordering small streams in the pine hills of extreme southeast Louisiana, southeastern Mississippi and much of Alabama.

On the eastern margin of the Loess Region bigleaf magnolia occurs in the areas where only thin veneer of loess overlies coarse sediments of Citronelle formation. With exception of the Steep Bluffs area, it is largely absent from the hardwood forests of the Mississippi Bluff including its "slope" section. In Homochito National Forest, bigleaf magnolia is a conspicuously abundant subcanopy component. But large trees reaching into the upper layer are not so frequent, and the bigleaf makes up, consequently, only 1.8% of the canopy structure.

The importance of drought-resistant species in Homochito National Forest increases considerably compared to Sicily Island - in part due to the more favorable successional situation, in part because of the more xeric conditions of the area. The canopy of Homochito ravine forest contains not only southern red oak (*Quercus falcata*) but also post oak (*Q. stellata*) which was not found in the ravines of Sicily Island area, although it occured there on the hilltops and upper slopes. Both xerophytic oaks form relatively large populations: taken aggregately, they make up in Homochito National Forest as much as 8.6% of the

canopy structure (compare it to only 1.3% made up by xeric oaks in Sicily Island). The Homochito assemblage was also marked by the highest diversity of hickories - four species were registered here on the sampling area of 1 hectare. The xeromorphic forms were predominant. This site was characterized, in particular, by considerably higher population density of mockernut hickory, than Sicily Island area. In Homochito, mockernut was joined by snagbark (*Carya ovata*), a "loessophobic species" which did not occur in the forests of the Mississippi Bluff, including even its "slope" section, and likewise was not present in Sicily Island. Snagbark is a component of various mesic to dry-mesic forests developed on the old geological surfaces in more temperate and interior regions of eastern North America but within the Coastal Plain it tends to gravitate to the poor sub-xeric sites on the well-drained sandy soils. The aggregate importance of the xeromorphic hickories increased from only 1.0% in the ravines of Sicily Island (where only mockernut was present) to as much as 5.0% in the ravines of Homochito National Forest.

Together with laurel oak and bigleaf magnolia, post oak and snagbark hickory should be, perhaps, identified as one of those "surplus" species whose presence in Homochito National Forest seems to be indicative of the more marginal and xeric status of the local hardwood assemblage compared to Sicily Island. Thus, the ravine hardwoods of Homochito

National Forest had more diverse overstory assortment of distinctively xeric or "loessophobic" components than any other site sampled in this project. Structurally, these forms even predominated over the mesic species. Eight distinctively xeromorphic taxa present in the ravine assemblage Homochito National Forest made up as much as 27.8% of canopy structure - as opposed to 23.5% in the Sicily Island area, 2.8% in Port Hudson area, as well as 0.7-1.6% to none in the moist-mesic to mesic forests of the Mississippi Bluff.

Due to the abundance and structural importance of the drought-resistant and "loess-phobic" trees, I tend to consider the hardwood assemblage of Homochito National Forest as biogeographically distinctive from the shallow-loess hardwood forests of the "white oak-blackgum" section. This forest is floristically very similar to the mesic hardwood formations developed on non-loessial (most commonly sandy and sandy-graveliferous) substrates along the creeks and in ravines in the longleaf pine matrix of the lower Coastal Plain. The major difference is that the major species of the Coastal Plain upland matrix, longleaf pine (*Pinus palustris*) is replaced in somewhat less pyrophytic uplands of Homochito National Forest by loblolly pine.

The Boundary between the Hardwood and Pine Matrixes

Spicer (1969) and Delcourt and Delcort (1974) suggested that in the early-historical times when large tracts of primeval timber existed in the Loess Region and biogeographic boundaries were sharper, the forests dominated by loblolly pine replaced hardwood forests in the section where loess deposits thinned to a depth of six to two feet. Hardwood forests dominated by beech and magnolia continued, according to the Delcourts (1974) persisted only in the ravines. Cuming who traveled in 1809 along the Mississippi Bluff from Baton Rouge to Natchez noticed that "...the pine woods... generally begin at from fifteen to twenty miles distance from the Mississippi river..." (Thwaites 1904: 353).

In effort to locate a more precise historical boundary between the hardwood belt and loblolly pine forests, I set several reconnaissance transects from the Bluff escarpment eastward. Equipped with the Geologic Map of Mississippi, I then traveled along those and observed the vegetation change along the way. Of course, the forests and woodlands I traveled through were secondary and early-successional in origin with only tiny ravine patches of what can be identified as left-overs of the late-successional forests. However, I noticed that even in the areas where pine was abundant, the pine-rich early-successional forests tended

to be loosely segregated along the edaphic gradient of thinning loess mantle into two sections.

In one of these sections which was typically adjacent to the Bluff, loblolly pine made up from one quarter to roughly a half but rarely much larger portion of the overstory structure. These were characteristically mixed, hardwood-coniferous woodlands. Secondly, here pine growth was typically concentrated on hilltops and did not extend into ravines: at the very best pines were limited to the upper slopes, while most of the vertical ravine gradient remained under pure hardwood cover. Additionally, exceptionally large broadleaf trees of mesophytic kinds, including solitary overstory beeches, that could be found here and there amidst the younger successional growth on uplands and upper slopes - undoubtedly left-overs of the mature, perhaps, late-successional phases - also served as important identification marks.

Taken together, these features suggested the relatively recent nature of pine expansion stimulated by anthropogenic disturbance. Such mixed forests contrasted rather strongly with the broad outer fringe where loblolly pine was an overwhelming dominant. The predominantly pine section generally overlapped with the area of more shallow relief, and although hardwoods could have played important role in bottoms, loblolly pine was abundant through the

whole edaphic gradient and frequently dominated slopes and shallow depressions.

For needs of my reconnaissance work, I assumed that conspicuously mixed, hardwood-pine woodlands were post-clearcut formations developed in the place of originally hardwood forests: abundance of white oak and relative frequency of blackgum in the overstory and subcanopy strata of these stands may have served as the distinctive marks of shallow-loess "Bluff-slope" hardwood forests as opposed to the moist-mesic hardwood forests of the deep-loess section. "Bluff-core" hardwoods developed within the deep-loess section. The forests of the more eastern section where loblolly pine was overwhelmingly important were identified as a second-growth formation which was predated by predominantly pine forests.

According to my rough approximations, the boundary between the hardwood and derived hardwood-coniferous formations of the Bluff slope to the thick and apparently "native" loblolly pine forest in Wilkinson, Amite, and Franklin counties of southwestern Mississippi generally overlaps with the interval where the loess mantle thins to a depth from 8 to 5 feet. It appears that originally a greater portion of Western Feliciana was under mesic hardwood forest than it is shown on the vegetation map of the Parish composed by the Delcourts (1974) where about 15% of its territory in the northwestern corner were under

"white oak-pine-beech" forest, although the Delcourts may have correctly distinguished this area as rich in *Q. alba*.

Only extreme northwestern section of this corner may have originally been under the forest with pine. Thompsons Creek, throughout almost all its length, except, perhaps, the extreme upper part above Cason Creek, seems to have been flanked by the hardwood forests. In East Feliciana Parish of southeastern Louisiana these hardwood forests appear to have formed a narrow strip which extended along at least two thirds of its western boundary.

The Dynamics of Potentially Dominant Species of the Shallow and Thin-Loess Sections

The ravine assemblage of the Port Hudson area representative of the shallow-loess "slope" section replicates most closely the original structure of the closed-canopy beech-magnolia forests. Here two primary shade-tolerant dominants, beech and magnolia, make up, respectively, 26.6% and 24.7% of the overstory structure and form aggregately slightly more than a half of the forest canopy. White oak which makes up 10.3% of the canopy structure is the third most important species. The co-dominant status of *Q. alba* is well profiled in this assemblage: although its population densities are considerably lower than those of the shade-tolerant components, they are well above those of any other light-dependent canopy species. Thus the dominant association of the Port Hudson site contains, quite clearly, only three

dominant species - beech, magnolia, and white oak - which is more or less in accordance with the conventional pattern of the closed-canopy beech-magnolia forest. Beginning from the fourth-rank taxon of the species list, *Carya glabra*, the relative importance values decrease here very gradually forming the "classic" diminishing succession of the accessory components.

The ravines of the Sicily Island area harbor a more heterogeneous and structurally complex forest type. This forest is co-dominated by as many as 5 canopy species, both shade-tolerant and highly light-dependent. American beech which makes up 28.8% of the canopy structure is by far the most important component of the dominant association. Four second-order co-dominants are loblolly pine (11.2%), southern magnolia (10,6 %), tulip tree (10,5 %), and white oak (8.9%). Tulip tree achieves the dominant status largely due to the abundance of slender-stemmed individuals which made it to the canopy relatively recently.

Much of the reproductive success of the light-demanding deciduous species in the Sicily Island seems to be related to the local importance of loblolly pine. As mentioned above, Sicily Island is the only area studied within this project where this conifer is present in the structure of the late-successional beech-magnolia forest. In the "conventional" second-growth forests, the beneficiary effect of anthropogenic disturbance on the

reproduction of the light-dependent hardwood species lasts only until a more or less contiguous shade-tolerant subcanopy is formed. The presence of a relatively large population of loblolly pine in the ravines of the Sicily Island contributed to the establishment of the milder successional regime. Thin canopies of the pine trees pass much light to the forest floor thus helping to maintain high reqruitement rates of even those hardwood species (such as tulip tree, white oak, sweetgum, blackgum, and red maple) whose reproduction by this stage of the successional process would have been otherwise inevitably hindered by the shade-tolerant species. What is more, many pine trees here either have already achieved the limit of their their growth or became infested by southern bark beetle (or some fungus disease) and now are declining. This resulted in even further thinning of the canopy cover and ongoing development of new gaps under dying trees.

Slender canopy-size individuals of the successional species, especially those of tulip tree, sweetgum, red maple, and sourwood, tend to congregate in small stands under such dying or dead pines, as well as in the places of their former locations. Although different in origin, this peculiar form of perpetual disturbance generates an ecological conditions rather similar to those of the escarpment sites. However, the structural heterogeneity of the Sicily Island assemblage is not accompanied - due,

perhaps, to the less favorable edaphic conditions - by the level of canopy diversity comparable to that of the Tunica Hills and Steep Bluffs areas.

The ravine hardwood assemblage of Homochito National Forest is dominated by the association which includes four major species - blackgum (12.6%), tulip tree (12.5), upland laurel oak (11.7%), and white oak (11.4%). Beech and southern magnolia which once dominated this forest now are only minor overstory components aggregately responsible for only 3.1% of the canopy structure. Like most of the early-successional stands, the Homochito assemblage is characterized by a rather smooth transition from the dominant association to the group of accessory species. The break between the two groups is filled by loblolly pine (8.1%) and sweetgum (6.2%) which can be categorized as the second-order co-dominants. Due to the very low importance of the shade-tolerant species in the canopy stratum, most of the structurally important light-dependent components, except loblolly pine and tulip tree, seem to be able to reproduce themselves perpetually in this forest.

Potentially Dominant Light-Dependent Species

Apart from beech and magnolia, there are five other species - white oak (*Quercus alba*), tulip tree (*Liriodendron tulipfera*), loblolly pine (*Pinus taeda*), blackgum (*Nyssa sylvatica*), and upland laurel oak (*Q. hemisphaerica*) - that show ability to build up large canopy

populations and assume the dominant status in the ravine hardwood forests of the shallow-loess and thin-loess sections.

White Oak. The most common feature of all forest assemblages developed on the periphery of the Loess Region is the structural importance of white oak which replaces here sweetgum as the most likely light-dependent co-dominant component of the canopy stratum. The question arises, of course, to which extent this trend may reflect the original canopy structure of the "marginal" forests.

Generally speaking, I find it doubtful that white oak could have been able to maintain populations that high in the canopy of the relatively undisturbed early-historical beech-magnolia forests. I noticed that white oak reproduces well only as far as canopy is dominated by oaks and pine but not beech and magnolia. This trend is indicated by many examples. The old-growth beech-magnolia forest managed by the Louisiana State Arboretum is surrounded with the early-successional post-cultivation assemblages where, within a sample area of 1 ha, white oak was represented.by 14 overstory and 49 understory specimens responsible respectively for 7.7 % and 8.5 % of the structural importance in these layers. In contrast, the 1 ha sample of the beech-magnolia old growth itself contains only one canopy tree and five understory saplings of this species which fact possibly suggest that white oak does not

reproduce well in the environment of the mature beech-magnolia forest.

The areas with *Q. alba*-rich overstories may also show different patterns of white oak reproduction depending on the successional characteristics of these sites. Within 1 ha sample of the gappy ravine forest of the Sicily Island Area where the significant portion of the overstory is controlled by shade-intolerant deciduous species and pines, I found as many as 34 more or less developed understory individuals of white oak responsible for 1 % of the understory structure. By contrast, in the late-successional forest of the Port Hudson area where the canopy is more closed and exceptionally rich in the shade-tolerant taxa, I registered only 4 understory individuals of *Q. alba* which accounted for 0.1 % of the understory structure. It appears that the reproduction capacity of white oak in this stand, despite its importance in overstory stratum, has come to the critical point.

One can possibly suggest that expansion of white oak to the level of the second-order dominant species in the survived beech-magnolia stands of both these areas is probably caused by the anthropogenic disturbance and must be, therefore, of the temporary nature. White oak has gotten a chance to expand in the second-growth ravine assemblages of the Sicily Island and Port Hudson areas following destruction of their original overstories by man.

Apparently, it is able to reproduce successfully up to the moment when the overstory is again reclaimed by the shade-tolerant dominants. The favorable reproduction regime for white oak is certainly over in the beech-magnolia ravines of the Port Hudson area. In the absence of any repeated disturbance, the massive recruitment of young oaks in this site ceased and the large population of *Q. alba* which had already entered the overstory as a result of the "successional impulse", remains persistent there as a mere relict of the earlier successional stage. More favorable successional situation in the beech-magnolia stands of the Sicily Island will probably enable white oak to maintain here relatively high recruitment rates within few coming decades.

Tulip Tree. Tulip tree also readily achieves the dominant status in the canopy of the dry-mesic sites but it does so only in the second-growth stands. A very strong dependence of tulip tree on direct sunlight and its extremely sparse understory population densities in all studied forests indicate that this species may expand to the dominant status following forest clearance. Sicily Island assemblages shows a unique example of more or less dynamic recruitment of tulip tree into the overstory from the subcanopy stratum but this phenomenon is generated by the chain of successional events which became possible as a result of the initial act of anthropogenic disturbance. Yet

even in this forest, the "perpetual" nature of tulip tree recruitment cannot be surely postulated because I did not find here much evidence for the dynamic replenishment of the midstory stratum with the understory individuals. The dynamics of *Liriodendron* suggest against the possibility that this taxon can maintain its canopy population densities in any of the observed assemblages indefinitely through time. Even in Sicily Island where there is a comparatively large midstory population, the recruitment into the canopy will decline when the subcanopy population pool is exhausted and a continuous deciduous canopy stratum is formed.

Upland Laurel Oak and Blackgum. The important fact regarding upland laurel oak (*Quercus hemisphaerica*) and blackgum (*Nyssa sylvatica*) distribution is that the both species reach the dominant status only in the early successional assemblage of Homochito National Forest where their reproduction is not hindered by the shade-tolerant species. However, both taxa can develop under their own or other light-dependent species' canopy. The effect of the closed-canopy beech-magnolia overstory over the reproduction rates of blackgum are evident from the comparison of its understory population in Homochito National Forest and Sicily Island where *Nyssa* was represented, respectively by 44 and 38 saplings with that of Port Hudson where, despite the relatively sizeable

canopy population, only a single sapling was found in the understory. Clearly, blackgum continues to reproduce dynamically in the latter stands but, similar to white oak, lost this ability in Port Hudson assemblage which makes a close replica of the old-growth beech-magnolia forest. To make such comparison for upland laurel oak is more difficult due to the more marginal nature of its distribution in the Loess Hills. But Ware (1988) pointed out that *Q. hemisphaerica* importance is generally dissociated from high beech importance. It is noteworthy that the both assemblages where upland laurel oak reaches some importance - apart from Homochito National Forest, another one is the upland early-successional assemblage of Chicot State Park in south-central Louisiana - are nearly devoid of the shade-tolerant components. The late-successional assemblage of the lake-facing slope in the Chicot State Park features only one subcanopy individual of laurel oak. As a matter of fact, it is the only specimen of *Q. hemisphaerica* found during this research in the late-successional forest.

Loblolly Pine. Loblolly pine (*Pinus taeda*) represents especial interests among the potentially dominant trees because of the ongoing discussion of its role in the composition and structure of the Coastal Plain hardwood forests and the undocumented and somewhat puzzling history of its diffusion into the Loess Hills. As an

accessory and even co-dominant species, loblolly pine is present in the most survived beech-magnolia stands throughout the non-loessial portion of the lower Coastal Plain (Quaterman and Keever 1962, Blaisdell et al. 1973, Schwartz 1974, Delcourt and Delcourt 1977, Harcombe and Marks 1977, Platt and Schwartz 1990, Batista and Platt 1997). It is still a matter of further research to establish whether or not loblolly pine is ecologically native to the non-loessial beech-magnolia forests (although, most likely, the answer is "no"). In any case, it is almost certain that *P. taeda* is not a native component of the forests developed in the loessial district, especially those of the Mississippi Bluff (Delcourt and Delcourt 1974, Platt 1994, personal communication).

When and how loblolly pine appeared in the Blufflands is still not completely understood. Platt (personal communication) has suggested that loblolly may have introduced in the Tunica Hills in the 1950s at which time the local uplands were clearcut and first pine plantations were established in the place of the destroyed hardwood forests. Glen Brown, an assistant forest manager of the Anderson-Tully Company, on the basis of the data available to him, suggested that loblolly pine seemed to have been already present in the section of the Mississippi Bluff in the vicinity of Vicksburg in the first decades of the 20th

century. Even the earlier time of invasion is suggested by the canopy structure of the old successional forest preserved by the Oakley Plantation, a historical site located in the vicinity of Saint Francisville, just south of the Tunica Hills. Along with giant oaks, the forest contains a fair number of exceptionally large trees of *P. taeda* whose origins are dated back to the time of the site's abandonment in 1863. This fact suggests that seed source of loblolly pine must certainly have been nearby.

Apparently, the early stage of establishment of *P. taeda* in the Blufflands is coincident with the period of development of the plantation agriculture. Some of the newcoming planters have probably brought loblolly pine originally as an ornamental tree from the east. With the abandonment of the previously cultivated areas as a result of the Civil War or even earlier *P. taeda* may have established itself in some of the former fields. If loblolly pine was locally present in the Blufflands in the beginning of the 20th century, it certainly benefited from the advent of the boll weevil in 1920 which resulted in the major loss of the cultivated land througout the region. (Agelasto, 1922; Wahlenberg 1960, Hurt 1994).

Known for its intolerance of any shading, *Pinus taeda* is apparently unable of reproducing in the hardwood forest of almost any kind. Despite the high overstory frequency of loblolly pine in the ravines of Sicily Island, its

regeneration within my sample area was represented by just one specimen found in the lower midstory. In the whole surveyed ravine area beyond the range of my transects only two understory specimens were registered but those seemed to have been in the declining state. Surprisingly, no regeneration of *P. taeda* was registered even in the surveyed ravines of the Homochito National Forest where the loblolly-dominated forests are far more extensive and representative. It seems that in both areas only the first generation of pines, namely those plants that were among the first colonizers of the cleared plots had chances to survive and reach the canopy. My observations from the peripheral loessial forests are quite in accordance with the data of Bryant et al. (1993) from the Piedmont forests of Georgia who proved that loblolly pine does not seem to benefit from natural gap formation. Even gaps as big as 0.1 ha are not suited well enough for pine regeneration. This fact suggests that the successional characteristics of *P. taeda* are quite unlike those of the most hardwood accessory species whose reproduction in the beech-magnolia forest is dependent primarily on gaps.

Since loblolly cannot maintain its permanent population in the hardwood forest by means of colonizing gaps as the broadleaf species do, it may expand only following destruction of the original hardwood canopy over relatively large areas. It seems that in the early-

successional forests only the first generation of pines - those that were among the first colonizers of the vacant plot have chances to survive and reach the canopy. Thus, at least in the Blufflands where hurricanes do not seem to be so disruptive the presence of *P. taeda* can be considered as a well-proved indicator of the intensive anthropogenic influence.

Other Species. What are the chances of the other species from Quarterman and Keever's list to reach the status of the canopy dominants? Apparently, we should decline all claims for such species as southern red oak and mockernut hickory. These do not approach to the status of the canopy dominants even in the early-successional assemblage of Homochito National Forest. Pignut hickory demonstrates its ability to build up relatively large populations only within very narrow "slope" section and only following the anthropogenic disturbance (clearcut). And yet even under the overlapping set of the most favorable edaphic and successional conditions it does not become important enough to fit the status of the dominant species.

Sweetgum demonstrates a relatively high importance indices in the canopy of all shallow- to thin-loess forests - but again only as a major accessory species. In the ravines of Sicily Island it is also represented by the rather high understory to midstory populations (after beech

it is the second most important potentially canopy species to be found in both layers). Yet, compared to the large population densities of the subcanopy recruits, the canopy population densities are remarkably modest (only 4.9%) - even though the Sicily Island site is characterized by the exceptionally favorable successional regime. Apparently, the marginal conditions of this shallow-loess, sub-xeric site to some extent suppresses the development of sweetgum so that not all understory and subcanopy tree are destined to make it into overstory. In the ravines of Homochito National Forest sweetgum expanded to the same overstory population size as it did in Sicily as e result of more recent clearcuts but here, judging by the modest subcanopy population densities and lack of reproduction in the understory, it appears to be unable to maintain even its current canopy status.

The Successional Trends and the Nature of the Original Old-Growth Forests

None of the presently co-dominant light-dependent species in the studied stands could have played the dominant role in the original forests. The expansion of all these species in the present-time second-growth forest is a result of the anthropogenic disturbance. This leaves only two species - American beech (*Fagus grandifolia*) and southern magnolia (*Magnolia grandiflora*) - as the potential dominants in the early-historical forests and no foundation for the concept of the Southern Mixed Hardwood Forest

regarding the shallow-loess margin of the Loess Hills. The forests of the shallow-loess section of the Bluff "slope", as well as those of Sicily Island and other western loessial outcrops were undoubtedly beech-magnolia in nature. And so were the hardwood ravine forests of the loblolly pine section east of the Mississippi Bluff. White oak (*Quercus alba*), blackgum (*Nyssa sylvatica*), and, perhaps, tulip tree (*Liriodendron tulipfera*) were likely to have been more important in these forests than within the deep-loess section of the Mississippi Bluff but they were only accessory - not co-dominant species. And so was upland laurel oak (*Quercus hemisphaerica*) on the piney eastern margin of the Loess Hills Region.

The subsequent anthropogenic disturbance - in the form of extensive forest clearence - served, in fact, as an important biogeographic factor which sharpened the floristic differentiation of the habitats and forest types along the edaphic gradient by selectively promoting the different assortments of the light-dependent species - sweetgum (*Liquidambar styraciflua*), tulip tree, and, perhaps, water oak (*Quercus nigra*) or bitternut hickory (*Carya cordiformis*) in the deep-loess section, white oak, tulip tree, and blackgum in the shallow-loess section, and blackgum, tulip tree, upland laurel oak, and loblolly pine (*Pinus taeda*) in the thin-loess section.

Few words must be said about the perspectives of natural evolution of the hardwood assemblages of Homochito National Forest which represents a relatively early stage of the natural succession. In the absence of the further clearing operations in Homochito National Forest within few decades from now, both tulip tree and sweetgum are destined to decline in importance and be partially replaced by the species that seem to be able develop under its own canopy - blackgum, white oak, hickories, bigleaf magnolia, white ash, and winged elm. Beech and magnolia would eventually prevail over all more light-dependent species but, judging by the relatively sparse population of both species in the understory stratum, their importance in the overstory may considerably increase only in 60 to 80 years from now.

Some ideas can be also suggested about the nature of the original matrix forests on the eastern margin of the Loess Region. I find it doubtful that loblolly pine could have dominated the uplands of the eastern margin of the Loess Region along with beech and white oak, as it was suggested by Delcourt and Delcourt (1974). Loblolly pine cannot maintain its dominance in any kind of hardwood forest, let alone the forest in which beech is important. Beech, on the other hand, does not tolerate fires which, in the absence of anthropogenic disturbance, were crucial for the *Pinus taeda* reproduction and maintenance of the pine-dominated ecosystem. White oak, as a more xeric-adapted

taxon, could have been one of the associate species but - due to the fire pressure - it is unlikely to have been as important as to claim the co-dominant status. Loblolly pine was probably accompanied in this section - as it is here today - by other, more xeric species of oaks and hickories such as southern red oak (*Quercus falcata*), post oak (*Quercus stellata*), and mockernut hickory (*Carya tomentosa*) but these taxa also do not tend to approach the dominant status. I suggest that the upland forests of the broad eastern margin of the Mississippi Bluff which were defined by the Delcourts as being dominated by the white oak-pine-beech association were, in fact, predominantly pine forests with the admixture of some drought- and fire-resistant hardwoods. Sweetgum undoubtedly played much less important part in these forests than it does today.

The narrow strips of hardwood forest dominated by beech and magnolia extended only in the ravines were fires extended less frequently. It appears that the boundary between the hardwood forest in the ravines and predominantly coniferous formation on the uplands was sharper than it is today because pine and beech are mutually exclusive, and so are pine and many other mesic species.

The Shallow-Loess Moist-Mesic Hardwood Forests on Terrace and Valley-Train Foundations

In the extreme southern end of the Loess Region - south of the Port Hudson area - where the Terrace deposits rich in clay and loam become a predominant substrate underlying the thinning loess mantle, the moisture-loving species again considerably increase in importance while the xero-mesic components shrink or drop out. Water oak (*Q. nigra*), with sweetgum (*Liquidambar styraciflua*) and cherrybark oak (*Q. pagoda*) as two major associates, is a primary dominant species in the mosaic of the early successional forests of Eastern Baton Rouge Parish. Pecan (*Carya illinoensis*) is an important accessory component in the forests of this area. Southward, the role of decidedly bottomland components, especially those adapted to the poor drainage and soil aeration, increases. One of the areas that exemplifies the broad physiographic and floristic transition from the loessial uplands to more bottomland landscape types is Hooper Forest in northern Baton Rouge.

The loessial surfaces and outcrops alternate here with the mosaic of very shallow and nearly flat depressions. This forest is strongly dominated by water oak, with cherrybark oak and sweetgum being the second and third most important canopy species. Willow oak (*Q. phellos*), accompanied by pecan and red maple (*Acer rubrum*), is a conspicuously important component of this forest. Another distinctive feature of this assemblage is abundance of

Chinese tallowtree (*Sapium sebiferum*), an introduced subtropical species from the forests of southern China. Tallowtree is predominantly a subcanopy component but some specimens reach into the overstory. More mesic species such as bottomland chestnut oak (*Q. michauxii*), white ash (*Fraxinus americana*), winged elm (*Ulmus alata*), and black cherry (*Prunus serotina*) are also present in this forest, especially on the elevated loessial outcrops. The sparkling presence of southern magnolia in the understory and midstory strata throughout the whole edaphic gradient of Hooper Forest indicates that this early-successional assemblage developed in the place of the former beech-magnolia or at least magnolia-rich forests.

The oldest of all loessial assemblages in the shallow-loess moist-mesic is Burden Plantation located in the southern section of Baton Rouge. This assemblage is also strongly dominated by moisture-loving species. The most important canopy taxa are sweetgum and water oak, followed by cherrybark oak. The floristic similarity of this site with Hooper Forest is marked by the presence of several specifically bottomland species such as willow oak, pecan, red maple and also Nuttall oak (*Quercus nuttallii*) which was not found in Hooper. The population densities of these bottomlanders in this site are somewhat lower than in Hooper Forest which can be probably explained by the decidedly upland location of Burden Plantation.

Nevertheless, willow oak, pecan, and red maple were all found in the quarter-a-hectare exemplary sample which also contained beech and southern magnolia.

Neither of the moist-mesic stands survived in East Baton Rouge Parish are mature enough to give idea of the original forests of this region. However, both southern magnolia and American beech are present in the canopy of the local mesic forests at least as far south as the southern portion of the City of Baton Rouge. Burden Plantation forest feature comparatively few large-sized beech trees. Most of them look somewhat weakened and do not reach a full canopy size - even in the stands which contain large canopy magnolias. I do not exclude the possibility that beech occurs in Burden stand on the extreme southern edge of its distribution. If so, it may have played a relatively modest role in the original forests of this area. Characteristically, William Bartram, who witnessed in 1775 the splendid old-growth mesic forests along Bayou Manchac south of Baton Rouge, did not even mention beech among the important species of this assemblage, although he put southern magnolia first in his list of "the trees of the first order in magnitude and beauty" (Harper 1958: 270).

Whatever could have been the role of beech, *Magnolia grandiflora* was undoubtedly one of major if not the most important species. The high potential importance of

magnolia in Burden Plantation Forest can be suggested based on its large subcanopy population. In few decades from now this subtropical species is likely to become a major canopy dominant, which would certainly affect the reproduction efficiency of the currently important light-dependent species. The original forest of Burden Plantation was, I suggest, the magnolia-beech-sweetgum, magnolia-sweetgum or magnolia-dominated forests where the other, presently dominant, species were confined to more or less accessory niches.

Brief Summary and Conclusions

The combined action of edaphic conditions, physiography and disturbance contributed to the establishment of at least five distinct forest canopy types in the southern Loess Hills. American beech (*Fagus grandifolia*) and southern magnolia (*Magnolia grandiflora*) were originally the dominant species in all of them. The differentiation of the canopy types is based largely on the distinct assortments of the light-dependent species.

The deep-loess deposits of the Mississippi Bluff originally harbored two distinct moist-mesic to mesic forest types. One of these forest types developed within the narrow section of the Bluff Escarpment characterized by exceptionally deep dissection of the loess mantle and perpetual physiographic disturbance. This is the most diverse and heterogeneous of all loessial forests. It has,

perhaps, the highest species diversity per unit area in Eastern North America north of Mexico. The southernmost escarpment forests (from West Feliciana Parish, Louisiana, north, perhaps, to Natchez, Mississippi) are dominated by beech-sweetgum-magnolia-water oak association and are characterized by high importance and diversity of the delicate mesic and bottomland-centered tree species. More northern escarpment forests (north of *Magnolia* range) seem to have been originally dominated by beech-sweetgum or beech-sweetgum-sassafras association and were characterized (at least, in northern Warren County, Mississippi) by the unusual mixture of the bottomland-centered taxa and tree species adapted to poor sandy soils and sub-xeric edaphic regimes. Both southern and northern escarpment forests have large assortments of rare, sparsely distributed, and highly-localized species which never or only occasionally sprinkle in the canopy of the "conventional" beech-magnolia forests. This is the only forest type, which is a relatively close replica of the Southern Mixed Hardwood Forest postulated by Quarterman and Keever (1962).

The closed-canopy beech-magnolia forests developed within the deep-loess portion of the Mississippi Bluff east of the Escarpment section characterized by little or no physiographic disturbance were originally dominated by only shade-tolerant species - American beech in the middle Blufflands, beech and southern magnolia from northern

Warren County (Mississippi) south to Saint Francisville (Louisiana). In the Tunica Hills area of West Feliciana Parish the dominant association was additionally diversified by American holly (*Ilex opaca*). The moist-mesic to mesic closed-canopy forests exemplify the second riches type of the loessial forests but they are characterized by a lower diversity of the rare and sparsely distributed species per unit area. Throughout the deep-loess section of the Mississippi Bluff the indicator canopy species are sweetgum (*Liquidambar styraciflua*), water oak (*Quercus nigra*), cherrybark oak (*Q. pagoda*) and bottomland chestnut oak (*Q. mischauxii*). In the closed-canopy late-successional forests these typically are among the first-rank accessory components. The ravine forests of the deep-loess section are also characterized by the presence in their canopy of a wide variety of the bottomland-centered and moisture-loving mesic species such as sycomore (*Platanus occidentalis*), boxelder maple (*Acer negundo*), sugarberry (*Celtis laevigata*), red and American elm (*Ulmus rubra* and *U. americana*), southern sugar maple (*Acer barbatum*), American basswood (*Tilia americana*), and red mulberry (*Morus rubra*) which are absent from the canopy of the shallow-loess forests. The eastern and southern "slope" of the Mississippi Bluff is underlain with shallower loess mantles and characterized therefore by poorer, more acidic soils and faster drainage which led to the establishment of the

mesic to dry-mesic edaphic regimes. This transitional section is still a domain of the hardwood forest but the local communities are characterized by the decreasing importance of the warm-temperate Coastal Plain oaks and sweetgum. Sweetgum does retain the status of the major accessory species in the mesic to dry-mesic sites but here it is essentially less important than in the deep-loess section. Thinner sweetgum populations tend to congregate in the ravine bottoms where the underground moisture is more readily accessible. The indicator trees here are white oak (*Quercus alba*) and blackgum (*Nyssa sylvatica*). White oak considerably increases in importance in this section and commonly attains the status of one of the second-rank dominant species. Blackgum is very ephemerally represented in the deep-loess section and is essentially absent from some moist-mesic samples such as that of Magnolia Glen preserve but becomes a major accessory species on the shallow-loess mantles.

On the broad eastern margin of the Loess Region, where the loess deposits are very thin and locally intermixed with sand, the uplands are dominated by loblolly pine (*Pinus taeda*). This is not mixed hardwood-pine or white-oak pine community as indicated by Braun (1950) and the Delcourts (1974) but a predominantly pine forest. Homochito National Forest in southwestern Mississippi represents one of the best and largest tracts of this forest type survived

on the margins of the Loess Region. A somewhat mixed aspect of the Homochito assemblage is given by the strips of the predominantly hardwood forest which cover the bottoms and lower slopes of the local shallow ravines. White oak and, particularly, blackgum which remain to be important components of this forest type are supplemented here by three other indicator species - loblolly pine, upland laurel oak (*Quergus hemisphaerica*) and bigleaf magnolia (*Magnolia macrophylla*).

The southernmost section of the Bluff slope in East Baton Rouge Parish is characterized by the structural decrease of American beech and increase of few bottomland species adapted to the poor drainage regimes such as pecan (*Carya illinoensis*) and willow oak (*Quercus phellos*). West of the Mississippi River and south of Opelousas beech drops out of the species composition and live oak (*Quercus virginiana*) becomes more or less regular component of the forest structure, gradually changing the appearance of the forest by the prevalence of the evergreen life forms.

Interestingly enough, the present-day biogeographic zonation of the loessial beech-magnolia forests appears to be strongly sharpened by the anthropogenic disturbance. The clearence of the original late-successional forests in the Loess Hills region that influenced selectivelly different groups of species depending on depth of the loess mantle. Although the original vegetation of the region was also

likely to have been characterized by a certain degree of differentiation along the edaphic and physiographic gradient, the original old-growth beech-magnolia forests were much less segregated due to the lower importance of the indicator species.

CHAPTER 11

BIOGEOGRAPHIC VARIATION IN THE MIDSTORY STRATUM

The middle stratum, midstory or subcanopy of the beech-magnolia forest, as it is understood in this work, is a section of the vertical gradient which includes trees ranging from 4 meters above the ground up to any height as far as they remain obstructed by the taller trees of the canopy stratum. Among the trees with unobstructed crowns related to the midstory stratum are those which are less than 12 m tall.

The midstory structure of the beech-magnolia forest is formed predominantly by two guilds of trees: the undergrowth of the canopy trees and the midstory or subcanopy specialists. The structural importance of the potentially canopy taxa decreases with every subsequent layer closer to the ground. The upper midstory or immediate subcanopy, which tends to be a relatively thinly populated layer in the old-growth forest, is typically dominated by advanced recruits of the canopy species. The lower midstory is commonly dominated by the midstory specialists and has essentially higher density of trees and more diverse assemblage of tree species.

The mature Loess Hills forests are characterized by the relatively sparse midstory in the areas strongly dominated by beech and magnolia. Such areas are conspicuously park-like, almost free of undergrowth.

Somewhat more dense midstory stands occur in the localities where beech and magnolia intermingle with other, less shade-tolerant trees. One should remember that, since nearly all surviving remnants of the beech-magnolia forests were or remain to be influenced by disturbance of various kinds, anthropogenic, post-anthropogenic or otherwise, the vast majority of the late-successional sites are characterized by relatively dense tree populations. Many of them may by, in fact, not completely identical to those observed in the region by the early-historical travellers and first settlers.

Midstory Specialists

The list of the midstory specialists registered on the aggregate area of 7.6 ha of the mature forests includes 27 tree species which control some 50 to 60 percent of the midstory structure. The midstory specialists can be related the species that demonstrate the routine ability to reach the status of small- to middle-sized tree commonly exceeding 4 meters in height.

The most convenient way to make a short comprehensive introduction of the subcanopy specialists of the beech-magnolia forest would be to subdivide their assortment into four major groups on the basis of their distribution patterns. One group represented mainly by the subtropical and, to the lesser extent, cool-temperate taxa shows a noticeable variation along the latitudinal gradient.

Another set of species which can be identified as the shallow-loess indicators, increase in importance from the Mississippi Bluff outward with the thinning of the loess mantle. A broad array of middle-size to small trees in the beech-magnolia forest appear to depend, to a varied extent, on certain types of natural disturbance. These respond in mosaic-like fashion to the local variations in the disturbance regimes. Related to this group can also be various sparsely distributed, localized and rare species which tend to congregate in the section of the Bluff Escarpment. Finally, to the forth group belong the species that are able to maintain the dominant status or, at least, are of regular occurrence in the subcanopy strata of all beech-magnolia forests.

The "Matrix" Association

Throughout the region, regardless the differences in edaphic conditions and disturbance regimes, the midstory of the late successional ravine forests is dominated by three relatively shade-tolerant cold-resistant temperate species, American hornbeam (*Carpinus caroliniana*), Eastern hophornbeam (*Ostrya virginiana*) and flowering dogwood (*Cornus florida*). These taxa together account approximately from one third to one half of the midstory structure and represent the most stable subcanopy component of the beech-magnolia forest. Two of them, American hornbeam and Eastern hophornbeam are worthy of reference as some of the most

broadly-distributed and cold-resistant Eastern American temperate trees. From nearly the Gulf coast these species extend as far north as the southern section of Ontario and the Saint-Lawrence River Valley where they are part of the northern hardwood-conifer assemblages in which beech is also present. Dogwood is a typical subcanopy component of various broadleaf deciduous forests from the southern tip of Ontario southward.

The successional status of *Carpinus-Ostrya-Cornus* association in the beech-magnolia forests causes some dispute. Platt and Schwartz (1990), for instance, refer to hornbeam, hophornbeam and dogwood as fugitive gap-colonizing pioneers. Indeed, all three species appear to benefit from gap dynamics but their responses to disturbance seem to be rather subtle. Seedlings of *Carpinus*, *Cornus* and especially those of *Ostrya*, apparently do need an exposure to some light in order to get established but all three species demonstrate a rather remarkable ability to form large midstory and understory populations under the closed canopy.

Among the late-successional sites, the population densities of these taxa generally tend to be larger in the assemblages with less developed beech-magnolia overstory and larger shares of the accessory trees but this indicates their preferential choice of more mixed-canopy forests rather than identifies them as pioneers. Moreover,

hornbeam, hophornbeam and dogwood are some of the very few and probably the most common of all subcanopy tree species that could be found persisting under the closed beech-dominated overstory in the most somber sections of the beech-magnolia forest. Such stands are characterized, of course, by much more sparse subcanopy growth but the dominant status of *Carpinus-Cornus-Ostrya* or *Carpinus-Cornus* association, always in combination with *Fagus*, remains here largely unchallenged.

Followed more frequently by *Cornus* and less frequently by *Ostrya*, *Carpinus* commonly is the most important member of this group. In the wide variety of habitats such as Tunica Hills, Port Hudson, Louisiana State Arboretum, Chicot State Park and Sicily Island it is also the most important tree in the midstory stratum. I observed that within almost any sampling area *Carpinus* generally tended to increase in importance downslope and congregate on the bottoms, while *Ostrya* increased in importance upslope and reached its peak on the hilltops. It poses the question whether the expansion of *Ostrya* is a function of the local edaphic changes (in this case it can be correlated with the transition to the better drained, drier upland soils) or it is stimulated by the highly successional nature of the secondary upland forests which are poor in, or devoid of beech and magnolia. Apparently, both factors are at play but the local change in the edaphic conditions appears to

be of special ecological significance for *Ostrya* does decrease toward the the wetter end of the mesic gradient. For example, I found that the relative importance of *Ostrya* in the moist ravines of Tunica Hills, despite pronounced physiographic disturbance of the local ravine slopes and gappy nature of the Magnolia Glenn forest, is essentially lower (2.7%) than in the less moist late-successional sites with better developed and more closed beech-magnolia overstory. The distribution of *Cornus* along the slope gradient seems to be more even, perhaps, with some increase toward its upper section.

Beech (*Fagus grandifolia*) is an unvariable component of the dominant "matrix" association in all late-successional midstory communities with the only exception of Chicot State Park where in the lake-slope forest its reproduction ability seems to be undermined by the hydrological disturbance. Although *Fagus* locally prevails over any other species in the midstory of beech coves and various other strongly overshaded areas, it frequenly loses to *Carpinus* the first-rank position in the overall subcanopy structure of the larger forest areas such as 1-hectar sampling units used in this research. *Carpinus* tended to take the upper hand in most of my plots, because, as a faster-growing species, it was able to take advantage of a wide range of successional situations always available at such a scale.

Subtropical and Evergreen Species

Beech, hornbeam, hophornbeam, and dogwood together form a general floristic background, which gives the interior of the beech-magnolia community so much of its somber and excessively cool-temperate outlook. Sharp contrasts of the beech-magnolia midstory become immediately evident where these distinctly cool-temperate taxa intermingle with the evergreen and subtropical species. Some components of this latter group are represented throughout the whole latitudinal extent of the southern Loess Hills. But the diversity and population densities of the subtropical species tend to increase gulfward in a way that they become structurally important only in the southern section of the beech-magnolia forest. In the Holarctic forests, the evergreen habit is most commonly found among those broadleaf trees and shrubs that are limited in their distribution to the zone of subtropical climate.

I make a deliberate distinction between the evergreen and subtropical taxa because not all evergreen trees of southern Loess Hills are subtropical in distribution and, vice versa, not all subtropical species are evergreen. There are three major species of evergreen subcanopy specialists characteristic the beech-magnolia forest - American holly (*Ilex opaca*), sweetleaf (*Simplocos tinctoria*) and Carolina laurelcherry (*Prunus caroliniana*).

One of them, American holly, is rather warm-temperate in its distribution. On the other hand, some decidedly subtropical midstory components of the loessial forests such as cowlick or two-wing silverbell (*Halesia diptera*) and pyramid magnolia (*Magnolia pyramidata*) are overwhelmingly deciduous. These two species are largely limited in distribution to the southern Gulf Plain only marginally extending into coastal South Carolina. Nevertheless both of them have close ecological and taxonomic counterparts in the forests of the Southern Appalachians which fact may give a hint about the origins of their deciduous habit. Two-wing silverbell is replaced in the latter region and adjacent sections of Piedmont by Carolina silverbell (*Halesia monticola*) which reaches there the size of a large canopy tree (Braun 1950).

Pyramid magnolia forms a close taxonomic pair with a highly localized south-Appalachian endemic *Magnolia fraseri* (Miller 1975, Treseder 1978). The morphological and genetic similarity between the two are such that pyramid magnolia was even suggested to have been a coastal plain variety of the letter taxon and given a synonymous name *M. fraseri* var. *pyramidata* (Treseder 1978). Still another subtropical tree, hercules-club (*Zanthoxylum clava-herculis*), conspicuous for its trunk covered with a thick armour of conical citrus-flavored spines, is characterized by the late-deciduous to semi-evergreen habit. *Zanthoxylum* is a

largely tropical genus that appears to be centered in the dry seasonal habitats of Mexico, Central America and - more marginally - in the American Southwest (Duncan and Duncan 1988). Given the biogeographic characteristics of the genus, it seems not surprising that its only Coastal Plain representative replicates some general leaf habits - such as folliage hardiness and persistence - of many semi-deciduous (but formerly, perhaps, evergreen) trees from the seasonal tropical forests.

Both pyramid magnolia and hercules-club are worth of reference as some of the most sparsely distributed and infrequent trees of the beech-magnolia forest. First found by William Bartram in coastal Geogria, *Magnolia pyramidata* is considered by Treseder (1978) as the second rarest species of *Magnolia* in the United States. Within our study region this tree is characterized by especially localized distribution - it was found exclusively in Tunica Hills. *Zanthoxylum* is a largely tropical genus with only two species in the eastern United States. Although somewhat less localized than pyramid magnolia, it was found only on 3 out of 8 late-successional sites, all within the moister section of the edaphic gradient. Only on one site was it represented by more than one specimen.

My impression is that the full-canopy stature and remarkable dbh sizes attained by pyramid magnolia and hercules-club in the old-growth forest of Magnolia Glenn

preserve are most likely a result of the unique set of the edaphic conditions and disturbance regimes characteristic for this highly eroded escarpment area. Other midstory specialists of Magnolia Glenn such as flowering dogwood, American holly and sweetleaf also reach here the size classes unparalleled by any other site except (but only for dogwood) the Steep Bluffs area.

The Role of the Light-Dependent Species

Generally speaking, nearly all subcanopy taxa, regardless how shade-tolerant they are, generally do better where more light is available in the subcanopy environment. The gappy forests with somewhat lower shares of beech and magnolia in the canopy tend to have more dense populations of the midstory specialists than do the more closed-canopy forests rich in beech and magnolia. Yet there is a large group of species whose dependence on light in the beech-magnolia forest is particularly pronounced. The most widespread of those are three relatively broadly-ranging temperate species, red mulberry (*Morus rubra*), devil's walkingstick (*Aralia spinosa*) and paw-paw (*Asimina triloba*). In the mesic to moist-mesic beech-magnolia forests they are commonly found in varying frequecies on nearly every 1 ha sample area.

All three exemplify different levels of shade-tolerance and strategies of dispersion. Devil's walkingstick is a typical fugitive species which is able to

germinate and develop only in the conditions of full or nearly full sunlight. Being overshaded as the gap is closing up, it immediately stops its growth, loses leaves and dies out. Consequently, *Aralia* is characterized by sparse, very spotty distribution always associated with relatively large breaks in the canopy. Paw-paw is also specialized on colonization of gaps and various sunny expositions. But, unlike devil's walkingstick, it seems to be capable of.germinating under nearly closed mixed-species overstory (areas strongly dominated by beech and magnolia are avoided) forming large populations of seedlings and small saplings in the lower midstory, roughly within up to 60 cm from the forest floor. These show ability to persist for some time in the conditions of dispersed sunlight but remain dormant or nearly so: their recruitment into higher layers of the understory and into the midstory depends on the availability of more or less direct sunlight. As a result, the high-understory to midstory populations of paw-paw tend to be clustered in relatively small pockets associated with gaps and various openings.

Due to the abundance of the potential recruits in the low understory, such congregations are characterized by essentially larger number of individuals than those of *Aralia* and almost any other midstory light-dependent species. In the older gaps paw-paw sometimes forms nearly monospecific higher-understory to lower-midstory stands.

Once the midstory size is achieved, paw-paw appears to become less sensible to the shortage of sunlight. Again, unlike *Aralia*, the larger individuals of paw-paw are able to continue their growth in partially or even almost completely closed gap as soon as at least some dispersed light is still available.

The third relatively common midstory species, red mulberry, although having been already mentioned among the species capable of reaching the overstory status, could also be listed as a subcanoppy specialist because of the variability of its life forms. Red mulberry is able to germinate under the closed canopy, sometimes in relatively somber conditions but its seedlings have an ephemeral lifespan unless not exposed to the sunlight. How much sunlight is needed not completely clear: my observations suggest that seedlings may survive and continue their vertical development under more ephemeral quantities of sunlight than those of two other species. Efficiency of recruitment may be higher in gaps, which is suggested by the larger midstory population of *Morus* in Magnolia Glenn and Steep Bluffs area, but gaps do not appear as crucial for red mulberry as they are for the other two species.

Generally speaking, mulberry can develop under relatively thin but closed mixed-species overstories. Yet the exposition does have its ecological significance. Depending on the availability of the sunlight, mulberry may

adopt two different growth forms. Its large-size canopy form characterized by tall trunk and elongated oval-shaped canopy seems to be associated with the old gaps where "lucky" individuals once avoided having been overshaded by other overstory species and managed to make a breakthrough into the canopy. Under closed or nearly closed mixed-species (but not beech-magnolia) canopy, mulberry tends to develop into the midstory life-form with relatively short trunk and broad, umbrella-shaped canopy well-suited to the conditions of dispersed sunlight.

Apart from the relatively common gap-colonizers, the loessial beech-magnolia forests also harbor a large assortment the rare, sparsely-distributed or highly-localized sun-loving species which includes persimmon (*Diospyros virginiana*), redbud (*Cercis canadensis*), black locust (*Robinia pseudoacacia*), winged sumac (*Rhus copallina*), smooth sumac (*R. glabra*), paulownia (*Paulownia tomentosa*), Chinaberry (*Melia azedarach*), paper mulberry (*Broussonetia papyrifera*), Chinese tallowtree (*Sapium sabiferum*), green ash (*Fraxinus pennsylvanica*), Carolina ash (*F. caroliniana*), roughleaf dogwood (*Cornus drumondii*), bigleaf magnolia (*Magnolia macrophylla*) and white walnut (*Juglans cinerea*).

Present in the list are more than a half of the midstory specialists by far found in the Loess Hills. This group includes both southern and relatively cold-resistant

temperate forms. Carolina ash is limited almost entirely to the low subtropical section of the Coastal Plain. Persimmon, bigleaf magnolia, paulownia, Chinaberry and paper mulberry are warm-temperate in distribution. Interestingly enough, the latter three species are East-Asian exotics which occur naturally in the mixed mesophytic forests of southern China. Most likely, they had been brought into the region during the Ante-Bellum Period and were originally cultivated as ornamental trees on plantations. Escaping from plantation and town gardens into surrounding wilderness, these exotics have gradually established self-sufficient forest populations thus contributing to the native flora.

The other five rare gap colonizers are temperate North American species characterized by relatively broad latitudinal ranges which extend from the vicinity of the Gulf coast to the Great Lakes region or nearly so: green ash extends to the northern boundary of the mixed "hemlock-hardwood" forest in southern Quebec and Nova Scotia, black locust and winged sumac can be found as far north as extreme southern Ontario, redbud terminates in southern Michigan and roughleaf dogwood extends to eastern Ohio (Duncan and Duncan 1988). Finally, white walnut is a component of distinctively cool-temperate interior flora. This species only very marginally extends onto the Coastal Plain and, perhaps, reaches the southernmost locations in

the eastern United States within the loessal belt. Among the subcanopy species of subtropical origin, two-winged silverbell, hercules-club, and pyramid magnolia also can be related to the category of the rare light-dependent midstory specialists due to their rather strong dependence on gaps and steep relief forms which allow a greater flexibility in avoiding obstruction by canopy trees.

Like in the case with the canopy species, the term "rare" implies here a rather broad spectrum of connotations: the above-mentioned species are rare in different ways and to a different extent. All of the species which I related to this category were found in only one or very few of the surveyed stands and all, except for bigleaf magnolia, were represented by characteristically sparse populations - typically one, more rarely two and only in a couple of cases - by three specimens per one hectare. Perhaps, the most conspicuous feature of this group's distribution pattern is that its members tend to be very strongly centered in the area of the Bluff escarpment.

The "most" genuinely "rare" appear to be two subtropical components, pyramid magnolia and hercules-club, which are occasional or highly infrequent throughout their narrow Coastal Plain ranges. The remainder of the above-mentioned species can be related to the category of the facultatively rare or habitat-rare trees. For persimmon, black locust, sumacs and Chinese tallow tree the limiting

factor is a late-successional status of the beech-magnolia community. These taxa are not uncommon in the various early-successional or strongly-disturbed vegetation types throughout the region but tend to be infrequent or extremely rare in the well-developed, tall forests. In the Tunica Hills sumacs and black locust typically colonize forest edges, various strongly disturbed areas and, again, wastelands. Both species appear to be intolerant to almost any overshading.

The presence of other species such as Carolina ash and roughleaf dogwood is suggestive of the bottomland connections. By contrast, bigleaf mognolia is adapted to the relatively poor and well-drained shallow-loess and non-loessial soils east of the Bluff Ridge and distributed rather broadly throughout the eastern shallow-loess margin of the southern Blufflands. Consequently, this taxon can be qualified as a "rare" species only for this section of the Blufflands but not for the areas east of the Bluff where, where, on the shallow-loess surfaces of Mississippi and southeastern Louisiana, it tends to be more or less common and locally even abundant.

On the southern, eastern and western periphery of the loessial mantle where sands and gravels of the Upland Complex (Autin et al. 1991) come closer to the surface, the dominant association include red maple (*Acer rubrum*) and sourwood (*Oxydendron arboreum*). Red maple is one of the

most cold-adapted temperate components of the mature forests ranging from the Gulf coast north almost to the southern boundary of the Canadian taiga. In the southern Loess Hills, this taxon seems to be represented by its southern form, *A. rubrum* var. *drumondii* which is limited to the lower Coastal Plain and Florida.

Sourwood is a moderately warm-temperate taxon centered in the south-Appalachian region, one of the distinctive components of the Mixed Mesophytic Forest Region (Braun, 1950). Extending along the Appalachian axis from West Virginia deep into the central portion of the Gulf Plain, this species reaches the extreme southwestern points of its distribution in the Homochito National Forest, in the Port Hudson area and in Sicily Island (Duncan and Duncan, 1988), without expanding, however, onto the loess-rich soils of the Mississippi Bluff proper. While the Port Hudson appears to be the southernmost point of sourwood's range, Sicily Island is the only locality where this taxon was discovered west of the Mississippi River (Duncan and Duncan, 1988). Both red maple and sourwood are moderately shade-tolerant species. They are nct necessarily associated with gaps and show ability to develop under closed mixed-species canopy except the spots overshaded by large beech and magnolia trees.

The Latitudinal Variation

Physiognomically, the midstory is one of the most "temperate-looking" layers in most beech-magnolia forests. The "temperate outlook" comes from the exceptionally important role of the *Fagus-Carpinus-Cornus-Ostrya* association and comparative scarcity of the evergreen and subtropical components - perhaps, with the only exception of the Tunica Hills area where the survived late-successional forests contain - in addition to the cool-temperate taxa just mentioned - relatively large populations of Carolina laurelcherry (*Prunus caroliniana*), two-winged silverbell (*Halesia diptera*), and American holly (*Ilex opaca*).

The presence of the subtropical species in the midstory of the beech-magnolia forest region generally tends to fade from the south to the north but not always it diminishes in a steady contiguous fashion. Some aspects of the site-by-site variation in abundance of the subtropical thermophiles may depend on the differences in the disturbance regimes. The overall relative importance of the midstory subtropical components, for instance, is highest - 19.5% - in the physiographically disturbed ravines of the Tunica Hills. It is here that the midstory subtropical thermophiles reached their highest diversity per unit area in the Loess Hills - 5 species per 1 hectare. From the Tunica Hills, the importance of the subtropical components

decreased to 15.7% in the beech-magnolia assemblage of the Port Hudson area and to 13.5% in the old-growth stand of Louisiana State Arboretum.

Among the southern sites, a rather strong negative deviation from the standard pattern was exhibited by the lake-slope assemblage of Chicot State Park where the aggregate importance of the subtropical components in the midstory was only 2.9%. Perhaps, the reproduction of some subtropical species, especially southern magnolia, was undermined here by the hydrological disturbance associated with the immediate proximity to the artificial Chicot Lake. In the northern part of the beech-magnolia region, the aggregate importance of the subtropical components sharply decreases and ranges from 1.8% in the Sicily Island site to only 0.4% (represented by *Magnolia grandiflora* only) in the Bluff Experimental Forest. North of Vicksburg, in the forests of the Steep Bluffs area the role of the subtropical life forms diminishes almost to a zero. The only subtropical tree found in one hectare sample of this forest site was a midstory-sized individual of *Zanthoxylum clava-herculi*.

The variation in the aggregate importance of the evergreen life forms (this assortment included American holly (*Ilex opaca*) but excluded the subtropical deciduous components) was characterized by a less conspicuous fluctuation. In all the southern sites, except for Chicot

State Park, the aggregate share of the evergreen species oscillated within a very narrow range - between 14.1% in the Tunica Hills and Port Hudson, and 13.5% in Louisiana State Arboretum. In the northern sites the evergreen midstory element was of negligible importance ranging from 0.9% in Sicily Island to 0.4% in the Bluff Experimental Forest.

The sharp decrease in importance of the subtropical and evergreen taxa occurs somewhere in the middle of the latitudinal extent of the beech-magnolia forest region, perhaps, north of Natchez, southwestern Mississippi. Port Gibson and Sicily Island sites are located already in the cooling "shade" of the "northern" zone.

Interestingly, most of the individual subtropical taxa showed a rather remarkable variation in population densities among the sites of even the same latitudinal category. This variation is particularly well profiled in the southern section of the loessial beech-magnolia forests. The subtropical taxa which are abundant in one southern site may considerably decrease in importance and even be replaced by another subtropical taxon or taxa in yet another southern site. In part, this variation may be associated with the differences in disturbance regimes. For example, *Prunus caroliniana* is structurally important only in the subcanopy of the Tunica Hills forest where it makes

up 7.6% of the lower midstory and 7.0% of the understory structure.

Outside the Tunica Hills, the more southern Port Hudson site exemplifies the only other late-successional forest where Carolina cherry was found in any substantial numbers but here its relative importance decreases to only 0.5% and 2.4% respectively. The moist, steep-slope forests of Tunica Hills are also characterized by exceptionally large population of *Halesia diptera*. This species is rather common throughout the southern and middle sections of the Blufflands - it makes up, in particular, 2.1% in the subcanopy of Port Hudson and 7.1% in the understory of Sicily Island forest. However, Tunica Hills is the only site where *Halesia* makes up as much as 10.5% of the lower midstory structure and attains the status of one of the four most important subcanopy dominants. Remarkably, both Carolina laurel cherry and two-winged silverbell are absent or nearly so in the beech-magnolia stand managed by the Louisiana State Arboretum.

Beyond my sampling plots I located here on slopes two understory-sized individuals of Carolina laurel cherry but, according to Glen Brown, the manager of the site, they were planted. The only individual of two-winged silverbell found in one of my plots was also likely to have been planted, although Glen Brown could not remember the exact time and circumstances of this case. The fact that neither of these

two species was also found in my nearby Chicot Bluff site suggests that they are generally absent from the entire region. Throughout Chicot Lake area Carolina laurel cherry and two-winged silverbell are replaced by sweetleaf (*Simplocos tinctoria*) which reaches the dominant status exclussively in the midstory stratum of the old-growth stand managed by the Louisiana State Arboretum and no other site.

Most of the subcanopy subtropical species do not extend into the nothernmost section of the beech-magnolia forest and many reveal the definitely south-centered patterns of distribution. One of the most conspicuous subcanopy evergreens, *Prunus caroliniana* is characteristic specifically of the southern and, to the lesser extent, the middle section of the "beech-magnolia" region, reaching the highest importance in the subcanopy of Tunica Hills forest and extending at least as far north as the southern end of the Natchez Trace where it occurs sporadically in the early-successional forests in the vicinity of the Emerald Mound. I failed, however, to find essential signs of *Prunus caroliniana* presence further north along the Bluff.

Two-winged silverbell, an important associate of Carolina laurel cherry in the subcanopy of the Tunica Hills and Port Hudson forests, is also absent on the northern fringe of the beech-magnolia region - in the Bluff Experimental Forest - but occurs in some moderately

northern sites such as Sicily Island. I noticed that within its range this taxon exhibits a rather peculiar latitudinal variation of its growth forms. In Sicily Island *Halesia* is one of the dominant understory components making up 7.1% of the shrub layer. As many as 225 understory individuals (of which 200 are less than 2 meters tall) of two-winged silverbell were found on one hectare sample area of this disturbed, gappy forest.

Theoretically, this site must have been characterized by one of the largest midstory population densities. Remarkably, only 5 individuals of *Halesia* were registered in the midstory stratum of the same site. Of course, the population densities of two-winged silverbell vary strongly throughout the beech-magnolia forest region. But even in the relatively "conventional" closed-canopy assemblage of the Port Hudson area *Halesia*, with its understory population densities as low as 27 individuals per one ha, was represented by 17 subcanopy trees. Under the more favorable disturbance regime characteristic for the ravines of Magnolia Glenn Preserve in Tunica Hills, the understory population of *Halesia* increases to 92 individuals (which is still less than in Sicily Island) while the equivalent number of the midstory trees increases to 66. One of the possible and most likely interpretations of this comparative trends can be based on the assumption that within the beech-magnolia region, *Halesia* responds to the

slight northward decrease of the winter temperatures first of all with the decrease of its midstory populations. Although this subtropical taxon is able to maintain large understory populations at least as far north as Sicily Island, only very few of understory individuals eventually reach here into the middle stratum - apparently because of the repeating action of more severe and probably more frequent freezes.

The local variation in midstory abundance of sweetleaf (*Simplocos tinctoria*), one of the few subtropical components which is found throughout the whole former beech-magnolia region, is generally latitudinal in nature but some aspects of its distribution are rather puzzling. Typically, *Simplocos* is relatively scarse in the midstory ranging from 7 specimens per 1 ha or 0.9% in Tunica Hills to 2 specimens per 1 ha or 0.3% in Sicily Island, with the Port Hudson site (4 specimens or 0.5% of the midstory structure) falling in between. On this general background, a somewhat exceptional abundance of *Simplocos* in the midstory of the Arboretum stand where this taxon is represented by 30 specimens per 1 ha and accounts for 6.4% of the subcanopy structure is rather startling.

The understory populations of *Simplocos* demonstrate more regular latitudinal dynamics. Sweetleaf is an important understory component throughout most of the "beech-magnolia" section of the Loess Hills extending north

to the Bluff Experimental Forest and terminating rather sharply some distance between the latter site and the Steep Bluffs area where not a single individual was found. The understory shares of this taxon decrease in more or less properly latitudinal fashion from 23.2% in the LSA stand and 10.2% in the Port Hudson forest to 6.9% further north in Tunica Hills, 5.6% in the ravines of Sicily Island and 1,6 percent in the Bluff Experimental Forest. Still, the surprisingly high population density of *Simplocos* in Louisiana State Arboretum (773 understory specimens per 1 ha as compared to 304 specimens in the next closest site in the Port Hudson area) left me wondering about the reasons for the uniqueness of the LSA stand. The dynamics of *Simplocos* in the Arboretum assemblage particularly perplexing given the fact of its comparatively modest population densities only about 1.5 miles away, on the lake-facing slope of Chicot State Park where I registered 120 understory and only 2 midstory individuals. Perhaps, the combination of the southern location and exceptionally old age of the LSA stand can be considered as the most likely reasons for its remarkably abundant *Simplocos* population.

A rather remarkable distribution dynamics are characteristic for the subcanopy populations of southern magnolia (*Magnolia grandiflora*). While being a dominant tree of the canopy stratum throughout most of its range,

magnolia plays a relatively important part in the midstory of only southern stands and decreases drastically northward - from 12.2% of relative importance in Port Hudson, 7.1% in Louisiana State Arboretum and 5.9% in the Tunica Hills to only 0.7% in Sicily Island and 0.4% in the Bluff Experimental Forest. The latitudinal decrease is particularly pronounced if the sizes of the sample populations are compared. The population densities of *Magnolia grandiflora* decrease from 52 and 48 individuals per 1 hectare in the Port Hudson and the Tunica Hills areas to only 5 individuals in the Sicily Island area and 2 individuals in the Bluff Experimental Forest. The sharp decrease of the population densities from the southern to the northern stands is also observed in the understory. Evidently, in the northern section of its natural range, magnolia experiences essential difficulties with reproduction and recruitment into the upper strata. This may imply a much higher vulnerability of these northern populations to even minor climatic fluctuations and anthropogenic disturbance. The boundary between the "northern" and "southern" patterns of *Magnolia* subcanopy distribution passes somewhere in the middle of the beech-magnolia forest region - perhaps, through the Natchez area or slightly north of Natchez.

Even in the southern sites *Magnolia* is no more than a second-order dominant species yielding in population

densities to beech (in LSA stand - also to sweetgum) and several major midstory specialists such as American hornbeam, Eastern hophornbeam, and flowering dogwood - plus paw-paw and sugarleaf in the LSA stand. Characteristically, the population sizes among the southern sites are essentially larger in the physiographically-disturbed assemblage of the Tunica Hills and second-growth assemblage of Port-Hudson than in the closed-canopy old-growth forests. In the midstory of Louisiana State Arboretum, for instance, magnolia is represented by only 19 individuals per hectare, i. e. by the sample population which is 2.5 times less than that of the Magnolia Glen preserve where 48 subcanopy specimens were registered.

Physiognomically, the most *Magnolia*-rich midstories are those of Magnolia Glen preserve in the Tunica Hills. The Port Hudson stand does contain more midstory magnolias but, remarkably, 45 (or 87%) of 52 midstory-sized trees were concentrated in the upper midstory, with the crowns "packed" immediately under those of the canopy trees. Thus, with the lower midstory population so remarkably sparse, the "middle space" of the forest looks here nearly as much pauperized in *Magnolia grandiflora* as in the northern stands. This rather unusual type of the population distribution among the strata seems to be indicative of the historical anthropogenic disturbance.

The overall pattern of the latitudinal dominance exemplified by the subtropical and evergreen species suggests that the beech-magnolia forests could be roughly subdivided into two parts: the southern half where the aggregate share of the subtropical and evergreen components are indicative of the "full-blown" structure of this forest type (such a forest was reconstructed for the Tunica Hills area by the Delcourts (1974); and northern half where the drastically decreased role of the subtropical and evergreen component suggests a more severe climate control. The latter are "marginal" beech-magnolia forests where the reproduction of the subtropical species and their recruitment into the upper strata becomes more complicated.

<u>The Species Increasing in Importance Northward</u>

Apart from the subtropical species, there are many species, primarily the canopy ones, that demonstrate more or less profiled north-centered distribution pattern. The midstory populations of American beech (*Fagus grandifolia*) in the second-growth beech-magnolia forests tend to increase from 25.2% in the Port Hudson area to 43.9% in the Bluff Experimental Forest and 53.3% in Port Gibson site. And so do few other less important accessory cold-resistant temperate species - white ash (*Fraxinus americana*), American basswood (*Tilia americana*), sassafras (*Sassafras albidum*), cucumber magnolia (*Magnolia acuminata*) which makes its first appearance in the subcanopy of the Bluff

forests north of Natchez, Mississippi, and gradually increases in importance further northward, as well as black walnut (*Juglans nigra*) which first appears in the subcanopy of the Steep Bluffs area. Within the deep-loess section of the Mississippi Bluff, white oak (*Quercus alba*) and blackgum (*Nyssa sylvatica*) also tend to increase in importance in the northern sites but this could be a function of some change in soil conditions.

In the closed-canopy beech-magnolia forests which are characterized by the most cool-temperate-looking midstories the aggregate importance of the cold-resistant temperate taxa ranges from 69.8% in the Port Hudson area and 75.0% in the old-growth stand of Louisiana State Arboretum to 89.4% in the Bluff Experimental Forest and 90.3% in Port Gibson site. The escarpment forests which are characterized by more mixed and heterogeneous midstory assemblages, the aggregate importance of the cool-temperate components is generally lower but in these forests, too, the role of the cool-temperate species increases from 60.4% in the Tunica Hills to 82.7% in the Steep Bluffs area.

The overall population densities of the canopy tree species in the midstrory stratum also tends to increase from the south to the north, at least in the closed-canopy forests - from 41.2% in Louisiana State Arboretum, 41.8% in Port Hudson, and 43.7% in the Tunica Hills to 66.0% in the Bluff Experimental Forest. The increase of the structural

importance of the canopy tree species occurs largely due to the decrease in diversity of the subcanopy specialists and increase of the population densities of the north-centered temperate tree species.

Remarkably, some warm-temperate tree species also demonstrate a trend toward the northward increase. Bigleaf magnolia (*Magnolia macrophylla*), for instance, appears only in the extreme northern Steep Bluff site beyond the range of southern magnolia. Although located in the section of the very deep loess deposits, the Steep Bluffs area is also marked by the somewhat increased importance of other species more typical for the shallow-loess margins of the Bluff, such as white oak and blackgum. It may suggest that the seemingly latitudinal distribution of bigleaf magnolia may be, in fact, determined by some specific properties of the soils of the Steep Bluffs area.

A more pronounced northern trend is demonstrated by southern sugar maple (*Acer barbatum*) which increases in importance from 1.2% in the Port Hudson area and 2.3% in the Tunica Hills to 3.2% in Port Gibson stand and finally culminates with 6.9% in the Bluff Experimental Forest. But the reasons for this variation do not necessarily involve a bioclimatic explanation. The point should be made that southern sugar maple shows the decided trend toward northward increase only in the closed-canopy stands; the escarpment sites are characterized by the lower population

densities and demonstrate no essential variation along the latitudinal gradient. It appears that southern sugar maple increases in importance northward not so much because of the progressive macro-climatic cooling trend but rather in positive response to the increasing importance of American beech.

Midstory Composition and Structure of the Moist-Mesic to Mesic Closed-Canopy Forests

The midstory stratum in the "conventional" closed-canopy beech-magnolia forests of the Loess Region is characterized by the exceptional importance of the "matrix" *Fagus-Carpinus-Cornus-Ostrya* association. The aggregate population density of the midstory individuals of these four species is always essentially higher in the second-growth than in the old-growth beech-magnolia forests, ranging from 49.8% in Louisiana State Arboretum to 60.3% in Port Hudson, and 73.9% in the Bluff Experimental Forest. Although the sample populations of all species increase, the most conspicuous increase in the northern stands is demonstrated by American beech which makes the first-rank dominant species both in Port Gibson stand (53.3%) and the the Bluff Experimental Forest (43.9%).

In the old-growth LSA stand and the Port Hudson assemblage where beech makes up respectively only 8.7% and 11.7% of the midstory stratum, the first-rank dominant species is *Carpinus* responsible for 20.3% of the midstory stratum in the Arboretum old-growth and 25.2% in the Port

Hudson area. The highest relative importance (28.1%) is achieved by American hornbeam on the lake-facing slope of Chicot State Park where it does not have to compete with beech in the midstory and much of the canopy is made up sweetgum and other not shade-tolerant species. The second-rank dominant taxon in the old-growth stand of Louisiana State Arboretum is *Cornus* but in most second-growth forests it is replaced either by *Carpinus* (Bluff Experimental Forest) or *Ostrya* (Port Hudson). *Ostrya* tends to increase in importance with the thinning of the loess mantle or raising relief.

Midstory strata of the closed-canopy forests may contain few other species but these are not permanent members of the dominant association: they replace each other from site to site depending on the latitude, site disturbance histories, the nature of adjacent habitats, and other circumstances. Southern magnolia typically occupies the niche of the second-order dominant species in the southern stands such as those of Louisiana State Arboretum and Port Hudson area. It should be emphasized that *Magnolia* population density in the closed-canopy old-growth stand managed by LSA are essentially lower than those of the "matrix" dominant taxa. With only 19 subcanopy individuals per 1 ha which is almost twice as less as beech, magnolia has comparatively high relative importance index (7.1%) only because of the low total number of midstory trees

available within this sampled area and its substantial dbh sizes.

The higher population densities exist in the southern second-growth forests such as the Port Hudson assemblage where *Magnolia* is represented by 52 subcanopy individuals responsible for 12.2% of the midstory structure. Evidently, this phenomenon is a successional syndrome: here magnolia probably had a chance to build up high subcanopy population densities during the period when the overstory was largely dominated by the light-dependent taxa. This is indicated by the fact that 45 out of 52 midstory magnolias were concentrated in the immediate subcanopy packing their crowns under those of tall overstory trees. When the closed shade-tolerant overstory became formed, recruitment rates of *Magnolia grandiflora* considerably decreased which is suggested by its exceptionally low population densities in the lower midstory (only 7 tress per 1 ha).

While the midstory strata of the northern beech-magnolia stands are conspicuously poor in *Magnolia* which is probably indicative of the problems related to the recruitment dynamics in the slightly cooler climate, southern sugar maple (*Acer barbatum*), on the contrary, increases in importance from the southern stands northward. This trend becomes noticeable in Port Gibson stand and culminates in the Bluff Experimental Forest where this taxon turns into one of the major members of the dominant

association. Increase of the midstory population densities of *Acer barbatum* to the level of the dominant midstory species is positively correlated with the structural increase of beech. Southern sugar maple seems to be one of the very few species which are positively associated with *Fagus*. The most likely explanation of this phenomenon is that beech fosters the development of large *Acer barbatum* populations by arresting the development of its more light-dependent competitors.

Sweetgum (*Liquidambar styraciflua*) is most likely to become one of the second-order midstory co-dominants in the moist-mesic to mesic sites which are immediately adjacent to the accessory floodplains. Typically, those sites where sweetgum is one of the dominant canopy species are also likely to have its relatively large subcanopy populations. Sweetgum, for instance is the second-order dominant species in Louisiana State Arboretum where it responsible for 6.9% of the midstory structure, and the first-order dominant on the lake-facing slope of Chicot State Park where it is responsible for as much as 16.7% of the subcanopy structure. However, it is not always the rule. For instance, sweetgum also co-dominates in the midstory assemblage of the Port Hudson area forming here two times larger sample population than in the midstory of the LSA stand.

Finally, some "random" species such sweetleaf or bitternut chicory may also assume the second-order dominant status in the midstory of certain mature beech-magnolia forests. The structural importance of such species may not be necessarily readily explained by some obvious factors and correlations.

The Case of the Tunica Hills. It was already pointed out that the ridgetops and some gentle slopes of the Tunica Hills area are characterized by an exceptional abundance of American holly (*Ilex opaca*). This feature is endemic to the Tunica Hills. Nowhere else American holly showed even remotely close population densities.

The subcanopy structure of the historical *Ilex opaca*-rich forests seems to have been quite different from the "conventional" closed-canopy beech-magnolia forests whose survived remnants we are more likely to observe today. In the small patch of the gentle-slope magnolia-beech-holly forest, which I discovered in the Tunica Hills Wildlife and Management Area, American holly made up as much as 56.5% of the midstory structure and 62.7% of the understory. The subcanopy of this small stand looked strikingly different from those of both the surrounding early-successional forest and any other late-successional assemblage in that it was overwhelmingly evergreen. With the addition of two other evergreen species, southern magnolia and Carolina

laurel cherry, the aggregate share of the evergreen taxa reached 67.2%.

American holly is able to produce a remarkably dense shade. The stands with the closed *Ilex opaca* midstory and overstory that I found in the Tunica Hills gave impression of some of the darkest and gloomiest forest type I have ever visited. In such stands holly seems to suppress the development of the "matrix" midstory species and probably somewhat complicates the recruitment of two dominant overstory species, American beech and southern magnolia. In the considered magnolia-beech-holly stand, the *Carpinus-Fagus-Cornus-Ostrya* association made up only 24.3% of the midstory stratum.

The Light-Dependent and Rare Subcanopy Specialists

Apart from the "matrix" cool-temperate taxa and several potentially important evergreen and subtropical components in the southern section of the region, the closed-canopy beech-magnolia forests are relatively poor in the midstory specialists. Only few light-demanding and even fewer rare and localized tree species were registered in these forests, and almost in all cases those were characterized by very low population densities. The midstory of the old-growth beech-magnolia forest managed by Louisiana Arboretum contained small populations of devil's walkingstick (*Aralia spinosa*), red maple (*Acer rubrum*), and red mulberry (*Morus rubra*) together responsible for about

1.5% of the subcanopy structure, as well as the large population of paw-paw (*Asimina triloba*).

The midstory of the Port Hudson assemblage was marked by the presence of only two conspicuously light-dependent subcanopy specialists - persimmon (*Diospyros virginiana*) and roughleaf dogwood (*Cornus drumondii*), each one represented by only one specimen. The Bluff Experimental Forest was characterized by the modest population density of red mulberry (0.9%), as well as the ephemeral presence of red maple (0.3%) and paw-paw (0.2%). Finally, each of the three mentioned sites was also marked by the sprinkling occurrence of oversized individuals of bigleaf storax (*Styrax americana*), an understory shrub which occasionally reaches into the lower midstory in the old gaps.

The Case of Louisiana State Arboretum. In one respect the old-growth forest of Louisiana State Arboretum represents a rather peculiar exception from the typical subcanopy pattern of the "conventional" closed-canopy beech-magnolia assemblage. In this forest I recorded the highest midstory population density of *Assimina triloba* (50 trees per 1 hectare) among all (not only closed-canopy) sites surveyed within this research. With the relative importance of 9.4%, paw-paw makes here the third major component of the dominant midstory association - along with American hornbeam, flowering dogwood, and beech. Such mixture of the "conventional" shade-tolerant species and

highly light-dependent pioneer in the dominant association is rather remarkable for the closed-canopy forest.

The nature of *Asimina* distribution in the Arboretum stand leaves no doubt that its currently high population density is, in fact, a very recent phenomena caused by the tornado strikes of 1995 and 1998. All larger specimens of paw-paw congregate in the spots where the canopy has conspicuous signs of fresh violent disruption. In contrast, the spared areas under the closed canopy are characterized by essentially "zero" subcanopy population of this species. Since the canopy gaps are still far from being filled, the local population of *Asimina* has a high potential toward further increase.

It appears that the sudden, abrupt change in the light conditions in a previously more or less closed-canopy beech-magnolia community stimulates a more vigorous response of paw-paw than does the perpetual physiographic disturbance in the steep-slope forests of the Bluff escarpment. *Asimina triloba* is a rather important midstory component of the ravine assemblages in the Tunica Hills and Steep Bluffs area, yet it is not so conspicuously abundant there as in the subcanopy of the LSA stand. One of the possible explanations for the abundance of paw-paw in LSA stand could be the fact that immediately following canopy disruption by tornado, this assemblage may have had more

area under fresh gaps or more gaps per unit area than typically has the Tunica Hills at any given period of time.

Interestingly enough, the anthropogenic disturbance associated with the large-scale destruction of the forest canopy typically does not result in the increase of paw-paw population densities in the early-successional regrowth which develops on such sites. On the contrary, nearly all early-successional forests are characterized by relatively low population densities of this species, particularly in the midstory. Preference for the small-scale, mosaic-like disturbance suggests that paw-paw is probably sensitive to the abrupt changes of the forest microclimate (both on the ground level and below) and loss (or intensive disturbance) of the upper humus layer which invariably happens due to plowing or severe post-clearcut erosion.

The Role of the Accessory Canopy Species

The midstory stratum of the beech-magnolia forest contains most of the canopy tree species present in the overstory. Quite typically, those mesic canopy species that play an accessory role in the canopy of the mature beech-magnolia forest, occupy the similar accessory niches in the midstory. In the midstory strata of the closed-canopy beech-magnolia stands, such accessory canopy species (beech, magnolia, sweetgum, and southern sugar maple are excluded from this list as the dominant or potentially dominant species) are represented by 13-17 species

responsible for about 10.9% to 18.5% of the midstory structure. With few exception, the subcanopy population densities of these taxa appear to depend on the degree of their shade-tolerance.

Those species which are able to develop under its own canopy such as bottomland chestnut oak, winged elm, white ash, as well as bitternut and pignut hickories are characterized by the comparatively high frequencies, ranging roughly from 7-8 to 13-15 subcanopy specimens per 1 ha. The most sizeable populations on the deep-loess sites are typically those of *Q. michauxii* ranging from 1.7% in Port Hudson to 2.1% in the Bluff Experimental Forest, winged elm and white ash ranging respectively from 3.7% and 1.1% in the LSA stand to 1.4% and 2.2% in the BEF stand, and bitternut hickory peaking to 5.8% in the Port Gibson site. In the northern sites, basswood and white oak also increase in importance, ranging respectively from 1.8% and 1.5% in Port Gibson site to approximately 1.3% and 1.4% in the Bluff Experimental Forest.

From the southern end of the Natchez Trace further northward along the Bluff there is a gradual increase of the midstory population densities of cucumber magnolia which is represented in the Bluff Experimental Forest by 4 individuals responsible for about 0.7% of the subcanopy structure. Red elm, although less shade-tolerant than the above-mentioned species, also tend to approach their

population densities ranging from 1.3% in Port Hudson to 1.0% in the BEF stand. It conspicuously expands in the midstory of the mesic slope forests immediately adjacent to the floodplains of the accessory streams ranging respectively from 3.7% in the LSA stand to as much as 5.2% on the lake-facing slope of Chicot State Park which is subject to the hydrological disturbance. In this respect, red elms shows the distribution trend similar to that of sweetgum. The major difference between these two species is the fact, that, unlike sweetgum, red elm fails to form any sizeable overstory populations: even in the sites where red elm is relatively important in the midstory, its overstory population densities typically range from only 1 to 2 specimens per 1 hectare. Apparently, even in the moist-mesic closed-canopy beech-magnolia forests the vast majority of *Ulmus rubra* trees never reach into the overstory stratum and are destined to die off in the midstory or understory.

By contrast, species totally dependent on gaps such as tulip tree, cherrybark oak, Shumard oak, water oak, sugarberry, sassafras, sycamore, and American elm are typically represented by very sparse populations, averaging from 1-2 to 3-5 specimens per 1 ha. To the latter category should be related some species which are able to develop under its own canopy but are generally infrequent in the overstory stratum or uncharacteristic for the moist-mesic

sites such as black cherry and blackgum. Typically, all the bottomland-centered species (except sweetgum and red elm) belong to the category of the sparsely distributed midstory components. Similar to red elm but to the lesser extent, sugarberry tends increase somewhat in importance only in the midstory of Chicot Bluff forest where the hydrological disturbance and canopy disruption produced by the recent tornadoes created more favorable conditions for its expansion. The midstory population densities of certain accessory canopy species such as basswood, white oak, and cucumber magnolia depend on latitude and increase in the midstory strata of the northern stands.

Midstory Composition and Structure of the Physiographically-Disturbed Moist-Mesic Forests

Within this section, the midstory assemblages have evolved in the conditions of extremely dissected physiography, permanent ravine erosion resulting in permanent small-scale disruption of the canopy stratum, and exceptionally moist microclimate. The physiographically-disturbed sites tend to have densier midstory populations - in part due to the abundance of gaps, in part because of the greater availability of dispersed sunlight. The vast majority of the midstory specialists demonstrate their preferential or exclusive choice for the moist, steep-sloped and physiographically-disturbed forests of the Bluff Escarpment. In overall, the Mississippi Bluff Escarpment is characterized by essentially more mixed and heterogeneous

associations of dominant midstory species than any other section of the Loess Region. The Escarpment forests also have far more diverse midstory assortments - both in terms of the total species numbers and numbers of the midstory specialists only - than any closed-canopy forest site.

In the Tunica Hills and Steep Bluffs, like elsewhere, the major dominants are again beech (*Fagus grandifolia*), American hornbeam (*Carpinus caroliniana*), and flowering dogwood (*Cornus florida*). These three species in aggregate make up 44.4% of the midstory structure in the Tunica Hills. Eastern hophornbeam (*Ostrya virginiana*) decreases in importance to only 2.7% in the Tunica Hills but remains one of the important dominant species in the Steep Bluffs area where it is responsible for 7.8% of the midstory structure. Throughout the whole Escarpment section the dominant association always includes sweetgum (*Liquidamabar styraciflua*) whose relative importance ranges from 5.1% in the Tunica Hills to 7.1% in the Steep Bluffs area.

In the southernmost section of the Bluff Escarpment exemplified by the assemblage of the Tunica Hills, the dominant association is additionally diversified by three subtropical species - two-winged silverbell (*Halesia diptera*), southern magnolia (*Magnolia grandiflora*) and Carolina laurel cherry (*Prunus caroliniana*) which collectively make up 17.4% of the midstory structure. Of course, these species also occur in the closed-canopy Bluff

forests. However, it is important to emphasize the fact that within their distribution ranges they contribute considerably to the midstory structure of only those sites that have perpetually disrupted overstories.

The comparison between *Magnolia* populations in the two old-growth forests is particularly indicative of this trend. While the midstory of Magnolia Glen assemblage in the Tunica Hills contained 48 subcanopy individuals of *Magnolia grandiflora*, the midstory strata of the LSA stand (which was until very recently a perfect sample of the closed-canopy beech-magnolia forest) had only 19. The lower midstory of the Port Hudson assemblage, which developed in the conditions of the closed-canopy beech-magnolia forest, had *Magnolia* population densities as low as 7 specimens per 1 ha which again was contrasting rather sharply with 34 specimens per 1 ha registered in the Tunica Hills. It is quite remarkable that, although being omnipresent in the southern half of the beech-magnolia region, Carolina laurelcherry and two-winged silverbell both reach the status of the dominant subcanopy trees only in the eroded ravines of the Tunica Hills where they make up, respectively, 4.5% and 7.7% of the midstory structure.

By contrast, their midstory population densities in the closed-canopy forests are typically rather sparse. For instance, while being represented by as many as 42 and 66 midstory individuals per 1 ha in the Tunica Hills, laurel

cherry and two-winged silverbell had respectively only 4 and 17 individuals in the midstory of the Port Hudson assemblage. It is not quite clear whether the exceptional importance of laurel cherry in the Tunica Hills Escarpment is stimulated only by the intense small-gap dynamics. Although this evergreen taxon benefits from numerous gaps, it also shows a relatively good ability to develop under the closed-canopy conditions. In the ravines of Magnolia Glen this species occurs relatively randomly throughout the forest, without showing much preference for the disturbed spots. In fact, as a relatively slowly-growing species, it is essentially less effective in colonizing gaps than the vast majority of the fast-growing deciduous taxa. I suggest that high population densities of *Prunus caroliniana* in the Tunica Hills may be additionally fostered by some special qualities of the local soils.

Unlike Carolina laurel cherry, *Halesia* is much more selective. Its distribution through the forest suggests a rather pronounced dependence on disturbance and steep relief forms characteristic for the escarpment. In the Tunica Hills this subcanopy specialist tends to congregate along the lower slopes and bottoms of steep ravines where it has higher chances to avoid being obstructed by overstory trees. In sections where the slope gradient is steep, the broad crowns of *Halesia* trees, alternating with those of the other species such as sweetgum, boxelder

maple, American hornbeam, and red mulberry, tend to form a loose quasi-canopy stratum 5-12 m high hanging over narrow bottoms. This stratum, with a distinctively dominant role of *Halesia* in it, is one of the eye-catching features of the Tunica Hills old growth.

Quite remarkably, neither Carolina laurel cherry nor two-winged silverbell appear to be stimulated by the anthropogenic disturbance. In the Tunica Hills, the upland early-successional forest does not contain midstory-sized individuals of silverbell and has the essentially lower midstory populations densities of laurel cherry (15 specimens per 1 ha) than the old-growth forest downslope in the ravines. The early-successional ravine forest along the Natchez Trace was characterized by the very sparse population of both laurel cherry and silverbell. It appears that both Carolina laurel cherry and two-winged silverbell are characteristic trees of the specifically mature, late-successional forests and may be in some cases considered as the important indicators of the ecosystem's antiquity and health.

American holly (*Ilex opaca*) is also more important in the midstory of the Tunica Hills old-growth ravine forest than in the midstory of any other stand, except the closed-canopy beech-magnolia forests of the Tunica Hills itself. But it makes up only 2.7% of the midstory structure and, unlike it was suggested by the Delcourts (1974), cannot

claim the status of the dominant species in the disturbed ravines, although apparently it could have done so on somewhat more stable ridgetops and gentle slopes. Another evergreen component, sweetleaf (*Simplocos tinctoria*), - despite its large understory population - has a relatively modest (0.9%) share in the midstory assemblage of the Tunica Hills which contrasts strongly with its importance in the subcanopy of the Arboretum stand. It appears that in most cases this species does not respond enthusiastically to the perpetual disturbance and, as a very shade-tolerant species, benefits more from the closed-canopy conditions which limit the competitiveness of more light-dependent taxa. In the Tunica Hills most of the midstory *Simplocos* trees were found in the poorly-lighted pockets of the forest under the closed canopy. It does not exclude, of course, the opposite examples. The largest and tallest specimen of *Simplocos* was registered, for instance, in the Tunica Hills and achieved here an exceptional size precisely because of the unique relief features of the area designed by the physiographic disturbance. This individual was found growing on the deposits of the loessial terrace created by the old medium-scale landslide.

It should be, of course, taken into consideration that all above-mentioned subtropical species, as well as subcanopy-sized form of American holly so peculiar to the

Tunica Hills, are completely lacking in the northern sample of the Escarpment forest - in the Steep Bluffs area.

The physiographically-disturbed Escarpment forests with their broken, perpetually disrupted overstories are also characterized by the high midstory population densities of paw-paw (*Asimina triloba*). By contrast, the closed-canopy late-successional assemblages (with the exception of tornado-struck LSA stand) such as the Bluff Experimental Forest typically have very low frequency of midstory-size individuals - this is despite the fact that such sites may harbor very large population pools of seedlings and small saplings. Ability of paw-paw to maintain large populations of potential recruits in the lower understory gives it an advantage over almost any other gap colonizer once disturbance event disrupts the canopy. The chronic disruption of the canopy stratum in Magnolia Glen and Steep Bluffs areas promotes the intensive and perpetual recruitment of paw-paw seedlings into the upper understory and subcanopy strata. Efficiency of *Asimina* recruitment into the subcanopy in the gappy, steep-slope forests of the Tunica Hills is suggested by the fact that, with the understory paw-paw population of about 81% of that of the Bluff Experimental Forest, the Magnolia Glenn Preserve has 8 times higher midstory population. The relative importance of paw-paw in midstory of the

Escarpment sites ranges from 1.3% in the Tunica Hills to 2.0% in the Steep Bluffs area.

The Escarpment sites are also characterized by the increased population densities of two other gap colonizers such as red mulberry (*Morus rubra*), which typically accompanies physiognomically somewhat similar two-winged silverbell on the lower slopes, and devil's walkingstick (*Aralia spinosa*) found throughout the forest in gaps.

The Rare and Highly Localized Subcanopy Specialists

One of the most conspicuous features of the physiographically-disturbed forests is exceptionally rich assortment of the rare or highy localized gap-colonizers. Of 12 species which can be categorized as rare, occasional or localized, 10 species were found in the physiographically-disturbed forests and 7 were endemic to these forests.

The assortment of the eroded ravines of the Tunica Hills represent the only late-successional community surveyed within this research where I found two highly light-dependent pioneer species, black locust (*Robinia pseudoacacia* L.) and winged sumac (*Rhus copallina* L.) common for young successional vegetation in recently disturbed areas but very unusual for the mature beech-magnolia forest. Persimmon (*Diospyros virginiana*), a warm-temperate pioneer tree indicative of the early stages of the forest succession on the abandoned fields but rare in

the closed-canopy communities, was likewise present in Magnolia Glenn. Pyramid magnolia (*Magnolia pyramidata*) represented mostly by the midstory-sized individuals and hercules-club (*Zanthoxylum clava-hercuis*) should be, of course, also mentioned among the subcanopy specialists highly dependent on disturbance: four out of five individuals of these two species were centered in the old slide gaps or grew on extremely precipitous, cliff-like slopes where no other tree could efficiently compete with them for light, and canopy was essentially disrupted.

Of a special interest was also the presence in this site of three warm-temperate exotic gap-colonizers native to Eastern Asia, pawlonia (*Paulonia tomentosa*), paper mulberry (*Broussonetia papyrifera*) and Chinaberry (*Melia azedarach*). The area of Tunica Hills escarpment is also marked by the presence of Chinese parasoltree (*Firmiana simplex*) but this species was found outside my sampling plots. Surprisingly, the Tunica Hills old-growth forest turned out to be the second richest site in the flora of exotic invaders in the Loess Hills leaving behind not only all other late-successional assemblages but also all early-successional anthropogenic forests with the only exception of Oakley Plantation.

Some relatively rare subcanopy species found in this area suggest both successional and edaphic trends. For instance, green ash (*Fraxinus pennsylvanica*), a prompt gap-

colonizer in the floodplain forests throughout nearly all eastern North America, indicates one of the many floristic between the Tunica Hills and the Lower Mississippi River Valley. Also found in Magnolia Glen was roughleaf dogwood (*Cornus drumondii*), a taxonomic counterpart of flowering dogwood in the midstory of the bottomland hydrophytic forests. The highly positive response of this species on disturbance in moist conditions is suggested by the fact that it nearly replaces flowering dogwood in highly successional ravine forest along the southern end of Natchez Trace.

Infrequent but steady occurrence of redbud (*Cercis canadensis*), sometimes represented by remarkably large individuals with dbh up to 42 cm, suggests both floral connections and edaphic similarities of the Tunica Hills area with the limestone-rich Low Interior Plateaus where this taxon is especially abundant. It appears that in the beech-magnolia forests, redbud is more dependent on gaps than in the limestone hills of Kentucky and southern Indiana where I observed large quantities of this species under relatively thin, mixed-species canopy composed of oaks, tulip trees and hickories. The benefits of the physiographic disturbance for redbud reproduction can be readily observed in the Magnolia-Glen forest where all seedlings and young understory individuals were found in the areas of the recent treefall, sometimes on the tip-ups

of the large collapsed beeches and oaks, and all large specimens, including one registered within the sample plot, were associated with the old gaps.

The similarly disturbed Steep Bluffs site north of Vicksburg is also characterized by a rich assortment of the light-dependent midstory trees which likewise includes redbud, persimmon, paulownia, paper-mulberry and hercules-club. Apart from these, it contains bigleaf magnolia (*Magnolia macrophylla*) which frequently attains here the stature of a canopy tree and white walnut (*Juglans cinerea*). Of all the mentioned "rare" species, bigleaf magnolia is probably the only one that has an ability to germinate and develop under the closed mixed-species overstory (largely in Homochito National Forest), although gaps are preferred. However, the reproduction of this tree in the Steep Bluffs area, where pine is absent and beech makes up a large portion of the overstory, is rather strongly limited to gaps.

<u>The Role of the Accessory Canopy Species</u>

Diversity of the accessory canopy species present in the midstory strata of the escarpment sites is also higher than in any closed-canopy stand. Potentially canopy components are represented by 23-24 species in Magnolia Glen preserve and by 25 species in the Steep Bluffs area. In the Tunica Hills, among the potentially dominant trees found in the subcanopy, there were two species - chinquapin

oak (*Quercus muehlenbergii*) and overcup oak (*Q. lyrata*) - which were not found in the overstory.

In comparison with the closed-canopy forests, the midstory strata of both sites were characterized by the increased populations of the bottomland and bottomland-centered species. In the Tunica Hills, the midstory stratum is especially rich in sugarberry (*Celtis laevigata*) (3.5%) which ranks eighths - immediately after sweetgum. Other bottomland-centered species with somewhat increased population densities are boxelder maple (*Acer negundo*) (1.6%), elms (*Ulmus rubra* and *U. americana*) (1.3%), and sycamore (*Platanus occidentalis*) (0.4%). Some more mesophytic species - and again, predominantly moisture-loving ones such as bottomland chestnut oak (2.7%) and water oak (1.5%) - as well as black cherry (1.4%) also have conspicuously increased population densities in the ravines of Magnolia Glen preserve. The midstory population of southern sugar maple (*Acer barbatum*) in Magnolia Glen, by contrast, tends to be smaller than in the closed-canopy Bluff sites (except the Port Hudson area). It appears that perpetual disturbance somewhat restrains the development of this shade-tolerant taxon as it facilitates the development of its more light-dependent competitors. Still, even with the somewhat lower midstory population densities (2.3%), southern sugar maple remains one of the major accessory components in the Tunica Hills subcanopy - next to sugarberry and bottomland chestnut oak. And so it also does

in the Steep Bluffs area. In the midstory stratum of this northern Escarpment site, the high importance of the bottomland-centered species (primarily, *Ulmus rubra*, *U. americana*, *Acer negundo*, *Platanus occidentalis*, and *Carya illinoensis*), as well as some common gap-dependent mesophytic species such as *Prunus serotina* was supplemented by the presence of the interior-centered temperate taxa - cucumber magnolia, black wallnut, American basswood, and sassafras.

Those mesic canopy species that play an accessory role in the canopy of the mature beech-magnolia forest occupy the similar accessory niches in the midstory. It implies that generally most (albeit not all) of the species which have vigourous midstory regrowth in the Tunica Hills are those represented by large or larger-than-average canopy populations. Similarly, many of those species in the Tunica Hills which demonstrate moderate or low overstory population densities such as bitternut hickory, pignut hickory, tulip tree, cherrybark oak, and American basswood tend to show moderate or low midstory population densities (in a 0.7:0.6:0.3:0.4:0.3 ratio) and no increase compared to the closed-canopy sites. Of course, the population densities of some species in the escarpment sites may also be influenced by latitude. For instance, the midstory population of water oak decreases from 10 specimens in the Tunica Hills to only 4 in the Steep Bluffs area. On the

contrary, the population of American basswood increases from 3 specimens in the Tunica Hills to 15 in the Steep Bluffs.

The Biogeographic Transition with the Tninning of the Loess Mantle

Change in the edaphic conditions from the main loess ridge outward appears to be responsible for the very conspicuous biogeographic change in the subcanopy of the beech-magnolia forest. The subcanopy strata of the deep-loess and shallow-loess communities are characterized by broad assortments of the mutually-exclusive or edaphically-centered species whose number and aggregate importance tend to increase from the canopy to the midstory and from the midstory to the understory.

The subcanopy strata of the moist-mesic sites are characterized by the presence of a very large assortment of species (as many as 27 found in the midstory strata only) which are absent or, perhaps, extremely infrequent in the peripheral shallow-loess forests. Their list includes first of all the undergrowth of many canopy trees that have been already listed in Chapter 9 - the vast majority of the moisture-loving mesophytes or bottomland-centered species such as southern sugar maple (*Acer barbatum*), American basswood (*Tilia americana*), bottomland chestnut oak (*Quercus michauxii*), American (*Ulmus americana*), sugarberry (*Celtis laevigata*), boxelder maple (*Acer negundo*) and sycamore (*Platanus oxidentalis*).

The aggregate relative importance of these exclusive or nearly so moisture-loving components in the deep-loess sites fluctuates from approximately 14.3% in the midstory of the Bluff Experimental Forest to 12.3% in the Tunica Hills old growth. In the Port Hudson area located in the transitional "slope" section their importance decreased to 5.5% but all species except boxelder maple were still present in varying densities. In the subcanopy assemblages of the two marginal sites, these species were either absent or represented by marginal quantities: of this group the Sicily Island contained a single individual of red elm, and a single specimen of bottomland chestnut oak was registered in Homochito National Forest.

Two relatively moist-mesic slope sites west of the Mississippi River, the old-growth ravine assemblage managed by Louisiana State Arboretum and lake-facing slope of Chicot State Park, were characterized by the impoverished subcanopy assortments of the "exclusive" moisture-loving trees. One of the very characteristic and locally abundant bluff species, southern sugar maple, seems to be absent from these western forests. Sycamore and boxelder maple (the latter being represented mostly by the understory to low-midstory growth form) occur in the adjacent accessory floodplains but do not appear to extend readily upslope into mesic slope communities as they normally do in the ravines of the Mississippi Loess Bluff. Finally, American

elm was found in neither section of the edaphic gradient, including the floodplains.

On the other hand, due to the presence of few other moisture-loving species, especially red elm, as well as bottomland chestnut oak, sugarberry and American basswood, the midstory strata of these sites resemble relatively closely those of the deep-loess areas. The undergrowth of the bluff-centered canopy species makes up respectively almost 11% in the midstory of Chicot State Park site where invasions of the moisture-loving components is more pronounced and 3.6% in Louisiana State Arboretum.

Interestingly enough, the midstory populations of two Coastal Plain oaks, *Q. nigra* and *Q. pagoda*, as well as sweetgum in the marginal sites do not show any considerable decrease in population densities compared to the moist-mesic sites, although such decrease is rather pronounced in the canopy strata. The midstory *Liquidambar* population in Sicily Island is even somewhat larger than in the Escarpment of the Tunica Hills and considerably larger than in Louisiana State Arboretum. This may suggest that many subcanopy specimens of the Coastal Plain oaks and sweetgum either slow down their development and never reach into the overstory or experience high mortality [rates] at the stage preceding to their recruitement into the canopy stratum.

The composition and the structure of the subcanopy stratum depends strongly on the combination of the edaphic

conditions and disturbance regimes. Of the potentially important midstory specialists, the nearly "exclusive" moist-mesic and Bluff-centered distribution patterns were demonstrated by paw-paw (*Asimina triloba*) and Carolina laurel cherry (*Prunus caroliniana*), among more sparsely distributed ones - by red mulberry (*Morus rubra*). Paw-paw abounded in almost any deep-loess Bluff site sampled within research, as well as in the moist ravines in the vicinity of Lake Chicot, but it was completely absent from my sampling areas in Sicily Island and Port Hudson, and it was very poorly represented in the ravines of Homochito National Forest. Red mulberry showed a decidedly Bluff-centered pattern of distribution with only minor occurence in the ravines of Louisiana State Arboretum, Chicot Lake Bluff, and Sicily Island.

Although Carolina laurel cherry (*Prunus caroliniana*) was reported from some decidedly non-loessial sites of the southern Gulf Plain (Quigley 1994), in our region, it was found exclusively in the forests of the Mississippi Bluff, with the peak in the Tunica Hills area of West Feliciana Parish, southeastern Louisiana. This delicate mesophyte may not be completely absent from Homochito National Forest but here its populations are greatly suppressed by periodic fires which is indicated by the presence of a remnant of a small laurel cherry stem burnt to the ground on one my sampling plots. Two-winged silverbell (*Halesia diptera*)

also shows a well-profiled Bluff-centered pattern of distribution, especially in terms of its large-sized subcanopy growth form. This taxon was found neither in the mesic ravines of the Chicot State Park and Louisiana State Arboretum west of the Mississippi River, nor within the thin-loess eastern margin of the Mississippi Bluff. However, *Halesia* cannot be related to the group of the "deep-loess specialists" *sensu strictu* for it was also found in large quantities in the ravines of Sicily Island.

Of 12 "rare" and localized midstory specialists registered in the moist-mesic forests of the Bluff Escarpment, only one - bigleaf magnolia - was shared with Homochito National Forest and none with the Sicily Island assemblage. Two species - persimmon and roughleaf dogwood - were shared with the Port Hudson assemblage. Finally, four species - paper mulberry (*Broussonetia papyrifera*), hercules club (*Zanthoxylum clava-herculis*), redbud (*Cercis canadensis*), and, again, persimmon - were shared with the Chicot Lake Bluff forest which also had a very complex disturbance history.

The Shallow-Loess Midstory Assemblages

On the southern, eastern and western peryphery of the loessial mantle where sands and gravels of the Upland Complex (Autin et al, 1991) come closer to the surface, the midstory association includes two very important indicator species - red maple (*Acer rubrum*) and sourwood (*Oxydendron*

arboreum) from *Ericaceae* Family. Generally speaking, red maple-sourwood midstory association is indicative of the edaphic zone where white oak (*Quercus alba*) and blackgum (*Nyssa sylvatica*) become important components of the overstory structure. With the further thinning of the loess mantles eastward and westward from the deep-loess section, sourwood and red maple further increase in importance within the marginal edaphic zone dominated by loblolly pine (*Pinus taeda*).

The spatial dynamics of red maple and sourwood raise some questions. The midstory share of sourwood increases from 2.8% in Port Hudson to 15.1% in the ravines of Sicily Island where *Oxydendrum* is the most important midstory tree yielding in frequency only to *Carpinus*. The similar increase is displayed by red maple which ranges from 2.1% in Port Hudson to 11.5% in Sicily Island. Finally, in the ravines of the Homochito National Forest where the beech-magnolia overstory is lacking, sourwood and red maple make up, respectively, 13.7% and 9.8% of the midstory structure. Thus the structural increase of both species occurs along the gradient of decreasing fertility and soil moisture and increasingly more favorable successional conditions which makes the degree of involvement of these two factors in the current biogeographic dynamics difficult to estimate.

The similar variation patterns were demonstrated by the midstory recruits of two major overstory edaphicators,

white oak (*Quercus alba*) and blackgum (*Nyssa sylvatica*). In the Port Hudson assemblage, the midstory population density of white oak is only 3 individuals (or 0,4% of the midstory structure) per 1 hectare which is a surprisingly thin population given its very high overstory importance. Blackgum is a more important taxon reaching as much as 1% of the midstory structure. Both marginal sites harbor the much more sizeable midstory populations of white oak and blackgum ranging from 4.8% and 4.9% in the Sicily Island area to, respectively, 5.6% and 6.9% in Homochito National Forest. With the thinning of the loess mantle, the aggregate importance of the "shallow-loess assortment" - even whith white oak excluded from the list for the sake of terminological "purity" - increases from 5.9% in Port Hudson to 31.9% in Sicily Island and 44.7% in Homochito National Forest. And so does its diversity. Apart from the major "shallow-loess specialists", the marginal sites are marked by the sprinkling presence of the less regular canopy xeromorphic species such as mockernut hickory (*Carya tomentosa*), red oak (*Quercus falcata*), and loblolly pine (*Pinus taeda*), with bur oak (*Q. macrocarpa*) limited to the Sicily Island and post oak (*Q. stellata*) represented in Homochito.

The midstory populations of all these taxa, with the exception of mockernut and red oak in Homochito National Forest, were represented in both sites by no more than 1-2

individuals per 1 hectare. The "thin-loess status" of the Homochito assemblage was, however, specifically emphasized by the presence of sweetbay (*Magnolia virginiana*), a species adapted specifically to poor and acidic soils of the non-loessial section of the Coastal Plain and characteristic of the forest communities developed in the coastal flatwoods and within the longleaf pine belt. Making up about 0.9% of the forest subcanopy, this taxon occurred occasionally in the ravines and shallow depression where the drainage must have been complicated by fragipan. Not unfrequently it was accompanied by communities of shrubs also indicative of poor drainage such as deciduous holly (*Ilex decidua*) and hawthorns (*Crataegus* spp.).

By contrast, the diversity and aggregate importance of "shallow-loess specialists" in the deep-loess and generally moist-mesic to mesic sites is very low. Four major species - sourwood, red maple, white oak and blackgum can be generally characterized as rare, very infrequent in or absent from the deep-loess forests. Sourwood is, perhaps, the most "alien" component: of all sites of the deep-loess section: here it was found in very small numbers only in the understory of the Steep Bluffs area where other "shallow-loess specialists" were also present. Red maple and blackgum are not completely lacking from the deep-loess sites but their frequencies everywhere are very low: one, sometimes two lower-midstory individuals per 1 ha.

The Tunica Hills, especially its Escarpment area seems to be particularly poor in all "shallow-loess specialists": blackgum was completely lacking from this area, whereas white oak and red maple each were represented here by a single low-understory sapling. White oak in very low densities appears in the midstory of the Natchez Trace forest and begins to increase gradually in the northern section of the beech-magnolia region reaching 1.5% in Port Gibson, 1.3% in the Bluff Experimental Forest, and 1.8% in the Steep Bluffs area. Of the less important xeric and xero-mesic species, only mockernut was found in the mature beech-magnolia forests of the deep-loess section (the Tunica Hills) but it was accompanied by no subcanopy population.

The highest (albeit still very modest compared to the shallow-loess sites) concentration and aggregate importance of the "shallow-loess specialists" among all deep-loess sites was registered in the midstory sample of the Steep Bluffs area north of Vicksburg where three most "loess-phobic" species (red maple, blackgum, and bigleaf magnolia) together made up 3.4% of the midstory structure.

Interestingly, the midstory strata of the shallow-loess forests are also considerably diversified by exceptionally large individuals of the typical understory shrubs. This trend is not characteristic of the forests developed within the moist-mesic section of the edaphic

gradient where occasionally only 1-2 oversized specimens can be found on the area of 1 hectare. In the shallow-loess forests, oversized shrubs, although not abundant in terms of numbers of individuals, are represented by a large number of species. Remarkably, the diversity of shrubs present in the midstory tend to increase with the thinning of the loess mantle. In the midstory of the Port Hudson forest understory specialists sampled on 1 hectare were represented by 7 exceptionally large individuals of yaupon (*Ilex vomitoria*), 3 stretched out specimens of bigleaf styrax (*Styrax grandifolius*), and 1 specimen of sparkleberry (*Vaccinium arboreum*). The midstory assortment of Sicily Island contained as many as 8 oversized shrubs - predominantly of "loessophobic" or distinctively upland varieties such as serviceberry (*Amelanchier arborea*), witch-hazel (*Hamamelis virginiana*), hawthorn (*Crataegus viridis*), arrowwood (*Viburnum dentatum*), and rusty blackhaw (*Viburnum rufidulum*) - but also some more or less broadly-distributed mesic species such as bigleaf styrax (*Styrax grandifolius*), Parsley hawthorn (*Crataegus marshalii*) and Mexican plum (*Prunus mexicana*). These were represented by 1-2 specimens per 1 hectare.

The midstory stratum of Homochito National Forest is also rich in oversized shrubs: here almost all their assortment is made up by the xeromorphic and upland species - yaupon, Carolina holly (*Ilex ambigua*), deciduous holly,

hawthorn (*Grataegus* spp.), arrowwood, and rusty blackhaw. Deciduous holly and Carolina holly tended to achieve the best development in the areas with complicated drainage but were also present on well-drained slopes.

The Diversity Trends

The overall midstory diversity of the subcanopy strata of the beech-magnolia forest appears to decrease somewhat along the latitudinal gradient due to the gradual dropping of the subtropical species northward. The northern margin of the former beech-magnolia region is particularly impoverished in subtropical taxa. The Bluff Experimental Forest, for instance, is lacking three common subtropical subcanopy trees, while the Steep Bluffs site does not have any except hercules-club. However, latitude is a relatively "weak" factor. It can be responsible for some variation only if compared are different sites within one physiographic or edaphic section.

On a larger scale of the Loess Region as a whole, the latitudinal pattern is inconsistent and easily obscured by the "strong factors", such as edaphic conditions, physiography, and disturbance, especially the physiographic disturbance. Regardless latitude, the physiographically undisturbed, closed-canopy forests strongly dominated by the shade-tolerant species tend to have the essentially lower midstory diversity than the disturbed forests with broken canopies. For instance, the midstory assemblages of

the Louisiana State Arboretum and the Bluff Experimental Forest, two sites located on the opposite margins of the beech-magnolia region, were found to contain, respectively, 25 and 26 tree species per one hectare. These two site samples are also characterized by the smallest assortments of the midstory specialists - accounting for 8 species in the LSA stand and only 6 species in the Bluff Experimental Forest. These somber, closed-canopy forests contain almost none (with the exception of persimmon registered in the overstory of the BEF stand) of those rare or sparsely distributed species that occur in the subcanopy of the steep-slope, physiographically-disturbed sites of the Bluff Escarpment, although they do have more common gap colonists such as paw-paw and red mulberry (in both sites), and (in the case of the LSA stand only) devil's walkingstick.

The biodiversity of the subcanopy strata in the Loess Region peaks in three sites characterized by the perpetual small-scale disturbance of the canopy stratum and representative of two very different physiographic and edaphic habitats - the Mississippi Bluff Escarpment and the Sicily Island area. The diversity of the midstory stratum is highest in the Escarpment forest in the Tunica Hills where as many as 43 species of trees were registered in a one hectare sample, among them 19 species of subcanopy specialists. This level of diversity is reached due to the presence in the Tunica Hills of a broad assortment of the

locally rare or sparcely distributed midstory specialists untypical of the closed-canopy beech-magnolia forest such as pyramide magnolia (*Magnolia pyramidata*), paulownia (*Paulownia tomentosa*), persimmon (*Diospyros virginiana*), redbud (*Cercis canadensis*), black locust (*Robinia pseudoacacia*), green ash (*Fraxinus pennsylvanica*), chinaberry (*Melia azedarach*), paper mulberry (*Broussonetia papyrifera*), winged sumac (*Rhus copallina*), and roughleaf dogwood (*Cornus drumondii*), as well as the rare canopy trees such as chinquapin oak (*Quercus muehlenbergii*) and overcup oak (*Q. lyrata*). The second-rank result - 13 species - was registered in Steep Bluffs site north of Vicksburg which also accomodates many light-dependent gap colonizers, many of them common with the Tunica Hills, but lacks the vast majority of the subtropical species.

The midstory of the ravine assemblage in Sicily Island site where thinning canopies of aging and dying pines create remarkable conditions for the development of the understory stratum contains 37 species and ranks second in general diversity. The major difference between this shallow-loess site and the perpetually disturbed forests developed within the deep-loess section of the Bluff Escarpment is in the number of midstory specialists available on 1 ha. By contrast with the escarpment assemblages, the sample of Sicily Island forest contained only 8 subcanopy trees. Apart from the "matrix" species of

the beech-magnolia forest, it was enriched by only two "shallow-loess specialists", sourwood (*Oxydendrum arboreum*) and red maple (*Acer rubrum*). The midstory diversity of the subcanopy specialists was somewhat higher in Homochito National Forest which contained several additional warm-temperate and warm-temperate to subtropical species such as American holly (*Ilex opaca*) (this taxon was represented in Siciliy Island only in the understory), bigleaf magnolia (*Magnolia macrophylla*), and sweetbay (*Magnolia virginiana*). Most of the shallow-loess specialists which contribute to the midstory diversity in both sites are represented by the undergrowth of the canopy trees (somewhat varied between the sites) such as blackgum (*Nyssa sylvatica*), mockernut hickory (*Carya tomentosa*), red oak (*Q. falcata*), post oak (*Q. stellata*), upland laurel oak (*Q. hemisphaerica*), bur oak (*Q. macrocarpa*), and loblolly pine (*Pinus taeda*).

Interestingly, much of the "surplus diversity" in the midstory of the Sicily Island and Homochito National Forest is made up by exceptionally large individuals of the typical understory specialists, both of xeromorphic and mesic varieties which were represented by as many as 8 species.

It is noteworthy that the assemblages characterized by the relatively high diversity of the midstory stratum all developed in the conditions of perpetual disturbance. Sites like Magnolia Glen preserve where such disturbance has

continued for the indefinitely long period of time tend to accumulate the most diverse and heterogeneous midstory assortments. The sites more or less continuously affected by some kind of post-anthropogenic disturbance also tend to have relatively high (but generally somewhat lower) diversity indices of the subcanopy strata. Both in Sicily Island and Chicot State Park perpetual disturbance is associated with the specific successional processes initiated by human agency. In Port Hudson, the similar effect may have been caused by recurring clearing episodes. During the last 140 years periodic disruptions of the canopy cover by humans modified the subcanopy strata of this forest by allowing the few understory specialists and some disturbance-dependent trees to get established or increase their frequencies in the midstory.

On the lake slope of Chicot State Park, the hydrological disturbance initiated the long-term process of canopy change (the replacement of beech by sweetgum). Coupled with the disturbance effect of two recent tornados this successional phenomenon created here favorable conditions for the development of the relatively species-rich subcanopy. The midstory of this site gave 32 species of trees some of which were quite unexpected for the beech-magnolia forest. The rise of the underground water table contributed to the upslope expansion of few bottomland and even swamp tree species such as Carolina ash (*Fraxinus*

caroliniana), bald-cypress (*Taxodium distichum*), and Chinese tallowtree (*Sapium sebiferum*). The sample has a rich assortment of the rare or sparsely distributed midstory specialists of which three - paper mulberry, redbud, persimon, and hercules club - are among the species present in the subcanopy of the Escarpment assemblages.

The fact that highest level of diversity of the subcanopy trees is characteristic specifically of the eroded moist-mesic assemblages of the Bluff Escarpment is rather remarkable. Why does perpetual disturbance not stimulate a comparable diversity of the midstory specialists in the peripheral dry-mesic forests? The answer to this question seems to be related to the fact that most of the subcanopy contributors which benefit from small-scale canopy disruptions in the Bluff Escarpment forests are the relatively moisture-loving species. These species either cannot be accommodated by the xero-mesic habitats or they behave here differently - by colonizing, for example, road edges or abandoned fields but not forest gaps.

Summary and Conclusions

The composition and structure of the midstory changes with latitude, physiograraphy, edaphic conditions and disturbance. There are five descrete midstory types characteristic for the beech-magnolia forest.

The midstory of the closed-canopy beech-magnolia forest is the stratum strongly dominated by the cool-

temperate taxa. The subtropical components become structurally important on the the southern section of the beech-magnolia forests. The midstory of the southern assemblages developed under the closed-canopy conditions are characterized by the high population densities of the warm-loving shade-tolerant taxa - *Magnolia grandiflora*, *Ilex opaca*, and *Simplocos tinctoria*. The southern end of the deep-loess section (the Tunica Hills area) appears to have been strongly dominated by *Ilex opaca* to the extent that this taxon seemed to have suppressed the reproduction of many other important midstory species. This is the only forest type where the matrix *Fagus-Carpinus-Ostrya-Cornus* association did not play important role. *Simplocos* seems to have reached the dominant status only in those stands where *Ilex opaca* was not important in the midstory. The northern beech-magnolia stands are all characterized by the greatly increased midstory population densities of *Fagus*. This midstory type is extremely poor in the evergreen and subtropical species and rich in *Acer barbatum*.

The midstory types characteristic of the Bluff Escarpment forests are different from those developed in the closed canopy communities. These are the most diverse midstory types that can be found in the Loess Hills Region, to begin with. They are almost twice richer in species than the midstories of the closed-canopy moist-mesic to mesic forests. Secondly, the escarpment midstory type is

characterized by a greater heterogeneity: there are more co-dominant tree species in this midstory than in the midstory of any closed-canopy forest. The great mixture of the shade-tolerant and light-dependent species is another pronounced feature of the escarpment midstories. Like in the closed-canopy forests, American beech (*Fagus grandifolia*), American hornbeam (*Carpinus caroliniana*) and flowering dogwood (*Cornus florida*) are here the most important dominant species (in fact, the latter two form somewhat larger populations than in closed-canopy forests). In addition, the dominant association of the Tunica Hills Escarpment contains three subtropical species: two-winged silverbell (*Halesia diptera*), Carolina laurel cherry (*Prunus caroliniana*), and southern magnolia (*Magnolia grandiflora*). Two former subcanopy specialists occur in the closed-canopy forests throughout the southern end of the Mississippi Bluff but this is the only midstory type in which they achieve such exceptionally high importance. Magnolia also has much larger subcanopy population in the forests of the Tunica Hills Escarpment than in the closed-canopy beech-magnolia forests.

The midstory strata of the escarpment forests are characterized by exceptionally high importance of two light-demanding canopy trees, sweetgum (*Liquidambar styraciflua*) and sugarberry (*Celtis laevigata*) which is indicative both of the disturbed conditions of these

forests and moist microclimate of the deep loessial ravines. By contrast, several species typically reach very high importance in the closed-canopy forests (*Ilex opaca* - in the Tunica Hills and *Acer barbatum* - in the more northernly stands), are less important in the assemblages of the Tunica Hills Escarpment - most likely due to their loss in competition to more light-dependent species. The failure to maintain high recruitment rates into the midstory] in Magnolia Glen assemblage is particularly conspicuous in the case of sweetleaf (*Simplocos tinctoria*). with its very high importance in the lower understory and sparse midstory populations.

The escarpment forests contain many species of subcanopy gap-colonizers. Some of them, particularly paw-paw (*Asimina triloba*), and, to a lesser extent, devil's walkingstick (*Aralia spinosa*) and red mulberry (*Morus rubra*) are conspicuously important in the midstory strata of these assemblages as compared to the closed-canopy forests. The escarpment forests are also characterized by the very diverse assortments of the rare, sparsely distributed, and highly localized species most of which were never registered in the closed-canopy forests. Although the presence of some rare or locally unusual subcanopy trees such as *Magnolia pyramidata* and *M. macrophylla* may be in part explained by the peculiar soil properties of the sites they were found in, the high

dependence of the vast majority of the species of this category upon direct sunlight seems to be the main reason for their high diversity in the perpetually disturbed escarpment assemblages.

The difference between the southern (the Tunica Hills area) and the northern (north of Vicksburg) escarpment sites is largely in the absence of the subtropical and evergreen species. *Prunus caroliniana* and *Halesia diptera* sharply decrease in importance north of Natchez and appear to drop from the species composition between Natchez and Port Gibson, Mississippi.

The *Carpinus-Fagus-Ostrya-Cornus* association is also a dominant matrix in the midstories of the forests developed on the shallow and thin loessal mantles, except the early successional assemblage of Homochito National Forest where beech is relatively unimportant. Nearly all forests of the mesic to dry-mesic end of the edaphic gradient demonstrate the structural increase of *Ostrya* and decrease of *Carpinus* which are particularly well-profiled in Homochito assemblage. The conspicuous compositional feature of both shallow-loess and thin-loess forests is high importance of two subcanopy and two canopy "shallow-loess specialists" - sourwood (*Oxydendrum arboreum*), red maple (*Acer rubrum*), blackgum (*Nyssa sylvatica*), and white oak (*Quercus alba*). These species generally tend to increase in importance with the thinning of the loess mantle from the southern slope of

the Mississippi Bluff to Sicily Island where all four species are part of the dominant midstory association. They retain the dominant status in the ravines of Homochito National Forest but here the population densities of sourwood and red maple somewhat decrease - most likely as a result of the controlled fires which occasionally extend from the loblolly-dominated uplands downslope. Another distinctive feature of the shallow-loess midstory types is a high diversity of the extra-sized understory specialists reching into the midstory.

CHAPTER 12

BIOGEOGRAPHIC VARIATION IN THE UNDERSTORY STRATUM

Shrubs have been typically paid comparatively little attention in the studies of the Coastal Plain mesic forests. Even less is our knowledge of the overall understory composition and structure of the Loess Hills forests.

The aggregate assortment of the understory specialists registered within this survey in the late-successional forest of the Loess Hills contains 36 species. It is characterized by more pronounced variation among the sites than assortment any other stratum. Shrubs and small can be subdivided into five major biogeographic groups.

Over a half of the understory specialists found in the beech-magnolia forests are represented by the southern forms with the warm-temperate distribution patterns. This group includes 15 species - such as storax (*Styrax grandifolius*), French mulberry (*Callicarpa americana*), Carolina buckthorn (*Rhamnus caroliniana*), buckthorn bumelia (*Bumelia lycioides*), deciduous holly (*Ilex decidua*), rusty blackhaw (*Viburnum rufidulum*), chalk maple (*Acer leucoderme*), fringe-tree (*Chionanthus virginicus*), Parsley hawthorn (*Crataegus marshalii*), southern haw (*C. flava*), *C. viridis*, Chicasaw plum (*Prunus angustifolia*), Eastern baccharis (*Baccharis halimifolia*), along with all three species of vacciniums (*Vaccinium elliotii*, *V. arboreum*,

V. stamineum) - which are known both from the Southeastern Gulf Coastal Plain and some of the older geological surfaces of the Upper Southeast.

Although frequently limited to the specific edaphic habitats and characterized by fragmented distribution and spotty occurrence, these warm-temperate species potentially may be found throughout the whole of most of the latitudinal extend of the Mississippi Bluff from Louisiana to Kentucky and southern tip of Illinois and thus seem to be unlikely to display any well-expressed latitudinal variation within beech-magnolia region. Red bucky (*Aesculus pavia*) is the only warm-temperate species with the distinctively Coastal Plain distribution pattern but its range, too, extends along the Mississippi Embayment north to Tennessee-Kentucky state line and into extreme southwestern Illinois.

The understory assemblage of the loessial beech-magnolia forests includes 7 species of more warm-loving subtropical shrubs native to the lower portion of the Coastal Plain. Of these, four species such as yaupon (*Ilex vomitoria*), chinese privet (*Ligastrum sinense*), wax-myrtle (*Myrica cerifera*), and, of course, bush palmetto (*Sabal minor*) are evergreen, while other two such as Virginia stewartia (*Stewartia malacodendron*) and Carolina holly (*Ilex ambigua*), are deciduous to semi-evergreen. One of the most peculiar among the semi-evergreen species is

trifoliate orange (*Poncirus trifoliata*), an East-Asian exotic shrub which became a part of the forest flora in the southern section of the Coastal Plain. Although shedding leaves for the winter like a regular deciduous component, this taxon continues to photosynthesize through its evergreen twigs and thorns.

Curiously enough, the understory of the southern and middle sections of the Loess Hills forests contain even one tropical species, *Erythrina herbacea*. This taxon tends to develop into a relatively large tree in the Caribbean rainforests and is known to reach the size of the small tree in southern Florida from where it spread to the southern Coastal Plain. As a tropical species, *Erythrina* is intolerant of any frost. North of Florida, tender twigs of this plant are killed to the ground by freezes almost every winter. To adapt to the harsher winters of the subtropical zone, the Coastal Plain variety of this plant adopted the life form of a dwarf perennial shrub and evolved an enlarged subterranean bulb-like stem. *Erythrina* tends to gravitate to the shallow-loess margins of the Loess Hills region but it was also found in the uplands of the Tunica Hills area.

Approximately 9 to 10 species of understory specialists present in the southern Blufflands are components of the cold-adapted temperate deciduous flora distributed over the eastern portion of the United States

and adjacent hardwood section of Canada. The ranges of two species, American elder (*Sambucus canadensis*) and serviceberry (*Amelanchier arborea*) project remarkably far north into southeast Canada embracing most of the region occupied by the northern mixed hardwood-conifer forest. The distribution of witch-hazel (*Hamamelis virginiana*) embraces the southern section of the same forest region. Three other shrubs, spicebush (*Lindera benzoin*), *Viburnum dentatum*, and strawberrybush (*Euonymus americanus*) range from the Gulf coast up to the extreme southern tip of Ontario. These are distinctive understory representatives of the temperate broadleaf forest flora. One temperate species, Mexican plum (*Prunus mexicana*) is centered in the region west of the Mississippi River extending here as far north as extreme southeastern Nebraska. This is an understory component of the somewhat drier hardwoods (such as the oak-hickory forests) of the forest-prairie ecoton. Occasional specimens of red cedar (*Juniperus virginiana*) which seems to be the only conifer species native to the Deep Loess section of the Blufflands may also be found in the understory of the slope forests. While reaching well into midstory on the disturbed upland rifges, this temperate conifer is limited in the ravines to the life-form of a small shrub.

Perhaps, the most omnipresent of all shrubby life-forms of the beech-magnolia forests is black raspberry (*Rubus* spp.) which may be represented by either one or few

closely related species. Although abundant, this semi-shrub was not quantified among with other shrub forms because of the physical dificulty to measure dbh values of its prickly sprouts. Besides, these sprouts are of rather ephemeral semi-woody nature, which makes most species of this group a sort of transitional between the real shrubs and herbaceous plants.

Latitudinal Variation of the Understory Specialists

The understory is potentially the most evergreen and the "most subtropical" stratum of the beech-magnolia forest. It is also a stratum where the latitudinal change is characterized by the most steep gradient. Despite the comparatively insignificant distance between Vicksburg and Port Hudson, the aggregate importance of the subtropical taxa present in the understory changes rather dramatically within the beech-magnolia region. The understory of the Port Hudson assemblage is nearly half evergreen (43%) and half subtropical: the relative aggregate importance of all subtropical elements here is 46.2%. The relative importance of the subtropical species then gradually decreases northward to 31% both in the physiographically-disturbed old-growth forest of the Tunica Hills and physiographically stable assemblage managed by the Louisiana State Arboretum.

The most evergreen understory (with the evergreens making up as much as 91.8% of the understory structure) is found within the small patch of the gentle-slope mature

forest in the Tunica Hills. But taxonomically this understory type is "less subtropical" than that of the Port Hudson area because it is heavily dominated by *Ilex opaca* (62.7%) which is warm-temperate in distribution. The aggregate importance of the subtropical components here is only 29.1%. A considerable decrease in the relative importance of the subtropical species occurs within the northern half of the southern Blufflands - to 14.9% in Sicily Island area, 12.2% in the Port Gibson site, and 4.1% in the Bluff Experimental Forest. The Steep Bluffs area's understory is completely lacking any subtropical components.

It should be noted that, the subtropical shrubs play a rather minor role in the understory structure of the forests developed on the deep loess mantles and vast majority of the moist-mesic sites in general. In the moist, deeply-dissected ravines of the Tunica Hills and further north along the Mississippi Bluff, as well as around Chicot Lake most of the understory subtropical populations are typically made up by the undergrowth of the subcanopy specialists such as *Simplocos tinctoria, Prunus caroliniana, Halesia diptera,* as well as saplings of *Magnolia grandiflora*. If understory specialists are considered alone, the latitudinal variation within the deep-loess section of the Mississippi Bluff is very gentle. Except for the ephemeral presence of Chinese privet, the

understory stratum on the northern edge of the beech-magnolia forest, in the Bluff Experimental Forest, is nearly devoid of the subtropical shrubs.

The only potentially subtropical species found in the slightly more northern Steep Bluffs site is trifoliate orange (*Poncirus trifoliata*), an East-Asian exotic shrub which became a part of the forest flora in the southern section of the Coastal Plain. Southward, along the Mississippi Bluff, the density and diversity of the evergreen subtropical shrubs slightly increases. Still, only 4 species (*Ligastrum cinense, Ilex vomitoria, Sabal minor*, and *Poncirus trifoliata*) were found in the ravines of the Magnolia-Glenn preserve and these together made up only 3.4% of the understory structure. In the understory of the similarly moist and heavily dissected Louisiana Arboretum site, the subtropical shrubs were represented by only two species - *Sabal minor* and *Ilex vomitoria* - which together made up only slightly more than 2.4% of its structure.

The diversity and structural importance of the subtropical shrubs generally tends to increase not only from the north to the south but also from the main bluff ridge to the areas underlain by shallower loess deposits. The distribution of yaupon is especially indicative of this trend. This species is centered in the maritime section of the Gulf Plain where it seems to achieve the best

development on relatively poor, frequently sandy soils. The distribution limits of yaupon in the deep-loess section seem to be shifted somewhat southward compared to its northern boundary in the areas where the loess mantle is either shallow or absent. For example, while *Ilex vomitoria* is relatively common in the southern section of the Homochito National Forest, within the Bluff Ridge it was not encountered on the forest sites located north of Tunica Hills. This species gravitates to the sloping southern margin of the Mississippi Bluff - its shallow-loess "shoulder" south of Saint Francisville.

Among all beech-magnolia sites, the best development and highest frequency of yaupon were documented in the Port Hudson forest where it makes up as much as 22,9% of the understory structure. The local environmental conditions appear to meet both of its requirements, that is the maximum geographic proximity to the warm maritime influences combined with the maximum edaphic proximity to the maritime sediments underlying the loess mantle. Only about 30 miles north, in the moist ravines of Tunica Hills area located in the southern end of the main bluff ridge understory importance of yaupon decreases to 0.7%: in this locality, the population densities of *Ilex vomitoria* and general vigor of its individuals tend to increase from the lower and middle ravine slopes to the ridgetops.

The understory of the beech-magnolia forest in the Sicily Island area which is likely to be a biogeographic counterpart of the Port Hudson site in the northeastern part of Louisiana does not contain yaupon because it is located apparently too far north from the climatic optimum of this warm-loving maritime species. Yaupon continues to increase in importance further southward along the Bluff - despite the trend to the moister and more poorly drained soils. Along with Chinese privet, *Ilex vomitoria* is a dominant species in the understory of the Burden Plantation where it makes as much as 20.5% of the understory structure. It appears that this shrub equally prefers marginal sites with either excessively well-drained or poorly-drained soils (as long as they are located within the zone of its bioclimatic optimum) but cannot buil up high population densities in the middle - on the fertile and moist but relatively well-drained soils of the deep-loess section.

The understory importance of another subtropical shrub, *Stewartia malacodendron*, decreases from 4.1% in the Port Hudson forest to 1.2% in the ravines of Sicily Island. Interestingly, that the structural share of the temperate associate of *Stewartia*, serviceberry decreases in the opposite direction, from Sicily Island (0.9%) to Port Hudson (0.03%). As for *Myrica cerifera* and *Ilex ambigua*, these taxa are sparsely distributed and play relatively

insignificant role in Sicily Island and Homochito National Forest, although there is an obvious trend toward their ctructural increase from Sicily to Homochito.

The strong subtropical flavor to the understory of the beech-magnolia forest is given by the occasional presence of bush palmetto (*Sabal minor*). Although relatively infrequent throughout most of the Loess Hills Region and confined here largely to the moist ravine bottoms, this dwarf palm is commonly present on almost every 1 ha site, except the northernmost section in the vicinity of Vicksburg where its population seems to become more sparse. In the ravines of the Mississippi Bluff Ridge, I did not register this subtropical species north of the Bluff Experimental Forest (where its population was very thin and I observed it only in a couple of instances - and each time outside of my sampling plots). Interestingly, in the more bottomland habitats *Sabal* remains competitive as far north as Poverty Point, northern Louisiana, and probably extends well into southern Arkansas.

The Understory Shrub Assortments of the Extreme Southern Extensions of the Loess Region

The most distinctive feature of the understory strata in the forests developed on the southern margin of the Mississippi Bluff, in East Baton Rouge Parish, is a remarkable increase in importance of the subtropical evergreen components, especially bush palmetto. Like in the case with yaupon, the structural increase of *Sabal* at the

southern edge of the Loess Region is a combined result of climatic and edaphic change related to the proximity of the Gulf of Mexico and lowering relief. As the latitude and relief decrease south of the Port Hudson area and the poorly drained Terrace deposits come closer to the surface due to the thinning of the loess mantle, the upland loessial habitats begin to experience an increasing pressure from the bottomland flora.

The hardwood bottomland forests bordering the southernmost extensions of the Loess Bluff have a vigorous palmetto understory, and, with the change of edaphic conditions and increasing influence of the tropical maritime airmass, *Sabal minor* turns into one of the most "enthusiastic" colonizers of the upper grounds. This taxon becomes a regular component of the understory structure in Hooper Forest (northern Baton Rouge) and assumes the status of one of the dominant species in Burden Plantation where it is responsible for as much as 24.4% of the understory structure.

The structural increase of two other subtropical species - yaupon (*Ilex vomitoria*) and Chinese privet (*Ligustrum sinense*) contribute to the evergreen and predominantly subtropical status of the understory stratum of this forest. Numerically, *Ligustrum* and *Ilex* predominate here over palmetto and any other species present in the understory. This understory type is in many respects - as

strongly dominated by shrubs and, most notably, by the subtropical shrubs - very different from those of the "classical" beech-magnolia forests further north. In Burden Plantation subtropical components aggregately make up as much as 88.6% of the understory structure. Secondly, unlike those of the "conventional" forests, this understory type is characterized by the comparatively low shrub diversity and prevalence of the bottomland-centered species. The few important accessory shrub species present in Burden are French mulberry (*Callicarpa americana*), deciduous holly (*Ilex decidua*), and waxmyrtle (*Myrica cerifera*).

The progressive generic impoverishment of the understory stratum is a characteristic trend of the loessial forests on the Mississippi Bluff south of the Port Hudson area and Opelousas Ridge south of Opelousas. Missing from these forests are many mesic, let alone sub-xeric shrubs of both cool-temperate and warm-temperate origins characteristic of "conventional" beech-magnolia forests.

The effect of diversity loss along the southern extensions of the Loess Region is very similar to a decrease in number of species, which occurs along many peninsulas and is known as the *peninsula effect* (Simpson 1964). Indeed, the southern extensions of the Mississippi Loess Hills resemble peninsulas of the upper ground, extending deep into the bottomlands and marshes of the Mississippi River Delta. The reasons for species loss are,

to a large extent, edaphic and physiographic (i. e. related to the decrease in complexity of the relief forms), in part - which is especially likely for the cool-temperate shrubs - bioclimatic (i. e. related to decreasing latitude and increasing influence of the tropical maritime airmass).

Another possible reason is generic competition. All three dominant species of Burden Plantation understory - Chinese privet, yaupon, and bush palmetto - have vigorously developed root system which may greatly affect the distribution of the other shrub species. Introduction of *Ligustrum* some time in 19th century - initially as an ornamental plant - is likely to have contributed to the considerable change of forest understories throughout much of East Baton Rouge Parish.

West of the Mississippi River and further gulfward, on the small isolated or nearly isolated upland surfaces of the salt-dome islands and southernmost extensions of Opelousas Ridge surrounded by the extensive bottomland landscapes of the Mississippi Delta, *Sabal* rules unchallenged. Throughout much of the surviving forest in Avery and Jefferson islands, it represents, perhaps, the most important understory species. In the understory of Forked Island assemblage the dominance of bush palmetto is overwhelming to the extent that it essentially suppresses the reproduction of the other components of the shrub layer and alone makes up 77.7% of the understory structure.

Because of the abundance of *Sabal*, the whole extreme southern margin of the Loess Region - including the southern half of Opelousas Ridge, as well as the salt-dome islands and Forked Island further south and southwest can be qualified as domain of a truly subtropical "palmetto" forest. It is, perhaps, the most structurally unusual and generically poor understory type present in the Loess Region.

Understory Dynamics of the Canopy Subtropical Species: the Case of Southern Magnolia

The understory dynamics of southern magnolia (*Magnolia grandiflora*) resemble those shown by this species in the midstory strata. Magnolia tends to accumulate relatively large population densities in the southern sites and decrease drastically in the northern section of the beech-magnolia region. The relative importance of magnolia in the understory fluctuates from 8.1% in the Tunica Hills and 5.2% in the stand managed by the Louisiana State Arboretum to 2.4% in the Bluff Experimental Forest and 0.6% in Sicily Island. The question may rise about certain discontinuity in the pattern: indeed, the more northern site of the Bluff Experimental Forest had 44 saplings of *Magnolia*, whereas more southern Sicily Island - only 18. In reality most of the registered "saplings" in both sites were sprouts growing from the underground parts of big trees. Of the treelets registered in Sicily Island, 10 were real saplings, of those found in the understory of the BEF

assemblage only 8 were "guaranteed" saplings developed from seeds.

For comparison, of 111 Magnolia treelets found in the understory of Magnolia Glen preserve, as many as at least 81 were "real" saplings. Of 145 registered in the understory of the LSA stand, about 100 were "real". This statistic reflects the drastic reduction of the reproductive efficiency of Magnolia in the northern section of its range and confirm the conclusion about "marginal" - in reproductive sense - and thus ecologically fragile equilibrium state of the northern beech-magnolia forests. It appears that in the northern forests magnolia tends to rely more on vegetative reproduction as a way to compensate for the smaller number of propagules and their greater loss. Most of the sprouts in the Bluff Experimental Forest were registered in the vicinity of two-three large trees only. Canopy-size magnolia trees tend to frequently develop an "aura" of sprouts around the trunk but in the BEF site this feature of the large individuals of *Magnolia grandiflora* was particularly pronounced. The result was, of course, highly clustered distribution of *Magnolia* understory growth as compared to the southern sites in which the distribution throughout the area was much more even.

The most immediate reason for such drastic latitudinal population reduction involves latitude and related

differences in winter temperatures among the southern and northern sites. Longer and stronger freezes in the northern portion of the former beech-magnolia forest region appear to be the primary factor involved. Although by no means irrelevant, this assumption can be supplemented by some accessory considerations. Having spent much time on my sampling plots, I observed, among other things, the behavior and browsing of the wildlife on *Magnolia* seeds. Part of the problem of *Magnolia* propagation may be related to the animal factor. In general, magnolia seems to be far less successful propagator than beech and many other trees. Its seeds are relatively large and far more attractive to wildlife than those of almost any other species. The fact that they come sealed in large "cones" also facilitates predation for *Magnolia* cones are fewer, larger and more conspicuous than fruits of the other trees. Consequently, magnolia may well experience highest "predation pressure" in the forest. In the fall, predation of *Magnolia* seeds reaches its apogee in the beech-magnolia forest. The vast majority of seeds never even reach the ground being consumed by squirrels immediately on fruit-bearing trees. Squirrels are followed by chipmunks and birds who collect seeds from the ground and, in fact, save some of them by burring. Generally, the predation of *Magnolia* seeds appears to be much more thorough than that of any other species.

In the more southern sites, a larger number of magnolias provide a larger amount of seeds. But with fewer trees of *Magnolia* available for a unit area in the northern sites and a thorough nature of predation, the number of survived seeds may be close to a critical value behind which magnolia, in the long-term perspective, would not be able to maintain its population in the forest. My hypothesis is that the animal predation represents, in fact, a very important secondary factor which may influence the biogeographic range and population densities of *Magnolia grandiflora*. Long-term and short-term fluctuations of climate and dynamics of the animal populations work together to shape and reshape the depth of the marginal zone contributing to the expansion or shrinking of *Magnolia* populations.

Latitudinal Variation among the Temperate Shrub and Tree Species

The latitudinal dynamics of the temperate taxa also play a rather important role in the understory structure. One of the cool-temperate shrub species conspicuously affected by the latitudinal variation is spicebush (*Lindera benzoin*). Its relative importance increase northward from 0.1% in the understory of the Arboretum stand and 3.7% in the Tunica Hills to 8.8% in the Bluff Experimental Forest. Understandably, this change is only evident in the moist-mesic forests, predominantly those of the deep-loess section of the Mississippi Bluff because spicebush does not

occur in the xero-mesic sites. Within the shallow-loess section, one can observe some essential structural differences between the forests of the sub-maritime zone exemplified by the assemblage of Port Hudson area, and their more northern and interior counterparts represented by the assemblage of Sicily Island. Of particular interest here are the paired latitudinal dynamics of warm-temperate *Vaccinium elliottii* and subtropical *Ilex vomitoria*. Both species are characterized by essentially similar growth forms, light preferences and modus of expansion which fact suggests that they occupy the same ecological niche.

Elliott's blueberry completely replaces yaupon in Sicily Island where it is a first-rank understory dominant making up 15.7% of the understory structure. As the competitiveness of yaupon increases gulfward, the populations of Elliott's blueberry shrinks. In the understory of the Port Hudson site where *Vaccinium elliottii* is largely replaced by yaupon its relative importance decrease to only 1,3%. The understory assemblage of the Homochito National Forest, where *Ilex vomitoria* is present but not as nearly as important as in the Port Hudson area, represents the transitional stage between the two mentioned extremes.

Within the deep-loess section, the understories of the beech-magnolia sites reflect the northward increase of the structural role of the canopy taxa - from 28.2% in the

Tunica Hills to 56.4% in the Bluff Experimental Forest. There is also a general northward increase in the aggregate structural importance of all cool-temperate understory growth forms which which is especially "steep" within the the moist-mesic to mesic section of the edaphic gradient where it progresses from 50.6% and 52.8% of the understory structure in the Louisiana State Arboretum stand and the Tunica Hills to 76.7% in the Bluff Experimental Forest.

The understory assemblages developed on the shallow loess mantles are characterized by the generally lower (largely because due to the marked presence of warm-temperate and subtropical shrubs), but also increasing aggregate importance of the cool-temperate components - from 31% in the Port Hudson area to 43.8% in the Sicily Island.

Edaphic Preferences of the Understory Specialists

One of the most conspicuous gradients of floristic variation between the understory assortments is associated with the variation in depth of the loess deposits from the main bluff ridge to the periphery of the loessial mantle. The related difference in edaphic regimes resulted in the development of two essentially distinct congregations of species.

The understory assemblages developed within the Deep Loess Section, on the soils characterized by the relatively high water-retention capacity, are dominated by a rich

assortment of mesophytes and moisture-loving species. Of 21 species of the understory specialists registered here, at least 4 species such as oakleaf hydrangea (*Hydrangea quercifolia*), spicebush (*Lindera benzoin*), elderberry (*Sambucus canadensis*), strawberry bush (*Euonymus americana*) and Chinese privet (*Ligastrum sinense*) seem to be strongly centered in the area of the central ridge and one species, chalk maple (*Acer leucoderme*), appears to be limited in its distribution to Tunica Hills. Apart from these "deep-loess specialists", the forests of the bluff ridge also contain the large assortment of the less delicate mesophytes such as bigleaf storax (*Styrax grandifolius*), French mulberry (*Callicarpa americana*), Carolina buckthorn (*Rhamnus caroliniana*), buckthorn bumelia (*Bumelia lucioides*), red bucky (*Aesculus pavia*), Mexican plum (*Prunus mexicana*) and Chicasaw plum (*P. angustifolia*) which are shared with the understory assamblages of the Shallow Loess Section.

The diversity of the shrub flora of the Mississippi Bluff can be in part attributed to the fact that this area is a meeting ground for the species with remarkably different edaphic requirements. Some taxa present in the ravines of the Bluff Ridge, such as already mentioned spicebush, elderberry and Chinese privet, along with deciduous holly (*Ilex decidua*), bush palmetto (*Sabal minor*) and Parsley hawthorn (*Crataegus marshalii*) are components of the bottomland-centered flora which extend here from the

lower grounds of the Mississippi River Valley and its accessorry floodplains.

The Mississippi Loess Bluff is probably one of the few, if not the only region of the Coastal Plain where such pronounced "bottomlander" as bush palmetto may occasionally be found on the slopes and even hilltops. On the other hand, some pronounced "uplanders" such as rusty blackhaw (*Viburnum rufidulum*), witch-hazel (*Hamamelis virginiana*) and yaupon (*Ilex vomitoria*) also occur in the both sections. Being well-adapted to the relatively low fertility and faster drainage of the soils developed on the sandy and sandy-loam deposits, these species appear to be more characteristic for the non-loessial surfaces of the Gulf Coastal Plain but retain their competitiveness in the moist ravines of the bluff ridge. Within the Deep Loess Section they gravitate ecologically to the upper slopes and hilltops.

It should be pointed out that the forests of Deep Loess Section are characteristically poor in *Ericaceae* and essentially devoid of such genera as *Azalea*, *Kalmia* and *Rododendron* which are very important in the Mixed Mesophytic Forest Region and throughout the sandy soils of the Gulf-Atlantic Coastal Plain.

The forests developed on the periphery of the loessial mantle are characterized by their own, very distinctive assemblage of the typical understory species. In relation

to the forests of the Mississippi Bluff, these can be conceived as "peripheral" species many of which are shared with the forests on the well-drained non-loessial surfaces throughout the remainder of the Gulf Plain. Generally, the nature of the shrub assortments found in the shallow-loess areas correlate relatively well with the idea of "two-step" subdivision of the shallow-loess zone into the intermediate white oak-blackgum-sourwood-red maple shallow-loess section proper and the broad thin-loess margin where the indicator species are, apart from those mentioned above, loblolly pine, upland laurel oak, and bigleaf magnolia. To identify these sections at the level of shrub communities, one should differentiate the shallow-loess zone "generalists", i. e. the shrubs which tend to occur throughout the whole shallow zone east and west of the Mississippi Bluff, and the species characteristic more specifically for one of the sections.

The most important indicators of the shallow-loess mantles are toothleaf viburnum (*Viburnum dentatum*) and three species of vacciniums - Elliott's blueberry (*Vaccinium elliotii*), sparkleberry (*V. arboreum*) and squaw-huckleberry (*V. stamineum*). Witch-hazel (*Hamamelis virginiana*) is also almost by any measure more important in the forests on the shallow-loess deposits than within the Deep Loess Section.

The diversity of the shrubs adapted to the soil drought seems to increase with the general thinning of the loess deposits. For instance, wax myrtle (*Myrica cerifera*), and Carolina holly (*Ilex ambigua*) are absent from the ravine sample of the Port Hudson forest located comparatively close to the main bluff ridge but [appear to be more regular components/sprinkle more or less regularly] in the ravine assemblages of the Sicily Island area and, especially, Homochito National Forest.

In turn, the understory assemblages of the Homochito National Forests where the potential thickness of the loess deposits decrease to a depth less than six feet (Spicer, 1969) additionally contain several species highly adapted to sandy, excessively poor and percolative soils such as fringe-tree (*Chionanthus virginicus*), possumhaw viburnum (*Viburnum nudum*), rhododendron (*Rhododendron canescence*), and lyonia (*Lyonia ligustrina*). These species were located neither in the Port Hudson area nor in Sicily Island. Of special reference is the distribution of two species with "intermediate" ranges, Virginia stewartia (*Stewartia malacodendron*) and serviceberry (*Amelanchier arborea*). These shrubs occurred in the ravine bottoms of only two areas, Sicily Island and Port Hudson. Unlike other "shallow loess specialists", they were found neither on the extreme thin-loess edge of the Loess Hills, in the Homochito National Forest, nor within the river-front section of the

Mississippi Bluff characterized by the deepest accumulations of loess.

This distribution pattern suggests that stewartia and serviceberry are likely to be ecologically associated with the certain edaphically transitional section of our region where the loessial mantle is not as deep as within the area of the Bluff Ridge but not as quite that thin as on the extreme margin of the Loess Region, in the Homochito National Forest. The understory assemblage of the Sicily Island's ravines additionally contains two exceptionally localized hawthorns, *Crataegus spatulata* and *C. viridis* (or *C. pruinosa*) which were not found anywhere else within the Loess Region.

The large group of the species which contributes to the diversity of the shallow-loess forests such as bigleaf silverbell (*Styrax grandifolius*), French mulberry (*Callicarpa americana*), deciduous holly (*Ilex decidua*), buckthorn bumelia (*Bumelia lucioides*), red bucky (*Aesculus pavia*), Mexican plum (*Prunus mexicana*) and Chicasaw plum (*P. angustifolia*) and Parsley hawthorn (*Crataegus marshalii*) show little or no variation with respect to the depth of the loessial mantle and more or less readily shared with the deep-loess section of the Mississippi Bluff. Thus the resulting pattern of the "peripheral zone" is intermingling of the "shallow-loess specialists" and the

above-mentioned "generalists" - under the structurally dominant role of the fewer "peripheral" species.

It is reasonable to mention that few species-generalists also demonstrate - although in a relatively gentle form - some edaphic preferencies. Paradoxically, two predominantly bottomland species, deciduous holly and Parsley hawthorn, tend to show a somewhat higher frequency in the drier peripheral forests than in moister and thus seemingly more favorable environments of the Mississippi Bluff. In the areas underlain with the shallow- and thin-loess mantles, these two shrubs seem to occur most readily in the localities with apparently complicated drainage and poor soil aeration.

In the Homochito National Forest, for instance, both species frequently congregate in shallow depressions where poor drainage and acidic soils are indicated by the presence of some species characteristic for bayheads such as *Magnolia virginiana* and *Lyonia ligustrina*. Although relatively rare in both sections, red bucky also tends to be slightly more common on the margins of the Loess Region which is particularly true for for the areas west of the Mississippi River. The presence of the Carolina buckthorn (*Rhamnus caroliniana*), on the other hand, appears to be slightly more pronounced in the deep-loess section – perhaps, because of the calcareous nature of the loessial soils. But this impression is largely caused by a rather

unusual abundance of *Rhamnus* in the forests along the southern end of the Natchez Trace and along the eastern, deep-loess edge of Macon Ridge (the Poverty Point site).

Although found in various frequencies throughout the whole Loess Region, bush palmetto also gravitates to the deep-loess section. The Mississippi Bluff is probably the only area of the Loess Hills Region where *Sabal* can be regularly found on the ravine slopes and even ridgetops. By contrast, on the periphery of the Loess region, this dwarf palm was limited exclusively to the ravine bottoms, where it occurred in the vicinity of small springs and bogs.

Importance of bush palmetto considerably increases at the southern margins of the Loess Region - in the forests of East Baton Rouge Parish, in the southern portion of Opelousas Ridge, and on the salt-dome islands. Most of these areas are underlaid by the relatively shallow loess mantles but the clayey to silty nature of the parent deposits beneath loess contributed to the development of the relatively poorly drained soils unlike those in the areas where loess was deposited over the Citronelle.

Light Preferences and Population Densities of the Understory Specialists

The forests of the Loess Hills are potentially very rich in the understory specialists, but the vast majority of the shrub species present in these forests are, to a various extent, dependent on sunlight and thus can only rarely be found in the areas with closed beech-magnolia

overstory. Strawberry bush (*Euonymus americanus*) is probably the most shade-tolerant of all shrubs present in beech-magnolia forests and the only shrub species which occur more or less regularly in those somber sections where beech-magnolia overstory achieves its best development.

While being relatively infrequent, bush palmetto (*Sabal minor*) seems to be another species able to develop under the closed canopy rich in beach. Small seedlings of few other species like Chinese privet (*Ligastrum sinense*), French mulberry, (*Callicarpa americana*), oakleaf hydrangea (*Hydrangea quercifolia*), witch-hazel (*Hamamelis virginiana*), along with thin, light-suppressed sprouts of *Rubus* spp. and seedlings of some lianas (particularly, *Parthenocissus quinquefolia* and *Bignonia capreolata*) may be found with certain regularity in such dark corners of the forest but none of these shrub seedlings, except probably Chinese privet and black raspberry appear to be able to persist in this somber environment for long. One can hypothesize that in the original early-historical forests, with their thick beech-magnolia overstory and very small amount of sunlight reaching the ground, most of the understory species were characterized by very low frequencies.

In the beech-magnolia-holly forests of the Tunica Hills, where access of sunlight to the forest floor was additionally blocked by several subcanopy layers of

Ilex opaca, the understory environment seemed to have been particularly somber. The 0.1 ha sample of the relict beech-magnolia-holly stand I managed to locate in the vicinity of the Magnolia-Glenn Preserve did not yield any shrub species. The understory stratum here was dominated by the extremely shade-tolerant undergrowth of American holly and sugarleaf. I extended my search of the understory specialists further downslope, into the section of the beech-magnolia-holly forest which was deliberately excluded from sampling area because it had been in part disturbed by Hurricane Andrew in 1992. The only shrub registered within additional 0.07 ha of the beech-magnolia-holly forest was a single individual of American elder. It was found, however, in the middle of the gap which owed its existence to powerful disruption of the canopy by Hurricane Andrew. Thus the trend to the relatively scarce and shrubless nature of the understory stratum in the beech-magnolia-holly grove in the Tunica Hills probably reflect the original conditions of the early-historical beech-magnolia-holly forests

In the original beech-magnolia and beech-magnolia-holly forests gaps formed either by hurricanes or as a result of the natural death and fall of individual canopy trees were probably the major means of reproduction for the vast majority of shrubs. In the most of the present-day stands, shrubs are characterized by somewhat higher population densities and more even distribution than could

be expected based on the "conventional" dynamics of the beech-magnolia forest. The explanation for this phenomenon seems to be related the fact that all surviving stands have been affected by disturbance of varied nature and intensity.

The anthropogenic disturbance is probably the most universal and widespread factor. As pointed out above, the modern second-growth beech-magnolia forests are commonly characterized by the relatively large canopy populations of the light-dependent trees whose crowns are less effective in blocking sunlight. With more dispersed sunlight passing to the understory, the understory population densities would likely to have become larger and less restricted in distribution. In the second-growth closed-canopy forests they aggregate not only in the canopy openings but also under the canopies of successional trees and in the areas where canopies contact. The exceptionally mature stands (presumably, analogues of the early-historical forests) exemplified by the closed-canopy sections of the Tunica Hills and LSA assemblages also contain successional trees but those are fewer and commonly stand isolated. The overstory stratum in such old-growth stands is so densely packed with tree canopies that the crowns of the successional tree species tend to be partially shaded by broad crowns of surrounding beeches.

In the physiographically-disturbed old-growth forests of the Tunica Hills and the Steep Hills site, where the broken nature of the overstory creates conditions for the generally greater availability of dispersed sunlight in the understory of these forests, the shrub diversity increases considerably compared to the undisturbed, closed-canopy beech-magnolia assemblages. Although landslide gaps abound in these forests, the vast majority of understory specialists here are not necessirally associated with treefall areas. It implies that most of the shrubs present in the late-successional assemblages are not typical pioneer species. In fact, the vast majority of shrubs occur in the dispersed sunlight conditions which prevail under irregular, discontiguous canopy on the steep slopes and in various physiographically complex expositions. Moreover, shrubs are not lacking even under the relatively closed mixed-species overstories, although their population densities in such areas, understandably, decrease. I assume that colonization of the relatively large landslide gaps by many shrub species could be complicated because of the thermally stressful microclimatic conditions which result from the exposure to the full sunlight. By contrast, the irregular, uneven overstory of the steep-slope forest acts as a filter which blocks much or most of the sun radiation but at the same time channels the mild amounts of sunlight down to the understory through the patchwork of various

ephemeral micro-gaps, older semi-grown up treefall gaps and unfilled or partly filled breaks among tree canopies. The establishment and survival of shrub populations under such natural filter may be also favored by the great variation in light intensity within relatively small areas.

By contrast, in the original forest, with their thick beech-magnolia canopy and very small amount of sun light reaching the ground, most of the understory species, except the most shade-tolerant ones, were characterized by very low frequencies. Gaps were likely to have been a crucial condition for the development of shrub populations in the primary old-growth forests strongly dominated by beech and magnolia. I postulate that a long history of the anthropogenic disturbance contributed to the development of the essentially different successional regimes which had a significant impact on the understory strata - in terms of the general increase of shrub populations.

First, certain species of shrubs may have expanded and established the larger populations after the clearance of the original shade-tolerant overstory. Secondly, the development of the early-successional forests with the relatively thin overstories and then the reestablishment of more mixed second-growth late-successional forests may have contributed to the further "entrenchement" of the shrub populations. Finally, the anthropogenic activity contributed to the establishment in the Loess Hills Region

of a few exotic species such as Chinese privet (*Ligustrum sinense*) and Japanese privet (*L. japonicum*) which may have influenced or even changed the understory structure in some forested areas such as Oakley and Burden Plantations.

One of the essential adaptations for survival under the closed-canopy conditions is a powerful root system which covers relatively large units of soil and is able to support not just one individual plant but a group or even several groups of sprouts. The larger population densities of shrubs in the forests on the shallow-loess surfaces and the general ability of these shrub populations to persist under the mixed closed canopy of many species of trees including beech is related to the fact that the shrubs with the extensive collective root systems are much more diverse in these forests than on the deep-loess surfaces.

All major dominant shrubs of the shallow-loess sections, both in sub-xeric and poorly-drained moist-mesic forest types, such as vacciniums (especially *Vaccinium elliottii*), yaupon, Virginia stewartia, and arrowwood are characterized by very vigorous, vital and extensive root systems. In the deep-loess moist-mesic section of the edaphic gradient this category of the understory specialists is represented by spicebush and Chinese privet. Once such shrubs expanded (through clearcuts and other anthropogenic disturbances), their populations appear to be capable of persisting for long even in the comparatively

unfavorable light conditions such as those of the Port Hudson ravine assemblage with its largely closed overstory and high importance of the shade-tolerant dominants.

Thus the long-term anthropogenic disturbance and associated ecological pressures were very important factors behind the understory evolution in the present-day beech-magnolia forests. They contributed to the development of the essentially more dense and specious understories than those characteristic of the original closed-canopy forests.

Species Diversity in the Understory Stratum

The beech-magnolia forest type of the Loess Hills seems to be one of the most shrub-rich, understory-rich forest in North America. However, the local indices of understory diversity in these forests may be extremely varyable depending on the regime of disturbance. The undisturbed patches of the exceptionally well-developed beech-magnolia and magnolia-beech-holly forest (existing now as a relatively compact sections within larger-sized and more heterogeneous late-successional units) suggest a very low shrub diversity and suppressed nature of the understory communities. Such sections are probably ilustrative of the structure of the original, closed-canopy beech-magnolia forests. The early-historical closed-canopy forests must have been characterized by a very localized, strongly gap-centered pattern of shrub distribution and

were likely to have had, consequently, a lower understory diversity - at least at the level of 1 ha visibility.

During the last two centuries of repeated clearing the nature of the shrub distribution and understory structure turned out to be strongly changed: shrubs were released from surpression and the differences in the biodiversity patterns became somewhat blurred. Today the well-developed secondary beech-magnolia forests in overall tend to have relatively abundant and specious understory populations.

The variation in the understory diversity has its distinctive features. The understory stratum of the beech-magnolia forest contains more subtropical species than any other stratum. The loss of these components along the south-north transect creates the effect of a somewhat more marked decrease of the understory diversity than in any other stratum.

Unlike in the overstory and midstory, there is no a marked decrease in the general understory or specifically shrub diversity with the thinning of the loess mantle. The shallow loess sites are lacking quite a few moisture-loving understory specialists but those are replaced, even with some surplus, by the shrubs adapted to the poorer and well-drained soils. Generally, under the closed-canopy conditions, the assemblages on the shallow-loess mantles appear to be potentially slightly more diverse in terms of the number of shrub species than their deep-loess

counterparts. But this preliminary conclusion needs to be tested on a greater number of stands.

In the present-day survived late-successional forests of the Loess Hills, the diversity of understory strata in general and shrubs in particular tends to increase from the closed-canopy forests to the more mixed forest types with partially disrupted, gappy canopies. The understory diversity peaks today in two nearly opposite sections of the Loess Hills - in the deep-loess moist-mesic forests of the Bluff Escarpment and in the disturbed dry-mesic to sub-xeric forests of the perypheral shallow-loess section. The latter trend is exemplified by the ravine assemblage of the Sicily Island area.

Brief Summary and Conclusions

The species composition and structure of the understory stratum change considerably along the latitudinal and edaphic gradients. Within the deep-loess section of the Mississippi Bluff, the major increase of the subtropical and evergreen components occurs largely due to the population increase of the canopy and subcanopy species. Only south of the Tunica Hills area, the evergreen shrubs become an important component of the understory communities. Thinning of the loess mantle results in the gradual replacement of the moisture-loving species with the subxeric and xeric ones. Shrubs are structurally more important on shallow and thin loess mantles than in the

deep-loess section. Some evergreen shrubs appear to go further north in the shallow-loess section than in the deep-loess section. Physiographic disturbance and xeric conditions are the primary factors that appear to be responsible for the increase of the shrub and understory diversity per unit area. It seems that the original beech-magnolia forests may have had lower diversity of shrubs per unit area than the modern mature forests.

CHAPTER 13

CONCLUSIONS

The Loess Hills forests of the Lower Mississippi Embayment represent the largest and by now the least explored block of the upland hardwood forest in the Southeastern Coastal Plain. The fertility and high moisture-holding capacity of the loessial material played a critical role in the development of these forests. Consequently, the variation of the depth of the loess mantle is one of the most important biogeographic factors.

In an effort to determine the status of the Loess Hills forests, one should not overlook their ancient origins and their unique role in the Pleistocene bioclimatic dynamics. Historically, the role of the loessial forests was that of a "floral heart" of eastern North America or, to put it in a more correct way, the central "floral artery" providing the temperate and warm-temperate broadleaf flora with both a refugium region for survival and a route for the gulfward migration. During the Pleistocene, the Mississippi Bluff funneled three or four migration cycles and "refugium periods" which, along with the deposition of loess, in the most profound way shaped the biogeographic pattern of these forests. During such Pleistocene fluctuations, the loessial forests appeared to host much if not the most of the eastern North American deciduous flora. They became a parental forest region

which, with the transition to the interglacial conditions like ours, repeatedly generated younger, in a geological sense more "successional" forest types. This gives a hint for an explanation of the mixed, somewhat undifferentiated biogeographic pattern of the loessial forests which share certain features with adjacent and even some disconnected forest regions such as, for example, the Mixed Mesophytic Forest. Viewed from such a perspective, the hardwoods of the Loess Hills are not even "just another" forest type or forest region but rather quite literally, a source, a "*cause d'etre*" of all modern forests of Eastern North America, ancestor forests of all its living forests.

Although the Loess Hills have been settled by humans since the time of the late Pleistocene, the anthropogenic activity turned into the important biogeographic factor only during the Hopewellian time (beginning approximately from A.D. 0) marked with the intensive building of the mound centers and first large towns. The ecological impact of the Loess Hills forests greatly increased in the middle Mississippian Period (after A.D. 1200) following the introduction and spread of the cleared-field maize-based agriculture. Both ceremonial and agricultural clearing reduced the area covered by the original "climax communities" and contributed to the expansion of the early-successional tree species. The growing populations of the successional species could, in turn, cause certain

influence on the population dynamics of the late-successional forest. A fairly considerable extent of clearence recorded in the Blufflands during the early-historical times by the European and European-American travellers suggests that even some of those survived tracts of the "old-growth" forest with no record of historical clearence, in fact, may have developed on previously cultivated land and thus be representative of the very advanced stages of natural succession. The long-term nature of the native agriculture combined with frequent use of fire undoubtedly rendered forest succession slower and more complicated, fostered the development of some species and retarded entrance of the others.

Apparently, the native inhabitants of the Loess Hills also practiced some agroforestry. On their fields they seemed to foster the development of certain economically important species such as persimon, various plums and cherries, mulberries and nut trees. The fact that tree orchards in various forms were literally grown by the protohistorical and early-historical Indians is indicated by the presence of the various fruit-bearing Old World trees such as pears, peaches, figs, and European apples which could have been maintained only through cultivation. When through several seres of successional communities the forest vegetation reclaimed abandoned fields and orchards, this led to the development of the forests enriched by the

economically useful species, both the native and exotic ones.

For how long the large populations of the economically useful species could maintain themselves in the natural communities is difficult to say. Whether some evidence of the native forest management can be found in the present-day forests of the Loess Hills, remains one of the most intriguing questions to answer. Sampling the forests located in the immediate vicinity from the old Indian sites such as Emerald Mound in southwestern Mississippi and Poverty Point in Arkansas, I found that these sites have conspicuously large population of some potentially useful trees and shrub species. Of special interest were outstandingly high population densities of two understory specialists, Carolina buckthorn, or Indian cherry (*Rhamnus caroliniana*) and Mexican plum (*Prunus mexicana*). The relatively large overstory population of pecan (*Carya illinoensis*) is another remarkable feature of the Natchez Trace site. Of course, the natural reasons for the explanation of these phenomena, perhaps, some peculiar qualities of the local soils, cannot be completely ruled out. But the exclusive correlation of high population densities of these three economically useful species with the old Indian sites is indeed remarkable and "suspicious".

The major ecological and biogeographic change happened in the Loess Hills Region during the period of the European

colonization and development. Most of the original forests of the region were cleared during the ante-bellum period for cotton monoculture. After the Civil War there were several decades of recovery but much of the recovered forest was then repeatedly cleared during the period from approximately 1890 to 1920 when cotton expanded again. The third wave of deforestation began in 1940s, peaked in 1950-60s and declined in the early 1970s. It was related to the expansion of the soy beans culture and was characterized by the emphasis on the industrial clearing. It was a period of the hardwood timber boom and intensive development of the timber industry in the region. During this period the last substantial tracts of the survived late-successional forest and much of the second-growth forest were cleared.

Consequently, during the last two centuries most of the loessial forests were cleared 2-3 times. The intensive clearing practices stimulated the development of the essentially different forest type which was nearly lacking the shade-tolerant components in the canopy and was dominated by the expanded populations of the various light-dependent species, particularly sweetgum, southern oaks, and tulip tree which had the accessory status in the original early-historical forests.

The species composition and the structure of the surviving late-successional forests are subject to biogeographic variation associated with the combined action

of latitude, physiography, edaphic conditions and disturbance, both natural and anthropogenic. The spatial analysis of the community variation associated with these factors leads to the recognition of four major directions or *vectors* of biogeographic change. The latitudinal vector of the vegetation change is determined by increasingly cooler winter conditions from Baton Rouge northward as the influence of the warm maritime airmass emanating from the Gulf of Mexico diminishes and the influence of the cool airmasses and polar front gradually grows stronger.

Physiography and edaphic conditions represent a set of closely related factors determined largely by the regional variation in thickness of the loess mantle. The high general capacity of the loessial material to preserve water combined with the pronounced physiographic dissection of the Mississippi Loess Bluff contributed to the establishment in this area of the ever moist and cool microclimate.

Particularly moist conditions are typical for the western flank of the Bluff immediately adjacent to the escarpment: this section is dissected by the web of exceptionally deep, narrow and steep ravines which provide the most effective impediment from overheating and excessive evaporation. The escarpment area is characterized, consequently, by the higher diversity and relative importance of moisture-loving components than the

remainder of the Mississippi Bluff, let alone more peripheral sections of the Loess Region. Likewise, the forests on shallow loess deposits contain an assortment of species adapted to the faster drainage regimes. These tend to enter progressively with the thinning of the loess mantle and gradually increase in aggregate importance in the direction from the deep-loess "core" outward. The associated vector of vegetation variation could be roughly categorized as nearly centrifugal because the species composition changes in a rather uniform manner east, west and south of the Bluff.

The most intensive and perpetual form of natural disturbance that affects the forest vegetation of the Blufflands is physiographic in nature - it is associated with the ongoing erosion of the loess mantle. Loess is a material very susceptible to erosion due to its loose physical structure. So, generally speaking, the erosion of the loess mantle is not unlikely to start and progress in almost any area where it is relatively thick. Indeed, the minor signs of such disturbance one can observe here and there throughout the Mississippi Bluff but they are localized and rather infrequent. Geographically, the zone of the intensive physiographic disturbance is localized in the western section of the Bluff, in the area immediately adjacent to the escarpment where the loessial deposits

achieve their maximum thickness and form a sort of a cap or crest over the remainder of the bluff ridge.

Anthropogenic disturbance is an important ecological factor overlaying all latitudinal, physiographic and edaphic variations within the beech-magnolia region. Almost all survived beech-magnolia stands were affected by human activities in this way or another. Yet the ecological impact of the anthropogenic disturbance, of course, varies strongly among the sites depending on its nature, intensity and historical longitude.

Despite the relatively short distance between Warren County, Mississippi, and the Gulf Coast, the hardwood forests of the southern Loess Hills are characterized by a rather sharp latitudinal gradient. Forests of northern Warren County exemplify the middle-Bluffland type characterized by the intensive intermingling of the cool-temperate and warm-temperate components and considerable importance of the interior-centered cool-temperate species which are either absent in the southern Blufflands or represented there by low population densities. These are all-deciduous forests lacking the subtropical and evergreen components in the canopy.

The forests of the "beech-magnolia" type begin some 19 to 26 miles north of Vicksburg and extend approximately to the middle East Baton Rouge Parish east of the Mississippi River and to Opelousas west of the River. Within most of

this section, *Magnolia grandiflora* decreases rather gently from the south to the north. The sharp biogeographic changes occur only at the opposite ends of the "beech-magnolia" forest region. The population densities of *Magnolia* decrease abruptly at the northern fringe of its range in the vicinity of Vicksburg, Mississippi, and increase dramatically south of West Feliciana Parish in Louisiana. At the northern margin, the distribution of magnolia throughout the forest becomes very spotty. Throughout most of the beech-magnolia region, the population densities of *Magnolia* are considerably lower than those of *Fagus*. Only at the southern edge of this forest type, at Port Hudson, it achieves the equal population densities with beech.

Magnolia is not the only subtropical species which may be present in the canopy of the beech-magnolia forest. But other potentially overstory species - *Quercus durandii*, *Zanthoxylum clava-hercules*, and *Magnolia pyramidata* - are either very sparsely distributed or highly localized.

The latitudinal change is further accentuated by the northward decrease of the population densities of water oak (*Quercus nigra*) and the parallel increase of the population densities of a large assortment of broadly-ranging and interior-centered cool-temperate deciduous taxa such as beech (*Fagus grandifolia*), tulip tree (*Lirirodendron tulipfera*), white ash (*Fraxinus americana*), sassafras

(*Sassafras albidum*), cucumber magnolia (*Magnolia acuminata*), black walnut (*Juglans nigra*), boxelder maple (*Acer negundo*), as well as southern sugar maple (*A. barbatum*).

The loessial forests of the "beech-magnolia" type can subdivided into four latitudinal sections: northern-fringe beech-magnolia forest, northern beech-magnolia forest, southern beech-magnolia forest, and southern-fringe beech-magnolia forest. The northernmost forest type was localized in the vicinity of Vicksburg and extended at least some 19 miles north of the present-time city limits. It was characterized by comparatively low importance and spotty distribution of *Magnolia gandiflora* and very high importance of American beech (*Fagus grandifolia*). Southern sugar maple (*Acer barbatum*) - a warm-temperate species - appears to have sharply increased in importance in this forest type and further north along the Bluff in response to the structural decline of evergreen magnolia and increasing importance of beech.

Northern beech-magnolia forest type extended approximately from southern Warren County to some point between Port Gibson and Natchez. West of the Mississippi River it included Sicily Island and southern section of Macon Ridge. The major structural difference between this forest and the northern-fringe forest type was in considerably increased *Magnolia* population densities.

However, both forest types were characterized by very high - higher than in southern forests - importance of beech and low importance of water oak (*Quercus nigra*). The second-growth northern beech-magnolia stands are characterized by the higher importance of several cool-adapted temperate species - such as tulip tree (*Liriodendron tulipfera*) and white ash (*Fraxinus americana*). Another conspicuous feature of both forest types is a relatively high importance of the interior-centered cool-temperate trees such as sassafrass (*Sassafras albidum*), cucumber magnolia (*Magnolia acuminata*), and black walnut (*Juglans nigra*) which are either absent or poorly represented in the southern forests. Sassafras and black walnut further increase in importance in the middle-Bluffland forests.

The southern beech-magnolia forests are characterized by somewhat higher population densities of evergreen magnolia and slightly lower population densities of American beech than the forests of the northern type. But magnolia still has here essentially lower (about two times) population densities than beech. The rare subtropical species are more likely to be found in these forests but the interior-centered cool-temperate species are either absent or characterized by very low population densities. Water oak, nearly semi-evergreen in these latitudes, is typically one of the most important accessory components after sweetgum in these southern forests.

The southern-fringe beech-magnolia forest type has surviving remnant only east of the Mississippi River, in the Port Hudson area. Historically it was probably limited to a very narrow segment of the Mississippi Bluff which extended from southernmost portion of West Feliciana Parish to northern East Baton Rouge Parish. This is the only beech-magnolia forest type where *Magnolia* achieves the equal population densities with *Fagus*.

The physiographicly disturbed forests of the Bluff Escarpment even in their southern section are characterized by essentially lower importance of the subtropical and evergreen components. On the other hand, these forests are likely to contain more species of subtropical and interior-centered cool-temperate trees per unit area than the closed-canopy beech-magnolia forests at the same latitude.

The transition to more southern than "beech-magnolia" forest types occurs in the middle and southern section of East Baton Rouge Parish where American beech seems to decrease in importance to the extent that it becomes a species of the secondary importance. Live oak (*Quercus virginiana*) is still not a part of this community: it begins to sprinkle only in the bottomland forests south of Baton Rouge city limits. The original forests of East Baton Rouge Parish were probably strongly dominated by *Magnolia grandiflora* (which is evident from the exceptional importance of this taxon in the subcanopy of Burden

Plantation forest). Sweetgum and water oak also seem to have been very important constituents of the original forests of this section and probably achieved the status of the second-order co-dominants.

The transition to a more evergreen and more subtropical forest type is more evident west of the Mississippi River, on Opelousas Ridge where beech declines approximately 1 mile north of Opelousas and live oak begins to sprinkle, gradually increasing in importance, in the mesic forests south of Opelousas.

The predominantly evergreen and subtropical forest type where live oak shares dominance with evergreen magnolia originally covered the southern third of Opelousas Ridge. The presence of the old-growth bottomland forest strongly dominated by live oak suggests that *Q.virginiana*-rich forest type originally extended at least as far north as Lafayette. Today live oak-magnolia forest type survived only in the immediate vicinity from the coast line on the salt-dome islands and Forked Island.

Throughout most of the southern Loess Hills, the original old-growth forests were undoubtedly dominated by the *Fagus grandifolia-Magnolia grandiflora* association. This was "beech-magnolia" forest, not the mixed undifferentiated association postulated by Quarterman and Keever (1962) under the name "Southern Mixed Hardwood Forest". Some of the surviving modern forests of the

"beech-magnolia" type are dominated by the associations which include not only the two shade-tolerant species but also several light-dependent trees - sweetgum (*Liquidambar styraciflua*), tulip tree (*Liriodendron tulipfera*), and bitternut hickory (*Carya cordiformis*) in the moist-mesic to mesic section and white oak (*Quercus alba*), tulip tree (*Liriodendron tulipfera*), and occasionally loblolly pine (*Pinus taeda*) on the periphery of the Loess Region.

The presence of these taxa in the dominant association may superfecially resemble the pattern of the Southern Mixed Hardwood Forest suggested by Quarterman and Keever (1962). But this does not seem to confirm the concept of SMHF because all the forests, in which these taxa shared the dominant status with beech and magnolia, were secondary in origin. The comparative analysis of the structural characteristics of old-growth and second-growth beech-magnolia forests shows rather clearly that the high importance of these and many other light-dependent species in the overstory of some second-growth assemblages is a temporary post-clearence phenomenon. The poor ability of nine to ten species (in the conditions of the middle- and upper-slope forest - including sweetgum) either to reproduce or to maintain high recruitment rates in the modern closed-canopy beech-magnolia forest suggests against the possibility that they could have claimed the status of

the dominant species in the early-historical assemblages or will claim it in the putative future climax.

The beech-magnolia-holly association suggested by Delcourt and Delcourt for the entire region of the southern Blufflands appear to be tenable only for the physiographicly undisturbed gentle slopes of the Tunica Hills area where the exceptional importance of American holly (*Ilex opaca*) may be related to the specific properties of the local soils.

Of nine to ten "core" species (other than beech and magnolia) mentioned by Quaterman and Keever, only sweetgum appears to be potentially capable of reaching the codominant status in the undisturbed closed-canopy late-successional forests - yet only within the moist-mesic section of the edaphic gradient. This gives us the idea of the beech-magnolia-sweetgum association which probably occupied the bottoms and perhaps the slope margins of some deep, ever moist ravines, especially those eroded in the thick loess deposits of the Mississippi Bluff or immediately adjacent to the floodplains of the tributary streams. It appears that sweetgum was, as it continues to be, a very important codominant taxon (more important than *Magnolia grandiflora*!) in the moist-mesic deep-ravine communities of the Bluff escarpment where intensive erosion of the loess mantle leads to the frequent disruption of the forest canopy by landslides. While somewhat different from

beech-magnolia or magnolia-beech-holly associations suggested by earlier workers, beech-magnolia-sweetgum association still is a long shot from the "Southern Mixed Hardwood Forest".

The narrow section of the Bluff Escarpment is characterized by exceptionally dissected relief, deep, steep-slope ravines and frequent landslides. Frequent disruptions in the canopy of these steep-slope moist-mesic forests led to the development of the very rich and heterogeneous forest type dominated by the beech-sweetgum-magnolia-water oak association which is unique to specifically this and no other section of the Loess Hills. This is a closest structural approximation to the putative Southern Mixed Hardwood Forest but its structural heterogeneity is maintained by the perpetual physiographic disturbance. Water oak is unable to reach the status of the dominant taxon in the closed-canopy forests.

The repeated disturbance such as periodic clearcuts may have probably made the initially beech-magnolia forest replicate the structure of the SHMF due to the increasing importance of the light-dependent taxa. Perhaps, some reservations should be made for the western portion of the Coastal Plain where hurricanes frequently disrupt the canopy thus maintaining local hammocks in the state of the constant successional flux. The resulting forest type may indeed fit the characteristics of the Southern Mixed

Hardwood Forest suggested by Quaterman and Keever (1962). But the hurricane influence on the forests of the Loess Hills is far from being even nearly as pronounced as in Florida and Georgia.

Due to the variation in the edaphic conditions and disturbance regimes, the beech-magnolia forests of the Loess Hills can be subdivided into five basic types.

In the forests of the deep-loess section of the Mississippi Bluff the indicator canopy species are sweetgum (*Liquidambar styraciflua*), water oak (*Quercus nigra*), cherrybark oak (*Q. pagoda*) and bottomland chestnut oak (*Q. mischauxii*). In the closed-canopy late-successional forests these typical are among the first-rank accessory components. The ravine forests of the deep-loess section are also characterized by the presence in their canopy of a wide variety of the bottomland-centered and moisture-loving mesic species such as sycomore (*Platanus occidentalis*), boxelder maple (*Acer negundo*), sugarberry (*Celtis laevigata*), red and American elm (*Ulmus rubra* and *U. americana*), southern sugar maple (*Acer barbatum*), American basswood (*Tilia americana*), and red mulberry (*Morus rubra*) which are absent from the canopy of the shallow-loess forests.

The eastern and southern "slope" of the Mississippi Bluff is underlain with shallower loess mantles and characterized therefore by poorer, more acidic soils and

faster drainage which led to the establishment of the mesic to dry-mesic edaphic regimes. This transitional section is still a domain of the hardwood forest but the local communities are characterized by the decreasing importance of the warm-temperate Coastal Plain oaks and sweetgum. Sweetgum does retain the status of the major accessory species in the mesic to dry-mesic sites but here it is essentially less important than in the deep-loess section. Thinner sweetgum populations tend to congregate in the ravine bottoms where the underground moisture is more readily accessible. The indicator trees here are white oak (*Quercus alba*) and blackgum (*Nyssa sylvatica*). White oak considerably increases in importance in this section and commonly attains the status of one of the second-rank dominant species. Blackgum is very ephemerally represented in the deep-loess section and is essentially absent from some moist-mesic samples such as that of Magnolia Glen preserve but becomes a major accessory species on the shallow-loess mantles.

On the broad eastern margin of the Loess Region, where the loess deposits are very thin and locally intermixed with sand, the uplands are dominated by loblolly pine (*Pinus taeda*). This is not mixed hardwood-pine or white-oak pine comminity as indicated by Braun (1950) and the Delcourts (1974) but a predominantly pine forest. Homochito National Forest in southwestern Mississippi represents one

of the best and largest tracts of this forest type survived on the margins of the Loess Region. A somewhat mixed aspect of the Homochito assemblage is given by the strips of the predominantly hardwood forest which cover the bottoms and lower slopes of the local shallow ravines. White oak and, particularly, blackgum which remain to be important components of this forest type are supplemented here by three other indicator species - loblolly pine, upland laurel oak (*Querqus hemisphaerica*) and bigleaf magnolia (*Magnolia macrophylla*).

The southernmost section of the Bluff slope in East Baton Rouge Parish is characterized by the structural decrease of American beech and increase of few bottomland species adapted to the poor drainage regimes such as pecan (*Carya illinoensis*) and willow oak (*Quercus phellos*). West of the Mississippi River and south of Opelousas *Fagus* drops out of the species composition and live oak (*Quercus virginiana*) becomes more or less regular component of the forest structure, gradually changing the appearance of the forest by the prevalence of the evergreen life forms.

Interestingly enough, the present-day biogeographic zonation of the loessial beech-magnolia forests appears to be strongly sharpened by the anthropogenic disturbance. The clearence of the original late-successional forests in the Loess Hills region that influenced selectively different groups of species depending on depth of the loess mantle.

Although the original vegetation of the region was also likely to have been characterized by a certain degree of differentiation along the edaphic and physiographic gradient, the original old-growth beech-magnolia forests were much less segregated due to the lower importance of the indicator species.

The midstory of the beech-magnolia forests are characterized by the dominant role of the "matrix" *Fagus-Carpinus-Ostrya-Cornus* association and several notable trends. From the north to the south, there is a conspicuous increase of the subtropical and evergreen species: in the gentle-slope closed-canopy forests of the Tunica Hills the dominant role in the midstory stratum is assumed by American holly (*Ilex opaca*) which may have been originally replaced in the other southern sites by sugarleaf (*Simplocos tinctoria*). In the southernmost section of the Bluff Escarpment - in the Tunica Hills - Carolina laurelcherry (*Prunus caroliniana*) and two-winged silverbell (*Halesia diptera*) become the dominant species, whereas holly and especially sugarleaf decrease in importance. In the southern sites, southern magnolia is everywhere is an important co-dominant taxon but its population densities are especially high in the ravines of the Tunica Hills Escarpment.

Northward along the Bluff in the subcanopy there is a structural increase of the canopy species, particularly

American beech and southern sugar maple (*Acer barbatum*) and drastic decrease in the population densities of magnolia - despite the fact that it continues to be one of the dominant species in the canopy stratum. One of the most distinctive features of the Bluff Escarpment forests is structural increase of several light-dependent gap colonists such as paw-paw (*Asimina triloba*), devil's walkingstick (*Aralia spiniosa*), and red mulberry (*Morus rubra*), as well as remarkable increase of diversity of the sparsely distributed and rare midstory specialists. The midstory strata of the shallow- and thin-loess sites are characterized by the important role of two subcanopy "shallow-loess specialists", sourwood (*Oxydendrum arboreum*) and red maple (*Acer rubrum*), supplemented by blackgum and white oak. Another distinctive feature of the shallow-loess sites is a high diversity of the extra-sized understory shrubs reaching into the midstory.

The understory stratum of the late-successional loessial forests varies rather pronouncedly along the latitudinal, edaphic, and physiographic. Along the latitudinal gradient it varies from all-deciduous and predominantly cool-temperate understory type in Vicksburg area to the overwhelmingly evergreen and subtropical understory types in the extreme southern margin of the Loess Hills Region in East Baton Rouge Parish, southern section of Opelousas Ridge, and the salt-dome islands.

Along the physiographic and edaphic gradient, there is a transition from moist-mesic to subxeric understory types. The perpetual physiographic disturbance in the narrow section of the Bluff Escarpment is responsible for the development of some of the most heteregeneous and diverse understory types abounding with rare shrub species.

The shift from the deciduous to the increasingly more evergreen understory types generally overlaps with the transition from the all-deciduous middle-Bluffland forest types to the beech-magnolia forests further south. The understory assemblage of the Steep Bluffs area almost does not contain the important subcanopy and understory species whose ranges can be identified as subtropical, although it does contain American holly.

The vegetation shift further south along the Bluff is reflected in increasing population densities of both *Ilex opaca* and the subtropical subcanopy components. The structural increase of the warm-loving evergreen components with the decreasing latitude was registered in other parts of North America. For instance, Schwartz (1988) showed a rather well-profiled decline of evergreen tropical species from the south to the north along Florida Peninsula. Little (1978) showed that among tropical evergreen species of Florida, the understory species more readily extend into higher latitudes than the overstory ones. The same trend is exhibited by subtropical and evergreen species in the

southern Loess Hills. A considerably higher diversity of the understory subtropical species in almost every site within the range of the beech-magnolia forest as compared to the canopy species suggests that the former tend to extend northward more readily than the latter. This may be due to the thermal protection provided by the forest canopy.

The hardwoods of the Loess Hills exemplify some of the most diverse, perhaps, the richest forest community of extra-tropical North America. The remarkable biodiversity of the Loess Hills forests is related to their location in the low subtropical latitudes, unique physiography, and, of course, their long and unique geological history. The Loess Hills forests appear to be truely relic forests whose evolution seems to have continued uninterrupted since at least the Miocene times.

During the Pleistocene epoch during which the Bluffland belt acted as a corridor for the continental migrations of, perhaps, the majority of tree and shrub species of the Eastern deciduous flora. Favorable edaphic conditions, disected physiography, as well as cool and moist microclimate of the loessial ravines were the primary factors that contributed to the "entrenchment" in this region of the great many temperate and cool-temperate hardwood species which became diversified during the Holocene by the advancing warm-temperate and subtropical

floras. The diversity was further enhansed by the unique set of geographic and physiographic conditions. Located on a rather sharp transition between the Mississippi Alluvial Valley and exceptionally well-drained xeric uplands further eastward, the the Mississippi Bluff tended to funnel through and host both the bottomland and xeric upland floras.

The bottomland species expand from their major "core" area in the Mississippi Alluvial Valley deep into the Bluff area through the network of deep, moist ravines, whereas the upland and xeric species extend toward the Bluff escarpment though the the system of ridgetops. Because of the edaphic conditions of the deep-loess deposits and sharp slope gradient, two floras are readily fusing one into another on slopes, with the upland and xeric species descending to the ravine bottoms and many bottomland species abounding on the hilltops.

The Global Biogeographic Status of the Hardwood Forests of the Loess Hills

Most of the studies of the East-American forests have been traditionally performed by ecologists and biologists, not biogeographers, which fact had some implications for their classification. Unfortunately, the American geography and ecology lacks a broadly recognized classification scheme and terminology that would provide an accurate bioclimatic zonation of the Eastern North American forests. American ecologists appear to have a well-rooted trend to

underestimate or overlook the necessity in the development of such a methodology. The classification schemes applied by many scholars do not go any further from the rather obscure and simplistic subdivision of the whole forest complex of Eastern North America into the "southern" and "northern" forests.

One of the results of this and other colliding trends was that the biogeographic classification and terminology applied by ecologists to the southeastern forests are frequently at odds with the classification of the ecological climate zones following the Koppen system as modified by Trewartha (1968). Despite the subtropical status of the Coastal Plain's climate the forests of even the lower section of this region were routinely identified as "temperate" by many American ecologists (Smith 1973, Barden and Woods 1974, Axelrod 1975, Olson 1983, Greller 1980, 1988, Platt and Schwartz 1990; Batista and Platt 1997).

Comparison of the Loess Hills Forests with the Structurally Similar Forest Ecosystems of China

The better understanding of the place of Loess Hills forests in the global perspective could be obtained by comparison of these forests with rather neatly classified Chinese forests. It should be pointed out in this regard that the forests of East Asia, especially those of China are often considered as the close biogeographic counterparts of the Eastern American forests (Hsu 1983,

Ying 1983). The similarities of the geographic characters, climatic conditions and taxonomic composition between the broadleaf forests of China and the eastern United States seem to be more pronounced than between China and any other region where the broadleaf deciduous forests occur (Ying, 1983). The eastern North America and eastern to southern China represent two out of three largest extratropical broadleaf forest regions of the world. In contrast to the other regions under the similar vegetation, including Europe, both regions are characterized by the continuity of the forest cover from the boreal tc the tropical latitudes.

The classification of the Chinese broadleaf forests developed by the Chinese ecologists and biogeographers is quite detailed compared to the models worked out in the United States in reference to the eastern North-American forests. The latitudinal biogeographic classification of China's forests developed by Wu (1980) and slightly modified by Hou (1983) recognizes seven bioclimatic forest zones placed as latitudinal belts ranging from the Russian-Chinese border douwn to the South-China Sea and Indochina. On the basis of the species composition and structural characteristics, five major forest belts have been identified.

The northeastern corner of China adjacent to Korea is dominated by the mixed broadleaf-coniferous forest ranging into the cold-temperate coniferous forest region in

northern Manjchuria. The broadest belts in the middle and southern sections of the country are made up repectively by the warm-temperate broadleaf forest and the subtropical broadleaf evergreen forest zones. The extreme southern margin of China was identified to belong to the tropical monsoon and rain forest region. In their classification system, the Chinese scholars gave a special attention to the identification of the transitional zones. Between the overwhelmingly deciduous warm-temperate forest and the overwhelmingly evergreen subtropical broadleaf forest, they identified the narrow transitional belt of north-subtropical forest where fewer evergreens are strongly mixed with the temperate and warm-temperate deciduous components. As described and visualized by Ying (1983), the evergreen life forms begin to enter the warmer section of the temperate belt as few small understory shrubs, southward, on the northern edge of the subtropics, they increase in importance to become an important part of the mixed evergreen-deciduous understory and reach into the midstory. It is within the north-subtropical forest zone where the evergreens taxa begin to sprinkle with increasing frequency in the canopy stratum gradually changing the appearence of the forest community by the prevalence of the evergreen life form. South of the Yangtze River the hydrothermal conditions become favorable enough for the evergreen species to replace most of the deciduous ones,

although some temperate deciduous components such as beeches (*Fagus* spp.) are also present in the structure of these predominantly everegreen communities.

To understand the place of the loessial beech-magnolia forests in the global system of the life zones, the biogeographic comparison of this North American ecosystem with the neatly classified forests of China may prove useful. Axelrod (1975) is certainly not quite correct when he suggests, with the only reservation of the narrow coastal strip from central Florida into North Carolina, that the subtropical forests of the East Asia do not have counterpart in the southeastern United States. The hardwood forests of the southern Loess Hills, with their evergreen flora and well-developed sinusia of lianas, do give feel and touch of the subtropical forest. Many subtropical taxa of these forests, such as *Magnolia*, *Simplocos*, *Ilex*, *Stewartia* are represented by the close relatives in the forests of southern China. The relative importance of the subtropical and evergreen components in the structure of the late-successional forests of the southern Loess Hills varies along the north-south gradient between Vicksburg and Port-Hudson from 6.5% to 24.7% in the overstory, 0.4% to 22.2% in the midstory and 5.4% to 48.9% in the understory.

With such structural characteristics the beech-magnolia forests resemble rather strongly the north-subtropical forest of southern China. The forests north of

Vicksburg, which are devoid of evergreen magnolia and most other subtropical taxa but harbor rich assortments of the warm-temperate deciduous trees and shrubs, biogeographically are a close match to the warm-temperate broadleaf deciduous forest of middle-eastern China. However, unlike in China, where the transition from the subtropical to the warm-temperate forests is gradual, the boundary between deciduous-evergreen beech-magnolia forest and entirely deciduous warm-temperate associations north of Vicksburg proved to be rather abrupt. The subtropical shrubs and small trees, both evergreen and deciduous, significantly decrease in importance and diversity within the beech-magnolia forest region and ultimately drop (or nearly so) from the species composition upon reaching the northern limit of *Magnolia grandiflora* range.

On the extreme southern margin of the Loess Region, the loess-capped salt-dome islands of coastal Louisiana harbour the remnants of the more southern and more evergreen forest type dominated by magnolia (*Magnolia grandiflora*) and live oak (*Quercus virginiana*). These forests resemble structurally the subtropical evergreen forests of southern China.

Although being similar in general structure the forests of the southern Loess Hills and southern China are characterized, however, by some important compositional differences. Compared to the forests of southern China, the

forests of the Loess Hills have the low diversity of the subtropical evergreen components, especially the overstory ones. *Magnolia grandiflora* is the only common overstory subtropical tree in the loessial beech-magnolia forest. Two other species, semi-evergreen *Zanthoxylum clava-herculis* and especially deciduous *Magnolia pyramidata* are too rare or local to be referred as the regular components of the canopy stratum. Evergreen *Ilex opaca* reaches the canopy only in the uplands of the Tunica Hills.

By contrast, the assortment of the canopy evergreens in the subtropical forests of China includes approximately as many as 15 to 22 common hardwood species, with the gradual increase from the east to the west (Hou, 1983). Neither it readily matches the diversity of the evergreen subtropical forests of southern Japan where Satoo (1983) refers to approximately 16 evergreen canopy species. The impoverished nature of the subtropical flora of the southern Loess Hills, as that of the rest of the Southeastern Coastal Plain, can be attributed to the long history of the climatic deterioration which started in the middle Eocene and culminated in a series of the Pleistocene glacial cycles (Axelrod 1968, 1975).

In the southeastern United States, the combination of the geographic, bioclimatic and edaphic conditions has put the Pleistocene remnants of the Madro-Tertiary evergreen flora in a very harsh survival situation. During the

Wisconsinan glacial advance, the Laurentide ice shield capped most of the American Midwest with its southern lobe reaching deep into southern Illinois. The associated cooling was severe enough to wipe out the warm-loving floras from the most of the Southeastern Coastal Plain. The subtropical and even the warm-temperate taxa were, for example, completely absent from the late-glacial hardwood assemblages of the Tunica Hills, southeast Louisiana. The southward migrations of the North American floras have been checked, naturally, by latitudinal limitations of the eastern North American landmass. Pressed to the northern Gulf coast, the warm-loving evergreen species could not migrate to Florida because the conditions there were too dry for them to endure. Neither they were able to cross the broad belt of the xeric environments that separated the Coastal Pain from the humid gulfward slopes of the Sierra-Madre Oriental where the closely-related thermophyles have been persisting in the mixed-species montane forests (Axelrod 1975).

Yet unfavorable edaphic conditions (excessively well drained or vice versa poorly-drained infertile soils) and fires are likely to have been among other important constrains which prevented establishment of the mesic deciduous—evergreen forests throughout most of the zone where the climate would have otherwise allowed them to survive. The relics of the Madro-Tertiary flora have

probably persisted in small pockets on suitable soils in the immediate vicinity from the shoreline. Such small isolated refugia are likely to have been extremely vulnerable to the oscillation of any environmental factor and mortality rates among some species may have been high enough to set them on the edge of extinction. As a result, only a small fragment of the subtropical Tertiary flora managed to survive in the American Southeast (Axelrod 1968, 1975).

Certain structural and physiognomic similarity between the late-successional forests of the Loess Hills and the Broadleaf Evergreen Subtropical Forest of southeast China is emphasized by the fact that the East-Asian evergreen-deciduous forests are, too, characterized by high importance of beech which is represented in southern China by two major species, *Fagus longipetiolata* and *F. lucida* (Ying, 1983). It is noteworthy, however, that, unlike in eastern North America and Japan, in China beeches are indicative of the subtropical forest types for these moisture-loving mesophytic trees are totally lacking from the temperate and warm-temperate deciduous forests which developed under a stronger influence of a drier continental climate. Like in the beech-magnolia forest of the southern Loess Hills, in southeast China, beeches (*Fagus* spp.) also seem to represent the most important temperate deciduous component. But, in overall, the general importance of the

temperate and warm-temperate deciduous components in the Subtropical Evergreen Broadleaf Forest of China (except, probably, the transitional zone of the north-subtropical evegreen-deciduous broadleaf forest) seems to be lower than in the both beech-magnolia and more evergreen live oak-magnolia forest of the maritime salt-domes.

The high importance and diversity of the cold-adapted temperate trees in the loessial forests is related first of all to the more complicated and dramatic paleo-history of the Loess Hills Region which was greatly affected by the Pleistocene climatic fluctuations and massive southward migrations of the cool-temperate broadleaf deciduous species. The tree flora of the southern Loess Hills contains a large number of "cool-temperate" deciduous species characterized by very broad adaptation characteristics and geographic ranges extending from nearly the Gulf of Mexico to the Great Lakes Region. This assortment includes quite a few north-centered and interior-centered species such as cucumber magnolia (*Magnolia acuminata*), red oak (*Quercus rubra* L. *(Q. borealis* Michx. f.)), bur oak (*Q. macrocarpa*), American basswood (*Tilia americana*), black walnut (*Juglans nigra*), white walnut (*Juglans cinerea*), boxelder maple (*Acer negundo*), redbud (*Cercis canadensis*), oakleaf hydrangea (*Hydrangea quercifolia*), Kentucky coffeetree (*Gymnocladus dioicus*), and pink locust (*Robinia hispida*).

A great variety of the delicate herbaceous mesophytes and a substantial number of the northern ferns appear to persist in these low subtropical latitudes due to the deep dissection of the loess mantle and the high water-retention capacity of the loess deposits. The southward expansion along the Mississippi Bluff of still few other interior-centered species such as chinquapin oak (*Quercus muehlenberggi*) and American smoketree (*Cotinus obovatus*) appears to be favored by the calcereous nature of the loessial soils.

One of the major reasons for generally more evergreen nature of the Asian forests seems to be paleohistorical. Neither China nor even northern Asia experienced such extensive glaciations as did North America and Europe. During the Pleistocene, most of Siberia was free of ice. In the middle, southern and even most of northeastern Siberia, the glaciations were local and limited largely to the mountain areas. The ice shield did extend from northern Europe onto the northern section of west Siberia but this area was, sure enough, too far away from southern China to influence its Subtropical Evegreen Forest even nearly as much as the Lawrentian ice shield influenced the late-Madrean vegetation of the Southeastern Coastal Plain.

Mountain glaciers expanded in the highlands of western and north-western China (Winkler and Wang 1993) but their inflence on eastern portion of China is difficult to

estimate. During the Quaternary the northern boundary of the subtropical evergreen forest in China shifted 3 to 5 southward compared to its location in the late Pliocene (Hsu, 1983). It appears, however, there was no major shift in the position of the Subtropical Evergreen Forest Region since the middle Pleistocene (Hsu, 1983).

<u>The Comparison of the Loess Hills Forests with the Other Forest Ecosystems of the American Southeast</u>

The diversity of the evergreen species in the Loess Hills forests is somewhat lower than in the Coastal Plain forests generally located on the same latitude but developed on poorer sandy soils. The deep-loess hardwood forests of the Bluffland belt lack few trees characteristic of the non-loessial forest types such as upland laurel oak (*Quercus hemisphaerica*) and sweetbay (*Magnolia virginiana*), as well as some understory evergreen specialists such as *Osmanthus americanus*, *Illicium floridanum*, *Persea* spp., and *Cyrilla racemiflora*.

On the other hand, with fewer species of evergreens as they are, the southernmost Loess Hills forests may be equally or even more evergreen than their counterparts developed on sands and sandy loams. In fact, there are some evergreen species that appear to be favored by the calcareous nature of the loessial soils. The physiognomic comparison of the West Feliciana forests developed on the thick loess deposits with the patches of the hardwood forests survived on sandy slopes along the small creeks in

southeast Louisiana and southern Mississippi suggest, for example, that few evergreen subcanopy components such as *Prunus caroliniana* and *Ilex opaca* tend to peak on the loessial rather than the non-loessial soils. Likewise, *Simplocos tinctoria* also seems to be much more abundant in the old-growth slope forest of the Louisiana State Arboretum than in any sandy stream forests that I visited.

Still another difference between the loessial forests and those developed on non-loessial surfaces throughout the rest of the Coastal Plain is the presence in the former of a variety of the bottomland species that are typically absent from the sandy, highly percolative soils of the Coastal Plain. The relatively common bottomland components of the loessial forests include sycamore, as well as American and red elms. Interestingly enough, the Loess Hills forests harbor even the components of the truely swamp communities and exceptionally moist, low-lying bottomland forests. Water hickory (*Carya aquatica*) and swamp cottonwood (*Populus heterophylla*), also with green ash, was found in a perfectly upland mesic forest along the southern end of the Natchez Trace. Biogeographic distinctiveness of the Loess Hills from the rest of the mesic forests of the Coastal Plain is further suggested by the sprinkling presence of the bottomland trees of the "circum-Mississippian" flora - sugarberry (*Celtis*

laevigata), pecan (*Carya illinoensis*), Nuttall and willow oaks (*Quercus nuttallii* and *Q. phellos*).

Some authors emphasize the floristic affinity of the southern Blufflands with the Appalachian forests (Braun 1950, Brown 1938, 1954, Kral 1966, Delcourt and Delcourt, 1974). Braun (1950) placed the middle and northern section of the Blufflands into the Western Mesophytic Forest Region and suggested the similarity of the Loess Hills forests south of Vicksburg with those of the Mixed Mesophytic Forest Region. Indeed, the Loess Hills share with the Appalachian forests a rather rich assortment of herbaceous mesophytes and few distinctive arboreal components such as cucumber magnolia (*Magnolia acuminata*), oakleaf hydrangea (*Hydrangea quercifolia*), and, marginally, sourwood (*Oxydendrum arboreum*). But more comprehensive analysis of the species composition and structure of the Loess Hills forests suggests that these assemblages by no means can be qualified as "... a mixed mesophytic community modified chiefly by the presence of evergreen magnolia as one of the dominants", as stated by Braun (1950).

Many very characteristic temperate components of both the Mixed Mesophytic Forest and Western Mesophytic Forest regions such as northern red oak (*Quercus rubra*), chestnut oak (*Q. montana*), sugar maple (*Acer saccharum*), sweet buckeye (*Aesculus octandra*), silverbell (*Halesia monticola*), birches (*Betula lutea* and *B. lenta*), do not

occur in the Loess Hills forests. Chinquapin oak (*Q. Muhlenbergii*) which is one of the dominant species in the Western Mesophytic Forest Region is rare in the Blufflands. The forests of Deep Loess Section are poor in *Ericaceae* and essentially devoid of such genera as *Azalea*, *Kalmia* and *Rododendron* which are very important in the Mixed Mesophytic Forest Region.

What would be then, the biogeographic status of the Loess Hills forests? Since these forests contain many Coastal Plain species and tend to converge in the late stages of succession into beech-magnolia forest type, they are, of course, generically related to the other Coastal Plain mesic hardwood forests collectively known as the Southern Mixed Hardwood Forest. And yet, they can be interpreted as SMHF type only in the most general sense (implying, perhaps, the importance of the Coastal Plain component).

The Loess Hills forests appear to represent a genuinely unique forest type different from both the mesic hardwood forests of the Southeastern Coastal Plain and more interior Appalachian forests, although it combines some important features of the both. They should be, perhaps, identified as a discrete forest type on the vegetation map of Eastern North America.

Oddly, despite the highly unusual character of these ecosystems, until very recently they were given

surprisingly little attention by ecologists and biologists. This research in part attended to this problem.

The future research may be extended over the whole length of the Lower Mississippi Embayment, to the salt domes of coastal Louisiana. The establishment of the new preservation areas along the loessial pathway should be a primary practical outcome of such a research.

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APPENDIX A
LIST OF SPECIES AND FAMILIES REGISTERED IN SAMPLING SITES

Taxonomic nomenclature follows Radford et al. (1985). For species not found in the range covered by Radford et al (1985), Clewell (1985) was consulted.

Azalea, Wild (Rhododendron canescens (Michaux) Sweet) - Ericaceae

Ash, Carolina (Fraxinus caroliniana Miller) - Oleaceae

Ash, Green (Fraxinus pennsylvanica Marshall) - Oleaceae

Ash, White (Fraxinus americana L.) - Oleaceae

Basswood, American (Tilia americana L.) - Tiliaceae

Bay, Sweet (Magnolia virginiana L.) - Magnoliaceae

Beech, American (Fagus granidolia Ehrhart) - Fagaceae

Blackgum (Nyssa sylvatica Marshall, Black G.) - Nyssaceae

Blackhaw, Rusty (Viburnum rufidulum Raf.) - Caprifoliaceae

Boxelder (Acer negundo L.) - Aceracea

Buckeye, Red (Aesculus pavia L.) - Hippocastanaceae

Bumelia, Buckthorn (Bumelia lycioides (L.) Persoon) - Sapotaceae

Buckthorn, Carolina (Rhamnus caroliniana Walter) - Rhamnaceae

Bush, Strawberry (Euonymus americanus L.) - Celastraceae

Cedar, Red (Juniperus virginiana L.) - Cupressaceae

Cherry, Black (Prunus serotina) Ehrhart - Rosaceae

Chinaberry (Melia azedarach L.) - Meliaceae

Cottonwood, Eastern (Populus deltoides Marshall) - Salicaceae

Cypress, Bald (Taxodium distichum L.) - Cupressaceae

Dogwood, Flowering (Cornus florida L.) - Cornaceae

Dogwood, Rougleaf (Cornus drumondii C. A. May) - Cornaceae

Elderberry (Sambucus canadensis L.) - Caprifoliaceae

Elm, American (Ulmus americana L.) - Ulmaceae

Elm, Red (Ulmus rubra Muhl.) - Ulmaceae

Elm, Winged (Ulmus alata Michaux.) - Ulmaceae

French Mulberry (Callicarpa americana L.) - Verbenaceae

Erythrina (Erythrina herbacea L.) - Fabaceae

Fringe-tree (Chionanthus virginicus L.) - Oleaceae

Haw, Southern (Crataegus flava Ait) - Rosaceae

Haw, Spatulate (Crataegus spathulata Michaux.) - Rosaceae

Hawthorn, Parsley (Crataegus marshalii Eggl.) - Rosaceae

Hawthorn, Southern (Crataegus viridis L.) - Rosaceae

Hercules-club (Zanthoxylum clava-herculis L.) - Rutaceae

Hickory, Bitternut (Carya cordiformis (Wang.) K. Koch) - Juglandaceae

Hickory, Mockernut (Carya tomentosa (Poiret) Nuttall) - Juglandaceae

Hickory, Pignut (Carya glabra (Miller) Sweet) - Juglandaceae

Hickory, Shagbark (Carya ovata (Miller) K. Koch) - Juglandaceae

Hickory, Water (Carya aquatica (Michaux. f.) Nuttall) - Juglandaceae

Holly, American (Ilex opaca Aiton) - Aquifoliaceae

Holly, Deciduous (Ilex decidua Walter) - Aquifoliaceae

Holly, Carolina (Ilex ambigua Michaux.) - Aquifoliaceae

Hophornbeam, Eastern (Ostrya virginiana (Miller) K. Koch.) - Betulaceae

Hop-tree (Ptelea trifoliata L.) - Rutaceae

Hornbeam, American (Carpinus caroliniana Walter) - Betulaceae

Hydrangea, Oakleaf (Hydrangea quercifolia L.) - Saxifragaceae

Locust, Black (Robinia pseudo-acacia L.) - Fabaceae

Locust, Honey (Gleditsia triacanthos L.) - Fabaceae

Laurel Cherry, Carolina (Prunus caroliniana Aiton) - Rosaceae

Magnolia, Cucumber (Magnolia acuminata) - Magnoliaceae

Magnolia, Southern (Magnolia grandiflora L.) - Magnoliaceae

Magnolia, Pyramid (Magnolia pyramidata Bartram ex Pursh.) - Magnoliaceae

Magnolia, Bigleaf (Magnolia macrophylla Michaux.) - Magnoliaceae

Male-berry (Lyonia ligustrina (L.) DC.) - Ericaceae

Maple, Chalk (Acer leucoderme Small) - Aceraceae

Maple, Red (Acer rubrum L.) - Aceraceae

Maple, Southern Sugar (Acer barbatum Michaux.) - Aceraceae

Mulberry, Red (Morus rubra L.) Moraceae

Mulberry, Paper (Broussonetia papyrifera (L.) Vent.) - Moraceae

Oak, Cherrybark (Quercus pagoda) Raf. - Fagaceae

Oak, Chinquapin (Quercus muehlenbergii) Engelm. - Fagaceae

Oak, Durand (Quercus durandii) Buckley - Fagaceae

Oak, Laurel (Quercus laurifolia Michaux.) - Fagaceae

Oak, Live (Quercus virginiana Miller)- Fagaceae

Oak, Overcup (Quercus lyrata Walter) - Fagaceae

Oak, Post (Quercus stellata Wang) - Fagaceae

Oak, Shumard (Quercus shumardii Buckl.) - Fagaceae

Oak, Southern Red (Quercus falcata Michaux.) - Fagaceae

Oak, Swamp Chestnut (Quercus michauxii) Nuttall - Fagaceae

Oak, Upland Laurel (Quercus hemisphaerica Bartr.) - Fagaceae

Oak, Water (Quercus nigra L.) - Fagaceae

Oak, White (Quercus alba L.) - Fagaceae

Oak, Willow (Quercus phellos L.) - Fagaceae

Orange, Trifoliate (Poncirus trifoliata (L.) Raf.) - Rutaceae

Palmetto, Bush (Sabal minor (Jacquin) Persoon) - Arecaceae

Parasol-tree, China (Firmiana platanifolia (L. f.) Marsili) - Sterculiaceae

Paw-paw (Asimina triloba (L.) Dunal) - Annonaceae

Paulownia (Paulownia tomentosa (Thunberg) Steudel) - Scrophulariaceae

Pecan (Carya illinoensis (Wang.) K. Koch) - Juglandaceae

Persimmon (Diospyros virginiana L.) - Ebenaceae

Pine, Loblolly (Pinus taeda L.) - Pinaceae

Plum, Chicasaw (Prunus angustifolia Marshall) - Rosaceae

Plum, Mexican (Prunus mexicana (S.) Wats.) - Rosaceae

Privet, Chinese (Ligustrum sinense Lour.) - Oleaceae

Privet, Japanese (Ligustrum japonicum Thunberg) - Oleaceae

Raspberry (Rubus L.) - Rosaceae

Redbud (Cercis canadensis L.) - Fabaceae

Saint Andrew's Cross (Hypericum hypericoides (L.) Crantz) - Hypericaceae

Sassafras (Sassafras albidum (Nuttal) Nees) - Lauraceae

Serviceberry (Amelanchier arborea (Michaux.f.) Fern.) - Rosaceae

Silverbell, Two-winged (Halesia diptera Ellis) - Styracaceae

Sourwood (Oxydendrum arboreum (L.) DC.) - Ericaceae

Sparkleberry (Vaccinium arboreum Marshall) - Ericaceae

Spicebush (Lindera benzoin (L.) Blume) - Lauraceae

Squaw-huckleberry (Vaccinium stamineum L.) - Ericaceae

Stewartia, Virginia (Stewartia malacodendron L.) - Theaceae

Storax, Bigleaf (Styrax grandifolius Aiton) - Styracaceae

Sugarberry (Celtis laevigata Willd.) - Ulmaceae

Sumac, Smooth (Rhus glabra L.) - Anacardiaceae

Sumac, Winged (Rhus copallina L.) - Anacardiaceae

Sweetgum (Liquidambar styracidlua L.) - Hamamelidaceae

Sweetleaf (Symplocos tinctoria (L.) L'Her.) - Symplocaceae

Sycamore (Platanus occidentalis L.) - Platanaceae

Tallowtree, Chinese (Sapium sebiferum L.) - Euphorbiaceae

Tulip Tree (Liriodendron tulipfera L.) - Magnoliacea

Vaccinium, Elliott's (Vaccinium elliottii Chapman) - Ericaceae

Viburnum, Toothleaf (Viburnum dentatum L.) - Caprifoliaceae

Viburnum, Possumhaw (Viburnum nudum L.) - Caprifoliaceae

Virginia Willow (Itea virginica L.) - Saxifragaceae

Walkingstick, Devil's (Aralia spinosa L.) - Araliaceae

Walnut, Black (Juglans nigra L.) - Juglandaceae

Walnut, White (Juglans cinerea L.) - Juglandaceae

Waxmyrtle (Myrica cerifera L.) - Myricaceae

Willow, Black (Salix nigra Marshall) - Salicaceae

Witch-hazel (Hamamelis virginiana L.) - Hamamelidaceae

Yaupon (Ilex vomitoria Aiton) - Aquifoliaceae

APPENDIX B
LIST OF SPECIES WITH INDICATION OF THE SITES IN WHICH THEY WERE ENCOUNTERED

Taxonomic nomenclature follows Radford et al. (1985). For species not found in the range covered by Radford et al (1985), Clewell (1985) was consulted.

Acer barbatum Michaux. (Aceraceae) - Steep Bluffs Area, Bluff Experimental Forest, Port Gibson, Magnolia Glen Preserve (Tunica Hills), Port Hudson Area

Acer leucoderme Small (Aceraceae) - Magnolia Glen Preserve (Tunica Hills, ravine section only)

Acer negundo L. (Aceraceae) - Steep Bluffs Area, Bluff Experimental Forest, Port Gibson, Natchez Trace Forest, Magnolia Glen Preserve (Tunica Hills), Port Hudson Area

Acer rubrum L. (Aceraceae) - Steep Bluffs Area, Bluff Experimental Forest, Port Gibson, Magnolia Glen Preserve (Tunica Hills), Port Hudson Area, Forked Island, Chicot State Park, Louisiana State Arboretum, Sicily Island, Homochito National Forest

Aesculus pavia L. (Hippocastanaceae) - Magnolia Glen Preserve (Tunica Hills), Chicot State Park, Sicily Island

Amelanchier arborea (Michaux.f.) Fern. (Rosaceae) - Port Hudson, Sicily Island

Aralia spinosa L. (Araliaceae) - Steep Bluffs, Magnolia Glen Preserve (Tunica Hills), Forked Island, Louisiana State Arboretum

Asimina triloba (L.) Dunal) (Annonaceae) - Steep Bluffs Area, Bluff Experimental Forest, Magnolia Glen Preserve (Tunica Hills), Chicot State Park, Louisiana State Arboretum, Homochito national Forest

Broussonetia papyrifera (L.) Vent. (Moraceae) - Steep Bluffs Area, Magnolia Glen Preserve (Tunica Hills, uplands),

Bumelia lycioides (L.) Persoon (Sapotaceae) - Steep Bluffs Area, Bluff Experimental Forest, Magnolia Glen Preserve (Tunica Hills), Port Hudson Area, Chicot State Park, Louisiana State Arboretum, Sicily Island, Homochito National Forest

Callicarpa americana L. (Verbenaceae) - Steep Bluffs Area, Bluff Experimental Forest, Port Gibson, Natchez Trace

Forest, Magnolia Glen Preserve (Tunica Hills), Port Hudson Area, Forked Island, Chicot State Park, Louisiana State Arboretum, Sicily Island, Homochito National Forest

Carya aquatica (Michaux. f.) Nuttall) (Juglandaceae) - Natchez Trace Forest

Carpinus caroliniana Walter (Betulaceae) - Steep Bluffs Area, Bluff Experimental Forest, Port Gibson, Natchez Trace Forest, Magnolia Glen Preserve (Tunica Hills), Port Hudson Area, Burden Plantation, Chicot State Park, Louisiana State Arboretum, Sicily Island, Homochito National Forest

Carya cordiformis (Wang.) K. Koch) (Juglandaceae) - Steep Bluffs Area, Bluff Experimental Forest, Port Gibson, Natchez Trace Forest, Magnolia Glen Preserve (Tunica Hills), Port Hudson Area, Chicot State Park, Louisiana State Arboretum, Sicily Island, Homochito National Forest

Carya glabra (Miller) Sweet) (Juglandaceae) - Steep Bluffs Area, Bluff Experimental Forest, Port Gibson, Natchez Trace Forest, Magnolia Glen Preserve (Tunica Hills), Port Hudson Area, Chicot State Park, Louisiana State Arboretum, Sicily Island, Homochito National Forest

Carya illinoensis (Wang.) K. Koch (Juglandaceae) - Steep Bluffs Area, Natchez Trace Forest, Burden Plantation

Carya ovata (Miller) K. Koch) (Juglandaceae) - Chicot State Park, Homochito National Forest

Carya tomentosa (Poiret) Nuttall) (Juglandaceae) - Magnolia Glen Preserve (Tunica Hills), Louisiana State Arboretum, Sicily Island, Homochito National Forest

Celtis laevigata Willd. - Steep Bluffs Area, Bluff Experimental Forest, Natchez Trace Forest, Magnolia Glen Preserve (Tunica Hills), Port Hudson Area, Burden Plantation, Chicot State Park, Louisiana State Arboretum

Cercis canadensis L. (Fabaceae) - Steep Bluffs, Bluff Experemental Forest, Magnolia Glen Preserve (Tunica Hills), Chicot State Park

Chionanthus virginicus L. (Oleaceae) - Chicot State Park, Homochito national Forest

Cornus drumondii C. A. May (Cornaceae) - Natchez Trace Forest, Magnolia Glen Preserve (Tunica Hills), Port Hudson Area

Cornus florida L. (Cornaceae) - Steep Bluffs Area, Bluff Experimental Forest, Port Gibson, Natchez Trace Forest, Magnolia Glen Preserve (Tunica Hills), Port Hudson Area, Burden Plantation, Chicot State Park, Louisiana State Arboretum, Sicily Island, Homochito National Forest

Crataegus flava Ait (Rosaceae) - Sicily Island

Crataegus marshalii Eggl. (Rosaceae) - Steep Bluffs Area, Magnolia Glen Preserve (Tunica Hills), Port Hudson Area, Burden Plantation, Forked Island, Chicot State Park, Louisiana State Arboretum, Sicily Island, Homochito National Forest

Crataegus spathulata Michaux. (Rosaceae) - Sicily Island

Crataegus viridis L. (Rosaceae) - Sicily Island

Diospyros virginiana L. (Ebenaceae) - Steep Bluffs Area, Bluff Experimental Forest, Magnolia Glen Preserve (Tunica Hills), Port Hudson Area, Chicot State Park, Louisiana State Arboretum, Sicily Island, Homochito National Forest.

Erythrina herbacea L. (Fabaceae) - Magnolia Glen Preserve (Tunica Hills - upland section), Port Hudson Area, Chicot State Park, Louisiana State Arboretum, Sicily Island, Homochito National Forest

Euonymus americanus L. (Celastraceae) - Steep Bluffs Area, Bluff Experimental Forest, Magnolia Glen Preserve (Tunica Hills), Port Hudson Area, Chicot State Park, Louisiana State Arboretum, Sicily Island, Homochito National Forest

Fagus granidolia Ehrhart (Fagaceae) - Steep Bluffs Area, Bluff Experimental Forest, Port Gibson, Natchez Trace Forest, Magnolia Glen Preserve (Tunica Hills), Port Hudson Area, Burden Plantation, Chicot State Park, Louisiana State Arboretum, Sicily Island, Homochito National Forest

Firmiana platanifolia (L. f.) Marsili (Sterculiaceae) - Magnolia Glen Preserve (Tunica Hills)

Fraxinus americana L. (Oleaceae) - Steep Bluffs Area, Bluff Experimental Forest, Port Gibson, Natchez Trace Forest, Magnolia Glen Preserve (Tunica Hills), Port Hudson Area, Forked Island, Chicot State Park, Louisiana State Arboretum, Sicily Island, Homochito National Forest

Fraxinus caroliniana Miller (Oleaceae) - Chicot State Park

Fraxinus pennsylvanica Marshall (Oleaceae) - Magnolia Glen Preserve (Tunica Hills), Forked Island

Gleditsia triacanthos L. (Fabaceae) - Natchez Trace Forest, Magnolia Glen Preserve (Tunica Hills)

Halesia diptera Ellis (Styracaceae)- Magnolia Glen Preserve (Tunica Hills), Port Hudson Area, Chicot State Park, Sicily Island Area, Homochito National Forest

Hamamelis virginiana L. (Hamamelidaceae) - Steep Bluffs, Bluff Experimental Forest, Magnolia Glen Preserve (Tunica Hills), Port Hudson Area, Chicot State Park, Louisiana State Arboretum, Sicily Island, Homochito National Forest

Hydrangea quercifolia L. (Saxifragaceae) - Steep Bluffs Area, Bluff Experimental Forest, Port Gibson, Natchez Trace Forest, Magnolia Glen Preserve (Tunica Hills), Port Hudson Area, Chicot State Park, Louisiana State Arboretum, Sicily Island

Hypericum hypericoides (L.) Crantz (Hypericaceae) - Magnolia Glen Preserve (Tunica Hills), Forked Island, Sicily Island Area

Ilex ambigua Michaux. (Aquifoliaceae) - Sicily island, Homochito national Forest

Ilex decidua Walter (Aquifoliaceae) - Steep Bluffs Area, Natchez Trace Forest, Magnolia Glen Preserve (Tunica Hills), Port Hudson Area, Chicot State Park, Louisiana State Arboretum, Sicily Island, Homochito National Forest

Ilex opaca Aiton (Aquifoliaceae) - Steep Bluffs Area, Bluff Experimental Forest, Port Gibson, Natchez Trace Forest, Magnolia Glen Preserve (Tunica Hills), Port Hudson Area, Forked Island, Chicot State Park, Louisiana State Arboretum, Sicily Island, Homochito National Forest

Ilex vomitoria Aiton (Aquifoliaceae) - Magnolia Glen Preserve (Tunica Hills), Port Hudson Area, Burden Plantation, Forked Island, Chicot State Park, Louisiana State Arboretum

Itea virginica L. (Saxifragaceae) - Port Gibson Site

Juglans cinerea L. (Juglandaceae) - Steep Bluffs

Juglans nigra L. (Juglandaceae) - Steep Bluffs, Magnolia Glen Preserve (Tunica Hills)

Juniperus virginiana L. (Cupressaceae) - Magnolia Glen Preserve (Tunica Hills), Louisiana State Arboretum

Ligustrum japonicum Thunberg (Oleaceae) - Burden Plantation

Ligustrum sinense Lour. (Oleaceae) - Bluff Experimental Forest, Magnolia Glen Preserve (Tunica Hills), Port Hudson Area, Burden Plantation, Forked Island

Lindera benzoin (L.) Blume (Lauraceae)- Steep Bluffs Area, Bluff Experimental Forest, Magnolia Glen Preserve (Tunica Hills), Port Hudson Area, Louisiana State Arboretum

Liriodendron tulipfera L. (Magnoliaceae) - Steep Bluffs Area, Bluff Experimental Forest, Port Gibson Site, Natchez Trace Forest, Magnolia Glen Preserve (Tunica Hills), Port Hudson Area, Burden Plantation, Chicot State Park, Louisiana State Arboretum, Sicily Island Area

Lyonia ligustrina (L.) DC. (Ericaceae) - Homochito National Forest

Magnolia acuminata L. (Magnoliaceae) - Steep Bluffs Area, Bluff Experimental Forest, Port Gibson, Natchez Trace Forest, Chicot State Park, Sicily Island

Magnolia grandiflora L. (Magnoliaceae) - Bluff Experimental Forest, Port Gibson, Magnolia Glen Preserve (Tunica Hills, ravine and upland section), Port Hudson Area, Forked Island, Chicot State Park, Louisiana State Arboretum, Sicily Island, Homochito National Forest

Magnolia macrophylla Michaux. (Magnoliaceae) - Steep Bluffs Area, Homochito National Forest

Magnolia pyramidata Bartram ex Pursh. (Magnoliaceae) - Magnolia Glen Preserve (Tunica Hills, ravine and upland section)

Magnolia virginiana L. (Magnoliaceae) - Homochito National Forest

Melia azedarach L. (Meliaceae) - Magnolia Glen Preserve (Tunica Hills)

Morus rubra L. (Moraceae) - Steep Bluffs Area, Bluff Experimental Forest, Port Gibson, Magnolia Glen Preserve (Tunica Hills), Port Hudson Area, Forked Island, Chicot State Park, Louisiana State Arboretum, Sicily Island, Homochito National Forest

Myrica cerifera L. (Myricaceae) - Burden Plantation, Sicily Island, Homochito National Forest

Nyssa sylvatica Marshall, Black G. (Nyssaceae) - Steep Bluffs Area, Bluff Experimental Forest, Port Hudson Area, Forked Island, Chicot State Park, Louisiana State Arboretum, Sicily Island, Homochito National Forest

Ostrya virginiana (Miller) K. Koch.) (Betulaceae) - Steep Bluffs Area, Bluff Experimental Forest, Port Gibson, Natchez Trace Forest, Magnolia Glen Preserve (Tunica Hills), Port Hudson Area, Chicot State Park, Louisiana State Arboretum, Sicily Island, Homochito National Forest

Oxydendrum arboreum (L.) DC. (Ericaceae)- Steep Bluffs Area, Port Hudson Area, Sicily Island Area, Homochito National Forest

Paulownia tomentosa (Thunberg) Steudel (Scrophulariaceae) - Steep Bluffs Area, Magnolia Glen Preserve (Tunica Hills)

Pinus taeda L. (Pinaceae) - Natchez Trace Forest, Magnolia Glen Preserve (Tunica Hills, uplands), Sicily Island
Prunus angustifolia Marshall (Rosaceae) - Bluff Experimental Forest

Platanus occidentalis L. (Platanaceae) - Steep Bluffs Area, Bluff Experimental Forest, Port Gibson Site, Natchez Trace Forest, Magnolia Glen Preserve (Tunica Hills), Port Hudson Area

Poncirus trifoliata (L.) Raf. (Rutaceae) - Steep Bluffs Area, Magnolia Glen Preserve (Tunica Hills)

Populus deltoides Marshall (Salicaceae) - Natchez Trace Forest

Prunus caroliniana Aiton (Rosaceae) - Natchez Trace Forest, Magnolia Glen Preserve (Tunica Hills), Port Hudson Area

Prunus mexicana (S.) Wats. (Rosaceae) - Bluff Experimental Forest, Port Gibson, Sicily Island

Prunus serotina Ehrhart (Rosaceae) - Steep Bluffs Area, Bluff Experimental Forest, Port Gibson, Natchez Trace Forest, Magnolia Glen Preserve (Tunica Hills), Port Hudson Area, Burden Plantation, Forked Island, Chicot State Park, Louisiana State Arboretum, Sicily Island, Homochito National Forest

Ptelea trifoliata L. (Rutaceae) - Steep Bluffs Area

Quercus alba L. (Fagaceae) - Steep Bluffs Area, Bluff Experimental Forest, Port Gibson, Magnolia Glen Preserve

(Tunica Hills), Port Hudson Area, Sicily Island, Homochito national Forest

Quercus durandii Buckley (Fagaceae) - Port Gibson

Quercus falcata Michaux. (Fagaceae) - Natchez Trace Forest, Magnolia Glen Preserve (Tunica Hills, uplands), Sicily Island Area, Homochito National Forest

Quercus hemisphaerica Bartr. (Fagaceae) - Chicot State Park, Homochito National Forest

Quercus laurifolia Michaux. (Fagaceae) - Forked Island

Quercus lyrata Walter (Fagaceae) - Magnolia Glen preserve (Tunica Hills Area)

Quercus michauxii Nuttall (Fagaceae) - Steep Bluffs Area, Bluff Experimental Forest, Port Gibson, Natchez Trace Forest, Magnolia Glen Preserve (Tunica Hills), Port Hudson Area, Chicot State Park, Louisiana State Arboretum, Sicily Island, Homochito National Forest

Quercus muehlenbergii Engelm. (Fagaceae) - Bluff Experimental Forest, Magnolia Glen Preserve (Tunica Hills), Sicily Island

Quercus nigra L. (Fagaceae) - Steep Bluffs Area, Bluff Experimental Forest, Port Gibson, Natchez Trace Forest, Magnolia Glen Preserve (Tunica Hills), Port Hudson Area, Forked Island, Chicot State Park, Louisiana State Arboretum, Sicily Island, Homochito National Forest

Quercus pagoda Raf. (Fagaceae) - Steep Bluffs Area, Bluff Experimental Forest, Magnolia Glen Preserve (Tunica Hills), Port Hudson Area, Burden Plantation, Forked Island, Chicot State Park, Louisiana State Arboretum, Sicily Island, Homochito National Forest

Quercus phellos L. (Fagaceae) - Magnolia Glen Preserve (Tunica Hills), Burden Plantation

Quercus shumardii Buckl. (Fagaceae) - Steep Bluffs Area, Bluff Experimental Forest, Port Gibson, Magnolia Glen Preserve (Tunica Hills), Port Hudson Area, Chicot State Park, Louisiana State Arboretum, Sicily Island, Homochito National Forest

Quercus stellata Wang (Fagaceae) - Sicily Island Area, Homochito National Forest

Quercus virginiana Miller (Fagaceae) - Forked Island

Rhamnus caroliniana Walter (Rhamnaceae) - Steep Bluffs Area, Bluff Experimental Forest, Magnolia Glen Preserve (Tunica Hills), Chicot State Park, Louisiana State Arboretum, Sicily Island

Rhododendron canescens (Michaux) Sweet) (Ericaceae) - Homochito National Forest

Rhus copallina L. (Anacardiaceae) - Magnolia Glen Preserve (Tunica Hills)

Rhus glabra L. (Anacardiaceae) - Chicot State Park

Robinia pseudo-acacia L. (Fabaceae) - Natchez Trace Forest, Magnolia Glen Preserve (Tunica Hills)

Rubus L. (Rosaceae) - Steep Bluffs Area, Bluff Experimental Forest, Port Gibson Site, Natchez Trace Forest, Magnolia Glen Preserve (Tunica Hills), Port Hudson Area, Burden Plantation, Forked Island, Chicot State Park, Louisiana State Arboretum, Sicily Island Area, Homochito National Forest

Sabal minor (Jacquin) Persoon (Arecaceae) - Magnolia Glen Preserve (Tunica Hills), Port Hudson Area, Burden Plantation, Forked Island, Chicot state Park, Louisiana State Arboretum, Sicily Island

Salix nigra Marshall (Salicaceae) - Sicily Island

Sambucus canadensis L. (Caprifoliaceae) - Steep Bluffs Area, Bluff Experimental Forest, Port Gibson, Natchez Trace Forest, Magnolia Glen Preserve (Tunica Hills), Burden Plantation, Forked Island, Chicot State Park, Louisiana State Arboretum

Sapium sebiferum L. (Euphorbiaceae) - Burden Plantation, Forked Island, Chicot State Park

Sassafras albidum (Nuttal) Nees Lauraceae - Steep Bluffs Area, Bluff Experimental Forest, Port Gibson, Natchez Trace Forest, Magnolia Glen Preserve (Tunica Hills), Port Hudson Area, Chicot State Park, Louisiana State Arboretum, Sicily Island Area, Homochito National Forest

Stewartia malacodendron L. (Theaceae) - Port Hudson Area, Sicily Island Area

Styrax grandifolia Aiton- Steep Bluffs Area, Bluff Experimental Forest, Port Gibson Site, Natchez Trace Forest, Magnolia Glen Preserve (Tunica Hills), Port Hudson

Area, Burden Plantation, Chicot State Park, Louisiana State Arboretum, Sicily Island Area, Homochito National Forest

Sweetgum (Liquidambar styracidlua L.) - Hamamelidaceae - Steep Bluffs Area, Bluff Experimental Forest, Port Gibson Site, Natchez Trace Forest, Magnolia Glen Preserve (Tunica Hills), Port Hudson Area, Burden Plantation, Chicot State Park, Louisiana State Arboretum, Sicily Island Area

Symplocos tinctoria (L.) L'Her. (Symplocaceae) - Bluff Experimental Forest, Port Gibson Site, Natchez Trace Forest, Magnolia Glen Preserve (Tunica Hills), Port Hudson Area, Burden Plantation, Chicot State Park, Louisiana State Arboretum, Sicily Island Area

Taxodium distichum L. - Chicot State Park

Tilia americana L. (Tiliaceae) - Steep Bluffs Area, Bluff Experimental Forest, Port Gibson, Natchez Trace Forest, Magnolia Glen Preserve (Tunica Hills), Port Hudson Area, Forked Island, Chicot State Park, Louisiana State Arboretum, Sicily Island

Ulmus americana L. (Ulmaceae) - Steep Bluffs Area, Bluff Experimental Forest, Magnolia Glen Preserve (Tunica Hills), Port Hudson Area,

Ulmus rubra Muhl. (Ulmaceae) - Steep Bluffs Area, Bluff Experimental Forest, Port Gibson, Natchez Trace Forest, Magnolia Glen Preserve (Tunica Hills), Port Hudson Area, Burden Plantation, Forked Island, Chicot State Park, Louisiana State Arboretum, Sicily Island

Ulmus alata Michaux. (Ulmaceae) - Steep Bluffs Area, Bluff Experimental Forest, Natchez Trace Forest, Magnolia Glen Preserve (Tunica Hills), Port Hudson Area, Burden Plantation Chicot State Park, Louisiana State Arboretum, Sicily Island, Homochito National Forest

Vaccinium arboreum Marshall (Ericaceae)- Port Hudson Area, Chicot State Park, Louisiana State Arboretum, Sicily Island Area, Homochito National Forest

Vaccinium elliottii Chapman (Ericaceae) - Sicily Island, Homochito National Forest, Port Hudson Area, Forked Island
Viburnum dentatum L. (Caprifoliaceae) - Sicily Island, Homochito National Forest, Port Hudson Area, Forked Island

Vaccinium stamineum L. (Ericaceae) - Sicily Island Area, Homochito National Forest

Viburnum nudum L. - Caprifoliaceae - Homochito National Forest

Viburnum rufidulum Raf. (Caprifoliaceae) - Steep Bluffs Area, Bluff Experimental Forest, Magnolia Glen Preserve (Tunica Hills), Sicily Island, Homochito National Forest

Zanthoxylum clava-herculis L. (Rutaceae) - Steep Bluffs Area, Magnolia Glen Preserve (Tunica Hills)

APPENDIX C
MAPS OF THE SAMPLING AREAS

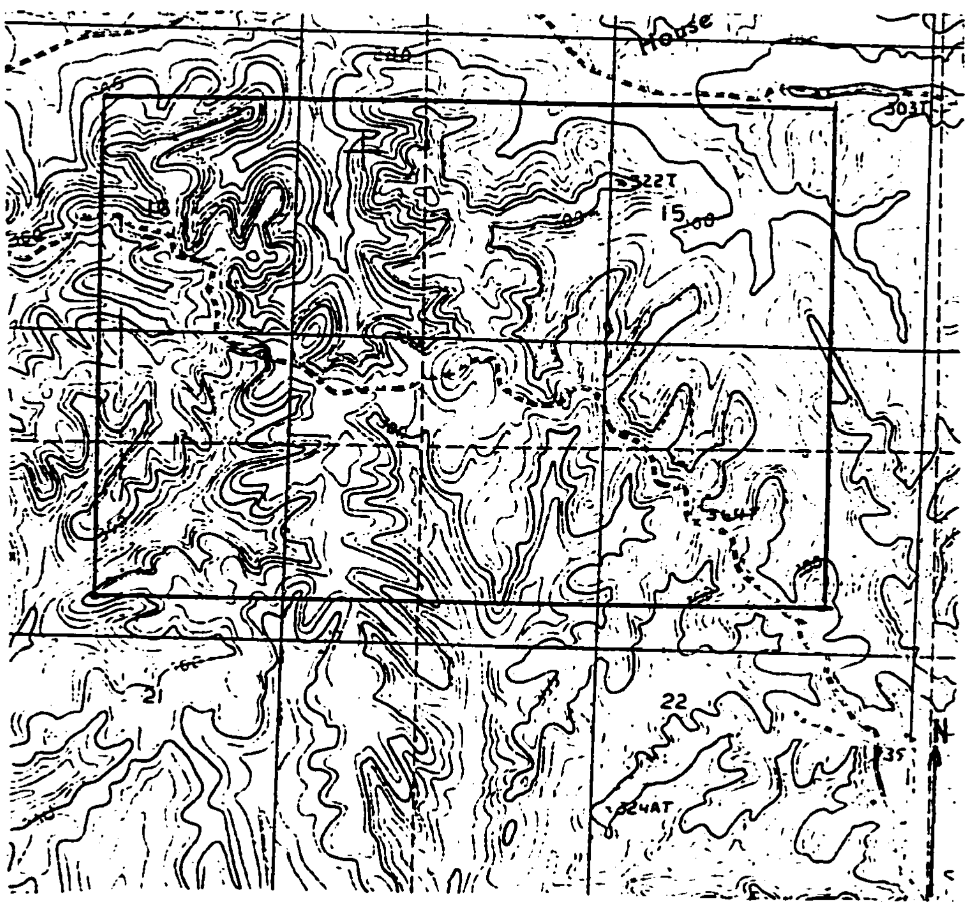


Figure 5. The Steep Bluffs Area, Warren County, Mississippi. Scale 1:24,000

Source: Eldorado Quadrangle, Mississippi, 7.5 Minute Series Topographic Map

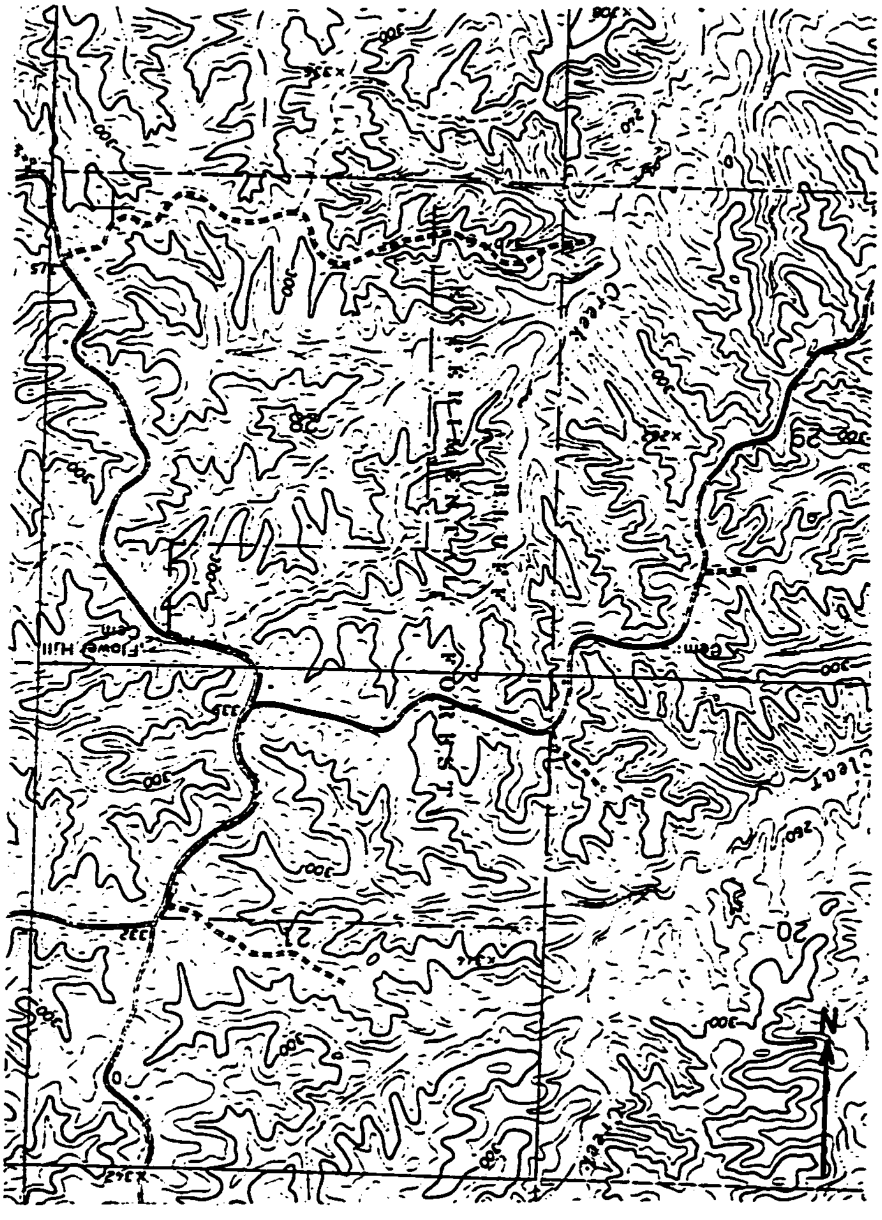


Figure 6. The Bluff Experimental Forest, Warren County, Mississippi. Scale 1:24,000

Source: Oak Ridge Quadrangle, Mississippi, 7.5 Minute Series Topographic Map

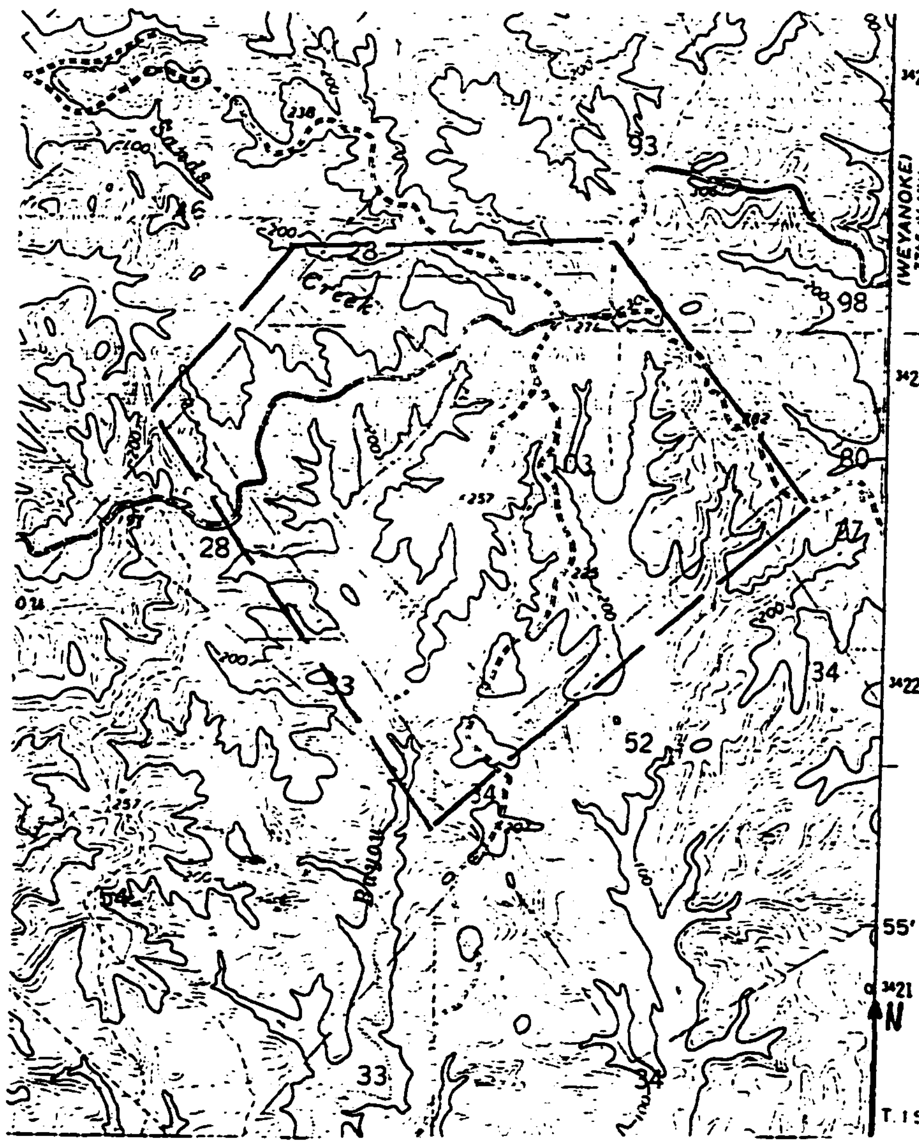
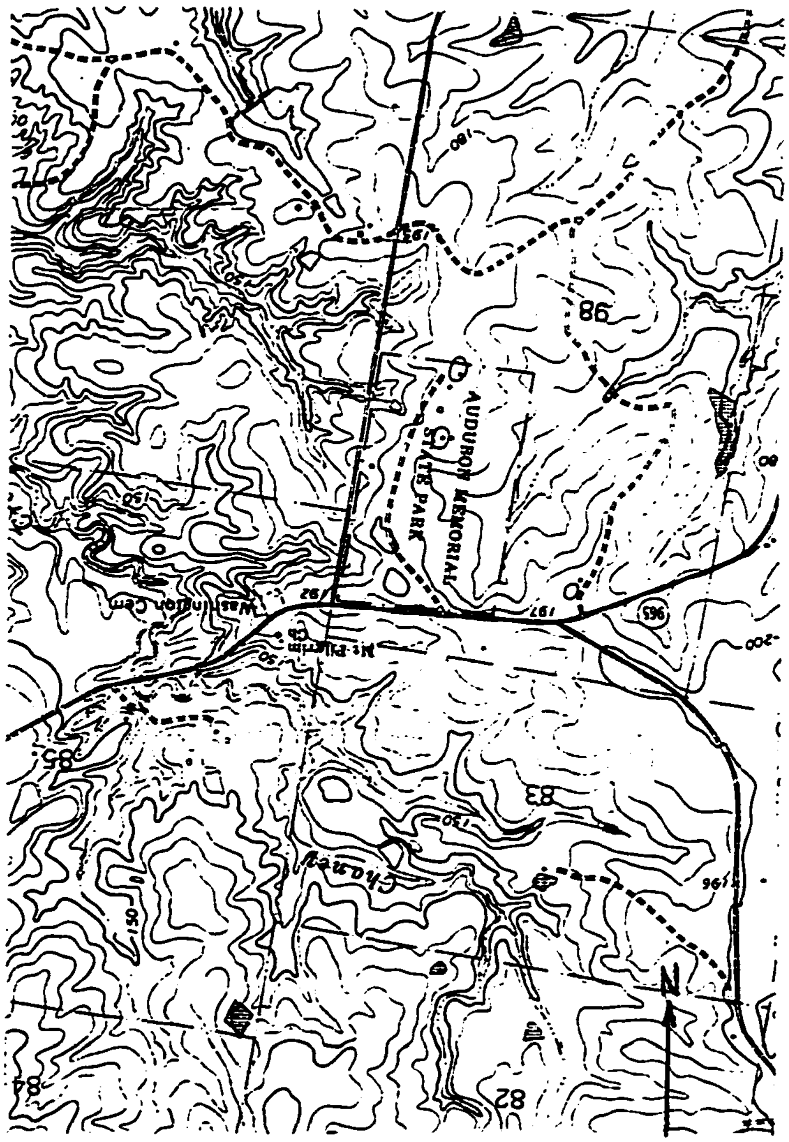


Figure 7. Magnolia Glen Preserve (The Tunica Hills Area), West Feliciana Parish, Louisiana. Scale 1:24,000

Source: Angola Quadrangle, Louisiana, 7.5 Minute Series Topographic Map



Source: Elm Park Quadrangle, Louisiana, 7.5 Minute Series Topographic Map

Figure 8. Audubon Memorial State Park (Oakley Plantation), West Feliciana Parish, Louisiana. Scale 1:24,000

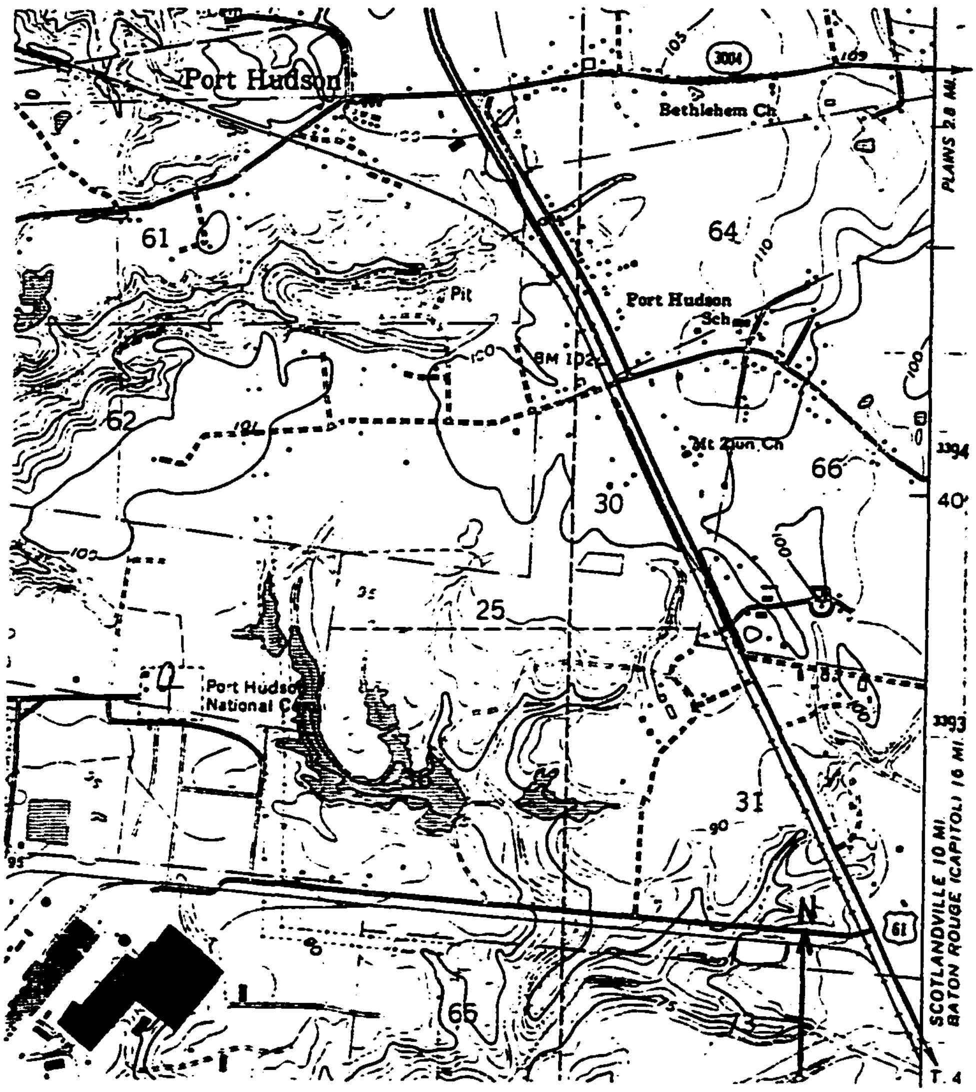


Figure 9. Port Hudson Area, East Baton Rouge Parish, Louisiana. Scale 1:24,000

Source: Port Hudson Quadrangle, Louisiana, 7.5 Minute Series Topographic Map

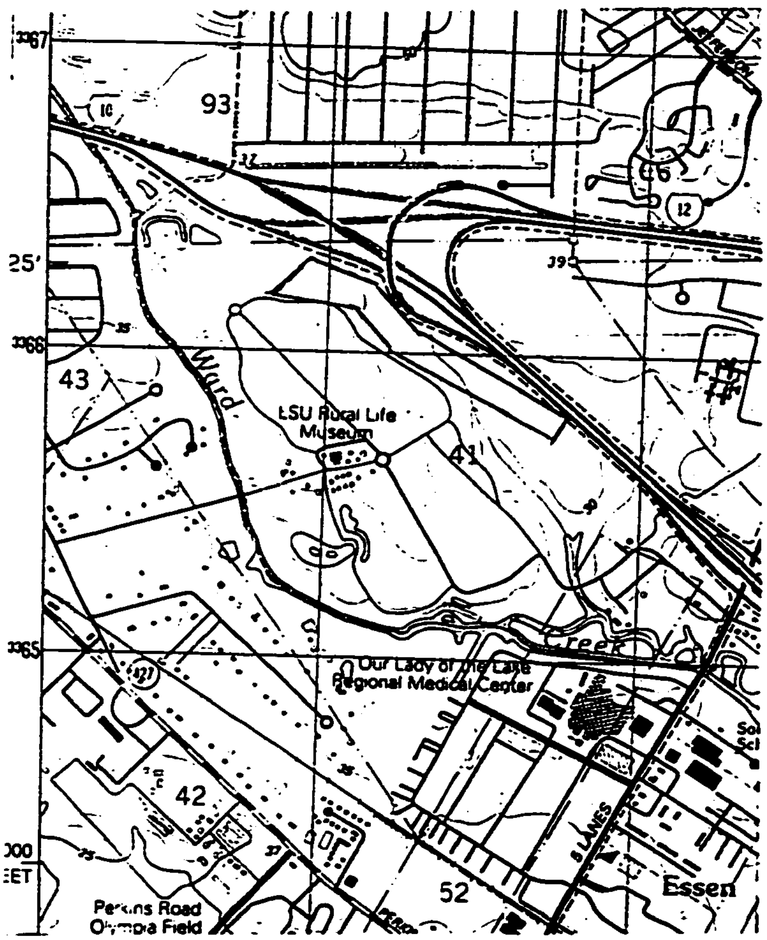


Figure 10. Burden Plantation, East Baton Rouge Parish, Louisiana. Scale 1:24,000

Source: Baton Rouge East Quadrangle, Louisiana, 7.5 Minute Series Topographic Map

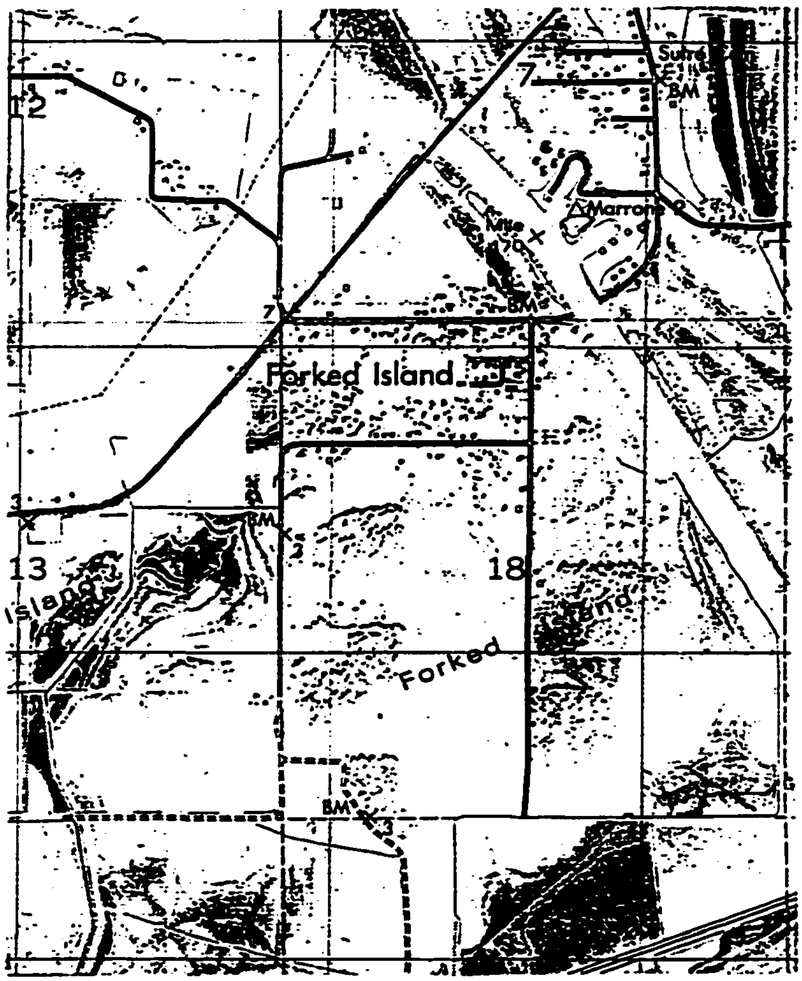


Figure 11. Forked Island Area, Vermillion Parish, Louisiana. Scale 1:24,000

Source: Forked Island Quadrangle, Louisiana, 7.5 Minute Series Topographic Map

Figure 12. Chicot State Park, Evangeline Parish, Louisiana Scale 1:24,000

Source: St. Landry Quadrangle, Louisiana, 7.5 Minute Series Topographic Map

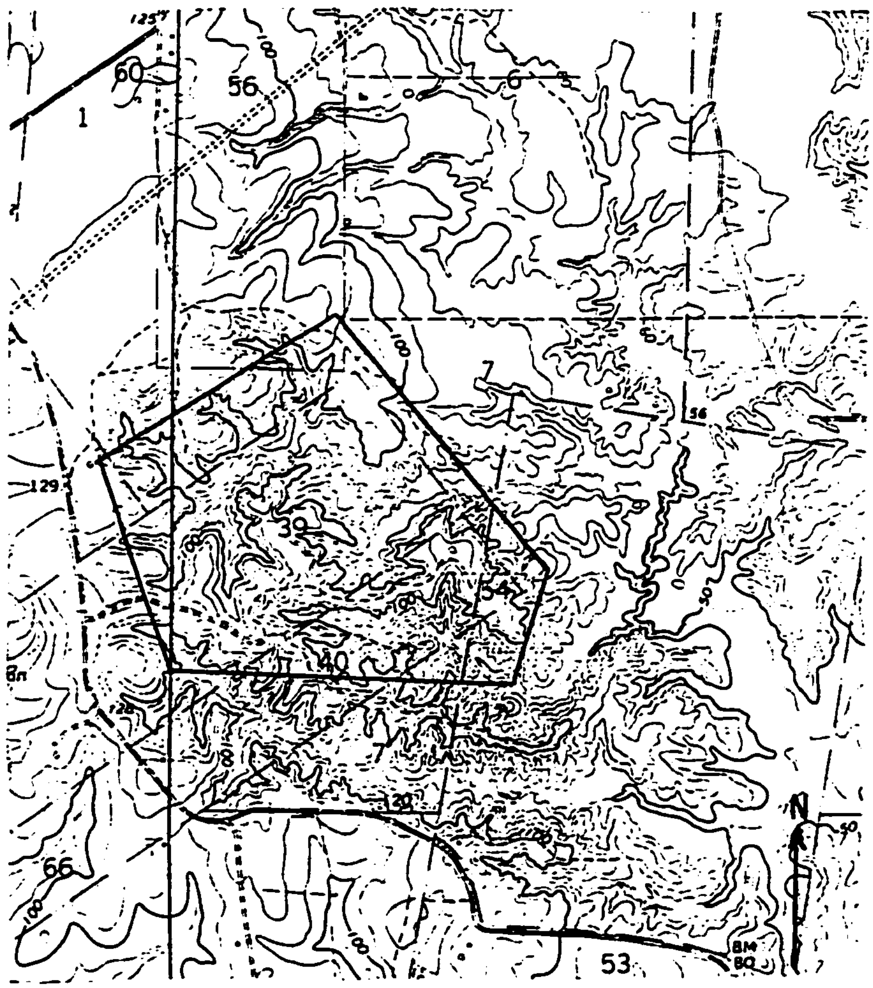


Figure 13. Louisiana State Arboretum, Evangeline Parish, Louisiana. Scale 1:24,000

Source: St. Landry Quadrangle, Louisiana, 7.5 Minute Series Topographic Map

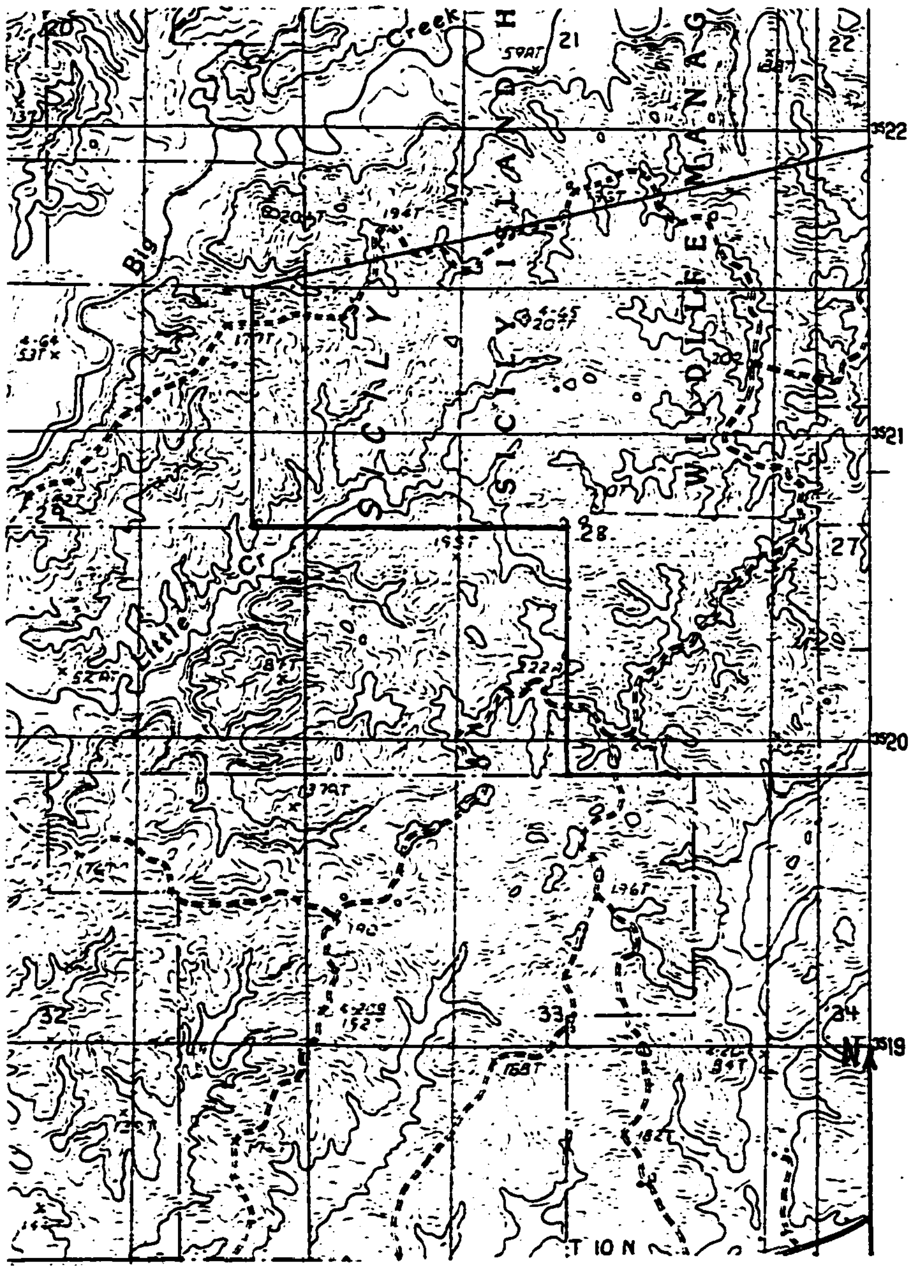


Figure 14. Sicily Island Area, Catahoula Parish, Louisiana. Scale 1:24,000

Source: Harrisonburg Quadrangle, Louisiana, 7.5 Minute Series Topographic Map

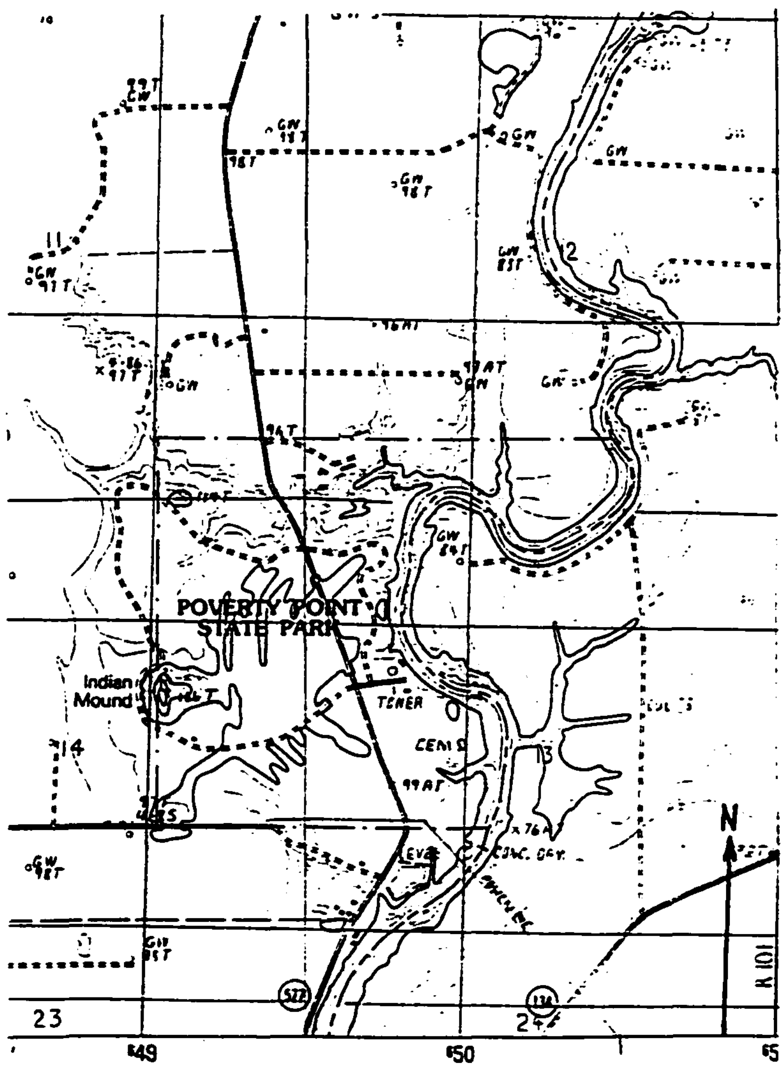


Figure 15. Poverty Point Area, West Carroll Parish, Louisiana. Scale 1:24,000

Source: Pioneer Quadrangle, Louisiana, 7.5 Minute Series Topographic Map

Figure 16. Clear Springs Area, Homochito National Forest, Franklin County, Mississippi. Scale 1:24,000

Source: Bude NW Quadrangle, Mississippi, 7.5 Minute Series Topographic Map

VITA

Igor Igorevich Ignatov was born on June 21, 1964, in Moscow, the Soviet Union. He attended public school 541 which he finished in 1981. In 1984 he entered Faculty of History of Moscow State University where he graduated with the "Red Diploma", equivalent of Master's degree in history, in 1990. He then attended the Department of Geography at the University of Wisconsin-Madison until entering the Department of Geography and Anthropology of Louisiana State University in 1992. He will earn the degree of Doctor of Philosophy in geography at the August commencement of 2001.

DOCTORAL EXAMINATION AND DISSERTATION REPORT

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Approved:

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William J Platt

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Date of Examination:

May 4, 2001