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Bottomland Hardwoods of the Mississippi Alluvial Valley: Characteristics and Management of Natural Function, Structure, and Composition

**Fayetteville, Arkansas
October 28, 1995**

Cover: Canopy and other forest vegetation in the Red Gum Research Natural Area (RNA) on the Delta National Forest, Sharkey County, MS. Red gum, so called by early loggers in the deep South for the red heartwood in old growth of this species, is one common name for sweetgum (*Liquidambar styraciflua* L.). This RNA contains remnant old-growth bottomland hardwood forest that still is dominated by sweetgum.

Photo by Lynda Wyant.

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Southern Research Station
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Bottomland Hardwoods of the Mississippi Alluvial Valley: Characteristics and Management of Natural Function, Structure, and Composition

Proceedings of a Symposium
Held during
The Natural Areas Conference
Fayetteville, Arkansas
October 28, 1995

Paul B. Hamel and Thomas L. Foti, Technical Editors

Preface

In October 1995 the symposium “Bottomland hardwoods of the Mississippi Alluvial Valley: characteristics and management of natural function, structure, and composition,” was held as part of the Natural Areas Conference in Fayetteville, AR. Dr. Scott Yaich, who now works for the Arkansas Game and Fish Commission, organized the symposium to provide managers with information necessary to restore composition, structure, and function to the forested ecosystem of the Mississippi Alluvial Valley. Symposium participants included managers of private, State, and Federal lands, as well as land management planners across a range of public and private jurisdictions.

Symposium presenters were invited to submit manuscripts; and only one manuscript previously had been submitted for journal publication (Kleiss, B.A. 1996. Sediment retention in a bottomland haradwood wetland in eastern Arkansas. Wetlands. 16(3): 321–333.). Subsequent to the symposium, Dr. Yaich asked us to compile and complete this volume. We acknowledge assistance provided by the many individuals who reviewed the submitted manuscripts.

All but one of the papers presented here were peer-reviewed by individuals unknown to the authors. That manuscript, the contribution of Dr. James T. Tanner who was then a professor of Zoology at the University of Tennessee, is included because it reflects the thinking of a biologist who studied the last extensive old-growth stand of bottomland hardwoods in the Mississippi Alluvial Valley. Dr. Tanner died shortly after completing the paper included in this volume.

Publication of these proceedings was underwritten by a grant made by the U.S. Fish and Wildlife Service to the Arkansas Natural Heritage Commission and by the USDA Forest Service, Southern Research Station.

—the editors

PEER REVIEW PROCESS

Each manuscript was reviewed by at least one and as many as three scientists selected by the editors for their subject-matter expertise. When the compiling editors decided to accept a submitted manuscript, they returned it and the peer reviews to the senior author, who then revised and resubmitted it in a form suitable for printing. Although each paper has been edited to reflect a uniform format and type style, responsibility for content and accuracy remains with the individual authors.

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NORTHERN ARKANSAS SPRING PRECIPITATION RECONSTRUCTED FROM TREE RINGS, 1023-1992 A.D.

Malcolm K. Cleaveland[1]

Abstract—Three baldcypress (*Taxodium distichum* (L.) Rich.) tree-ring chronologies in northeastern Arkansas and southeastern Missouri respond strongly to April-June (spring) rainfall in northern Arkansas. I used regression to reconstruct an average of spring rainfall in the three climatic divisions of northern Arkansas since 1023 A.D. The reconstruction was validated by comparing it to independent observed data. The reconstruction shows highly variable hydroclimatic conditions in the past, with considerable long-term low frequency variation. Managers who wish to know the "natural" state of ecosystems must consider ecosystem response to climate and the long-term changes in climatic averages and variability that have shaped the adaptability of the ecosystems. This adaptability may translate into resilience in the face of anthropogenic climate change.

INTRODUCTION

Climate varies considerably, not only at high frequencies, e.g., year-to-year, but at much lower frequencies, over decades and centuries (Bradley 1999, Crowley and North 1991). The observed (instrumental) data, rarely much longer than 100 years in the United States, give little insight into the nature of such low frequency climate variability, such as the occurrence of long duration extreme drought (e.g., Stahle and others 2000). Annual rings from climate-sensitive trees serve as proxies to investigate past climate (Cook and others 1999, Fritts 1976, Stockton and others 1985). The reconstruction presented here forms part of a network of long spring precipitation reconstructions (Stahle and Cleaveland 1992, 1996). Eventually these reconstructions will cover most of the Southeastern United States and the lower Mississippi Valley.

DATA

Tree-Ring Data

The tree-ring data come from baldcypress (a long-lived, deciduous conifer) at three sites (fig. 1, table 1). The samples were extracted with increment borers from many trees at each site above the basal swelling, a nondestructive sampling technique. Some cross-sections were cut from down trees to extend chronologies into the past. Core samples were glued into wooden mounts and the transverse surfaces of all samples sanded until polished.

Trees may not grow a ring everywhere when stressed, leaving a ring missing from the chronological sequence. On the other hand, many trees will occasionally form false rings, i.e., intra-annual features that look like real rings but create an error if included in the chronological sequence (Fritts 1976, Stokes and Smiley 1996, Swetnam and others1985). All samples were crossdated to detect false and missing rings. Crossdating involves pattern matching between many ring sequences at a site and nearby sites to ensure correct dating of each ring (Stokes and Smiley 1996). The dated series were then measured to 0.01 mm.

Tree-ring series contain nonclimatic growth trends that must be removed to make them statistically stationary (Fritts 1976). I used program ARSTAN (Cook 1985, Cook and others 1990) to fit an exponential curve declining to a constant or a regression line to each series, then divided each ring width by its corresponding curve value. The dimensionless indices derived by this process have a mean of 1.0 (eliminating differences in mean growth rates of the series) and relatively stable variance. Because the negative exponential curves and regression lines do an imperfect job of detrending in many cases, I further detrended the indices with a "stiff" cubic smoothing spline (Cook and Peters 1981, Peters and Cook 1981). The flexibility of the smoothing spline is controlled by setting a parameter equal to the wavelength of a sine wave which will have 50 percent of its variance removed by indexing (Cook 1985, Cook and Peters 1981, Peters and Cook 1981). For example, a 10-year spline

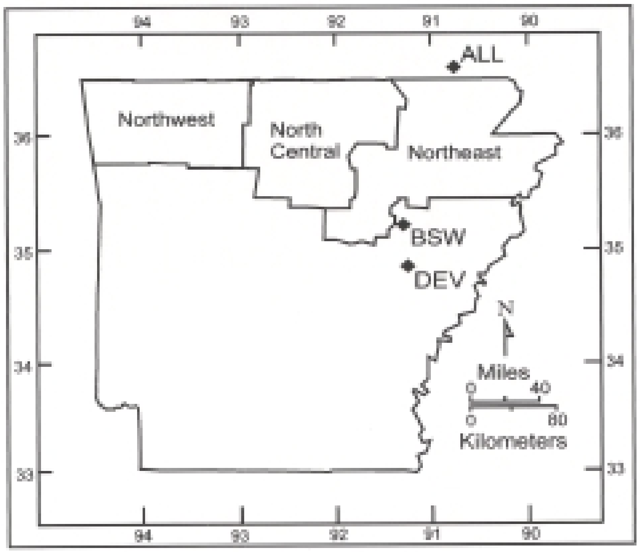

Figure 1—Locations of the tree-ring chronologies (table 1) used to reconstruct total spring (April–June) precipitation averaged from the three northern Arkansas climatic divisions.

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Table 1—Characteristics of tree-ring chronologies used to reconstruct spring (April-June) precipitation in northern Arkansas

Site/code name	Dates[a]	Latitude/ longitude	Standard deviation	Radii/ trees
All Lake, MO (ALL)	1188–1992	36^0,34’N 90^0,29’W	0.38	63/ 32
Black Swamp, AR (BSW)	1023–1980	35^0,09’N 91^0,18’W	0.39	61/ 31
Bayou DeView, AR (DEV)	1137–1985	34^0,57’N 91^0,13’W	0.42	60/ 28

[a] Residual (whitened) chronology (Cook 1985, 1987).

would fit the variation in a time series much more closely than a 100-year spline, the minimum stiffness used in detrending indices.

Tree-ring series usually contain persistence caused by physiology (Fritts 1976). Autoregressive (AR) modeling and removal of the persistence (“whitening”) make the climatic signal in tree rings clearer (Cook 1987, Meko 1981). The individual detrended series were AR modeled with the pooled multivariate AR model and the resulting whitened series were then averaged with an algorithm that weights values that fall near the mean higher than outliers (Cook 1985, Cook and others 1990). If significant AR persistence remained in the average, the chronology was rewhitened. The result was the “residual” chronology (Cook 1985). I averaged the three residual chronologies together to form a whitened regional tree-ring composite.

Climate Data

The precipitation data came from the National Climatic Data Center (NCDC) Historical Climatology series (Karl and others1983), a CD-ROM (NCDC n.d.) and updates to the CD-ROM. Exploratory correlations with the 12 months from the northern and central Arkansas and southern Missouri climate divisions showed that April-June rainfall in the three northern Arkansas climate divisions (Northwest, North Central and Northeast; fig. 1) correlated best with growth of the three tree-ring chronologies. Although the tree climate divisions reconstructed contain none of the tree-ring chronologies, they are nonetheless well correlated with the averaged tree growth because the trees respond to broad patterns of regional climate over hundreds of kilometers (Cook and others 1996). Monthly precipitation from the three northern Arkansas climatic divisions (fig. 1; NCDC n.d.) were averaged 1895-1992. The average of the three divisions was an AR-0 process, i.e., it contained no significant persistence (SAS Institute Inc. 1993).

CALIBRATION, RECONSTRUCTION AND VALIDATION

Calibration

Although the chronology average goes to 1992, I terminated the calibration period in 1985 because only one of the three chronologies extends further (table 1). I regressed (Draper and Smith 1981, SAS Institute Inc. 1989b) the regional tree-ring average against the northern Arkansas spring climate average for 1895-1985 and for two subperiods, 1895-1939 and 1940-1985 (fig.2, table 2). The 1895-1985 calibration equation used for reconstruction was:

$$Y_t = 113.7 + 241.7X_t \tag{1}$$

where Y_t is the total April-June rainfall for year t (average of the three climate divisions) and X_t is the average of the three residual chronologies. The results were excellent, accounting for more than 64 percent of the climatic variance 1895–1985. The Durbin-Watson test (Draper and Smith 1981) showed the residuals from regression 1895-1985 to be significantly serially correlated (r = 0.18), as were the residuals 1940-1985 (r = 0.29). Nevertheless, inspection of scatterplots of the residuals (not shown) appear to contain no marked departures from linearity.

Reconstruction and Validation

The regression coefficients (eqn. 1) were applied to the entire tree-ring series to produce estimates of spring rainfall (fig. 3) from averaged annual growth. The other calibrations

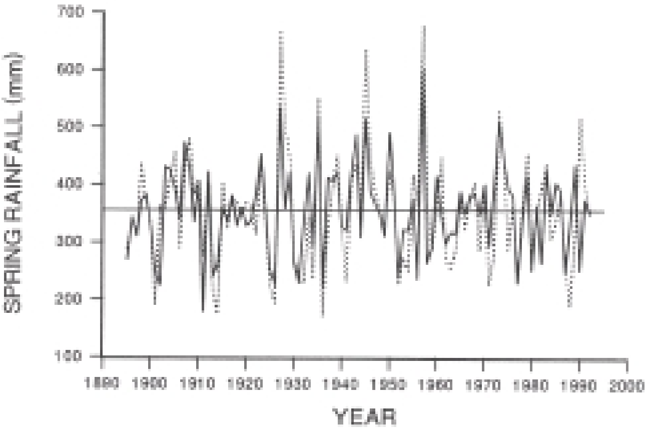

Figure 2—Observed (dashed line) and reconstructed (solid line) total spring (April-June) precipitation averaged from the three northern Arkansas climatic divisions, 1895–1992 (Karl and others 1983, NCDC n.d.).

Table 2—Calibration and validation statistics for reconstruction of spring (April-June) precipitation (mm) in northern Arkansas. B_0 and B_1 are the intercept and slope of the regression line, respectively. There is no significant difference ($P > 0.05$) between the parameters in the two subperiods, 1895-1939 and 1940-1985

Calibration period	R^2adj[a]	B_0	B_1	Residual autocorrelation[b]
1895-1985	0.644	113.7	241.7	0.18*
1895-1939	.673	107.2	250.4	.06NS
1940-1985	.604	120.2	233.5	.29*

Validation period	Correlation[c]	t-test diff. of means[d]	Sign test +/-[e]	Reduction of error[f]
1940-1985	.783***	.02NS	36/9***	.62
1895-1939	.825***	.00NS	36/9***	.68

* = $P < 0.05$; *** = $P < 0.001$; NS = $P > 0.05$, not significant

[a] Multiple correlation coefficient adjusted for loss of degrees of freedom (Draper and Smith 1981).

[b] Autocorrelation of residual tested with the Durbin-Watson statistic (Draper and Smith 1981, Neter and Wasserman 1974).

[c] Pearson product-moment correlation coefficient (Steel and Torrie 1980).

[d] Two-tailed paired observation test of difference between observed and reconstructed precipitation means (Steel and Torrie 1980); failure to find a significant difference is a good result.

[e] One-tailed test on the agreement between signs of departures from the means of the observed and reconstructed series (Conover 1980); positive shows agreement on the direction of the departures.

[f] The reduction of error statistic varies between negative infinity and positive 1.0; any positive number indicates skill at recovering paleoclimatic information (Fritts 1976).

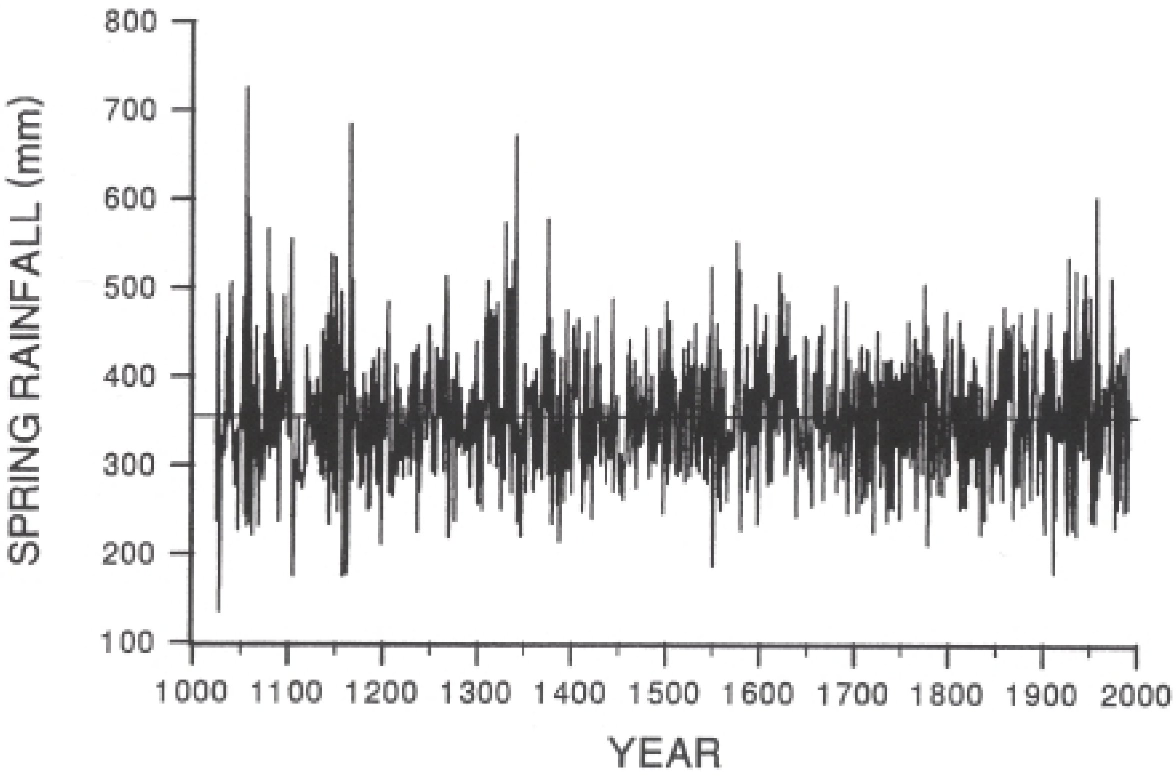

Figure 3—Reconstructed total spring (April-June) precipitation averaged from the three northern Arkansas climatic divisions, 1023–1992.

permitted validation of the series, because the observed data not used in the short calibrations could be tested for accuracy (Snee 1977). All tests of model estimates versus independent data indicate that the models have been validated (table 2). In addition, tests of the regression coefficients verify their essential equality in the two subperiods (Neter and Wasserman 1974, SAS Institute Inc. 1989a). The reconstruction variance appears quite high in the earliest three and a half centuries (fig. 3). This is probably an artifact of lower sample size in the early part of the time series, not a real phenomenon.

CLIMATIC VARIATION

It has been shown that average drought indices may vary over periods of several decades (Stahle and Cleaveland 1992, Stahle and others1988, 2000). Climate variability may also change considerably over decades (e.g., Cleaveland and others 1992, Cleaveland and Stahle 1996). One way of visualizing changes of climate is through cubic spline smoothing curves like those used to detrend tree-ring growth series. Figure 4 shows 10- and 30-year cubic spline curves for observed and reconstructed spring precipitation 1895-1992. The low frequency curves agree in their main features, although the last 30 years of the 30-year splines appear to be at least partially out of phase.

The spline curves offer insight into past variation (fig. 5). The addition of a very stiff 100-year spline derived from the long reconstruction shows quite clearly that there are century-long average-to-dry periods (e.g., 1100-1250 and 1370-1500; fig. 5) that might be expected during the Medieval Warm Period usually set from the ninth to the fourteenth or mid-fifteenth centuries (Hughes and Diaz 1994). On the other hand, in some places the Medieval Warm Period may have been both warmer and wetter than present, e.g., the Colorado Plateau in the southwestern United States (Petersen 1994). Petersen (1994) also characterizes the Little Ice Age (ca. 1500-1850) as colder and drier than present conditions in that region. This appears to have been a period of low variability in northern Arkansas, but the period 1645-1715, usually thought of as the heart of the Little Ice Age (Frenzel and others 1994) does not appear to have been anomalously dry (fig. 5). Stahle and others (2000) postulate a very long, extremely severe “megadrought” in the last half of the sixteenth century that appears to have affected northern Mexico and much of the United States. A very bad drought occurs in northern Arkansas during this period (fig. 5).

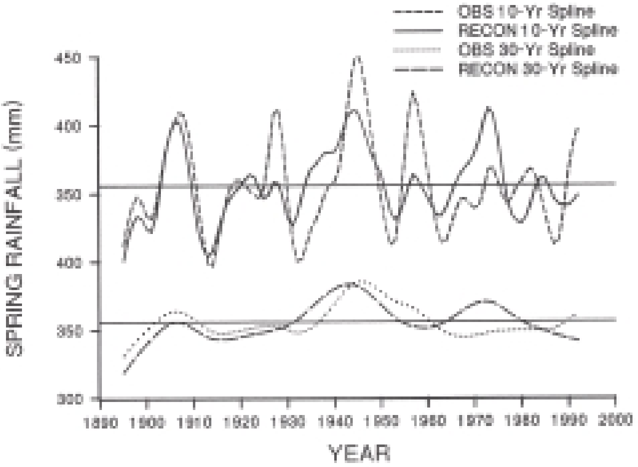

Figure 4—Smoothing spline curves showing variation from the long-term mean of observed and reconstructed total spring (April–June) precipitation averaged from the three northern Arkansas climatic divisions, 1895–1992.

Changes in variability and occurrence of extremes occur throughout the reconstruction. Two conspicuous periods of few extremes and low variability shown by the 10- and 30-year splines are ca. 1480-1550 and 1670-1810 (fig. 5). The twentieth century appears to have been a period of average to above average rainfall in northern Arkansas.

Another way to investigate the variability of climate is to look at the distribution of extremes. In table 3 the 100 wettest and 100 driest years (20.6 percent of the 970 reconstructed years) were classified by which century they fell into. The twentieth, eleventh and fourteenth centuries had more extremes than the other centuries. The balance was very different, however. The twentieth century had many more dry extemes than wet (18/9), while the eleventh century had 11 dry and 16 wet extemes. It is interesting to note that although most of the twentieth century 100-year spline curve is above average (fig. 5), this century has twice as many dry extemes as wet. The directions of anomalies in the smoothed curves do not necessarily govern the directions of anomalies in extreme values.

SUMMARY AND CONCLUSIONS

I used an average of three long tree-ring chronologies to reconstruct spring (April-June) total precipitation averaged from the three northern Arkansas climatic divisions. Tree-ring growth accounted for more than 64 percent of the climatic variance 1895-1985 and the regression model validated well against independent data.

Past spring precipitation varied considerably through time, with averages of long periods above and below the modern mean values. Several prolonged periods of drought exceeding anything in the twentieth century appear to have occurred in the past. The occurrence of extreme wet and dry years was unevenly distributed through time. Variability

Table 3—The reconstructed wettest and driest springs (April-June) in northern Arkansas, 1023–1992

Century	Wet	Dry	Total
11th (1023–1100)	16	11	27
12th (1101–1200)	10	12	22
13th (1201–1300)	6	6	12
14th (1301–1400)	14	11	25
15th (1401–1500)	7	6	13
16th (1501–1600)	9	6	15
17th (1601–1700)	12	5	17
18th (1701–1800)	6	14	20
19th (1801–1900)	11	11	22
20th (1901–1992)	9	18	27

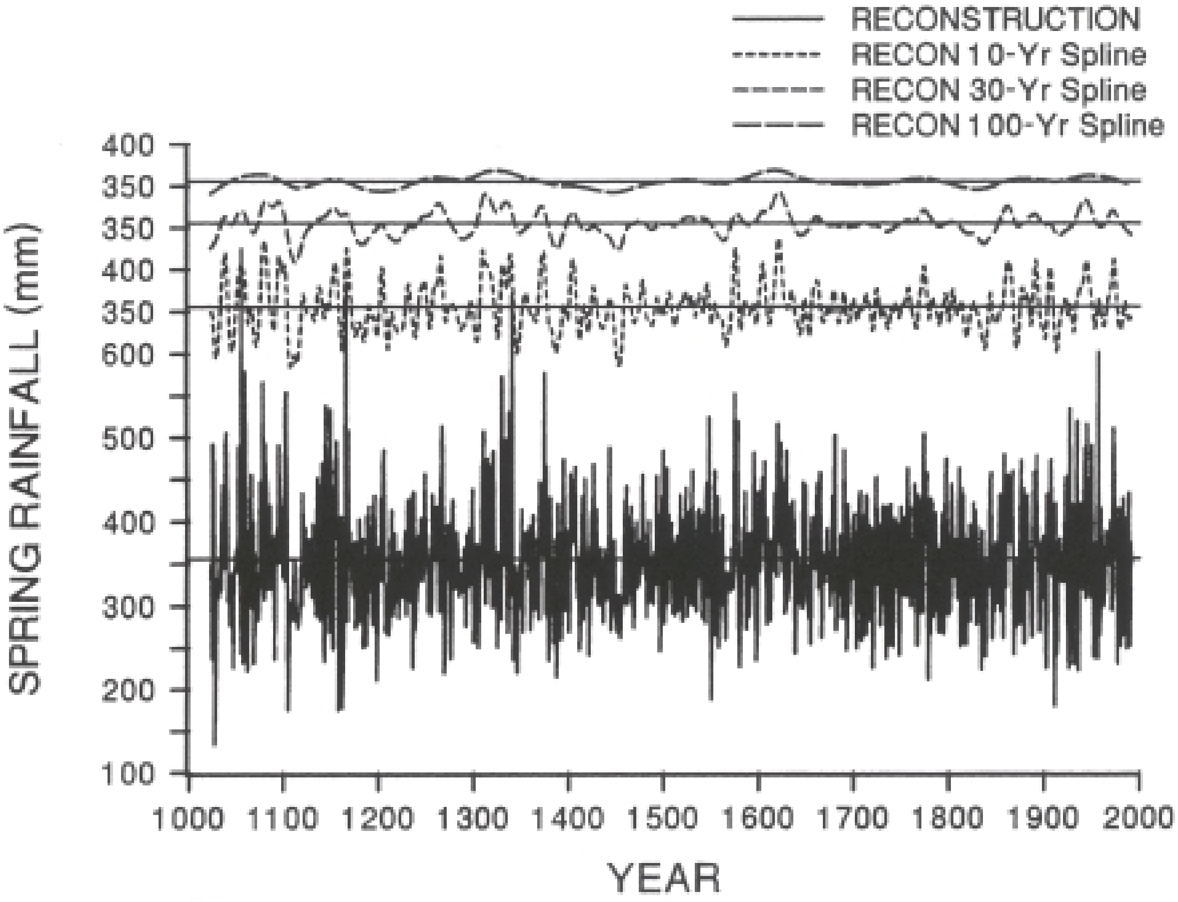

Figure 5—Smoothing spline curves showing variation from the long-term mean of reconstructed total spring (April-June) precipitation averaged from the three northern Arkansas climatic divisions, 1023–1992.

occurs on all scales, from year-to-year to centuries. Managers of natural areas can add another source of disturbance to their list of influences in the ecosystems they work with: Natural Climatic Change. However, ecosystems that have not been degraded may show a surprising degree of adaptability to anthropogenic change in climate (e.g., Houghton and others 1996), because those ecosystems have evolved with the highly variable climatic states seen in the reconstruction. This adaptation to climatic change is apparently a major source of biological diversity in ecosystems and ecosystems depend on biodiversity for their adaptive responses (McCann and others 1998, Polis 1998).

ACKNOWLEDGMENTS

I am grateful to the agencies that funded this research and have supported the University of Arkansas-Fayetteville Tree-Ring Laboratory: The National Science Foundation Climate Dynamics Program (grants ATM-8914561 and ATM-9222506) and the National Park Service Global Change Program (which has since been transferred to the U.S. Geological Survey) (cooperative agreement CA6000-1-8013). The Department of Interior Fish and Wildlife Service sponsored my attendance at the 22nd Natural Areas Conference and invited me to present this paper in the Symposium on Bottomland Hardwoods of the Mississippi Alluvial Valley. I also thank the reviewers who suggested improvements to the paper.

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PRESETTLEMENT FORESTS OF THE BLACK SWAMP AREA, CACHE RIVER, WOODRUFF COUNTY, ARKANSAS, FROM NOTES OF THE FIRST LAND SURVEY

Thomas L. Foti[1]

Abstract—Relationships between forest vegetation and soil were reconstructed from field notes of the 1846 Public Land Survey (PLS) along a portion of the Cache River including Black Swamp. Locations of corners were digitized along with species, diameter, and distance from section or quarter-section corners. Trees were grouped for analysis according to occurrence on groups of ecologically meaningful soil units (similar texture, flood frequency and saturation) using a digitized county soil map. Trees occurring at corners were treated as point-quarter samples to calculate density and dominance; these and relative abundance were used to calculate importance value (IV). Five bottomland and two upland types were defined, based on ecological distinctions in site characteristics. Based on ordination by Detrended Correspondence Analysis, these were shown to occupy a moisture gradient from frequently flooded bottomlands, through less flooded and better-drained bottomlands to well-drained uplands and dry uplands. These types are analyzed to allow restoration biologists maximum flexibility in using them in setting or analyzing restoration goals. One bottomland type occurred on sites where hydrologic regime has been altered by flood control levees to the extent that restoration to the presettlement forest is no longer possible. One of the upland types has not been previously documented and may have been primary habitat for a now-rare plant species, *Cyperus grayoides* Mohlenbrock.

INTRODUCTION

Clearing, drainage and other forms of ecosystem alteration have been and continue to be extensive in the Mississippi Alluvial Plain. Currently, national and international attention is being given to restoration and management needs within this region, such as the North American Waterfowl Management Plan (Arkansas Game and Fish Commission 1988). A number of programs exist that encourage reforestation within the region, perhaps most significantly the USDA Wetland Reserve Program and Conservation Reserve Program. In the Arkansas portion of the region ("the Arkansas Delta") State and Federal agencies as well as private organizations are actively acquiring land, most extensively for addition to the Cache River National Wildlife Refuge and White River National Wildlife Refuge.

On these newly acquired public lands, reforestation is occurring as needed. On Federal lands, ecosystem management is emphasized, that attempts to ". . . restore and sustain ecosystem integrity (composition, structure and function) and produce ecologically acceptable levels of sustainable multiple uses (U.S. Fish & Wildlife Service 1994). Such a management strategy implicitly requires knowledge of baseline ecological conditions against which to compare management alternatives.

Surveyors' notes compiled during the Public Land Survey (PLS) conducted by the General Land Office (GLO) in the 19th Century provide the only systematic survey of the vegetation of the mid-continent during that time, prior to massive timber cutting and settlement. When correlated with physical site characteristics, 19th century vegetation data can be used to develop understanding of and models of plant community composition and structure, as well as distribution on the landscape (Bourdo 1956).

A model of early vegetation of an area does not define a restoration or management goal; it is necessarily incomplete and uncertain. Conditions controlling vegetation may have changed or current needs may preclude restoration to this vegetation. However, even under these circumstances the model is useful in providing one baseline to be used in evaluating the feasibility of and progress toward such a goal.

The primary purpose of this study was to use existing surveyor's notes to develop a model of early vegetation of Black Swamp. A secondary objective was to undertake an initial assessment of the utility of the model to assist in development of reasonable goals for ecosystem restoration in the Lower Mississippi Alluvial Valley in eastern Arkansas.

METHODS

Study Area

The study area selected was Township 6 North, Range 3 West (T6NR3W or The Township) along the Cache River (fig. 1). Acquisition is actively underway in this area for the Cache River National Wildlife Refuge. The study area includes a portion of the Arkansas Game and Fish Commission Black Swamp/Rex Hancock Wildlife Management Area, designated under the Ramsar Convention as Wetlands of International Importance. The Arkansas Natural Heritage Commission (ANHC) holds a conservation easement on a part of the Wildlife Management Area. The study area includes naturally forested wetlands as well as cleared and farmed bottomlands and uplands. This area was chosen partly because of the availability of Geographic Information System (GIS) data layers and other digital data that facilitate the spatial analysis of GLO data.

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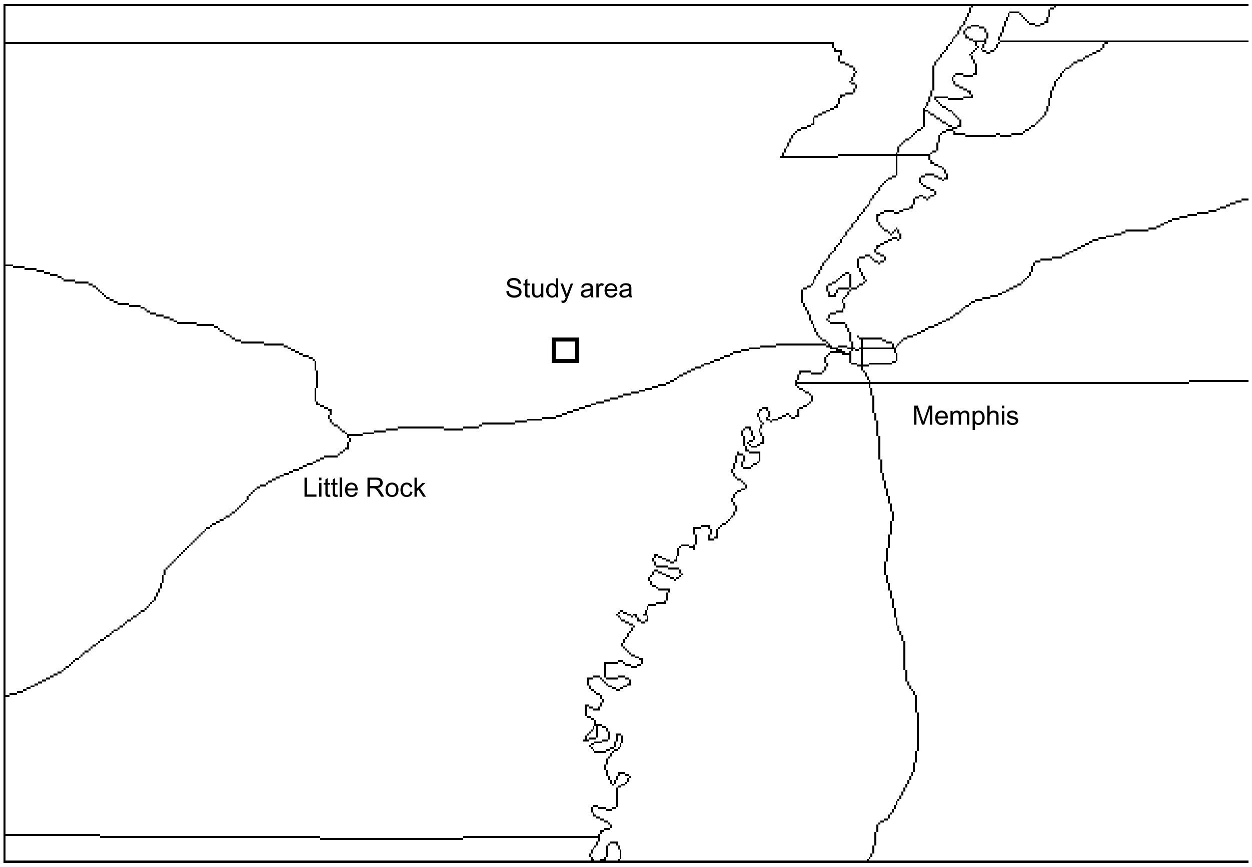

Figure 1—Location of the study area.

The Cache River is the longest tributary of the White River that lies entirely within the Mississippi Alluvial Plain. In the study area, it and its floodplain are usually distinctively incised below the level of the surrounding uplands, but natural levees and terraces within and above the floodplain create variations in flood depth, duration and frequency. Soils and geological substrate of the uplands vary from poorly drained clay flats to productive loamy and sandy upland soils to excessively drained sandy hills. A variety of upland and bottomland vegetation types occur in relationship to flood regime, soil characteristics and other physical features. On lowest, semi-permanently flooded sites is black swamp itself, dominated by water tupelo (*Nyssa aquatica* L.), with baldcypress (*Taxodium distichum* (L.) Rich.) common along watercourses. Buttonbush (*Cephalanthus occidentalis* L.) is a common shrub species. On higher bottoms are areas dominated by overcup oak (*Quercus lyrata* Walt.), Nuttall oak (*Q. texana* Buckl.), willow oak (*Q. phellos* L.) and others. Upland forests have generally been cleared for row-crop agriculture, principally soybeans and rice.

VEGETATION SAMPLING

I obtained survey notes on T6NR3W from the office of the Arkansas State Land Commissioner. David Garretson surveyed The Township in 1846.

Surveyors of the PLS traversed the western and northern sides of each section of 1 mile (1.6 km) square, which were organized into townships of 6 by 6 sections. They monumented corners of each section and gave the distance and direction to a tree in each quadrant of the compass (four trees). Species and sizes of these witness or bearing trees were noted. At the halfway point of each side of each section the surveyor marked the "quarter corner" and noted distance and direction to a witness tree of stated species and size north and south of the monument (two trees). The surveyor also noted two additional "line trees" along each side and recorded species and size. Crossing points of major features, such as rivers, canebrakes, etc. were located. At the end of the traverse of each side (1 mi or 1.6 km) the quality of the land, the kind of "timber" and the "undergrowth" characteristic of the mile were noted.

Plant identification by the surveyors was in some cases problematical. The identity of "cucumber" is unknown. Although cucumber magnolia (*Magnolia acuminata* L.) occurs in Arkansas, it does not occur on sites similar to those in the study area. The identity of "black oak" in the survey notes is an important question of identification. This name is recorded in most of the communities identified here, in both bottomlands and uplands. Black oak (*Quercus velutina* Lam.) does occur on upland sites in the vicinity of the study area, but not in bottomlands. It is likely that in bottomlands the term black oak in the notes refers to Nuttall oak (*Q. texana* Buckl.), which was not described for more than 85 years after this survey; to cherrybark oak (*Q. pagoda* Ell.), or possibly even to water oak (*Q. nigra* L.). In the uplands the term may apply either to black oak or to southern red oak (*Q. falcata* Michx.); in 19th-century contemporary surveys the latter was usually referred to as "Spanish Oak." I take "white oak" to mean *Q. alba* L., but the name occurs in the notes not only in upland forests, but also on bottomland forests, where *Q. alba* should not occur. This is particularly problematic to interpret; both swamp white oak (*Q. michauxii* Nutt., not *Q. bicolor* Willd., which does not occur in Arkansas) and overcup oak (*Q. lyrata* Walt.) are recognized by the surveyor. However, the name "swamp white oak" occurred only one time (in MCCROR, one of the wettest community types). Therefore, my assumption is that the term "white oak" means *Q. michauxii* Nutt. in the bottoms and *Q. alba* L. in the uplands. "Pin oak" in the lists may refer to *Q. palustris*, or perhaps to another of the red oaks, such as Nuttall oak. Although willow oak (*Q. phellos* L.) is often called pin oak locally, willow oak was recognized separately by the surveyor. These uncertainties will be discussed further in community descriptions. Spelling of common names in the descriptions that follow will be that of the surveyor, rather than an assumed accepted common name or scientific name.

Further difficulties occur in interpreting the importance of cypress and tupelo. Instructions to surveyors were unclear as to where the diameter of trees was to be measured, but there is a mention of diameter at the base (White 1983). Even if diameter were measured at breast height, the diameter and consequently basal area and IV of species with buttressed or swollen bases, such as cypress and tupelo, would have been exaggerated.

ANALYSIS PROCEDURES

Universal Transverse Mercatur (UTM) positions of 49 section corners were determined from USGS topographic maps. The UTM coordinates of the quarter-corners, line trees and distinctive features were calculated from the surveyor's noted direction and distance from each section corner. Locations of 455 trees were digitized. For one location, a cypress knee was used as a line marker, but since it was not a "tree" and no diameter or distance was noted, it was not included in the data set for analysis. The locations were read into a sites file in GRASS geographic information system.

Recorded distances and directions from points to trees of recorded species and size allowed use of the point-quarter sample method (Cottam and Curtis 1956) to estimate species composition, density and basal area.

In this study area a digitized map of soil series (map units) produced by the University of Arkansas in cooperation with the USDA Natural Resources Conservation Service served as the primary physical basis for sorting trees into potentially distinguishable communities. A digital map of the floodplains of the 1-, 3- and 100-year frequency floods developed by the U.S. Army Corps of Engineers provided an additional physical basis for grouping GLO trees. To simplify analysis, I aggregated the 39 soil map units into a smaller set of ecologically meaningful and distinct groups. The bottomland groups were distinguished based on duration of inundation or saturation of the soil series, based on descriptions in the county soil survey. Upland soil groups included a group of sandy loam soils along with soils of well drained natural levees and soils with sodium or magnesium salts (termed in the analyses "natric" soils), all of which have dry-mesic character. A separate upland group consisted of soil of loamy fine sand (one soil only—Bulltown) that is xeric.

I sorted trees into groups based on physical features (soil series or groups of series) important in plant community distribution. I used all trees from each data source (corner, quarter-corner and line) to calculate relative abundance and relative basal area (relative dominance). In the case of section corners and quarter corners where distance data were recorded, I calculated additional quantitative measures of forest structure, including absolute and relative density, absolute and relative basal area and geometric mean diameter, the diameter at which mean basal area occurs. I calculated importance value for each species within each group as the averaged sum of relative abundance and relative basal area calculated from all trees, and relative density based only on corner trees (IV = [RA + RBA + RD]/3).

I used relationships among the groups analyzed by multivariate statistical analysis: Detrended Correspondence Analysis (DCA or DECORANA; Hill and Gauch 1980) placed the communities along a continuum based on species composition.

In the discussions that follow, density and diameter are sometimes given. These are not included in the tables that follow, but are available from the author.

RESULTS

The Township includes 12,597 ha (31,131 ac), of which 15 percent lies within the 1-year floodplain, 28 percent within the 3-year floodplain and 70 percent within the 100-year floodplain of the Cache River and tributaries.

Forest Over the Entire Study Area

The surveyor recorded 31 genera or species in The Township (table 1 includes scientific names). Most of these are common taxa in the area today, but a few are uncertain.

Over the whole study area (table 2), cypress was the most important species with an IV of 16.6 percent, followed by white oak at 12.6 and tupelo gum at 11.2, the only other species with IV > 10. Sweet gum, ash, black oak, elm and hickory had IV's between 5 and 10. White oak was the most numerous species with 64 individuals recorded, followed by ash, sweet gum, tupelo gum, black oak, elm, cypress, and hickory. On corners with measured distances to witness trees, ash and white oak had the greatest density of 12.7 per ha (5.1 per ac) each, followed by sweet gum and tupelo gum; average density computed from all corner and quarter corner trees was 114/ha (45.6 per ac). Cypress had the largest mean diameter at 75 cm (30"), followed by white oak, sweet gum, black walnut (one tree only) and tupelo gum. While only white oak compares in importance with cypress and tupelo, and only these three have IV > 10, it is important to note that the combined IV of all oaks is virtually identical to that of cypress and tupelo combined. Thus, the forest of The Township may be described as cypress-tupelo-oak on wetter sites and oak-mixed hardwoods on drier sites.

Table 1—Common names of tree species as recorded by surveyor with scientific names of presumed actual taxa

Common name (scientific names)
Ash (*Fraxinus* L. sp. - F. *pennsylvanica* Marsh, *F. americana* L.)
Black gum (*Nyssa sylvatica* Marsh)
Black oak (*Quercus velutina* Lam., *Q. falcata* Michx., *Q. texana* Buckley, *Q. pagoda* Ell.; see text)
Black walnut (*Juglans nigra* L.)
Box elder (*Acer negundo* L.)
Cherry (*Prunus serotina* Ehrh.)
Cucumber (identification uncertain, see text)
Cypress (*Taxodium distichum* (L.) Rich.)
Dogwood (*Cornus florida* L.)
Elm (*Ulmus* L.sp. - *U. americana* L.)
Hackberry (*Celtis laevigata* Willd.)
Hickory (*Carya* Nuttall sp.)
Horn beam (*Carpinus caroliniana* Walt.)
Locust (*Gleditsia* L. sp. or *Robinia* L. sp.)
Maple (*Acer* L. sp. - *A. rubrum* L., *A. saccharinum* L.)
Mulberry (*Morus rubra* L.)
Overcup oak (*Quercus lyrata* Walt.)
Pawpaw (*Asimina triloba* (L.) Dunal)
Pecan (*Carya illinoensis* (Wang) K. Koch)
Persimmon (*Diospyros virginiana* L.)
Pin oak (*Quercus palustris* Muench, *Q. texana* Buckley)
Post oak (*Quercus stellata* Wang.)
Red bud (*Cercis canadensis* L.)
Sassafras (*Sassafras albidum* (Nutt.) Nees)
Slippery elm (*Ulmus rubra* Muhl.)
Swamp elm (*Planera aquatica* (Walt.) Gmelin)
Swamp white oak (*Quercus michauxii?* Nutt.)
Sweet gum (*Liquidambar styraciflua* L.)
Tupelo gum (*Nyssa aquatica* L.)
White oak (*Quercus alba* L., *Q. michauxii* Nutt., see text)
Willow oak (*Quercus phellos* L.)

DEFINITION OF SOIL GROUPS FOR VEGETATION ANALYSIS

Thirty-nine soil map units (plus water) occur in the township and GLO survey trees occurred on 27 of these. These 27 soil map units were aggregated into 7 soil groups (see table 3 for the codes by which the groups are referred to elsewhere). No GLO trees occurred on 12 soil series (table 4). These are not included in the analysis, but have been aggregated in mapping. In aggregate they cover about 7 percent of the study area.

Analysis of Soil/Vegetation Groups

The distribution in the study area of the following soil/vegetation types, even in generalized form, is a complex one (fig. 2). Tree species listed as “most important” below are the ones with IV > 10 percent.

TUCKER Forest (Tupelo-Cypress)—Tuckerman silty clay loam occurs in the lowest bottoms, immediately adjacent to the Cache River within the floodplain (fig. 2). The group includes a few trees on small watercourses outside the floodplain of the Cache River. A total of 91 trees of 16 species were recorded on this soil. The most important trees were tupelo gum and cypress (table 2). Tupelo gum was the most numerous species followed by cypress and overcup oak. Total density was 120 per ha (48 per ac), with tupelo gum having the highest density followed by persimmon and overcup oak. Cypress had largest mean diameter, followed by tupelo gum and white oak (2 trees only).

KOBFRQ Forest (Cypress-Oak-Tupelo-Maple)—This group is primarily comprised of Kobel frequently flooded soils that occur primarily below Black Swamp in the floodplain of the Cache River (fig. 2). A total of 21 trees of 13 species were recorded. The most important trees were cypress followed by white oak (presumed *Q. michauxii* Nutt.), tupelo gum and maple. No species were particularly abundant, with all species having from one to three occurrences in the data set. White oak, tupelo gum and maple had higher density than other species, and the total density was 175 per ha (70 per ac), the second-highest of the site types. Cypress had the greatest mean diameter, followed by swamp white oak (one tree only) and tupelo gum.

MCCROR Forest (Cypress-Sweetgum-Ash-Oak)—McCrory fine sandy loam soil occurs primarily east of and within the floodplain of the Cache River (fig. 2), on terraces slightly elevated above the adjacent Tuckerman soil. A total of 59 trees of 13 species were recorded on this site type. The most important were cypress, followed by sweet gum, ash, white oak (presumed *Q. michauxii* Nutt.) and overcup oak. Cypress was the most abundant species, followed by sweet gum, white oak, overcup oak and ash. Ash and sweet gum had the highest density, and the total density of 122 per ha (49 per ac) was moderate in comparison to other types. Cypress had the greatest mean diameter, followed by white oak and sweet gum.

KOBLEV Forest (Oak-Sweetgum-Ash-Cypress)—The principal soil of this group is Kobel silty clay loam, ponded. It occurs primarily west of the Cache River. The several other soil mapping units that are found on poorly drained natural levees are distributed primarily as linear bands within larger areas of Kobel frequently flooded soil and Kobel ponded soil. They occur elsewhere in the Cache floodplain and in the uplands along watercourses as well. A total of 117 trees occurred on these sites. The most important tree species was white oak (presumed *Q. michauxii* Nutt.), followed by sweetgum, ash and cypress. The most abundant species was white oak, followed by ash, sweet gum and elm. Ash had the highest density followed by white oak and sweetgum. Cypress had the greatest mean diameter, followed by sweet gum and tupelo gum. “Black oak” in this type was probably *Q. pagoda* Ell. or *Q. texana* Buckl.

ASKEW Forest (Sweetgum-Ash-Elm-Hackberry)—Askew fine silt loam is found on small, elevated areas within the floodplain of the Cache River, generally surrounded by Kobel or McCrory soil (fig. 2). A total of only 9 trees of 7 species were recorded on these sites (table 2), but they were analyzed separately because of the distinctive differences in site characteristics. The most important tree species was sweet gum, followed by ash, elm, and hackberry. Ash and

Table 2—Importance values of trees of the soil/vegetation groups[a] [b]

	Soil type / forest group							
Species	TUCKER	KOBFRQ	MCCROR	KOBLEV	ASKEW	UPLAND	UPSAND	ALL
Tupelo gum	35.9	11.3		4.6				11.2
Cypress	25.0	25.0	31.3	10.1				16.7
Overcup oak	8.1	4.5	10.6	4.3		0.8		4.6
Persimmon	8.0	2.3		2.9				2.6
Ash	5.8		12.1	12.9	20.3	5.4		7.9
Pecan	2.7	6.5	2.3	1.0				1.4
Elm	2.7	4.5	6.7	6.4	10.6	9.0		5.8
Maple	2.4	10.0		4.0				2.0
White oak	1.9	11.8	11.9	17.4	4.2	21.0	21.3	12.6
Swamp elm	1.8		3.0	.7				.9
Willow oak	1.3		2.1	.8		1.7		.1
Locust	1.0		.7	1.4				.7
Pin oak	.9	2.3	.7					.4
Hackberry	.9	4.1	1.5	1.8	10.0			1.2
Black gum	.9			2.2		5.1		1.9
Sweet gum	.6	4.9	15.4	13.9	44.5	10.6	8.4	9.4
Swamp white oak		6.6						.3
Hickory		6.1		4.5	6.2	11.9	14.8	5.3
Cucumber			1.6					.4
Black oak				6.3		18.9	26.4	7.4
Sassafras				1.5		.6		.6
Red bud				.7				.2
Horn beam				.6	4.1			.2
Pawpaw				.7		.9		.2
Box elder				.6		2.3		.7
Dogwood						6.1	9.3	2.2
Mulberry						1.7		.5
Black walnut						.9		.2
Post oak						.9	19.7	1.0
Cherry						.6		.2
Slippery elm						1.4		.4
Total trees	91	21	59	117	9	137	21	455
Corner trees	68	14	38	90	6	90	18	324

[a] Detailed data on which the IV's are based are available from the author.

[b] In calculations of IV, relative abundance was based on all trees in the database, while relative basal area and relative density were based on corner trees only.

sweet gum were the only species to have 2 individuals in the data set. The total density was the highest of any of the site types at 407 per ha (163 per ac), but this is based on only 3 corners. Sweet gum had the largest mean diameter among the species.

UPLAND Forest (White Oak-Black Oak-Hickory-Sweetgum)—This group, including well-drained natural levees, upland loamy and natric soils (table 3), occurs outside the floodplain on both sides of the Cache (fig. 2). It contains areas that are poorly drained bottomlands and the following excessively well-drained xeric type. Soils in this group are typically well drained. For this analysis it was not possible to eliminate all the poorly drained areas. A total of 137 trees of 17 species occurred on these sites (table 2). The most important species were white oak (probably *Q. alba* L.) and black oak (probably *Q. velutina* Lam. on these dry sites, or *Q. falcata* Michx.), followed by hickory and sweetgum. Most abundant trees were white oak and black oak, followed by hickory, elm, sweetgum, and dogwood. Black oak, white oak and elm had the highest density; the total density of 116 per ha (47 per ac) was moderate. Black walnut, post oak and willow oak had greatest mean diameter.

UPSAND Forest (Black Oak-White Oak-Post Oak-Hickory Woodland)—This type was comprised of one soil only - Bulltown loamy fine sand. These sites are generally excessively well drained, leading to droughty conditions. A total of 21 trees of 6 species occurred on these sites (table 2). Overall density of the forest (34 per ha or 14 per ac), characterizes it as a woodland or savanna. The most

Table 3—Soil groups used in analysis, with descriptions of constituent soils

Code – Name Texture, slope, hydrology, location, landform	Hydric?	Ac	Ha
TUCKER – Tuckerman			
Tuckerman SiClLm, 0–1 percent, frqfld, fldpln	Yes	3,753	1519
Tuckerman FnSaLm, 0–1 percent, frqfld, sm drains	Yes	870	352
Tichnor SiLm, 0–1 percent, frqfld, fldpln	Yes	74	30
KOBFRQ – Kobel silty clay loam			
Kobel SiClLm, 0–1 percent, frqfld, Cache backswamp	Yes	2,621	1061
MCCROR – McCrory fine sandy loam			
McCrory FnSaLm, 0–1 percent Cache terraces	Yes	3,663	1482
KOBLEV – Kobel and poorly drained natural levees			
Kobel SiClLm, 0–1 percent, ponded, Cache backswamp	Yes	1,910	773
Arrington SiLm, 0–3 percent, rarely fld	No	198	80
Yankopin (Commerce) SiClLm, <3 percent, rarely fld	No	845	342
Yankopin (Commerce) SiClLm, 0–3 percent, frqfld	No	1,275	516
Dundee SiLm, 0–1 percent	No	271	110
Amagon SiLm, 0–1 percent, terraces	Yes	326	132
Forestdale SiClLm, –1 percent, frqfld, fldpln	Yes	332	134
ASKEW – Askew fine sandy loam			
Askew FnSaLm, 1–3 percent, knolls in bottoms	No	930	376
UPLAND – Various			
Well-drained natural levee			
Dubbs SiLm, 0–1 percent	No	153	62
Bosket FnSaLm, 0–1 percent	No	345	140
Bosket FnSaLm, 1–3 percent	No	1,024	414
Bosket FnSaLm, 3–8 percent	No	412	167
Natric – sodium or magnesium Salt			
Lafe SiLm, 0–1 percent	No	16	6
Hillemann SiLm, 0-1 percent	No	46	19
Foley-Bonn complex, 0–1 percent	No	419	169
Grubbs SiLm,1–3 percent	No	790	320
Grubbs SiLm, 3–8 percent, eroded	No	464	188
Grenada SiLm, 1–3 percent	No	540	218
Upland sandy loam			
Wiville FnSaLm, 0–1 percent, near Bulltown	No	2,493	1009
Wiville FnSaLm, 1–3 percent, on edge of bottoms	No	1,902	770
Wiville FnSaLm, 3–8 percent, on edge of bottoms	No	373	151
UPSAND – loamy fine sand			
Bulltown LmFnSa, 1–8 percent, on dunes	No	2,067	836

Cl = clay(ey); fld = flood(ed); Fn = fine; frq = frequently; Lm = loam(y); pln = plain; Sa = sand(y); Si = silt(y); sm = small.

Table 4—Soils on which no witness trees occurred and the group with which they were combined for mapping purposes

Name, texture, slope, hydrology	Group	Ac	Ha
Kobel SiClLm, 0–1 percent	KOBLEV	56	23
Calhoun SiLm, 0–1 percent	KOBLEV	395	160
Calloway SiLm, 0–1 percent	UPLAND	396	160
Calloway SiLm, 1–3 percent	UPLAND	49	20
Overcup SiLm, 0–1 percent	KOBLEV	664	269
Jackport SiClLm, 0–1 percent	KOBLEV	10	4
Patterson FnSaLm, 0–2 percent	KOBLEV	161	65
Dubbs SiLm, 1–3 percent	UPLAND	152	61
Oaklimeter SiLm, 0–2 percent, occasionally flooded	KOBLEV	1	0
Arrington SiLm, 0–3 percent, freq. flooded	KOBLEV	30	12
Hillemann SiLm, 1–3 percent (natric)	UPLAND	210	85
Grenada SiLm, 3–8 percent (natric)	UPLAND	540	218
Water		355	144

Cl = clay(ey); fld = flood(ed); Fn = fine; frq = frequently; Lm = loam(y); pln = plain; Sa = sand(y); Si = silt(y); sm = small.

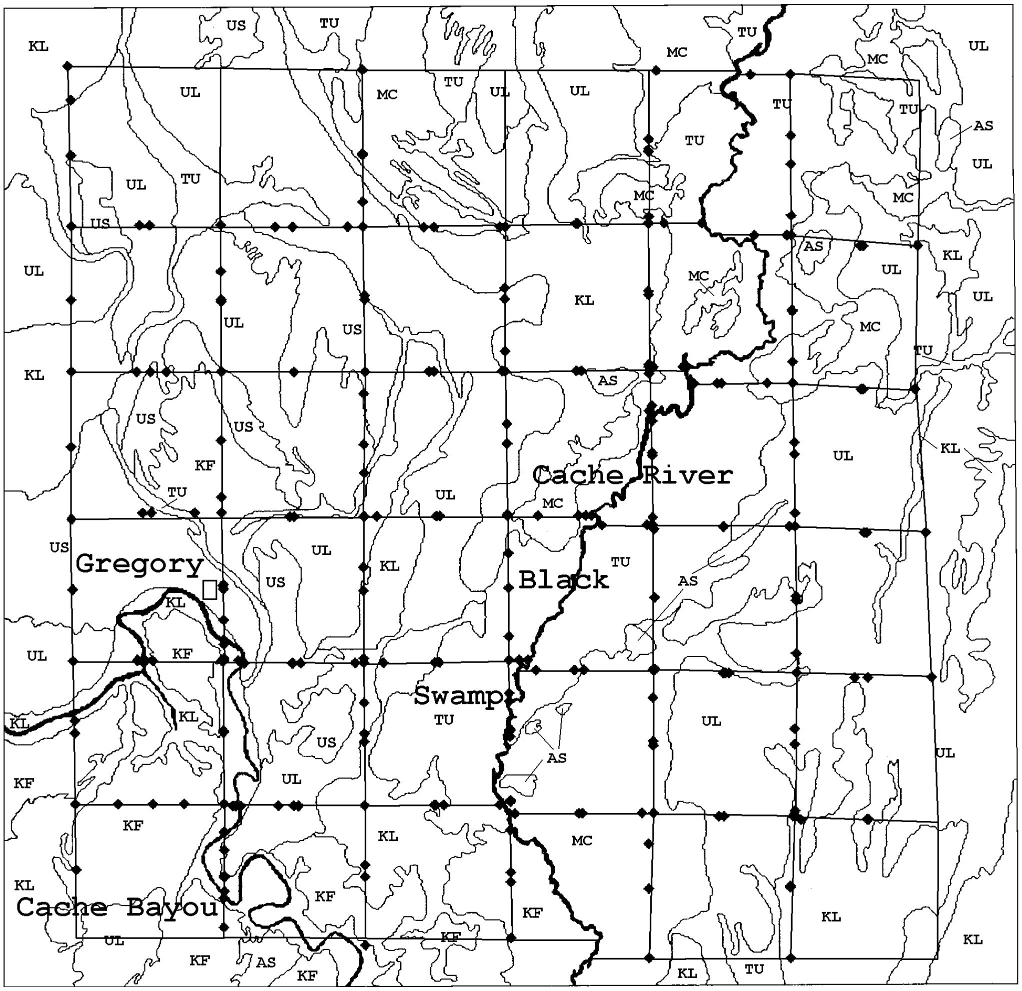

Figure 2—Generalized map of soil groups with General Land Office corners and line trees, approximate section lines and major features shown. Arkansas Highway 33 runs N-S through the western part of the study area but is not shown because it lies on section lines and would obscure witness tree locations. Section lines do not match at Cache River because surveys were conducted separately on each side of the river. The surveyor measured (approximately) and noted the discrepancies. Locations of General Land Office trees are indicated with a ♦. Soil groups are abbreviated: AS = ASKEW, KF = KOBFRQ, KL = KOBLEV, MC = MCCROR, TU = TUCKER, UP = UPLAND, US = UPSAND.

important species was black oak (probably *Q. velutina* Lam.), followed by white oak (probably *Q. alba* L.), post oak and hickory. The most abundant species in the sample was black oak, followed by post oak and hickory. Black oak had the highest density, followed by post oak and hickory. Sweet gum (1 individual) had the highest diameter followed by white oak.

Relationships Among Soil/forest Groups—Detrended Correspondence Analysis placed the soil/vegetation groups along a continuum that apparently represents a moisture gradient, as judged by species composition. From wettest to driest, the order was TUCKER, MCCROR, KOBFRQ, KOBLEV, ASKEW, UPLAND and UPSAND (fig. 3). Scores of the species at positive and negative extremes of Axis 2 indicate that Axis 2 primarily separates the KOBLEV soil/vegetation group from the ASKEW type. While these are adjacent and in close proximity on Axis 1, they are clearly separated on Axis 2. On this axis, horn beam, hackberry and sweetgum occupy one extreme. They are all high or present in ASKEW and low or absent in KOBLEV. At the other extreme, sassafras, pawpaw and red bud are all present in KOBLEV and absent from ASKEW. These differences separate the vegetation on KOBLEV poorly drained natural levees from that of similar ASKEW high mounds within the floodplain.

DISCUSSION

The seven soil/forest groups categorized here represent adaptations to a moisture gradient, ranging from extremely wet bottomlands through well-drained bottomlands and moist uplands to dry uplands. Because these communities are related to particular soils they should provide useful guidance to restoration efforts within and near the study area. Most of the types are similar to those found on little-disturbed sites of the same soil today, so inspection of the extant sites can provide details on overstory, midstory and understory composition of the communities, propagules for restoration, and the ability to do functional assessments of the types. In such cases, the 1846 community model serves only to provide the perspective that the existing forest is not simply an artifact of human management or mismanagement in the past 150 years, but is in fact a variant of the “natural” forest of the region. However, at least two of the types provide interesting and perhaps unexpected insights:

1. KOBFRQ (Kobel silty clay loam, frequently flooded) occurs in the second most hydric position on the moisture continuum, and consequently in a more hydric location than the related soil group KOBLEV (Kobel silty clay loam, ponded and poorly drained natural levees). Yet today KOBFRQ is virtually all cleared and in agriculture, while large areas of KOBLEV are still forested. This is because most areas of KOBLEV are within the floodplain of Cache River, which at this point is not channelized or leveed. In contrast, most areas of KOBFRQ lie outside the Cache floodplain along Cache Bayou, which was a distributary of the White River at the time of the GLO survey. Flood control levees along the White have since disconnected the source and dramatically reduced flooding in this area, allowing row-crop agriculture. From a restoration standpoint, this is a clear demonstration that the early forest may not be the appropriate goal for current restoration efforts. In the case where hydrologic regime has been dramatically and

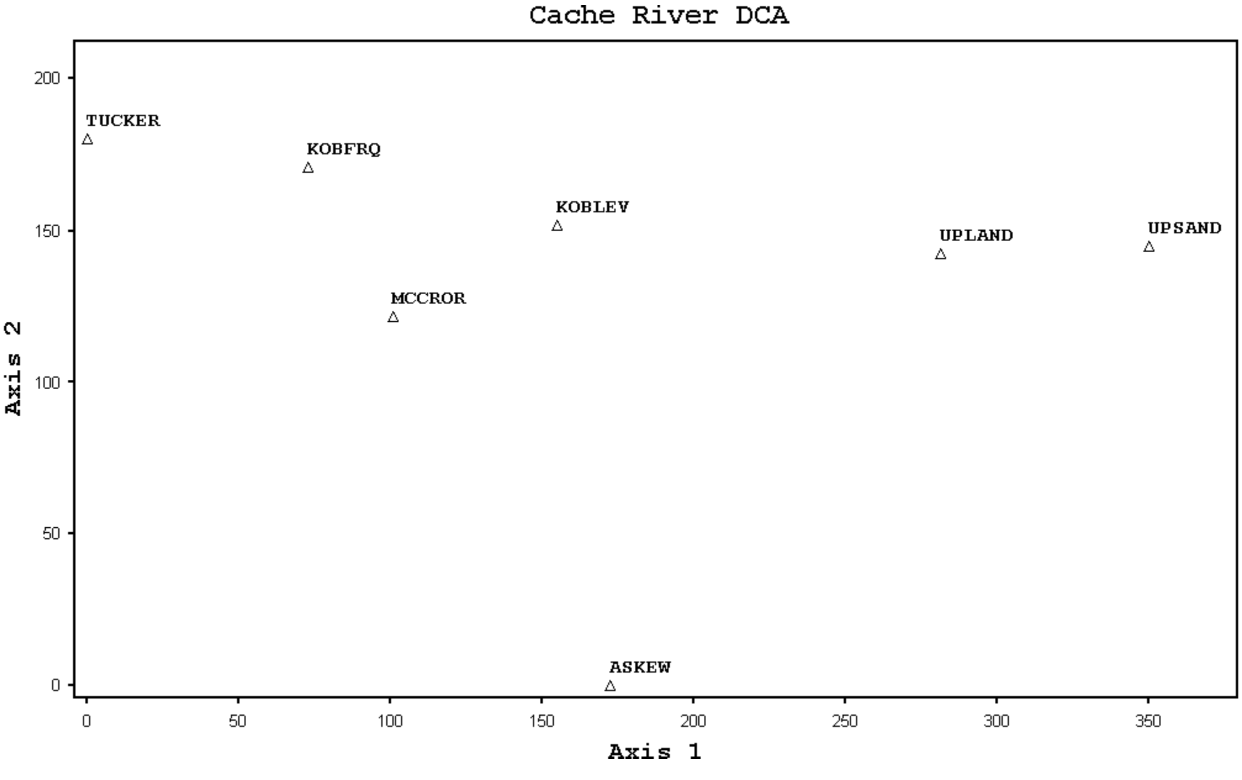

Figure 3—Soil/vegetation groups plotted on Axis 1 vs. Axis 2 of Detrended Correspondence Analysis.

unalterably changed from the “natural”, forest species suited to the new conditions will have to be propagated.

2. True upland forest (white oak-black oak-hickory) occurred in this area, with dogwood as a diagnostic species, limited to the uplands, as it is today. To many, the LMV was synonymous with bottomland hardwood forest. Nevertheless, large areas were covered with upland hardwood forest, pine forest or prairie, depending on site conditions. Many of these less appreciated vegetation types have been decimated even more than the bottomland hardwoods. A perhaps very rare and dramatically impacted community in this study area is represented by UPSAND, the community occurring on Bulltown loamy fine sand. This community, previously undocumented, was dominated by widely spaced trees. This community is typically referred to as savanna, barrens or woodland (a community with 25-60 percent canopy cover of trees). Searches by the ANHC have failed to locate any extant sites occupied by this type, even in degraded form. The presence of enough fine material in this soil, along with ease of removing the few trees, probably led to early clearing of the sites. At this point, little is known about the overall composition and structure of this community, but its importance may be illustrated by the occurrence in Missouri of the sedge *Cyperus grayoides* Mohlenbrock on similar lowland sandy sites. After failing to find suitable habitat in the vicinity of this study site, ANHC botanist John Logan discovered the species in Arkansas by looking in sandhill woodlands in the West Gulf Coastal Plain 300 km to the south (Personal communication. 1996. Logan, J. Arkansas Natural Heritage Commission, Suite 1500, Tower Building, 323 Center St., Little Rock, AR 72201). Restoration of the community on appropriate sites should be a high priority.

ACKNOWLEDGMENT

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APPLICATION OF GENERAL LAND OFFICE SURVEY NOTES TO BOTTOMLAND HARDWOOD ECOSYSTEM MANAGEMENT AND RESTORATION IN THE LOWER MISSISSIPPI VALLEY—AN EXAMPLE FROM DESHA COUNTY, ARKANSAS

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Abstract—The lower Mississippi River floodplain supported about 9 million ha of hardwood forests, and now less than 2 million. Reforestation is a priority of resource agencies, but efforts are hampered by uncertainties about species composition and site relations of plant communities. We compared the first land survey notes for an area along the Mississippi River in the 1800's to modern forest. The results suggest that (1) geomorphic surfaces generally provide a good basis for discriminating general patterns of plant community structure and composition, (2) modern forests differ from the forests of the early settlement era in importance of dominant species, suggesting that modern forests may not be appropriate restoration models, and (3) future distribution of plant communities will be altered because the lower Mississippi River has been stabilized, affecting future environments of deposition. Importantly, oak species, the primary material for restoration efforts, have never been particularly dominant on these sites.

INTRODUCTION

Bottomland hardwood forests blanketed most of the alluvial valley of the lower Mississippi River at the time of European/American settlement. These forests were highly diverse, supporting many species of resident, migratory, and wintering wildlife, including several that have since become extinct or regionally extirpated (Fredrickson 1978). Agricultural development has since reduced the original forest from about 10 million ha to less than 2 million ha (Forsythe 1985). Much of the remaining forest is located adjacent to the Mississippi River, inside the mainstem levee system, where flooding conditions and forest composition limit the overall quality and diversity of wildlife habitat available (Klimas 1991). Most remaining forests on the former floodplain are small fragments unconnected to major forest blocks.

In recent years a variety of programs have been initiated to encourage reforestation of floodplains (Allen 1990). These include the Conservation Reserve Program and Wetland Reserve Program, administered by the U.S. Department of Agriculture. Federal and state wildlife agencies are acquiring agricultural land for restoration to meet wildlife objectives. Planning a reforestation project involves selection of species, planting techniques, and maintenance requirements. Traditional forest re-establishment for wildlife or other purposes tends to focus on a few species selected to meet project needs. However, where ecosystem restoration for wildlife habitat is the principal concern, the objective is often to establish a forest community with a species composition and structure reflecting natural conditions for the site (U.S. Fish and Wildlife Service 1994), although usually species that produce hard mast for desired wildlife are emphasized, particularly oak species.

Ecosystem management has recently received emphasis as a direction for management of public lands, including National Forests and National Wildlife Refuges. Ecosystem management is here defined as management "...to restore and sustain ecosystem integrity (composition, structure and function) and produce ecologically acceptable levels of sustainable multiple uses" (USFWS 1994). In the context of ecosystem restoration, this objective requires that fairly specific compositional and structural models be available to guide the restoration design. Modern forests, even those regarded as "old growth" based on structural criteria, may not be appropriate models for restoration projects because of the likelihood that they have been substantially altered by human activity, particularly with respect to the relative abundance of non-dominant trees or of major understory species. Information from early observers and surveyors can provide insights into the character of the pre-settlement ecosystem, but development of fairly specific community characterizations to guide restoration requires a mechanism to relate historic data to specific site conditions in the modern landscape.

The objectives of this study are to

1. Characterize the vegetation documented by the first land survey of the study area in 1837, both over the entire study area and stratified according to ecologically meaningful landforms.

2. For those portions of the study area where the existing vegetation has been characterized, compare existing vegetation as described by Klimas (1991) with that documented by the first land survey.

3. Qualitatively describe the understory vegetation on the selected landforms using the mile notes of the surveyors.

METHODS

Overview

The study area is a portion of Desha County, Arkansas, southwest of the confluence of the Arkansas and Mississippi Rivers (fig. 1). It was selected because of the variety of

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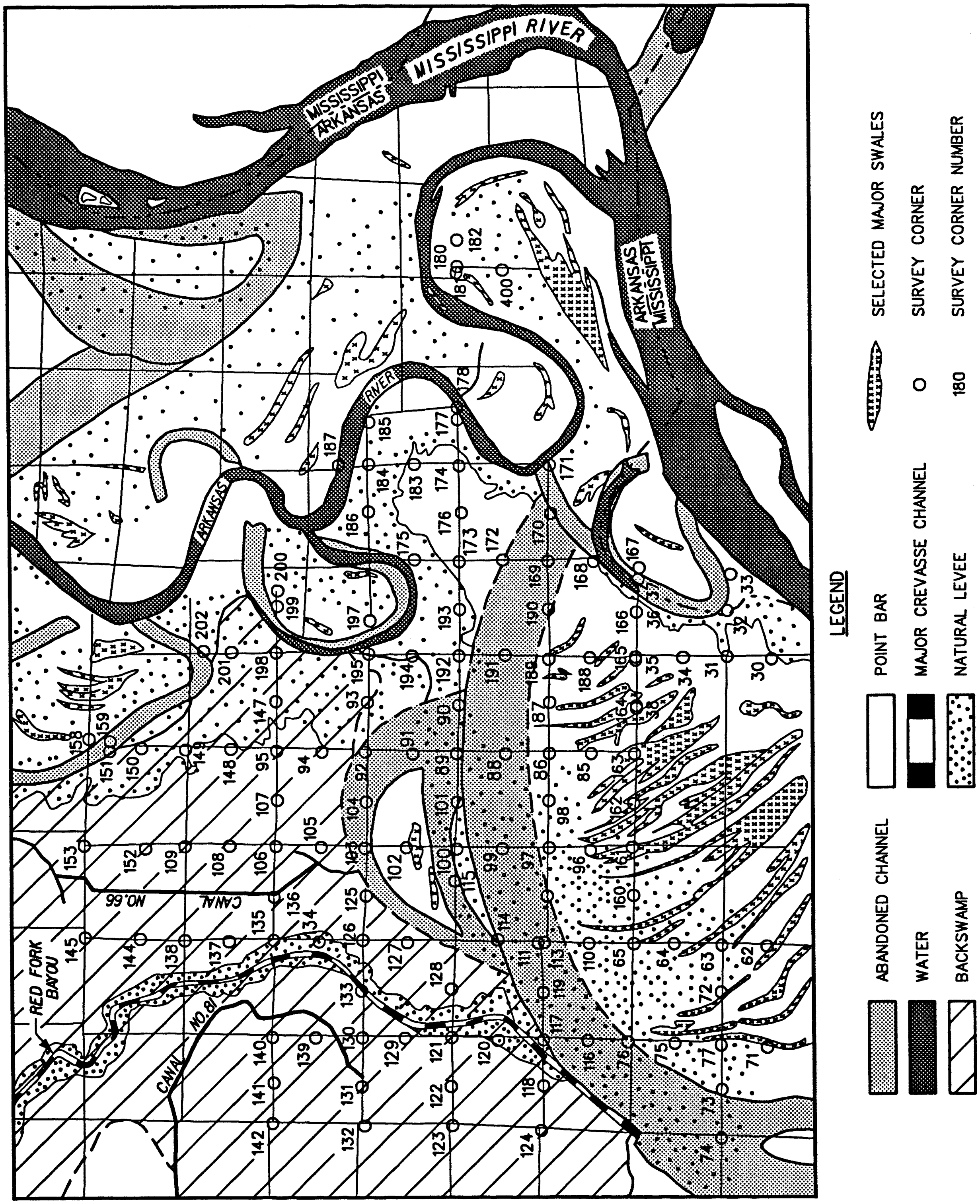

Figure 1—Vicinity map showing the location of the study area relative to the confluence of the Arkansas and Mississippi Rivers.

pertinent information available, and because it is typical of a fairly large segment of the lower Mississippi River alluvial valley with regard to the distribution of major landforms, the distribution and composition of modern forests, and land use history. The resources used included:

1. General Land Office (GLO) notes from the Desha County surveys of 1824 and 1837 (hereafter referred to as the 1837 survey) provided information on land and forest conditions as well as witness tree data suitable for use in deriving quantitative information on forest structure and composition. In this instance, “structure” refers to basal area and density of trees per unit area, by species. The notes recorded the work of two separate surveyors, Nicholas Rightor and Daniel Miller, both of whom recorded witness tree data in consistent and comparable terms. A testament to the difficulty of the working conditions is that Mr. Rightor had six men desert his employ during his first week of work. Data recorded included diameter and species of each tree used to witness section and quarter-section corners, as well as the distance and direction from the corner to the tree. Also, diameter and species of two “line” trees per mile were usually noted (Bourdo 1956, White 1983).

2. The principal source of information on modern forest and site conditions was the Lower Mississippi River Environmental Program (LMREP), which is an inventory and research program initiated and administered by the Mississippi River Commission, U.S. Army Corps of Engineers (Kolb and others 1968). The modern forest data were compiled by Klimas (1988), who sampled 1,100 sites within the confined (leveed) floodplain of the lower Mississippi River in 1984 and 1985 as part of the LMREP. He collected detailed information on overstory and understory composition and structure within one-tenth acre plots, and used multivariate analyses to isolate discrete community types. He then tested those types for their fidelity to specific site conditions reflecting flooding regimes, soil conditions, and similar variables. He found that most of the identified communities are associated with particular combinations of alluvial deposition (as reflected in the CERDS layer Environments of Deposition) and substrate age (as reflected in the meander history mapping described below); this finding is the basis for designating the four major Site Types described below and in table 1.

Table 1—Site type classification

{Private} site type code	Geomorphic description	General interpretation
A	Point bars	Basic alluvial site type
B	Point bars with natural levee deposits	Better drained, often with newer soils
C	Large swales within point bars; abandoned channels; backswamps	Poorly drained
D	Backswamps with natural levee deposits; abandoned channels with natural levee deposits	Poorly drained sites with better drained surface soils

3. One additional resource employed in this study, and also used to construct the vegetation models described in Klimas (1988) is a set of maps of the lower river showing channel meander history since 1765 (Mississippi River Commission 1881-97, 1938, 1941). These allowed us to eliminate from consideration all 1837 witness trees occupying sites that had since been reworked by lateral river migration (and for which, consequently, no ca. 1837 physical site data exist). Thus the mapped geomorphic features could be assumed to be the same basic landforms extant at the time of the survey. Klimas (1988) identified 4 major site types: Point Bars (well-drained sandy deposits); Point Bars with natural levee deposits (better drained than the previous and with newer soils); Swales, Abandoned Channels and Backswamps (poorly drained sites); and Backswamps and Abandoned Channels with natural levee deposits (poorly drained sites but with better internal drainage than the previous) (table 1). Figure 2 shows the geomorphic map and distribution of GLO survey points used in this study.

4. The various resources described above were employed here to investigate the possibility that the modern forest may offer an incomplete model to guide restoration efforts. In particular, we wished to determine if modern communities provide good models of the species composition and dominance patterns appropriate for the sites they occupy, and whether any particular community types are under-represented in the modern forest relative to conditions prior to major modifications due to clearing, differential harvest, and river regulation.

In order to meet the objectives of the study, the following analyses were conducted:

Characterize the vegetation documented by the first land survey of the study area in 1837, both over the entire study area and stratified according to ecologically meaningful landforms.

The witness trees were grouped according to their occurrence on each of the four major landforms or site types (table 1). Initial analysis concentrated on the relative abundance of all trees in the samples, including both corner trees and line trees. Then the data from corner trees only were summarized in terms of tree composition, density, and basal area. . This analysis was limited to corners that had not been reworked by rivers since 1837, as determined by Mississippi River Commission maps of the lower river showing channel meander history since 1765 (MRC 1881-97, 1938, 1941), as reported by Klimas (1988). These corners were eliminated because the site type of reworked corners would not necessarily be the same as that occurring at that corner in 1837, and therefore comparisons of 1837 to present would be meaningless. The analyses are based on treating the trees at each section and quarter-section corner as point-centered quarter samples used to calculate absolute and relative density and basal area for each species after the method of Cottam and Curtis (1956). Programs were checked against examples in Mueller-Dombois and Ellenberg (1974). Relative density and relative

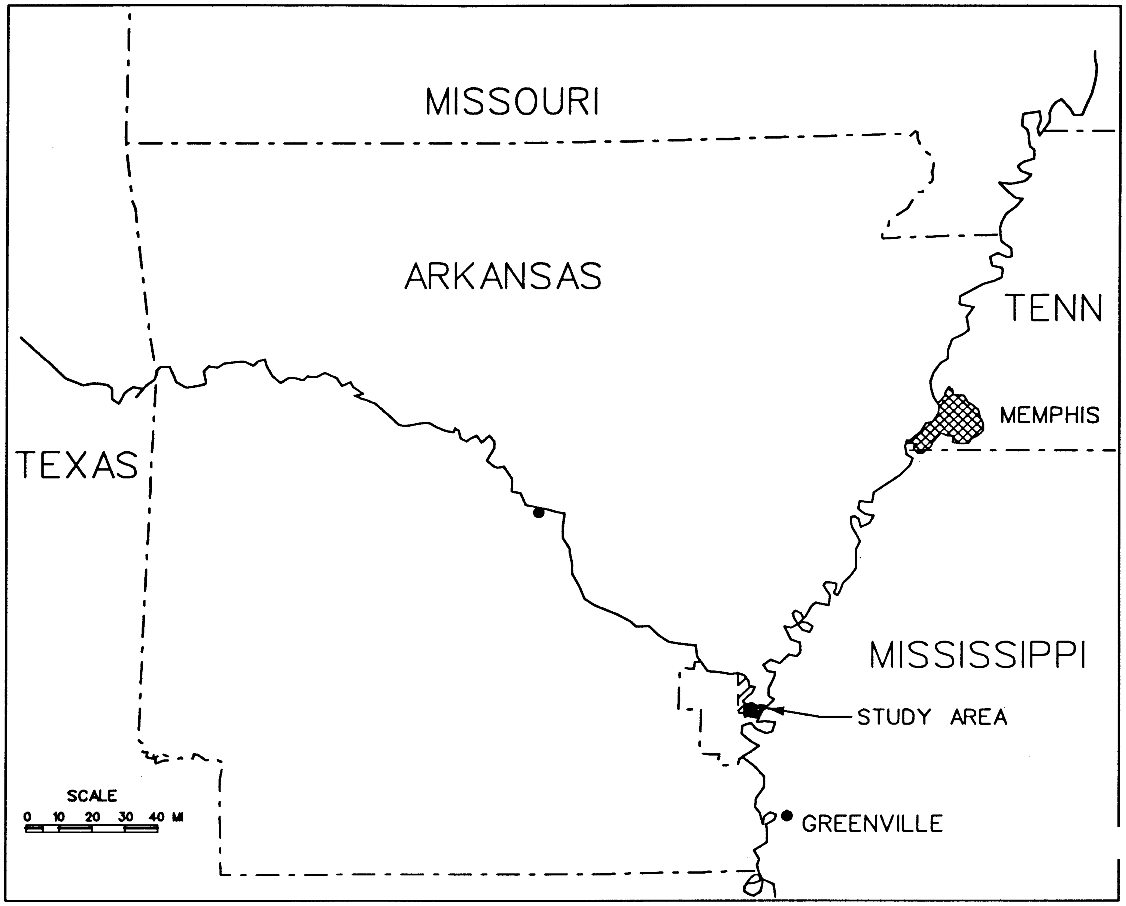

Figure 2—Geomorphology map of the study area displaying the locations of survey corners.

basal area were averaged to obtain species' importance values (IV). Relative frequency was not used in calculations of IV because in corners where only two trees were sampled, frequency could only take one of three values. Other measures which were calculated included geometric mean diameter (the diameter at which the mean basal area occurs) and absolute density.

Two-way Indicator Species Analysis (TWINSPAN; Hill 1979b) as implemented in PC-ORD Version 4 (MJM Software, Gleneden Beach, OR) was used to investigate the relationships among vegetation types.

For those portions of the study area where the existing vegetation has been characterized, compare existing vegetation as described by Klimas (1988) with that documented by the first land survey.
Those trees located on sites inside the modern levee system were summarized by site type. This allowed comparison of the modern forest, which is restricted almost entirely to sites on the river side of levees, to the 1837 forest on the same sites. It also ensured compatibility with data produced by Klimas (1988), who only studied forest on the river side of the levees.

Klimas (1988) described 51 separate plant community types in the lower Mississippi valley. Twenty-seven of these were considered compositionally and structurally consistent with modern forest conditions within the Desha County study area under consideration here. Those 27 communities were described based on 567 plots, which in this study were distributed among the four major geomorphic Site Types in proportion to the area occupied by each Site Type. Thus the modern forest data used in the analysis were not necessarily measured within the study area, but were a synthesis of data taken from those site types across the Lower Mississippi Valley.

For each Site Type, the modern forest data were summarized for all trees greater than 14 cm d.b.h., which is approximately the minimum size of trees selected by the GLO surveyors as witness trees. The data were summarized by combining relative density and relative dominance data, then dividing by two to yield an Importance Value equivalent to the IV calculated for the GLO data.

Two methods were used to compare GLO vegetation/site types to modern forests.

The first comparison involved only those GLO corners that were on the river side of the levees (inside the levees), presently naturally vegetated, and consequently mapped in CERDS. Each tree in the GLO database was associated with the current CERDS cover type for the site. GLO trees having a common current CERDS classification were grouped to investigate correlation between GLO and current vegetation. The IV of each species within each CERDS type was computed. GLO data were also summarized for each Site Type (geomorphic classification) to assess the uniqueness of the associated vegetation communities.

For the second method of comparison, the GLO data were summarized for each Site Type on sites both inside and outside the levee, except those sites that had been reworked by the river subsequent to the survey. This provided additional data points for quantitative comparisons of overstory composition and structure, as well as the understory analysis described below.

Qualitatively describe the understory vegetation on the selected landforms using the mile notes of the surveyors. The surveyor's observations concerning understory conditions were summarized by landform/vegetation types.

The GLO surveyor's comments on suitability of the land for cultivation, apparent flooding depths, general timber type, and understory composition were reasonably consistent within geomorphic site types. The major source of potential confusion was the characterization of these attributes over long distances, often an entire section line (one mile). In some instances he would differentiate segments of the line, for example:

"Land the first 15.49 Chs 1st rate cane bottom The ballance Swamp. Timber Oak gum Cypress Ash &c ("&c" is the GLO surveyor's abbreviation for "etc.") undergrowth green briers privy vines &c" (sic.)

"Land South half tolerable good bottom cane vines &c North half Swamp 10 feet overflow Timber Cypress Oak Ash &c undergrowth vines briers &c" (sic.)

Unless the site was within a zone of river meander activity during the intervening years, such descriptions invariably corresponded well with variations in site type on the modern landscape, when compared to the geomorphic map. In other cases the observation point was within a large area of fairly uniform terrain, and the comments could be assumed to apply to the basic site type dominant in the area. Generally, all comments that could be associated with particular site types were reasonably consistent in describing flood depths and understory. Timber types were more variable, possibly because small stands were included in the overall description. Thus cypress frequently is mentioned in association with almost all site types, suggesting that its occurrence in small swales and channels was sufficient to catch the surveyor's attention. In any case, canopy tree descriptions may be more biased than witness tree data, which are preferable.

However, in the case of the understory the surveyor's observations are the only source of information. As noted above, these observations seem quite consistent, as these examples indicate:

POINT BAR
"...Undergrowth Cane Vines &c"
"...undergrowth vines &c"

POINT BAR WITH NATURAL LEVEES
"...Undergrowth cane & Vines"
"... undergrowth heavy cane vines &c"

ABANDONED CHANNELS, SWALES
"...undergrowth vines brier &c"
"...Undergrowth Cane & Green briers"

BACKSWAMP
"...undergrowth privy vines green briers &c"
"...Undergrowth Switch cane palmetto &c"

BACKSWAMP WITH NATURAL LEVEE
"...undergrowth heavy cane"
"... very heavy cane..."

RESULTS

Table 1 shows the general site types related to vegetation that were designated as the basis for subdividing the data set. Table 2 shows the number of sample trees in each of the designated site types, as well as the distribution of sites in relation to the modern levee system.

Twenty-five species were named in the GLO notes (table 3) along with the likely scientific name to which they refer. Uncertainty as to correct nomenclature exists and is reflected in the table.

Distinctiveness of Site/Vegetation Types

Table 4 shows the composition of each of 4 vegetation/site types based on all trees in the database, both corner trees and line trees. Quantities include number of trees in the database and relative abundance, by species. A total of 229 trees were included in this analysis. Hackberry, sweetgum and ash occurred on all 4 site types and were the most abundant species, averaging from 15 percent to 17 percent of total trees. Persimmon and white oak also occurred on all 4 types, but in much lower abundance, making up just over 5 percent and just under 4 percent of total trees, respectively. Cypress occurred in three site types, and made up over 28 percent of the trees on swales, channels and backswamps (site type C). Pecan occurred on three site types as well, and made up 15 percent of the trees on point bars (site type A).

The summary IV data based only on corner trees are shown in table 5. Detailed data on absolute and relative density and dominance, along with geometric mean diameter by species are available from the third author. As measured by IV, which includes both density and size of trees, sweetgum and ash scored highest, improving on their abundance scores, while hackberry declined somewhat, falling below the IV of cypress, which, because of its large size scored much higher in IV than in abundance. The buttressing of cypress trees may well cause an overestimate of its basal area and IV, relative to density. Persimmon and white oak also score lower in IV than abundance. Considering average IV values over all site types, ash was the most important species, followed by sweetgum, cypress and hackberry. The importance of all oaks combined did not equal the importance of any one of these species.

TWINSPAN analysis (table 6) shows differences in species IV among the site types. Cypress is important only in the

Table 2—Distribution of corner trees with respect to levees (total trees per site type in parentheses)

{Private} site type code	No. trees inside levee	No. trees outside levee	Total number of trees
A	43 (51)	0 (1)	43 (52)
B	32 (44)	8 (11)	40 (55)
C	22 (33)	12 (19)	34 (52)
D	13 (15)	41 (55)	54 (70)
Total	110 (143)	61 (86)	171 (229)

Table 3—Tree species listed in the 1837 GLO surveyor's notes, with probable modern equivalent and scientific name. Unidentified indicates illegibility of the surveyor's notes. "Maple" was not used in the analysis since it occurred only in excluded sites

Surveyor name	Scientific name
Ash	*Fraxinus* sp.
Black oak	*Quercus nigra, falcata, texana*?
Boxelder	*Acer negundo*
Cottonwood	*Populus deltoides*
Cypress	*Taxodium distichum*
Dogwood	*Cornus florida*
Elm	*Ulmus* sp.
Hackberry	*Celtis laevigata*
Honey locust	*Gleditsia triacanthos, G. aquatica*?
Hickory	*Carya* sp.
Maple	*Acer* sp.
Mulberry	*Morus rubra*
Oak	*Quercus* sp.
Overcup oak	*Quercus lyrata*
Pecan	*Carya illinoensis*
Persimmon	*Diospyros virginiana*
Pin oak [willow oak?]	*Quercus palustris, phellos*
Redbud	*Cercis canadensis*
Red oak [cherrybark oak?]	*Quercus pagoda*?
Red priv(e)y [swamp privet]	*Forestiera acuminata*
Sassafras	*Sassafras albidum*
Sycamore	*Platanus occidentalis*
Sweetgum	*Liquidambar styraciflua*
White oak [cow oak?]	*Quercus alba* [*Quercus michauxii*]?
Willow	*Salix nigra*
Cane	*Arundinaria gigantea*
Palmetto	*Sabal minor*
Green briers (or briers)	*Smilax* spp.
Privey (or red privey)	Probably *Forestiera* spp.

poorly drained types (C and D). Hackberry, while important in all types, achieved highest importance in the poorly drained types. Cottonwood and pecan only achieved high importance on the best-drained type (B).

GLO Site/Vegetation Types and Modern Vegetation—Overstory Comparisons

Initial analysis sorted GLO trees according to the CERDS Land Cover type that today occupies the site types where they were located. All trees (corner and line) located on sites that are inside the modern levee were included in the initial analysis, and percentage of total in the CERDS type sites was calculated (table 7).

Ten or more GLO trees occurred in three CERDS vegetation types. Therefore compositional analysis (relative abundance) was limited to GLO trees of Cottonwood (17 trees), Hackberry/American Elm/Green Ash (64 trees, including two that were mapped as pure Hackberry) and Sycamore/Sweetgum/American Elm (59 trees) sites. CERDS vegetation types with fewer than 10 GLO trees include Black Willow, Cypress/Tupelo, Overcup Oak/Bitter Pecan, Pecan, Scrub, Sweetgum and Sweetgum/Oak.

Sites presently mapped as Cottonwood type were dominated by cottonwood (23 percent) in 1837 as well, followed by sycamore, sweetgum and hackberry. Present Hackberry/American Elm/Green Ash cover type sites were dominated in 1837 by ash (25 percent) and sweetgum (23 percent), followed by hackberry and cypress. Today's Sycamore/Sweetgum/American Elm areas were dominated by ash (22 percent), followed by hackberry, sweetgum and cottonwood.

The compositional comparisons between the 1837 forests and modern stands on the same sites are of interest, but composition alone is a limited attribute to compare communities of sites in 1837 to those of today. It is necessary to establish a relationship between identifiable GLO communities, based on both abundance and size, and modern landscape features, such as our site types. Table 8 summarizes importance values and species composition of the four site types within the levees. As measured by importance values, ash, sweetgum and hackberry dominated, in that order. Cottonwood was important only in the relatively well-drained site type A at almost 16 percent. Cypress was only important (34 percent) in swales, backswamps and other poorly drained sites (type C). Pecan was most important on point bars (type A, 9 percent), and honey locust (probably actually water locust) was only important on swales, channels and other poorly drained sites (type C, 9 percent).

These analyses demonstrate that geomorphic Site Types are effective discriminators of GLO overstory vegetation described in terms of both composition and structure. Therefore the summaries of all of the GLO data (except for sites reworked by the river after the survey) were then compared to modern forest data summarized by Klimas (1988) for the same site types to further illustrate differences and similarities between the 1837 forests and those sampled in 1985.

Table 4—Composition of four GLO vegetation/site types based on relative abundance of all trees in the database—corner and line

	Vegetation/site type									
Species	A		B		C		D		Total trees	
	No.	*Percent*	*No.*	*Percent*	*No.*	*Percent*	*No.*	*Percent*	*No.*	*Percent*
Ash	11	21.15	9	16.36	9	17.31	11	15.71	40	17.47
Black oak	2	3.85	—	—	—	—	—	—	2	.87
Boxelder	1	1.92	3	5.45	—	—	1	1.43	5	2.18
Cottonwood	4	7.69	3	5.45	—	—	1	1.43	8	3.49
Cypress	2	3.85	—	—	15	28.85	5	7.14	22	9.61
Dogwood	1	1.92	—	—	—	—	—	—	1	.44
Elm	1	1.92	3	5.45	1	1.92	6	8.57	11	4.80
Hackberry	6	11.54	10	18.18	7	13.46	15	21.43	38	16.59
Hickory	—	—	2	3.64	—	—	—	—	2	.87
Honey locust	—	—	—	—	3	5.77	1	1.43	4	1.75
Mulberry	—	—	3	5.45	—	—	—	—	3	1.31
Oak	—	—	—	—	—	—	1	1.43	1	.44
Overcup oak	—	—	—	—	1	1.92	—	—	1	.44
Pecan	8	15.38	2	3.64	—	—	1	1.43	11	4.80
Persimmon	1	1.92	5	9.09	4	7.69	2	2.86	12	5.24
Pin oak	—	—	—	—	2	3.85	1	1.43	3	1.31
Red bud	—	—	—	—	—	—	2	2.86	2	.87
Red oak	—	—	—	—	1	1.92	3	4.29	4	1.75
Red privey	—	—	—	—	1	1.92	1	1.43	2	.87
Sassafras	1	1.92	1	1.82	—	—	1	1.43	3	1.31
Sweetgum	12	23.08	9	16.36	4	7.69	10	14.29	35	15.29
Sycamore	—	—	2	3.64	—	—	3	4.29	5	2.18
Unidentified	—	—	—	—	—	—	1	1.43	1	.44
White oak	2	3.85	2	3.64	1	1.92	4	5.71	9	3.93
Willow	—	—	1	1.82	3	5.77	—	—	4	1.75
Total	52	100.00	55	100.00	52	100.00	70	100.00	229	100.00

Table 9 contrasts the importance values of dominant species (all species with an IV of 10 or greater) of the GLO forests on each major site type (inside and outside the modern levee system) with the modern forests inside the levee system. The modern forest descriptions are summarized from sample data taken along the river between Memphis, TN and Baton Rouge, LA. Although this sample area extends well beyond the study area, Klimas (1988) determined that forest communities within this reach are consistent in terms of composition and structure. Although species compositions in 1985 were similar to those in 1837 it is clear that some species have decreased in dominance (sweetgum, cypress, ash) while others have increased (hackberry and boxelder).

GLO Site/Vegetation Types and Modern Vegetation—Understory Comparisons

To summarize numerous observations stated in the mile notes, cane was noted on all site types, but was rare on the heaviest soils (backswamp and abandoned channels – site type C), and reached its greatest importance on natural levee soils wherever they occurred. Palmetto was mentioned occasionally, usually on backswamp sites. Green briers or briers and privey or red privey also were largely restricted to backswamps or abandoned channels, and was not noted on point bars or on natural levee deposits. These latter sites were almost invariably occupied by unspecified vines, unless completely covered by dense canebrake.

A variety of other observations turned up in the notes. The presence of large “windfalls” and references to “prairie cane” suggest that large openings within the canopy were common at the time of the survey. No references to fire were noted, but on at least one occasion the surveyor noted that cypress logs had been downed and prepared to be rafted out of the forest during high water. Occasional mention of farm buildings and roads as reference points make it clear that this was not wilderness. On the other hand, comments about provisioning campsites and difficulties traversing large areas make it equally clear that much of the area had not been substantially altered by the white settlers.

Understory conditions in the modern forest are far more diverse than the GLO notes indicate, but this is certainly a reflection of the surveyor’s disinterest in understory plants unless they impeded his progress. Klimas (1988) recorded hundreds of plant species in the forests flanking the lower Mississippi River, including more than two dozen vine species. The species the surveyors noted with regularity are present in the modern forest on the same sites and with the

Table 5—Summary Importance Value (IV) data on all site/vegetation types used in analysis of distinctiveness of site/vegetation types

	Site/vegetation types					
Species	A	B	C	D	Frequency	Average IV
Ash	19.77	17.88	21.05	17.91	4	19.153
Black oak	4.83	—	—	—	1	1.208
Boxelder	1.30	5.63	—	1.18	3	2.028
Cottonwood	15.60	2.36	—	1.00	3	4.740
Cypress	1.78	.3	7.10	12.85	3	12.933
Dogwood	1.21	—	—	—	1	.303
Elm	1.40	1.60	—	6.21	2	2.303
Hackberry	7.70	15.01	10.96	15.69	4	12.340
Pecan	10.82	1.95	—	1.48	3	3.562
Persimmon	1.49	6.74	7.06	2.70	4	4.498
Sassafras	1.40	4.45	—	1.18	3	1.758
Sweetgum	28.53	24.91	2.94	15.18	4	17.890
White oak	4.17	5.29	1.84	3.37	4	4.498
Hickory	—	3.34	—	—	1	.835
Mulberry	—	4.93	—	—	1	1.233
Sycamore	—	4.31	—	11.19	2	3.875
Willow	—	1.60	6.25	—	2	1.963
Honey locust	—	—	6.03	1.26	2	1.823
Pin oak	—	—	5.08	—	1	1.270
Red privey	—	—	1.69	1.18	2	.718
Oak	—	—	—	.93	1	.233
Red oak	—	—	—	3.29	1	.823
Red bud	—	—	—	2.29	1	.573
Unidentified	—	—	—	1.11	1	.278
Total IV	100.00	100.00	100.00	100.00		100.00
Total species	13	14	10	18		

same general patterns of abundance, with the exception of cane. In the modern forest cane tends to follow a similar pattern with respect to general site affinities, with its most extensive and consistent occurrence on natural levee deposits. However, the large, dense canebrakes and cane prairies described by the surveyors are no longer a common feature, and most stands of cane are localized or sparsely distributed in comparison to the conditions described in the early 1800s.

DISCUSSION

The overall objective of this study was to determine if information from the GLO survey could be used to help guide ecosystem restoration activities in the lower Mississippi Valley. Ecosystem restoration implies many possible considerations relating to the ability to recover a broad suite of ecosystem functions, but a basic tenet of most restoration plans is that restored plant communities should eventually have compositional and structural characteristics that reflect undisturbed conditions as closely as possible. In the lower Mississippi Valley, the principal remaining examples of extensive bottomland forests are located along the Mississippi River within the confines of the mainstem levee system. These forests do not meet the “undisturbed” criterion because of a long history of cutting and hydrologic modification, and therefore other sources of information must be employed to develop models to guide restoration.

Klimas (1988) has demonstrated that distinct modern forest types within the levee system are associated with particular geomorphic surfaces (as mapped in CERDS), which suggests a convenient basis for designing forest restorations on cleared lands. However, Klimas (1991) expressed skepticism that modern forest remnants within the levee system provide accurate models of “appropriate” community characteristics for those sites because the existing forests have been subjected to multiple and chronic stresses that may tend to favor certain opportunistic tree species and reduce representation of less resilient species. Stresses in the modern confined floodplain include altered hydrology, altered sediment distribution patterns, arrested channel movement, and a long history of differential harvest of valuable timber species. Much of the modern forest also occupies sites that were farmed in the past. These considerations cast doubt on the use of modern forests to serve as models for restoration, and there is little basis for determining which characteristics of the modern forest are “appropriate” and which are artifacts of human disturbance.

Table 6—TWINSPAN analysis of IV all corner trees, both inside and outside of modern levees. (Value is generalized measure of IV)

	3	1	2	4	
Cypress	4	1	–	3	000
Hickory	–	–	2	–	00100
Mulberry	–	–	2	–	00100
Willow	3	–	1	–	001010
Pin oak	3	–	–	–	001011
Black oak	–	2	–	–	001100
Dogwood	–	1	–	–	001100
Cottonwood	–	4	1	1	001101
Persimmon	3	1	3	1	00111
Honey locust	3	–	–	1	0100
Pecan	–	3	1	1	0101
Ash	4	4	4	4	01100
Hackberry	3	3	4	4	01100
Sweetgum	1	4	4	4	01101
White oak	1	2	3	2	01101
Sassafras	–	1	2	1	01110
Boxelder	–	1	3	1	01111
Red privey	1	–	–	1	10
Sycamore	–	–	2	3	1100
Elm	–	1	1	3	1101
Oak	–	–	–	1	111
Red oak	–	–	–	2	111
Red bud	–	–	–	1	111
Unidentified	–	–	–	1	111
	0	0	0	1	
	0	0	1		
	0	1			

The observations of the GLO surveyors represent a potential opportunity to resolve this uncertainty. The forests they described had certainly been influenced by Native Americans and early European settlers, but they had not been subjected to the fundamental and extensive disruptions imposed over the past century of exploitation and river engineering. However, the unique, site-specific insights contained in the GLO notes cannot be applied to restoration planning without a mechanism to translate the information into community descriptions that can be associated with identifiable features of the modern agricultural landscape.

The analyses described in this paper demonstrate that the information contained in the GLO notes can be usefully translated to the modern landscape on the basis of geomorphic setting. GLO witness tree data describe unique communities when summarized within the same major geomorphic settings used by Klimas (1988) to discriminate among modern forests. This requires consideration of structural data, as simple composition (species presence/absence) does not always differentiate among communities.

Comparisons of GLO data to modern stand data within geomorphic site types indicate that significant shifts in dominance have taken place, and that modern forests may provide misleading models for restoration projects. Shifts may have resulted from biases in harvest or changes in hydrology or other reasons. If the changes noted here are due to biases in removal, then restoration to “original” composition is warranted. If changes are due to hydrologic modifications, then restoration to new communities is needed. Sweetgum and/or ash were the leading dominants on Site Types A and B in the early 1800s, but neither

Table 7—GLO trees of sites occupied today by three CERDS land cover types

Species	Cottonwood		Hackberry/elm/ash		Sycamore/swtg/elm		Total	
	No.	Percent	No.	Percent	No.	Percent	No.	Percent
Ash	1	5.88	16	25.00	13	22.03	30	21.44
Black oak	1	5.88	1	1.56	1	1.69	3	2.14
Boxelder	1	5.88	1	1.56	3	5.08	5	3.57
Cottonwood	4	23.53	1	1.56	6	10.17	11	7.86
Cypress	—	—	7	10.94	1	1.69	8	5.71
Dogwood	1	5.88	1	1.56	—	—	2	1.43
Elm	—	—	—	—	4	6.78	4	2.86
Hackberry	2	11.76	11	17.19	7	11.86	20	14.29
Honey locust	—	—	—	—	1	1.69	1	.71
Mulberry	—	—	1	1.56	2	3.39	3	2.14
Overcup oak	—	—	1	1.56	—	—	1	.71
Pecan	1	5.88	6	9.38	4	6.78	11	7.87
Persimmon	—	—	—	—	5	8.47	5	3.57
Sassafras	—	—	—	—	1	1.69	1	.71
Sweetgum	2	11.76	15	23.44	7	11.86	24	17.14
Sycamore	3	17.65	—	—	2	3.39	4	3.57
White oak	1	5.88	2	3.13	2	3.39	5	3.57
Willow	1	1.56	—	—	1	.71	—	—
Total	17	100.00	64	100.00	59	100.00	140	100.00

Table 8—Summary of inside-the-levees importance values

	Vegetation types										
Species	A		B		C		D		Total	Mean	
	No.	*IV*	*No.*	*IV*	*No.*	*IV*	*No.*	*IV*	*Number*	*Number*	*IV*
Ash	9	19.77	6	21.28	5	28.10	4	35.02	24	6.00	26.04
Black oak	2	4.83	—	—	—	—	—	—	2	.50	1.21
Boxelder	1	1.30	2	4.48	—	—	1	4.92	4	1.00	2.68
Cottonwood	4	15.60	—	—	—	—	—	—	4	1.00	3.90
Cypress	1	1.78	—	—	5	34.09	—	—	6	1.50	8.97
Dogwood	1	1.21	—	—	—	—	—	—	1	.25	.30
Elm	1	1.40	1	1.96	—	—	—	—	2	.50	.84
Hackberry	5	7.70	6	14.01	3	8.99	3	17.06	17	4.25	11.94
Hickory	—	—	2	4.08	—	—	—	—	2	.50	1.02
Honey locust	—	—	—	—	3	9.09	—	—	3	.75	2.27
Mulberry	3	6.05	—	—	—	—	3	.75	6	1.51	2.08
Oak	—	—	—	—	—	—	1	3.85	1	.25	.96
Pecan	5	10.82	1	2.36	—	—	—	—	6	1.50	3.30
Persimmon	1	1.49	3	6.13	—	—	—	—	4	1.00	1.91
Pin oak	—	—	—	—	1	3.20	—	—	1	.25	.80
Red oak	—	—	—	—	—	—	1	4.61	1	.25	1.15
Sassafras	1	1.40	1	5.24	—	—	—	—	2	.50	1.66
Sweetgum	10	28.53	5	29.22	1	4.34	1	5.84	17	4.25	16.98
Sycamore	—	—	2	5.20	—	—	1	23.32	3	.75	7.13
White oak	2	4.17	—	—	1	2.79	1	5.38	4	1.00	3.09
Willow	—	—	—	—	3	9.40	—	—	3	.75	2.35
Total trees	43	100.00	32	100.00	22	100.00	13	100.00	110	27.50	N/A
Total species	13		11		8		8				

species is particularly important on those sites today. They have been replaced by boxelder and/or hackberry as the leading dominants. In 1837 hackberry was second or third to these species on Site Types A and B and was the leading dominant on site type D. Boxelder had low IV in the 1837 data, but may have been selected against by the surveyors as a short-lived tree. Secondary species (pecan, cottonwood, and sycamore) continue to be present at levels comparable to those noted at the time of the GLO survey on these Site Types. On Site Type C, baldcypress was by far the most important species at the time of the GLO survey, but it now ranks fourth in importance on those sites, having been largely replaced by hackberry, black willow, and boxelder. This change may be real, or may indicate a preference for cypress as a witness tree by the surveyors, or an overestimate of importance because of its buttressed base.

The modern forest inside the mainstem levee system has become dominated by opportunistic species (hackberry and box elder, in particular), largely at the expense of sweetgum and ash on drier sites, and baldcypress on poorly drained sites. Secondary species that were noted in the GLO survey are present in the modern forest, and presumably most understory species continue to occupy their characteristic sites. Thus, overall plant community composition has not been significantly altered, but dominance patterns and community structure have changed dramatically.

GLO surveyor's observations regarding understory conditions are anecdotal and limited to a few common species for the most part. They do not suggest any major changes over time, with one exception. The formerly abundant cane has clearly declined dramatically. This fact has been well-recognized as a region-wide phenomenon, and suggested mechanisms contributing to the decline have included cattle grazing, conversion of cane sites to agriculture, fire suppression, and a reproductive cycle that tends to delay recovery following disturbance (Remsen 1986). The potential significance of such changes is illustrated by the changes that have occurred in abundance over the past 150 years. Even though this species is still common, it no longer dominates community character on many sites, which has implications for a variety of ecosystem elements. For example, the loss of extensive canebrakes has been proposed as a likely cause of extinction for at least one wildlife species, Bachman's Warbler (Remsen 1986) and likely declines in another species, Swainson's Warbler. The wholesale shifts in overstory dominance patterns are likely to have had similarly significant impacts on ecosystem functions, and restoration

Table 9—Comparison between 1837 (GLO) and 1985 (Klimas 1988) dominant vegetation on each of four geomorphic site types

Site type A
Point bars

1837 Forests		1985 Forests	
Leading dominants	IV	Leading dominants	IV
Sweetgum	28	Hackberry	20
Ash	20	Boxelder	17
Cottonwood	16	Pecan	13
Pecan	11	Cottonwood	12
All other species	25	All other species	38

Site type B
Point bars with natural levee deposits

1837 Forests		1985 Forests	
Leading dominants	IV	Leading dominants	IV
Sweetgum	25	Boxelder	18
Ash	18	Hackberry	18
Hackberry	15	Pecan	12
All other species	44	All other species	40

Site type C
Abandoned channels, backswamps, and large swales

1837 Forests		1985 Forests	
Leading dominants	IV	Leading dominants	IV
Baldcypress	37	Hackberry	32
Ash	21	Black willow	14
Hackberry	11	Boxelder	12
All other species	31	All other species	22

Site type D
Abandoned channels, backswamps, and large swales with natural levee deposits

1837 Forests		1985 Forests	
Leading Dominants	IV	Leading Dominants	IV
Ash	18	Boxelder	28
Hackberry	16	Black willow	20
Sweetgum	15	Sycamore	10
Baldcypress	13		
Sycamore	11		
All other species	27	All other species	42

planning should attempt to recover the original dominance patterns.

In addition to providing general guidance regarding the composition and structure of relatively undisturbed forests, this study illuminates some fundamental difficulties in achieving forested wetland restoration within the lower Mississippi Valley. In particular, the relationship between forest characteristics and geomorphic surfaces highlights the potential significance of the relative lack of geomorphic dynamics in the modern floodplain. Certain species tend to regenerate on substrates that are made available by channel migration, such as cottonwoods on point bars and baldcypress in recently cutoff oxbows. With the stabilization of the river, these habitats are no longer being created to any great extent. Simple analysis of cover type distributions shows that these species remain as common dominants in the region, but more detailed evaluations (Klimas 1988) show that the majority of their occurrences are as relicts of older stands, or on sites recently disturbed by human activity rather than river movement. Much of the remaining baldcypress in the study area, for example, is associated with the perimeter of old, stabilized oxbows or it exists as scattered large trees in stands with other, drier-site species in the understory. Similarly, extensive cottonwood is found most commonly in abandoned agricultural fields, plantations, or on disturbed soils adjacent to levees or borrow pits. There are some extensive cottonwood stands on river islands and similar habitats subjected to regular extreme scour and deposition, but there are relatively few cottonwood sites that correspond to the classic succession patterns on accretion topography such as newly-formed point bars. Whatever unique characteristics such stands had may not be well represented in the modern forest. In the case of baldcypress, the implications are even more problematic, in that the majority of existing stands appear to be remnants of former stands that will not regenerate, and the sites that are typically invaded by cottonwood (old fields, disturbed soils) are not likely to be appropriate baldcypress habitat. The lack of suitable habitat for baldcypress regeneration will cause the gradual loss of this unique component of the Mississippi Valley ecosystem unless special restoration approaches are devised to ensure its persistence.

In general, plant communities are dependent on riverine processes and features and unless we restore the processes we cannot expect the same communities to return.

SUMMARY

GLO information interpreted in the context of geomorphic surfaces appears to provide a good basis for establishing goals regarding restoration of forest composition and structure within the study area. The established relationship between modern forests and geomorphology suggest that this approach is likely to be appropriate throughout the Mississippi Alluvial Valley, if the quality of the surveyor's notes is comparable to those we used. The required geomorphic mapping is available for the entire region (see Saucier and Snead 1989 for basic references).

This study demonstrated that modern forests inside the mainstem levee system do not provide good models for overstory restoration. Chronic severe disturbance has altered their composition and structure substantially. They remain the best available source of information on potential understory conditions, except that the characteristics of the modern cane populations have been shown to be substantially different from pre-settlement conditions.

The application of GLO/geomorphic models to restoration must be approached thoughtfully. For example, changes in flooding patterns would affect the applicability of GLO data, although the consistent site affinities of secondary and understory species tend to offset this concern. A more fundamental consideration has to do with the curtailment of river meander behavior. Although existing forests do not yet fully reflect this change, it is inevitable that communities which are directly associated with river migration, such as many black willow, cottonwood, and baldcypress forests, will eventually be greatly reduced as elements of the overall forest matrix. Restoration planners should strive not only to reestablish appropriate patterns of community composition and structure, but also find ways to offset the chronic disturbance and loss of ecosystem dynamics that have resulted from wholesale stabilization and confinement of the river.

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COMPOSITION, POTENTIAL OLD GROWTH, FRAGMENTATION, AND OWNERSHIP OF MISSISSIPPI ALLUVIAL VALLEY BOTTOMLAND HARDWOODS: A REGIONAL ASSESSMENT OF HISTORIC CHANGE

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Abstract—Recent Mississippi River Alluvial Valley (MAV) bottomland hardwood forest surveys revealed a larger proportion of intermittent flood zone (inundated 1 to 2 months), early successional (primarily hackberry-elm-ash), and permanent flood zone (inundated > 6 months annually, primarily baldcypress-water tupelo) community types than in the 1930s. For the same time period, these same surveys showed a smaller proportion of nonpermanent (inundated < 6 months), late-successional community types (overcup oak-water hickory and mixed bottomland hardwood) than in the 1930s. Sporadic flood zone (inundated < 1 month), shade-tolerant community types were less common in the MAV than elsewhere in the South-Central United States (Alabama, Arkansas, Louisiana, Mississippi, east Oklahoma, Tennessee, and east Texas). Most forests with old-growth conditions (site productivity-based minimum basal area, net growth near zero, and no recent commercial harvest activity) were in private ownership and characteristic of select community types. Findings were based on a reexamination of systematic sample-based forest surveys of the region. Annual change in bottomland hardwood area was diminishing (-1.1 percent, 1970s to 1980s; +0.3 percent, 1980s to 1990s), but the frequency of large (> 2,023 ha) forest fragments continued to decline (-2.4 percent, 1970s to 1980s; -4.0 percent, 1980s to 1990s). To reconstruct the historic mix of bottomland hardwood community types, renew forest cover, and retain or enhance associated resource values, this assessment suggests a primary focus on conserving large fragments, shifting nonpermanent flood zone, early successional community types toward late-successional types, and restoring occasional flooding regimes and forest cover adjacent to small remnant bottomland hardwood fragments.

INTRODUCTION

Nonforest cover represents the majority land use in the formerly extensive bottomland hardwood region known as the Mississippi Alluvial Valley (MAV). At present MAV forest communities contain no designated wilderness and few forest plantations. Yet the region's forest cover is comparatively roadless and more closely tied to hunting activities than other regions of the South-Central United States (Alabama, Arkansas, Louisiana, Mississippi, east Oklahoma, Tennessee, and east Texas) (Rudis 1998). Potential wood productivity of MAV forests is greatest among all regions of the South (Rudis 1998). Reforestation goals include timber production with economically valued species, but also the maintenance of threatened black bear and other forest-dependent wildlife populations and primitive recreation opportunities. Other goals include sequestering elemental carbon within species native to the region, conserving forested habitats and flooding regimes for indigenous plant and animal species, and improving water quality and other economically valued forest recreation like ecotourism. Attaching priority to these multiple goals requires an understanding of the region's historic bottomland hardwood communities and anthropogenic threats to current communities.

In the MAV, historic bottomland hardwood composition and old-growth (mature, stable forests unmodified by post-European settlement) forest conditions are not well documented. Bottomland hardwood forests in the MAV were almost certainly extensive, contiguous, undisturbed by modern anthropogenic uses, and a different mix of community types than found today.

The earliest systematic observations on record were from the 1800s Land Office, i.e., land surveyors' field notes of bearing, or witness, trees. Though not necessarily representative of all conditions, surveyors' accounts provide clues to former MAV forest composition. From one such account dated 1821 for West Feliciana, LA, Delcourt (1975) noted that surveyors referenced comparatively few witness trees in swampland. Nevertheless, in ravines and tributary stream bottoms, dominant witness trees were (southern) magnolia, (American) beech and (American) holly, with baldcypress and (water) tupelo in alluvial swamps. In 1975, the surveyed study area had only a few large (American) beech trees (Delcourt 1975). By the 1980s, modern-day surveys (McWilliams and Rosson 1990) reported none but baldcypress and water tupelo among the 14 species with $\geq$3 percent importance by volume for the MAV region.

Recent systematic, extensive area surveys noted that more than one-half of the 1930s MAV bottomland hardwood forest area has disappeared (McWilliams and Rosson 1990, Rudis and Birdsey 1986), and the majority area converted to agricultural uses (MacDonald and others 1979). A Yazoo River basin report (Anonymous 1944) noted in the 1940s that better drained floodplain forests were cleared first, followed by land clearing of poorly drained areas—a pattern likely repeated through the rest of the MAV. Following land clearing, subsequent agricultural improvements included drainage structure installation, nearby stream channelization, and changes to the regional flooding regime (Turner and others 1981). These changes fragmented bottomland hardwood forests with agricultural fields and roads and indirectly caused soil deposition and reforestation along new stream channels.

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Forests that are no longer contiguous may not sustain a region's existing mix of species and resources, nor improve selected desired resources, such as black bear habitat (Rudis and Tansey 1995) or primitive recreation opportunities (Rudis 1987). Sample-based inventories of forest fragments, i.e., contiguous forests ≥ 0.4 ha and unbroken by nonforest cover ≥ 37 m wide, noted significant associations by tree species (Rudis 1993), empirical community type and resource indicators for existing bottomland hardwood communities across the south-central region. These studies showed that the smaller the forest fragment, the more likely the forest was an early successional community characteristic of nonpermanent flood zones (inundated < 6 months). The smaller the fragment, the more frequently it had anthropogenic intrusions, e.g., fences, evidence of livestock use, and rubbish, and the closer it was, on average, to developed roads and agricultural and urban land. The larger the fragment, the more likely the forest had evidence of hunting, and the more likely the sampled tree community was characteristic of a permanently wet community type (inundated > 6 months). Fragment size was also directly associated with timber volume. The largest fragments were less likely to have evidence of harvest since the prior survey. These findings suggested that the potential for vegetation disturbance by land-use activities was inversely associated with fragment size. If old-growth conditions were typical of undisturbed conditions, then the probability of finding such conditions was greatest in the largest fragments.

OBJECTIVES AND METHODS

To test the hypothesis that nonpermanent flood zone, bottomland hardwood community types in the MAV were removed or otherwise altered, I summarized published community-type surveys since the 1930s and compiled associated data on forest fragment size and community types since the 1970s, and old growth by owner class for the most recent survey period.

Because community types before European settlement were poorly documented, I compared the current distribution of MAV bottomland hardwood community types with a surrogate for what might have existed from recent surveys for the entire South-Central United States. I also selected old-growth criteria compatible with available forest survey data to suggest the likely distribution of area in remnant old-growth condition by community type and ownership class.

Surveys from the Forest Inventory and Analysis Research Work Unit (FIA) of the U.S. Department of Agriculture Forest Service were the primary data sources. Detailed FIA bottomland hardwood community types for 1932–35 (Eldredge 1938; Stover 1942; Winters 1939a, 1939b; Winters and others 1938) were for a region roughly comparable to the MAV, including west Kentucky, southeast Missouri, and west Tennessee, but excluding southern Illinois. County boundaries in the delta survey units of Arkansas, Louisiana, and Mississippi (fig. 1) were the boundaries in subsequent survey reports (McWilliams and Rosson 1990, Rudis and Birdsey 1986, Sternitzke and Putnam 1956).

The early forest surveys reported summary findings with limited documentation compared to today. Nevertheless, such accounts embody the only detailed extensive area estimates by foresters of the time. Surveys from the 1930s through the 1960s used community-type estimates from systematic field observations and temporary plots (Frayer and Beltz 1985, Sternitzke and Putnam 1956). The FIA community types before the 1970s likely came from ocular estimation of dominant tree species. Between the 1970s and 1990s, FIA calculated community types from sampled tree species equidistant at 20-m intervals, > 10 m inside forest edges at 10 points within a 0.4-ha plot area (5 points and a 0.2-ha area for Louisiana's 1984 survey). Observations were from permanent plots spaced 4.8 km apart that FIA classed as forested (land with ≥ 10 percent tree crown cover and land temporarily < 10 percent tree crown cover not developed for other uses, ≥ 0.4 ha in size and ≥37 m wide).

Because the history of sampled areas is often unknown and forests have often been periodically disturbed, many sampled plots are classed as mixed-age class. A surrogate for age class is stand-diameter class, often referenced in timber resource reports as stand-size class, which is a classification of the height and size of trees. Stand-diameter classes are: sawtimber (≥ 50-percent stocked with live trees

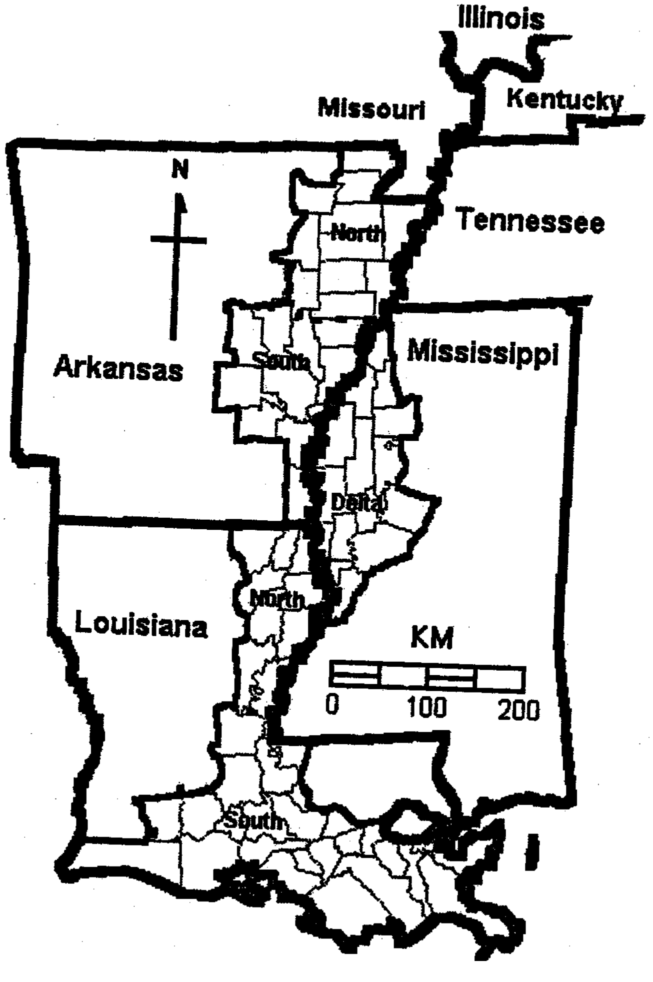

Figure 1—Counties in the Arkansas, Louisiana, and Mississippi Delta survey unit, Mississippi Alluvial Valley.

≥ 12.7 cm d.b.h. and ≥ 50-percent stocked with live trees ≥ 22.9 cm softwood, and ≥ 27.9 cm hardwoods; poletimber (≥ 50-percent stocked with live trees ≥ 12.7 cm, and < 50-percent stocked with sawtimber trees); and smaller (< 50-percent stocked with live trees < 12.7 cm).

This study examined only sampled plots characterized as bottomland-community type (< 25 percent pine stocking, judged by field crews to be in a wetland physiographic class, or having ≥ 50 percent overstory in bottomland species). Tree sampling recorded live tree stems ≥ 12.7 cm (1.4 m) d.b.h., on variable radius (8.6-m^2 factor) prism plots and live tree stems 2.5 to 12.6 cm on fixed (2.2-m radius) plots around three points. Additional details are provided elsewhere (Faulkner and others 1995, Rosson 1995, Rudis 1995).[2] Definitions for these and other common FIA terms are in the appendix.

Numerical FIA estimates are typically most reliable for a large proportion of the sampled population and least reliable for a smaller one. Louisiana's 1991 survey (Rosson 1995), for example, noted 67-percent confidence that a 502 000-ha estimate was within 5000 ha (1 percent of 502 000 ha) of the actual amount; and 67-percent confidence that an 810-ha estimate was within 200 ha (25 percent of 810 ha) of the actual amount. Because technology, field procedures, and forest-type estimation may change between surveys, care is advised in interpreting results. Shifts in forest-type area may be a result of procedural changes before 1974. Readers should refer to the original survey reports for further documentation. Because one cannot avoid procedural differences, caution is advised in concluding that forest-type classification, areal adjustments, and sample area expansion procedures are comparable to those used today.

Composition

I estimated the likelihood of finding forest land within a range of flood zones, shade tolerances, and empirical community types. This forest occurrence probability used forest-plot information on flood zone and shade tolerance selected at random for an approximately equal number of nonforest plots.

For forest plots, flood zone, shade tolerance, and community type were the dominant species by importance (average occurrence frequency, basal area, and number of stems per plot) value derived from trees tallied on sampled plots. Flood zone values were averaged by plot, with ordinal values assigned by species typical of flood zones inundated (1) permanently, (2) periodically, (3) intermittently, (4) sporadically, and (5) inundated only in wet years, after Wharton and others (1982). Shade tolerance values were averaged by plot, with ordinal values assigned by species as: (1) very tolerant, (2) tolerant, (3) intermediate, (4) intolerant, and (5) very intolerant, after Burns and Honkala (1990).

I cross-referenced these results with an earlier study of plots classed by ordinal flood zone and shade tolerance values for the South-Central United States. The earlier study (Rudis 1995) established 32 empirical community types for that region's 2,666 bottomland hardwood plots with distinctive and internally similar tree species importance. [The process employed hierarchical clustering to minimize the residual (error) sum of squares using FASTCLUS and Ward's method (SAS Institute Inc. 1990).]

For the MAV region, I used flood zone and shade tolerance estimates from the forest plots that occurred in the MAV (Rudis 1995). Because half of the region's bottomland hardwood forests had been cleared since the 1930s, I conservatively assumed that there was at least an equal area (represented by about an equal number of plots) of nonforest land today that was formerly in bottomland hardwood forests. I combined the sample of flood zone and shade-tolerance values from forested plots with the random array of values from nonforest plots to calculate occurrence probabilities. I also applied identical procedures to calculate occurrence probabilities for bottomland hardwood forests of the South-Central United States.

Occurrence probability was 1.00 (100 percent) at a flood zone and shade-tolerance location represented by a forested sample and 0.00 (0 percent) otherwise. G3GRID (SAS Institute Inc. 1991) generated grid patterns that afforded visual comparisons of forest occurrence probability distributions calculated from both regions. Grid patterns were interpolated linearly, between 0.00 and 1.00 in 0.02-percent increments, between flood zone 2, shade value 1 (permanently flooded, very shade tolerant) and flood zone 6, shade value 5 (inundated only in wet years, very shade intolerant). Occurrence probability was set to 0.00 for values outside that range.

Potential Old Growth

To date, no systematic survey of old-growth conditions has been attempted for the entire MAV. I estimated area of potential old growth from an *a posteriori* analysis of an existing database, namely sample-based FIA surveys. There is no one, widely agreed definition of old growth that one can generally accept from an *a posteriori* analysis. Unlike Frelich's (1995) reexamination of North-Central United States from FIA data, FIA surveys in the South-Central United States classed age as mixed if ≥ 2 strata with a > 10-year age difference existed. Other criteria used in old-growth assessments, i.e., a standing dead tree tally, live-to-dead tree ratio, and other disturbances (Devall and Rudis 1991), were not available for all plots.

I selected two types of old-growth criteria: one based on size, the second based on biological maturity. The first used the ratio of basal area of trees ≥ 50 cm diameter at 1.4 m (d.b.h.) divided by basal area of trees ≥ 12.7 cm d.b.h. to provide estimates of forest land with large trees. The second used three progressively restrictive biological maturity criteria designed to estimate forests: (1) likely to be old or mature, (2) having net growth approximately zero, and (3) having no recent harvest evidence. The first biologically mature criteria selected samples with basal area equal to or greater than that averaged for 45- to 65-year-old bottomland

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[2] U.S. Department of Agriculture, Forest Service, Forest Inventory and Analysis Research Work Unit. 1993. Forest survey inventory work plan, Mississippi 1993-1994. 128 p. On file with USDA, Forest Service, Southern Research Station, P.O. Box 928, Starkville, MS 39760–0928.

hardwood forests. (Age and basal-area data came from the east Texas’ 1986 forest survey. I used this region to characterize bottomland hardwood stand age, as that region used precise estimates from a special survey of dominant tree age.[3] Other States and years used 10-year and mixed age classes.) The second criterion selected samples with net growth (current minus past volume from the prior survey a decade earlier) close to zero. The third selected samples with no commercial harvest or cutting activity since the previous survey.

Fragmentation

Between 1974 and 1995, FIA surveys defined the areal extent, i.e., forest fragment size, associated with each 0.4-ha forested plot in south-central States as contiguous, ≥0.4 ha, unbroken by nonforest cover ≥37 m wide. Each forest fragment was inventoried by size class: 0.4 to 4; 5 to 20; 21 to 40; 41 to 202; 203 to 1012; 1013 to 2023; and ≥2023 ha. The FIA field crews estimated forest fragment area from aerial photography and field observations. Image and scale of aerial photographs varied from black and white, 1:20,000 or 40,000 in the 1970s and early 1980s, to color infrared, 1:58,000 after 1986.

RESULTS AND DISCUSSION

Forest Surveys

Conducted in the 1930s, the first extensive forest surveys of the MAV recorded 9 percent of the 5 190 500 ha of forests as old growth, and an additional 18 percent as having been cut but with some old-growth conditions (table 1). Forests near New Orleans and other development centers had already experienced extensive cutting for wood products by the mid-1930s. Remnant uncut old growth at the time was chiefly on poorly drained and clay-dominated soils. Many species became commercially important only after World War I, e.g., trees in sweetgum-water oak communities, or had no commercial value, trees in overcup oak-water hickory community type (table 1).

Table 1—Bottomland forest area by type and condition, Mississippi Alluvial Valley, 1932–35

Forest type	All conditions	Second growth[a]	Old growth[b]		
			Partial[c]	Uncut[d]	
	1000 ha				*%*
Baldcypress-water tupelo	684.9	521.4	131.4	32.1	5
Overcup oak-water hickory	857.0	331.6	285.4	239.9	28
Cottonwood and willow[e]	558.0	558.0	—	—	—
Mixed bottomland hardwood					
Sweetgum-mixed	1,017.3	794.0	129.3	93.9	9
Hackberry-elm-ash	814.0	571.8	199.6	42.6	5
Water oaks[f]	422.6	320.6	88.7	13.3	3
Other mixtures	836.7	729.0	86.1	21.6	3
Total	5,190.5	3,826.5	920.6	443.4	9

[a] Vegetative growth habits typical of abandoned clearings, recent catastrophic disturbances, or new riverbank soil deposits (Winters and others 1938).
[b] Stands composed of sawtimber trees with the characteristics of the original mature trees of the region (Eldredge 1937).
[c] = 10 percent volume removed but characterized by residual trees from the old-growth forest (Eldredge 1937).
[d] < 10 percent volume removed (Eldredge 1937).
[e] Early successional types defined in the 1930s as transitional, having no maturity potential (Winters and others 1938).
[f] Water, Nuttall, and willow oak.
Sources: Eldredge 1938; Stover 1942; Winters 1939a, 1939b; Winters and others 1938.

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[3] U.S. Department of Agriculture, Forest Service, Southern Research Station, Forest Inventory and Analysis Research Work Unit. 1985. Forest survey inventory work plan, 1985. 56 p. Administrative report. On file with: U.S. Department of Agriculture, Forest Service, Southern Research Station, Starkville, MS 39762–6124.

These early surveys recorded a paucity of old growth in southeastern Arkansas and points north (table 2) and east in Mississippi (table 3). The MAV maps of the period also indicated extensive land described as formerly forested but cleared for agricultural crops for the area north of the Arkansas River. Most uncut old growth, primarily overcup oak-water hickory was in Louisiana (table 4).

Apart from the steep declines since the 1930s, community-type comparisons reveal a greater proportion of hackberry-elm-ash and baldcypress-water tupelo and a lesser proportion of overcup oak-water hickory and mixed bottomland hardwood types represented today (fig. 2). Changes between the 1930s and 1990s show that the loss of bottomland hardwood area slowed only in the past

Table 2—Mississippi Alluvial Valley bottomland forest area by type and condition, east Arkansas, west Kentucky, southeast Missouri, and west Tennessee, 1935

			Old growth[b]		
Survey region and forest type	All conditions	Second growth[a]	Partial[c]	Uncut[d]	
	- - - - - - - - - - -	*1000 ha*	- - - - - - - - - - -		*%*
Southeast Arkansas					
Baldcypress-water tupelo	36.6	24.8	9.3	2.6	7
Overcup oak-water hickory	136.8	72.2	42.7	21.9	16
Cottonwood and willow[e]	81.9	81.9	—	—	—
Mixed bottomland hardwood					
Sweetgum-water oaks[f]	184.3	150.0	24.1	10.3	9
Hackberry-elm-ash	169.2	116.6	44.0	8.7	5
Water oaks[f]	129.1	104.1	21.5	3.5	3
Other mixtures	351.0	297.0	42.4	11.6	3
Total	1,089.1	846.6	184.0	58.5	5
Northeast Arkansas, west Kentucky, southeast Missouri, and west Tennessee					
Baldcypress-water tupelo	109.5	91.7	15.6	2.2	2
Overcup oak-water hickory	67.0	52.0	11.2	3.8	6
Cottonwood and willow[e]	106.3	106.3	—	—	—
Mixed bottomland hardwood					
Sweetgum-water oaks[f]	177.1	153.2	10.5	13.4	8
Hackberry-elm-ash	191.2	164.7	20.4	6.1	3
Water oaks[f]	107.9	101.5	5.7	0.6	1
Other mixtures	209.7	195.7	12.5	1.6	1
Total	968.8	865.1	76.0	27.8	3

[a] Vegetative growth habits typical of abandoned clearings, recent catastrophic disturbances, or new riverbank soil deposits (Winters and others 1938).

[b] Stands composed of sawtimber trees with the characteristics of the original mature trees of the region (Eldredge 1937).

[c] = 10 percent volume removed but characterized by residual trees from the old-growth forest (Eldredge 1937).

[d] <10 percent volume removed (Eldredge 1937).

[e] Early successional types defined in the 1930s as transitional, having no maturity potential (Winters and others 1938).

[f] Water, Nuttall, and willow oak.

Sources: Eldredge 1938, Winters 1939a.

Table 3—Mississippi Alluvial Valley bottomland forest area by type and condition, Mississippi, 1932

Forest type	All conditions	Second growth[a]	Old growth[b]		
			Partial[c]	Uncut[d]	
	- - - - - - - - - -	*1000 ha*	*- - - - - - - - - -*		*%*
Baldcypress-water tupelo	58.3	31.2	25.6	1.5	3
Overcup oak-water hickory	182.4	82.7	83.0	16.7	9
Cottonwood and willow[e]	87.9	87.9	—	—	—
Mixed bottomland hardwood					
Hackberry-elm-ash	126.5	93.5	31.2	1.9	1
Water oaks[f]	50.0	36.7	11.1	2.1	4
Other mixtures	54.6	49.7	4.9	—	—
Total	705.7	495.3	179.6	30.9	4

[a] Vegetative growth habits typical of abandoned clearings, recent catastrophic disturbances, or new riverbank soil deposits (Winters and others 1938).

[b] Stands composed of sawtimber trees with the characteristics of the original mature trees of the region (Eldredge 1937).

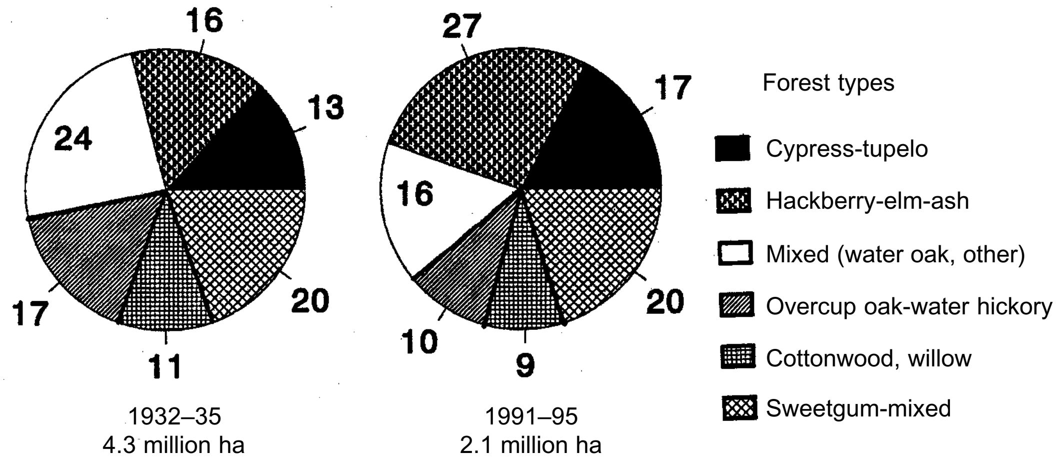
[c] = 10 percent volume removed but characterized by residual trees from the old-growth forest (Eldredge 1937).

[d] < 10 percent volume removed (Eldredge 1937).

[e] Early successional types defined in the 1930s as transitional, having no maturity potential (Winters and others 1938).

[f] Water, Nuttall, and willow oak.

Source: Stover 1942.



1932–35
4.3 million ha

1991–95
2.1 million ha

Figure 2—Percent bottomland-hardwood forest area by forest type and total forest area of Arkansas, Louisiana, and Mississippi Delta survey units, 1932–35 and 1991–95.

Table 4—Mississippi Alluvial Valley bottomland forest area by type and condition, Louisiana, 1934–1935

Survey region and forest type	All conditions	Second growth[a]	Old growth[b]		
			Partial[c]	Uncut[d]	
	- - - - - - - - - - *1000 ha*	- - - - - - - - - - - -			%
Northeast Louisiana, 1934					
Baldcypress-water tupelo	38.5	24.0	8.5	6.0	16
Overcup oak-water hickory	328.7	71.4	107.8	149.5	45
Cottonwood and willow[e]	88.6	88.6	—	—	—
Mixed bottomland hardwood					
Sweetgum-water oaks[f]	276.0	186.2	42.4	47.5	17
Hackberry-elm-ash	163.5	64.9	75.4	23.2	8
Water oaks[f]	78.9	42.3	30.0	6.6	17
Other mixtures	99.9	76.7	22.1	1.0	1
Total	1,074.1	554.1	286.2	233.8	22
South Louisiana Delta, 1935					
Baldcypress-water tupelo	442.0	349.7	72.4	19.8	14
Overcup oak-water hickory	142.0	53.3	40.6	48.0	22
Cottonwood and willow[e]	193.2	193.2	—	—	—
Mixed bottomland hardwood					
Sweetgum-water oaks[f]	233.9	191.1	28.6	14.1	6
Hackberry-elm-ash	163.6	132.1	28.6	2.8	2
Water oaks[f]	44.2	36.0	7.8	0.4	1
Other mixtures	133.9	109.9	16.6	7.4	6
Total	1,352.8	1,065.3	194.6	92.6	7

[a] Vegetative growth habits typical of abandoned clearings, recent catastrophic disturbances, or new riverbank soil deposits (Winters and others 1938).
[b] Stands composed of sawtimber trees with the characteristics of the original mature trees of the region (Eldredge 1937).
[c] = 10 percent volume removed but characterized by residual trees from the old-growth forest (Eldredge 1937).
[d] < 10 percent volume removed (Eldredge 1937).
[e] Early successional types defined in the 1930s as transitional, having no maturity potential (Winters and others 1938).
[f] Water, Nuttall, and willow oak.
Sources: Winters 1939b, Winters and others 1938.

decade (table 5). Since the 1970s, only baldcypress-water tupelo and willow community types have increased.

The 1967 delta survey unit in Mississippi documented that two-thirds of its forest land, about 170 000 ha, were soybean fields cleared since the 1957 survey (Beltz and Christopher 1967). Forests cleared for agriculture between 1957 and 1967 were about 28 percent overcup oak-water hickory, 37 percent sweetgum-mixed oaks, 13 percent hackberry-elm-ash, and 22 percent other community types (Beltz and Christopher 1967). Overcup oak-water hickory—characteristic of poorly drained clay flats—was preferentially removed, i.e., the proportion of area removed was larger by 8 percent than what existed in the Mississippi 1946–48 survey (Sternitzke and Putnam 1956).

Though Sternitzke and Putnam (1956) attributed much of the change in the MAV's forest composition to clearing of forests in areas suitable for agricultural production, they also noted heavy cutting during World War II for selected species. Overcup oak and the then undifferentiated tupelo, i.e., today's blackgum, swamp tupelo, or water tupelo, sawtimber

Table 5—Bottomland forest area by type and survey period, Arkansas, Louisiana, and Mississippi Delta survey units, 1930s to 1990s

Forest type	Change since the 1930s	Survey period 1991–1995	1984–1988	1974–1978	1964–1969	1947–1954	1932–1935[a]
	Percent	*1000 ha*					
Baldcypress-water tupelo	-34	380.4	412.9	363.4	NA	439.8	573.5
Overcup oak-water hickory	-71	210.4	217.7	286.8	NA	549.6	717.6
Cottonwood-willow	-59[b]					327.8	467.2
Willow		146.3	135.4	127.7	NA	NA	NA
Cottonwood		43.9	42.7	57.1	NA	NA	NA
Mixed bottomland hardwood						2,239.0[c]	
Sweetgum-mixed	-53	402.1	399.3	494.7	NA	NA	851.8
Hackberry-elm-ash	-9	565.4	545.1	590.2	NA	NA	618.6
Other mixtures	-69		287.4	366.0	NA	NA	1,054.4
Total	-52	2,080.1	2,040.5	2,285.9	2,702.2	3,556.2	4,346.1

NA = not available.

[a] 1932–35 adjusted to this three-State region by multiplying Mississippi Alluvial area estimates in table 1 by 0.84 (4,364.1 divided by 5,190.5).

[b] Cottonwood and willow.

[c] Sweetgum-mixed, hackberry-elm-ash, and other mixtures; no details available.

volume declined 27 percent between the 1930s and 1947–54 survey period (Sternitzke and Putnam 1956), which is limited evidence suggesting that the 1930s remnant old-growth forests dominated by these species were extensively logged. During the same period, baldcypress sawtimber volume increased by 33 percent—limited evidence suggesting the 1930s remnant old-growth forests dominated by baldcypress were not extensively logged.

By the 1947–54 surveys, poletimber and smaller diameter class area represented 45 percent of bottomland hardwood communities, and almost one-half were in the mixed types. Sternitzke and Putnam (1956) ascribed the predominance of younger age conditions to extensive cutting and some to reversion to forest after farm abandonment during the Depression and World War II.

Area in poletimber and smaller diameter class was greater for the 1947–54 survey period than subsequent years (fig. 3). Baldcypress-water tupelo area in sawtimber diameter class increased between the 1947–54 period and 1990s. With this exception, area in sawtimber diameter class was also greater for the 1947–54 period than in subsequent years. Later surveys showed declines in nearly all bottomland hardwood community types classed as poletimber and smaller diameter class, and a slower, smaller increase in the sawtimber diameter class (fig. 3).

Comparisons of Bottomland Hardwood Community Type in the South-Central United States

Based on an ocular comparison of a forest occurrence probability grid by flood zones and shade tolerance, community types today appear to occupy more of the grid in South-Central United States' bottomland hardwoods (fig. 4A) than in the MAV (fig. 4B). To gain a better understanding of the community types depicted in the above grids, I cross-referenced Rudis's (1995) empirically defined community types with FIA community types. Lines in figure 5 join empirical community types containing at least 50 percent of each FIA community type. For the most part, FIA community types represented a narrow range of flood zones. Exceptions were sweetbay-swamp tupelo-red maple type which occupied a broad range of flood zones, and swamp chestnut oak-cherrybark oak type, which was in the sporadic flood zone but had no majority affiliation with any empirical community type.

Closer inspection of the forest occurrence probability grids for the South-Central United States (fig. 4A) and MAV (fig. 4B) show a gap around flood code 5, shade code 2.5, which corresponds to blackgum (NY) and American holly (IO) empirical community types, and swamp chestnut oak-cherrybark oak FIA community type in figure 5. A second, smaller gap in the MAV grid occurs around flood code 3, shade code 3.5, which corresponds to the swamp tupelo

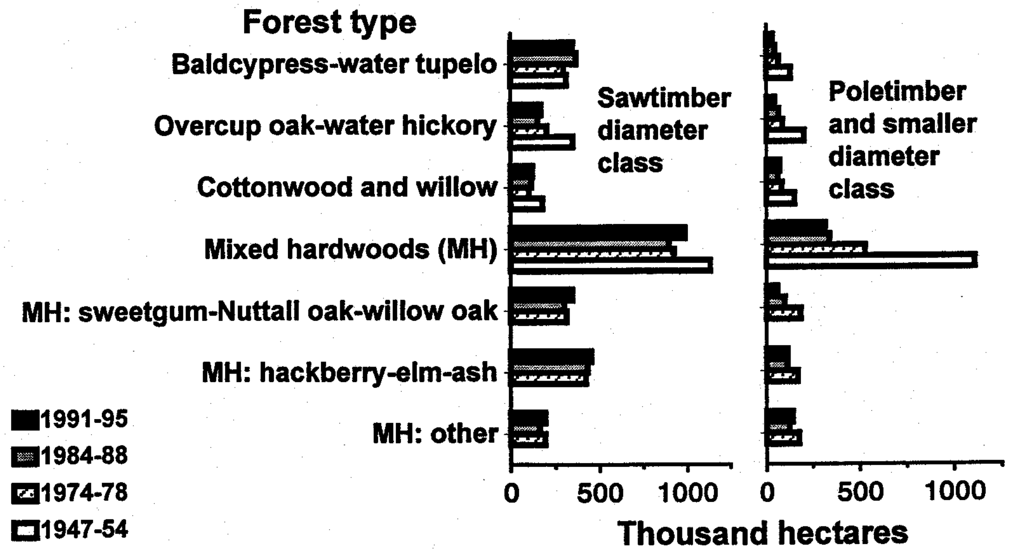


Figure 3—Forest area by diameter class for Arkansas, Louisiana, and Mississippi Delta survey units, 1947–95. For 1947–54 surveys, no data within mixed hardwood (MH) types. Sawtimber diameter class, 1947–54: forests with hardwood trees ≥ 27.9 cm, softwoods ≥ 22.9 cm, and net volume > 1,500 board feet (*sic*, no metric equivalent); 1974 and later: ≥ 50-percent stocked with trees ≥ 12.7 cm diameter, and ≥ 50-percent stocked with trees > 27.9 cm (hardwoods), > 22.9 cm (softwoods). Poletimber and smaller-diameter class: forests with trees not meeting sawtimber-diameter class criteria.

Table 6—Bottomland hardwood forest area by forest type and proportion of large tree basal area in the Arkansas, Louisiana, and Mississippi Delta survey units, 1991–1995

			Percent large tree basal area[a]			
Forest type	All areas	None	>0.1	0.1–20	21–40	>40
	- - - - - - - - - - - - - - - - - 1000 ha - - - - - - - - - - - - - - -					
Baldcypress-water tupelo	380.4	39.0	341.4	188.9	111.9	40.7
Overcup oak-water hickory	210.4	14.9	195.5	60.0	76.5	59.1
Willow	146.3	60.3	90.0	30.9	14.8	40.3
Cottonwood	43.9	8.0	35.9	7.6	5.2	23.1
Sweetgum-Nuttall oak-willow oak	402.1	19.0	383.1	120.7	135.5	126.9
Hackberry-elm-ash	565.4	58.1	507.4	127.1	224.3	156.0
Sweetbay-swamp tupelo-red maple	47.7	11.8	36.0	17.2	14.8	3.9
Sycamore-pecan-elm	60.0	16.2	43.8	16.9	15.5	11.4
Other mixed	221.0	38.8	185.2	74.6	63.2	47.4
Total	2,080.1	266.0	1,814.2	643.8	661.6	508.7

[a] Basal area of live trees ≥50 cm diameter at 1.4 m (d.b.h.) divided by basal area of live trees ≥12.7 cm d.b.h.

(NB) empirical community type, or the FIA swamp tupelo-sweetbay community type (fig. 5).

Quantitative species-based comparisons corroborate these qualitative comparisons. Species representing ≥3 percent dry weight importance in the east or west south-central Gulf Coastal Plain, but not the MAV, include: blackgum, cherrybark oak, hickory, laurel oak, loblolly pine, sweetbay, swamp tupelo, and yellow-poplar (McWilliams and Rosson 1990).

Old-Growth Potential

By selecting only sampled forests with >0.05 percent basal area from trees >50 cm d.b.h. (table 6), one obtains estimates from forests visually perceived as older stands. Community distribution along the flood zone-shade

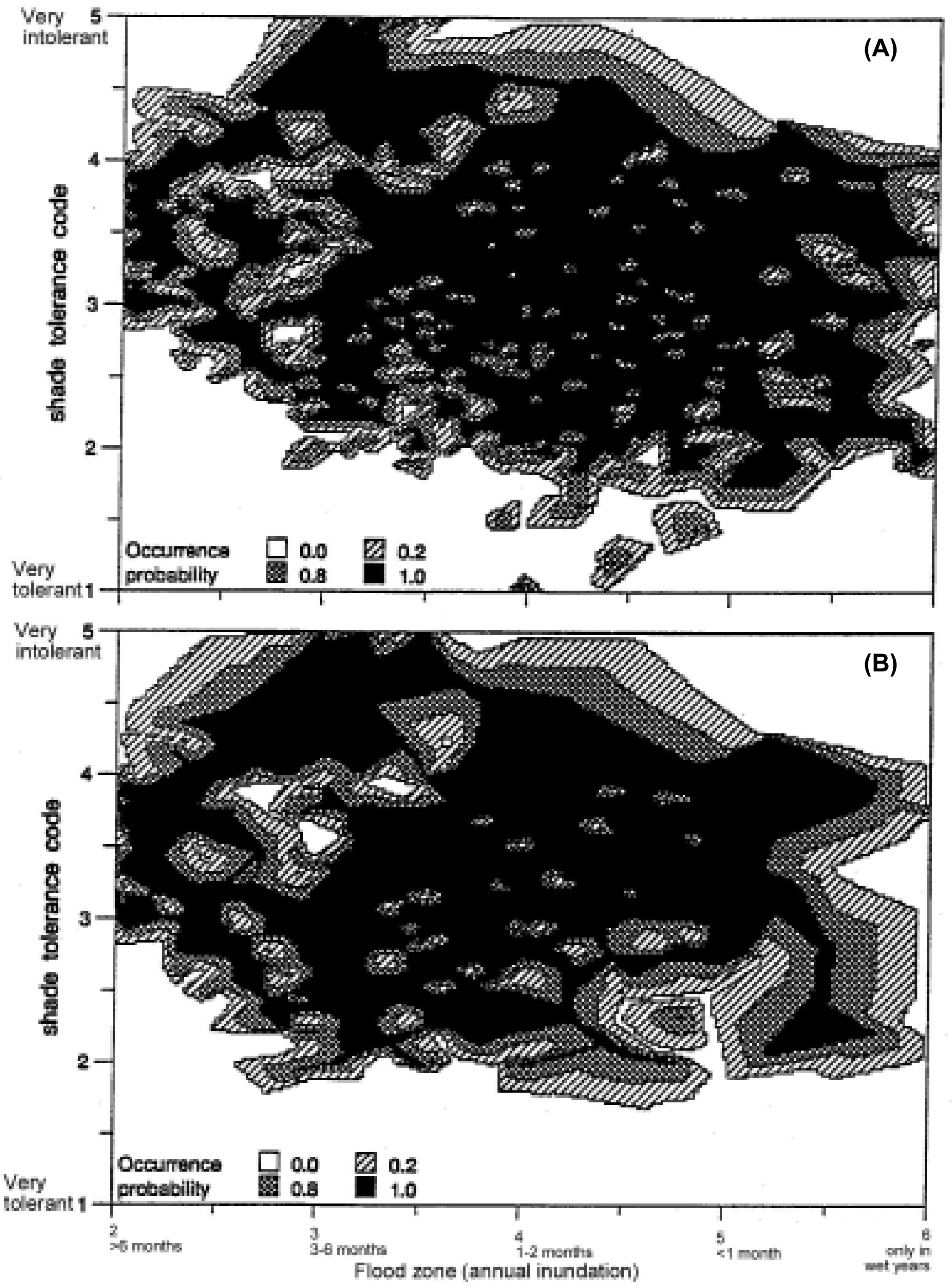


Figure 4—Predicted bottomland-hardwood occurrence by average flood zone and shade tolerance: (A) South-Central United States bottomland hardwoods, 1986–91. (Sample size: 5,366, i.e., 2,666 estimates from forest area samples based on tree importance values and 2,700 randomly assigned estimates representing nonforested, former bottomland hardwood forests; (B) Arkansas, Louisiana, and Mississippi Delta survey units, 1987–91. (Sample size: 1,724, i.e., 824 estimates from forest area samples based on tree importance values and 900 randomly assigned estimates representing nonforested, former bottomland hardwood forests).

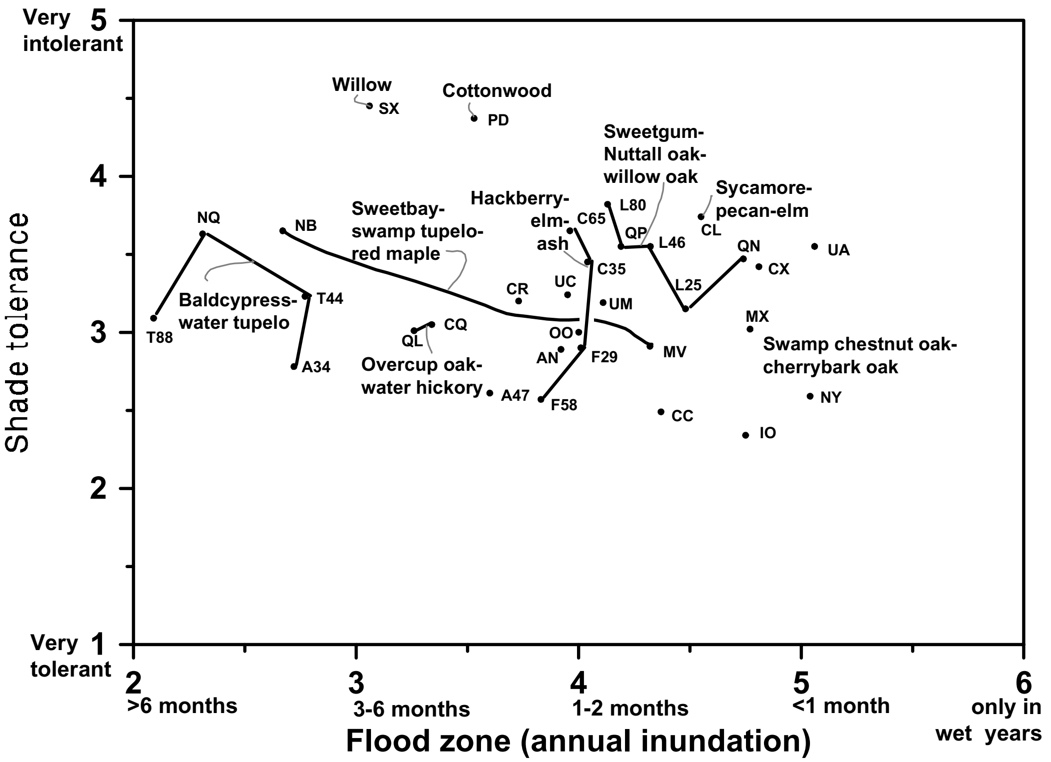


Figure 5—Forest Inventory and Analysis (FIA) community types and empirical-community types by average flood zone and shade tolerance value, South-Central United States bottomland hardwoods. Linked are empirical types that also categorize ≥ 50 percent of the FIA community type. Empirical community type codes by dominant species (additionally coded by percent importance if characteristic of more than one type): A34-red maple, A47-red maple, AN-boxelder, C65-hackberry, C35-hackberry, CC-blue-beech, CL-pecan, CQ-water hickory, CR-hawthorne, CX-other hickories, F58-green ash, F29-green ash, IO-American holly, L80-sweetgum, L46-sweetgum, L25-sweetgum, MV-sweetbay, MX-mixed, importance < 5 percent for any one species, NB-swamp tupelo, NQ-water tupelo, NY-blackgum, OO-no trees, > 2.5 cm at 1.4 m, PD-cottonwood, QL-overcup oak, QN-water oak, QP-willow oak, T44-baldcypress, T88-baldcypress, UA-winged elm, UC-cedar elm, UM-American elm (after Rudis 1995). Sample size = 2,666 plots.

tolerance grid shows a very limited occurrence in flood zone codes 4 through 6 and shade tolerance codes 2 and 3 (fig. 6).

A more conservative distribution of potential old-growth types emerges with the biological maturity criteria (table 7). Most communities in flood zone codes 5 disappear. These correspond to FIA community types like swamp chestnut oak-cherrybark oak and sycamore-pecan-elm. Primarily it is flood codes 2 through 4, i.e., baldcypress-water tupelo, overcup oak-water hickory, cottonwood, and willow, that have basal area equal to or greater than the range associated with mature forests (fig. 6B). Basal area from mature, i.e., 45- to 65-year-old southern bottomland hardwood, forests range from 20.9 to 29.6 m^2 per hectare (table 7). This range compares favorably with one 1990 27.4-m^2-per-hectare estimate from three southern floodplain research natural areas known to contain old-growth trees (Devall and Ramp 1992) and Martin's (1992) 25-m^2-per-hectare minimum for mixed mesophytic, old-growth forests.

Additional criteria [net growth 0±1.4 m^3 per hectare per year (fig. 7A) and no harvest since the previous survey (fig. 7B)], reveal that the greatest old-growth potential occurs in the wettest community types. Combining the three biological maturity criteria with the size criterion shows that estimates even smaller (table 8).

Ownership is largely in private hands, even when estimating area with old-growth potential (table 9). By forest type, corporate owners—frequently banks, insurance firms, agricultural businesses, and, in Louisiana, companies with oil production interests—control a large percentage of baldcypress-water tupelo area, even when based on the most restrictive old-growth criteria (table 10).

Fragmentation and Changes 1970s to 1990s

If small in area, a forest fragment is more likely than a large forest fragment to show evidence of livestock use and selected human intrusions (beverage, food, and other containers; trash; buildings; foundations; and fences); to be closer to agricultural and urban areas, roads and fences; and to contain less timber growing stock (Rudis 1995). If large, a forest fragment is more likely to have Spanish moss (*Tillandsia usneoides* L.) and signs restricting hunting activities (Rudis 1995). Larger forest fragments are from the permanent flood zone types; smaller fragments are from sporadic, intermittent, and periodic flood zone, early successional community types (Rudis 1995). These indices suggest change in the uses and resource values of remnant

Table 7—Maturity criteria, bottomland forest area, and sample size by potential site productivity and maturity class, Arkansas, Louisiana, and Mississippi Delta survey units, 1991–1995

Potential site productivity class	Maturity criteria[a]		Arkansas, Louisiana, and Mississipppi Delta survey units			
	Basal area	Sample size	All areas		≥Maturity criteria	
m^3/ha/yr	*m^2/ha*	*Number*	*1000 ha*	*Number*	*1000 ha*	*Number*
15.8 or more	29.6	3	92.0	39	23.1	10
11.6 to 15.7	25.6	10	223.8	94	83.8	35
8.4 to 11.5	23.7	15	381.0	154	179.9	74
6.0 to 8.3	22.6	19	681.0	279	356.6	145
3.5 to 5.9	21.8	17	623.9	253	361.3	146
1.4 to 3.4	20.9	6	78.4	34	37.8	16
Total			2,080.1	853	1,042.5	426

[a] Average stand basal area and sample size for 45- to 65-year-old bottomland forest stands. Stand age represents the mean of five dominant trees spaced ≥20 m within a 0.4-ha area. Source: East Texas 1986 surveys.

Table 8—Bottomland forest area by forest type and growth criteria for the Arkansas, Louisiana, and Mississippi Delta survey units, 1991–1995

Forest type	All areas	Growth criteria[a]			A, B, C, and percent large tree basal area[b]			
		A	A, B	A, B, C	1–100	1–20	21–40	>40
	1000 ha							
Baldcypress-water tupelo	380.4	290.1	75.9	37.5	34.7	14.7	10.2	9.8
Overcup oak-water hickory	210.4	110.6	20.2	13.1	13.1	4.2	2.3	6.6
Willow	146.3	54.3	14.7	4.6	4.6		2.7	1.9
Cottonwood	43.9	12.6	—	—	—	—	—	—
Sweetgum-Nuttall oak-willow oak	402.1	204.5	38.5	15.9	15.9	4.6	5.1	6.2
Hackberry-elm-ash	565.4	264.9	80.0	18.3	18.3	7.3	6.8	4.3
Sweetbay-swamp tupelo-red maple	47.7	25.2	—	—	—	—	—	—
Sycamore-pecan-elm	60.0	15.4	2.6	2.6	2.6	—	2.6	—
Other mixed	221.0	65.0	19.1	14.5	9.3	2.4	6.9	—
Total	2,080.1	1,042.5	209.1	106.5	98.5	33.3	29.5	35.7

[a] A is average basal area of 45- to 65-year-old bottomland hardwood stands (table 7); B is net growth on live trees = 0 ± 1.4 m^3 per hectare per year; C is no evidence of commercial harvest since prior surveys (about 7 years earlier).

[b] Basal area of live trees ≥ 50 cm diameter at 1.4 m (d.b.h.) divided by basal area of live trees ≥ 12.7 d.b.h.

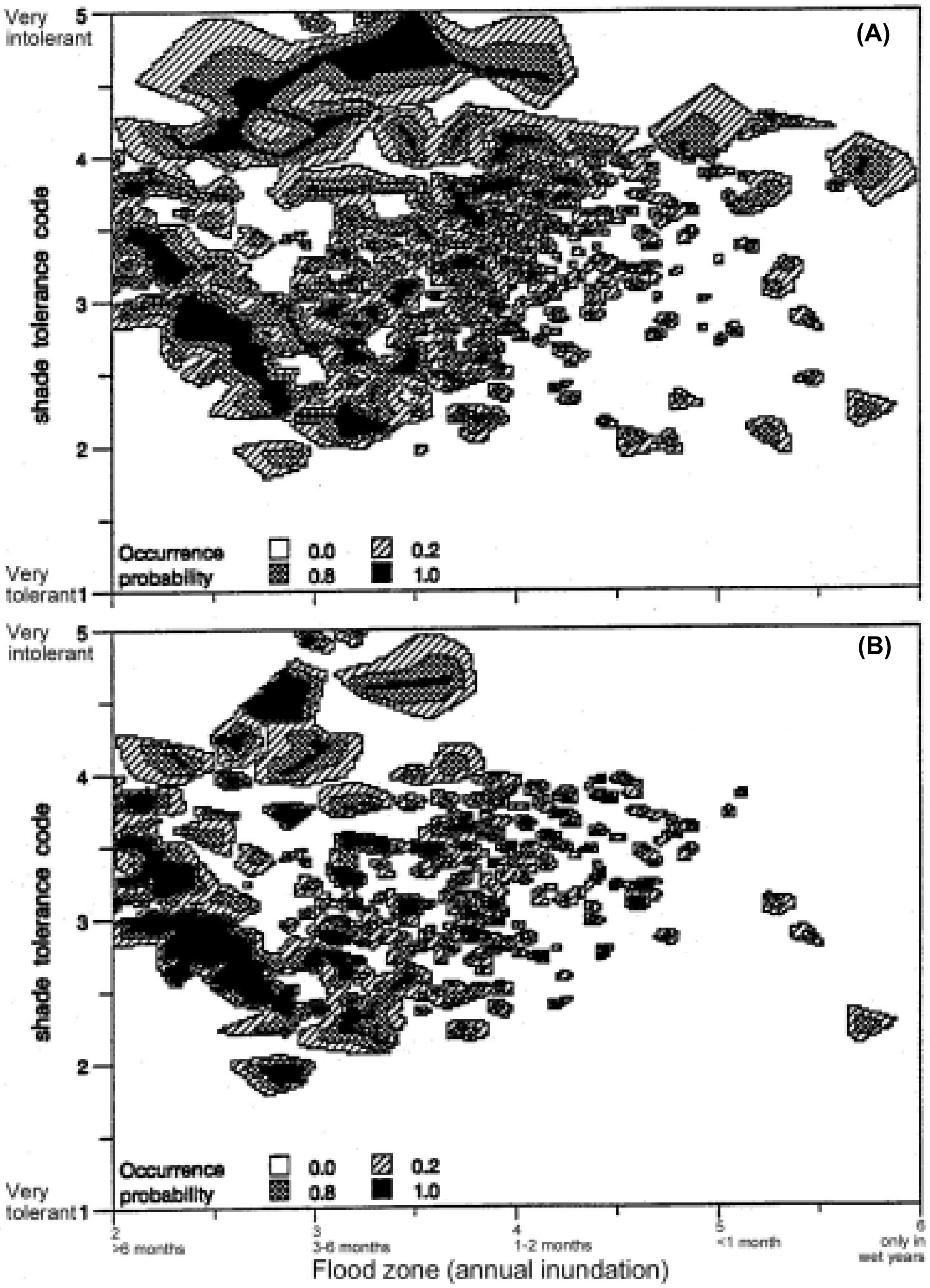


Figure 6—Predicted bottomland-hardwood occurrence, Arkansas, Louisiana, and Mississippi Delta survey units by average flood zone and shade tolerance for forests with: (A) large trees (> 0.1 percent basal ≥ 50 cm diameter at 1.4 m (d.b.h.) divided by basal area of live trees > 12.7 cm d.b.h.; (B) basal area ≥ average for 45- to 65-year-old southern bottomland-hardwood communities by potential site productivity class (20.9 to 29.6 square meters per hectare, productivity classes 1.4 to ≥15.8 cubic meters per hectare per year [see table 7]).

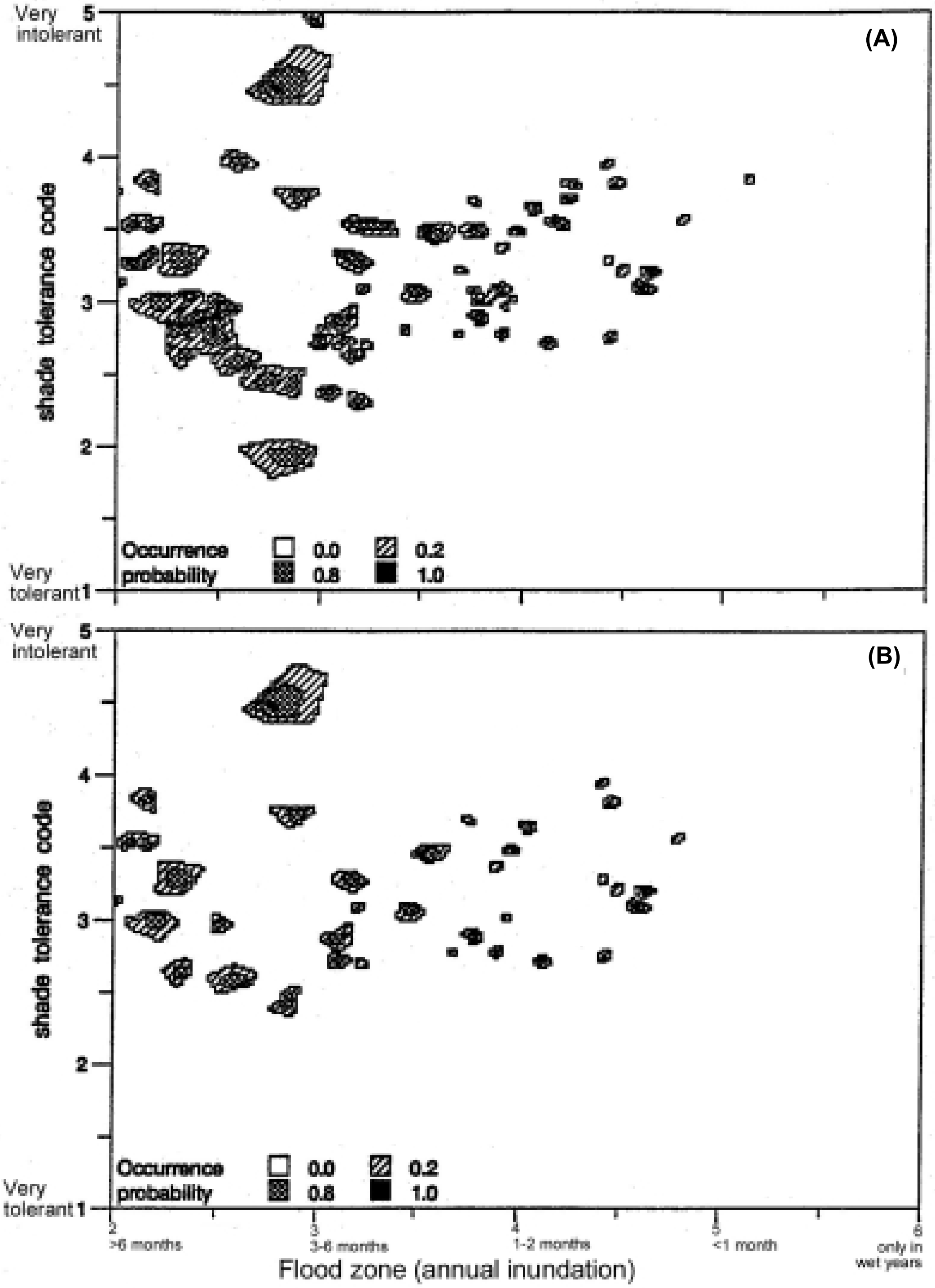


Figure 7—Predicted bottomland-hardwood occurrence, Arkansas, Louisiana, and Mississippi Delta survey units by average flood zone and shade tolerance for (A) forests with basal area >= potential site-productivity averages for 45- to 65-year-old southern bottomland-hardwood communities and net growth = 0 + or - 1.4 cubic meters per hectare per year; (B) forests with conditions listed in (A) and no evidence of commercial harvest activity.

Table 9–Bottomland forest area by forest type and growth criteria in the Arkansas, Louisiana, and Mississippi Delta survey units, 1991–1995

			Growth criteria[a]					
Forest type	All areas		A		A, B		A, B, C	
	1000 ha	*%*	*1000 ha*	*%*	*1000 ha*	*%*	*1000 ha*	*%*
Public	300.6	14	148.4	14	11.9	6	7.7	7
Other corporate[b]	526.9	25	308.9	30	67.1	32	29.9	28
Forest industry	272.3	13	123.5	12	23.4	11	14.4	14
Farmer	405.2	19	171.8	16	46.2	22	25.3	24
Other private[c]	575.1	28	289.9	28	60.6	29	28.6	27
Total	2,080.1	100	1,024.5	100	209.1	100	106.5	100

[a] A is ≥average basal area of 45- to 65-year old bottomland hardwood stands (table 7); B is net growth on live trees = ± 1.4 m^3 per hectare per year; C is no evidence of commercial harvest since prior surveys (about 7 years earlier).

[b] Other than forest industries.

[c] Other than farmers and corporate owners.

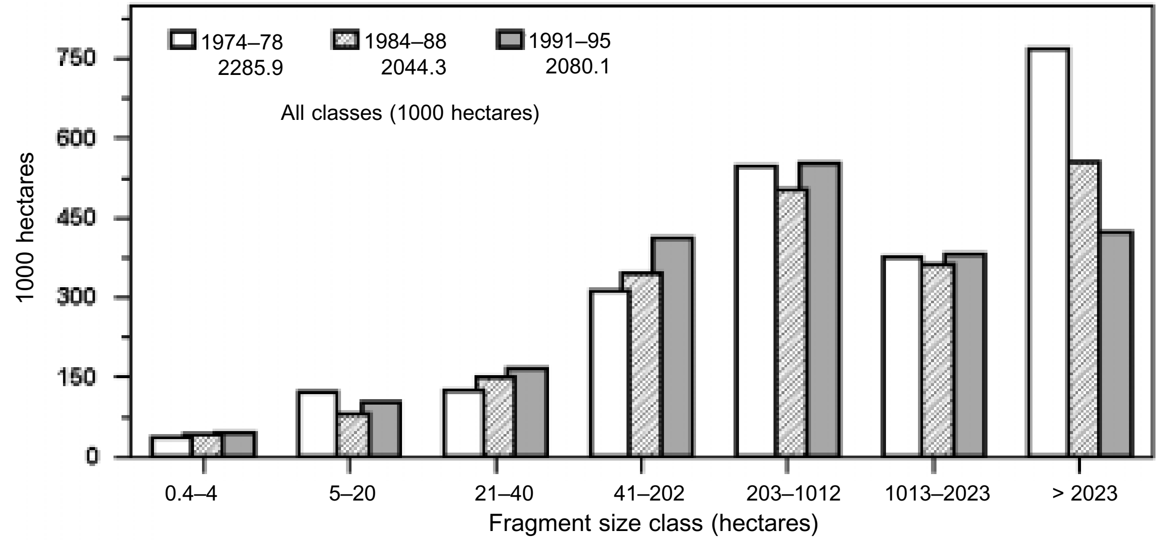


Figure 8—Bottomland-hardwood forest area by fragment size class and survey year, Arkansas, Louisiana, and Mississippi Delta survey units, 1974–78, 1984–88, and 1991–95.

or regenerated forests. On average, fragmented forest cover is less likely to retain or recover the resource values associated with the region's once large, contiguous forests.

Between the 1970s and 1990s, total forest area in the MAV changed only slightly, from 2.3 to 2.1 million ha, but there was a shift to fragment size classes < 2000 ha (fig. 8), and to baldcypress-water tupelo community types (table 11). For the largest (> 2023 ha) fragment size class, the decline was primarily in mixed hardwoods and hackberry-elm-ash (table 11). Declines in the largest fragment class were 9 percent in baldcypress-water tupelo, and above 30 percent in all other community types examined.

SUMMARY AND IMPLICATIONS

Comparisons with historical MAV data showed that the sporadic flood zone, late-successional community types, especially mixed bottomland hardwoods, were the most

Table 10—Bottomland forest area by forest type, owner, and growth criteria in the Arkansas, Louisiana, and Mississippi Delta survey units, 1991–1995

Forest type and owner class	All areas		Growth criteria[a]					
			A		A, B		A, B, C	
	1000 ha	*%*	*1000 ha*	*%*	*1000 ha*	*%*	*1000 ha*	*%*
Baldcypress-water tupelo								
Public	15.0	4	12.7	4	1.4	2	—	—
Other corporate[b]	166.5	44	133.4	46	35.3	47	15.5	41
Forest industry	39.9	10	34.2	12	7.7	10	7.7	21
Farmer	57.2	15	19.8	7	5.1	7	5.1	14
Other private[c]	101.8	27	90.0	31	26.3	35	9.2	25
Total	380.3	100	290.1	100	75.9	100	37.5	100
Overcup oak-water hickory, cottonwood, and willow								
Public	98.1	26	47.1	27	3.9	11	3.9	22
Other corporate[b]	92.0	22	39.5	22	12.5	36	7.3	41
Forest industry	51.8	13	22.7	13	5.1	15	—	—
Farmer	64.2	17	29.4	17	6.9	20	4.2	24
Other private[c]	94.5	22	38.7	22	6.6	19	2.2	13
Total	400.6	100	177.4	100	35.0	100	17.6	100
Sweetgum-Nuttall oak-willow oak								
Public	60.8	15	33.2	16	—	—	—	—
Other corporate[b]	64.1	16	30.1	15	7.9	21	—	—
Forest industry	42.3	11	20.0	10	6.3	16	4.3	27
Farmer	101.6	25	52.9	26	14.6	38	6.5	41
Other private[c]	133.3	33	68.3	33	9.7	25	5.1	32
Total	402.1	100	204.5	100	38.5	100	15.9	100
Hackberry-elm-ash								
Public	84.3	15	34.9	13	—	—	—	—
Other corporate[b]	144.2	26	79.7	30	6.1	16	2.0	11
Forest industry	104.7	19	40.2	15	2.0	5	—	—
Farmer	86.9	15	40.0	15	17.2	45	9.5	52
Other private[c]	145.4	26	70.0	26	12.8	34	6.9	37
Total	565.4	100	264.9	100	38.0	100	18.3	100
Mixed hardwoods (sycamore-pecan-elm, sweetbay-swamp tupelo-red maple, and other mixed)								
Public	42.4	15	20.5	26	6.5	30	3.9	22
Other corporate[b]	38.4	14	14.3	18	5.3	24	7.3	41
Forest industry	31.7	11	4.4	5	2.4	11	—	—
Farmer	88.4	31	25.0	31	2.4	11	4.2	24
Other private[c]	82.9	22	16.2	20	5.2	24	2.3	13
Total	283.9	100	80.4	100	21.7	100	17.6	100

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[a] A is ≥ average basal area of 45- to 65-year old bottomland hardwood stands (table 7), B is net growth on live trees = ± 1.4 m^3 per hectare per year, C is no evidence of commercial harvest since prior surveys (about 7 years earlier).

[b] Other than forest industries.

[c] Other than farmers and corporate owners.

Table 11—Bottomland forest area by forest type, survey period, change since the 1970s, and forest fragment size class in Arkansas, Louisiana, and Mississippi Delta survey units

Forest type and survey period	All size classes	Forest fragment size class (hectares) 0.4 to 40	41 to 202	203 to 1,012	1,013 to 2,023	>2,023
	1000 ha					
Baldcypress-water tupelo						
1974–1978	363.4	23.9	19.9	63.7	78.3	177.6
1984–1988	412.9	23.0	48.7	78.0	72.2	190.8
1991–1995	380.4	28.6	58.0	62.6	69.8	161.4
Change	17.0	4.7	38.1	-1.1	-8.5	-16.2
Percent	5	20	2	-2	-11	-9
Overcup oak-water hickory, cottonwood, and willow						
1974–1978	471.6	54.3	71.0	130.1	83.9	132.4
1984–1988	395.8	44.9	62.6	118.5	53.3	118.4
1991–1995	400.6	55.3	82.9	88.1	82.4	92.0
Change	-71.0	1.0	11.9	-42.0	-1.5	-40.4
Percent	-15	2	17	-32	-2	-31
Sweetgum-Nuttall oak-willow oak						
1974–1978	494.7	106.4	90.0	128.7	86.9	82.6
1984–1988	399.3	78.9	95.0	91.7	70.0	64.2
1991–1995	402.1	80.2	87.1	121.4	71.3	42.0
Change	-92.6	-26.2	-2.9	-7.3	-15.6	-33.7
Percent	-19	-25	-3	-6	-18	-41
Hackberry-elm-ash						
1974–1978	590.2	50.7	69.3	150.7	83.8	235.8
1984–1988	545.1	70.4	73.7	147.2	121.4	132.7
1991–1995	565.4	74.4	101.8	167.8	129.1	92.4
Change	-24.8	23.7	32.5	17.1	45.3	-143.4
Percent	-4	47	47	11	54	-61
Mixed hardwoods (sycamore-pecan-elm, sweetbay-swamp-tupelo-red maple, and other mixed)						
1974–1978	366.0	49.8	62.2	72.4	42.4	139.2
1984–1988	287.4	58.6	65.0	66.8	48.8	49.4
1991–1995	331.6	74.0	81.0	112.1	29.1	35.3
Change	-34.4	24.2	18.8	39.7	-13.3	-103.9
Percent	-9	49	30	55	-31	-75
All forest types						
1974–1978	2,285.9	285.1	312.5	545.5	375.2	767.6
1984–1988	2,044.3	275.8	344.9	502.3	365.8	555.6
1991–1995	2,080.1	312.6	410.8	552.0	381.7	423.0
Change	-205.8	27.5	98.3	6.5	6.5	-344.6
Percent	-9	9	31	1	2	-45

vulnerable to anthropogenic intrusions. The permanent flood zone community types typified by baldcypress-water tupelo, and the intermediate flood zone, early successional community types typified by hackberry-elm-ash were the least vulnerable. Since the 1970s, the largest (> 2023 ha) forests have continued to decline, with the nonpermanent flood zone types most affected. Based on old-growth criteria (potential site productivity-based minimum basal area, net growth near zero, and absence of harvest activity), permanent flood zone bottomland community types were associated with the most old-growth potential and large forest fragments and were primarily in private ownership. Nonpermanent flood zone types were associated with small forest fragments and the least old-growth potential. Clewell and Lea (1989) and Zedler and Weller (1989) describe associated forested wetland creation, maintenance, restoration, and research needed.

National reforestation programs to restore forested communities, such as the 1970s Forestry Incentive Program and the 1980s Conservation Reserve Program, have not traditionally focused on regional shifts in species or community types or forest fragmentation. If restoration of historic community types is also a desired future goal, these programs require approaches sensitive to regional changes. Declines in large forest fragments suggest losses in their associated values, e.g., optimal habitat for black bear (Rudis and Tansey 1995) and primitive recreational opportunities (Rudis 1987, 1995). Hoover and Shannon (1995) suggest social and political institutions and processes to maintain regional conservation land corridors and mitigate fragmentation, e.g., formal regional planning, informal adjacent landowner cooperation, and more stakeholder participation in the planning process.

If restoration of the 1930s proportion of MAV bottomland hardwood community types is desired, these programs will require focused efforts that (1) shift area of hackberry-elm-ash toward late-successional types, (2) establish species typical of likely missing bottomland hardwood types, e.g., swamp chestnut oak-cherrybark oak, (3) conserve remaining late-successional, nonpermanent flood zone types, and (4) foster occasional flooding characteristic of sporadic, intermittent, and periodic flood zones. Localized reforestation along rivers and streams and reconnection among existing small bottomland hardwood remnants also improve chances for recovery of landscape and regional scale values, e.g., water quality and habitats for selected wildlife species characteristic of floodplain forests (Hamel 2001).

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APPENDIX A

Common and scientific names as listed in the text (Little 1979*)*:

Common name	Scientific name
Ash	*Fraxinus* spp.
Green ash	*F. pennsylvanica* Marsh.
White ash	*F. americana* L.
Baldcypress	*Taxodium disticum* (l.) Rich. var. *distichum*
American beech	*Fagus grandifolia* Ehrh.
River birch	*Betula nigra* L.
Blackgum	*Nyssa sylvatica* var. *biflora* (Walt.) Sarg.
Blue-beech	*Carpinus caroliniana* Walt.
Boxelder	*Acer negundo* L.
Cottonwood	*Populus tremuloides* Michx.
Elm	*Ulmus* spp.
American elm	*U. americana* L.
Cedar elm	*U. crassifolia* Nutt.
Winged elm	*U. alata* Michx.
Hackberry	*Celtis laevigata* Willd. *C. occidentalis* L.
Hawthorn	*Crataegus* spp.
Hickory	*Carya* spp. *C. illinoensis* (Wangenh.) K. Koch
Water hickory	*C. aquatica* (Michx f.) Nutt.
American holly	*Ilex opaca* Ait
Southern magnolia	*Magnolia grandiflora* L.
Red maple	*Acer rubrum* L.
Oak	*Quercus* spp.
Cherrybark oak	*Q. falcata* var. *pagodifolia* Ell.
Delta post oak	*Q. stellata* var. *paludosa* Sarg.
Laurel oak	*Q. laurifolia* Michx.
Nuttall oak	*Q. nuttallii* Palmer
Overcup oak	*Q. lyrata* Walt.
Shumard oak	*Q. shumardii* Buckl.
Swamp chestnut oak	*Q. michauxii* Nutt.
Water oak	*Q. nigra* L.
White oak	*Q. alba* L.
Willow oak	*Q. phellos* L.
Pecan	*Carya illinoensis* (Wangenh.) K. Koch
Persimmon	*Diospyros virginiana* L.
Loblolly pine	*Pinus taeda* L.
Slash pine	*P. elliottii* Engelm.
Sweetbay	*Magnolia virginiana* L.
Sweetgum	*Liquidambar styraciflua* L.
Sycamore	*Platanus occidentalis* L.
Swamp tupelo	*Nyssa sylvatica* var. *biflora* (Walt.) Sarg.
Water tupelo	*N. aquatica* L.
WIllow	*Salix* spp.
Yellow-poplar	*Liriodendron tulipifera* L.

APPENDIX B

Definition of Terms

Flood zones—Sporadic, intermittent, nonpermanent, permanent zones.

Forest types—Community types recognized by Forest Inventory and Analysis and named by the species that comprise the majority of the stocking. These include: baldcypress-water tupelo associates include green ash, red maple, and sweetgum. This type occurs chiefly on very wet sites where surface water is present throughout the growing season in years of normal rainfall. Cottonwood associates include willow, white ash, green ash, and sycamore. Sites are along stream banks where bare moist soil is available, e.g., along river and stream margins. Hackberry-elm-ash associates include water oak, willow oak, laurel oak, sweetgum, water hickory, and boxelder. Sites are typical of river margins and moist bottoms. Overcup oak-water hickory associates include green ash, hackberry, American elm, red maple, and persimmon. Sites are in low-lying, poorly drained flats with clay or silty-clay soils. Sycamore-pecan-elm associates include boxelder, green ash, hackberry, cottonwood, willow, sweetgum, and river birch. Sites are on alluvial flood plains. Swamp chestnut oak-cherrybark oak associates include white oak, Delta post oak, Shumard oak, white ash, and hickories. Sites are on terraces or ridges in first bottoms. Sweetbay-swamp tupelo-red maple associates include slash pine, and moist site hardwood species. Sites normally have saturated soils throughout the growing season, such as along branch heads, drains, bays, and swamp borders. Sweetgum-Nuttall oak-willow oak associates include cottonwood, green ash, sycamore, pecan, American elm, red maple, and boxelder. This type occurs chiefly on sites with exposed moist soil such as stream banks and pond margins.

Saplings—Live trees with stems 2.5 to < 12.7 cm in d.b.h.

Seedlings—Live trees with stems < 2.5 cm in d.b.h. and > 3.0 cm tall for hardwoods, > 1.5 cm tall for softwoods.

Stand diameter class—A classification of the height and size of trees in a stand. Sawtimber diameter class stands are ≥ 50 percent stocked with live trees ≥ 12.7 cm d.b.h. and ≥ 50 percent stocked with sawtimber (≥22.9 cm softwood and ≥ 27.9 cm hardwood) trees. Poletimber stands are ≥ 50 percent stocked with live trees ≥ 12.7 cm and < 50 percent stocked with sawtimber trees. Smaller diameter class stands, typically composed of saplings and seedlings, are < 50 percent stocked with live trees < 12.7 cm.

Stocking—Degree of occupancy of land by live trees. It is measured by basal area or number of trees by size and spacing, or both, as a percent of a specified standard, which is the basal area or number of trees, or both, required to utilize the tree growth potential of the land.

THE EFFECT OF HERBIVORY BY WHITE-TAILED DEER AND ADDITIONALLY SWAMP RABBITS IN AN OLD-GROWTH BOTTOMLAND HARDWOOD FOREST

Margaret S. Devall, Bernard R. Parresol, and Winston P. Smith[1]

Abstract—Forest openings create internal patchiness and offer different habitat qualities that attract wildlife, especially herbivores, that flourish along forest edges. But intense herbivory in these openings can reduce or eliminate herbaceous and woody species and thus influence local species composition and structure of the forest. This study in an old-growth bottomland hardwood forest in southeastern Arkansas compares plant colonization among experimental plots, which excluded white-tailed deer (*Odocoileus virginianus*), deer and swamp rabbits (*Sylvilagus aquaticus*), and control plots. After the third year, plant species composition and abundance were significantly affected by herbivores.

INTRODUCTION

Old-growth forests of various types, which had developed with only low-intensity human disturbance, occupied much of the presettlement landscape of Arkansas (Holder 1970). European exploration and settlement of Arkansas began in the 16th century. Although the forests provided a valuable source of wood to European settlers, they were an impediment to farming. Wetland forests were especially threatened because at the time of European colonization wetlands were considered useful only after they were drained. The Swamp Land Acts of 1849–1850 granted swamplands in Federal ownership to the States to be reclaimed and disposed of; thereafter, widespread destruction of forested wetlands proceeded at a rapid rate (Turner and Craig 1980). Since colonial times almost half of the wetlands in the United States have been destroyed, and until recently thousands of acres were lost each year (MacDonald and others 1979). As a result, while old-growth forests are becoming less common throughout the United States, old-growth forested wetlands are even scarcer.

Although much is unknown about old-growth forests, it is obvious that many of their characteristics are different from those of younger forests (Juday 1988, Runkle 1991). While numerous definitions of old-growth forests have been suggested, two features occur in many of these definitions: (1) trees die singly or in small groups, creating openings or gaps in which regeneration of seedlings can occur; and (2) large logs and snags account for many of the values of the forests (Runkle 1982, 1991). For example, they provide food, shelter, or germination sites for various plant and animal species (Harmon and others 1986). Conversely, in many younger eastern forests large-scale disturbances occur often enough to be the dominant influence on their structure and composition (Runkle 1982, 1991).

Increased densities of deer (*Odocoileus virginianus*) and other herbivores that thrive in fragmented forests can alter plant species composition and structure (Alverson and others 1988). Swamp rabbits (*Sylvilagus aquaticus*) can be serious deterrents to the establishment of tree seedlings in wetlands. They clip seedlings at various heights above the ground and eat the tender parts (Blair and Langlinais 1960). Although there have been numerous studies of the effects of white-tailed deer on forests (Anderson and Loucks 1979, Alverson and others 1988, Griffin 1976, Richards and Farnsworth 1971, Ross and others 1970, Stewart and Burrows 1989), deer habitat and behavior vary considerably from one part of the country to another, and their effects on different plant species vary. Therefore, local studies are indispensable in answering questions about the effects of deer on a particular forest type (Strole and Anderson 1992). Moreover, the consequences of disturbance regimes and herbivory on old-growth bottomland hardwood forests are not well known because there have been few studies on the remaining old-growth wetland forests. The purpose of this study is to determine the effects of white-tailed deer and swamp rabbits on plant species diversity. Specific objectives include testing the hypotheses that species composition of tree regeneration is independent of white-tailed deer or combined white-tailed deer and swamp rabbit use of gap openings; and that plant species richness, abundance, and diversity within gaps are independent of white-tailed deer or white-tailed deer and swamp rabbit use.

The study area (Moro Bottoms) is a 40-ha old-growth bottomland hardwood forest located in Cleveland County, AR. It is part of a larger area owned by the Arkansas Natural Heritage Commission and the Arkansas Nature Conservancy. Dominant tree species at Moro Bottoms are oaks (*Quercus falcata* var. *pagodifolia* Ell., *Q. nigra* L., *Q. lyrata* Walt., *Q. alba* L., *Q. phellos* L., *Q. michauxii* Nutt., *Q. velutina* Lam.), sweetgum (*Liquidambar styraciflua* L.), and baldcypress [*Taxodium distichum* (L.) Rich.], with several hickory species [*Carya tomentosa* (Poir.) Nutt., *C. ovata* (Mill.) K. Koch and *C. cordiformis* (Wangenh.) K. Koch]. The small tree and shrub layer includes ironwood (*Carpinus caroliniana* Walt.), Carolina ash (*Fraxinus caroliniana* Mill.),

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and hollies (*Ilex opaca* Ait., *I. decidua* Walt.).[2] Moro Bottoms is an excellent example of a late transition bottomland hardwood forest becoming old growth through gap regeneration. Trees, especially sweetgum and cherrybark oak, are quite large (up to 149 cm)[3] with exceptionally good form. Moro Bottoms provided an ideal opportunity to study the effects of large mammalian herbivores on biodiversity in wetland forest gaps. A severe windstorm during the late summer of 1989 caused windthrows, which created gaps in the overstory ranging from 0.1 to 0.5 ha. A cursory survey before the study suggested moderate use of the area by deer in late fall and greater use by swamp rabbits.[4] Johnson and others (1995) noted that older forests generally provide the best foraging conditions for deer in fall and winter.

MATERIALS AND METHODS

Thirty paired plots consisting of herbivore exclosures and adjacent unmanipulated controls were installed within windthrow gaps. Each of the paired plots was randomly placed on one side of a north-south line located approximately through the center of each windthrow gap. Exclosures were approximately 2.5 by 4 m and were constructed of 5- by 10- cm welded wire fencing and 2.4-m metal posts. The fence was elevated 15 cm from the ground to allow entry of swamp rabbits. Within each exclosure ten 0.5- by 1.0-m quadrats were randomly located. These were fenced with 2.5- by 5-cm welded wire 0.6 m high to additionally exclude swamp rabbits. The remaining ten 0.5- by 1.0-m plots were available to swamp rabbits, but were protected from deer use. Adjacent to each exclosure was a control plot with three fence posts along one side. The control plot was divided into 10 contiguous 0.5- by 1-m quadrats. The exclosures were constructed in 1990 during winter prior to the growing season. While it would have been ideal to set up a separate set of fencing to exclude only swamp rabbits, and not to nest the rabbit exclosures inside the deer exclosures, operationally it would have been extremely difficult to accomplish. The logistics were such that the only practical course was to nest the treatments.

Data were collected during spring, summer, and fall of 1990, 1991, and 1992. Percent cover for herbaceous species (0 to 5, 6 to 15, 16 to 25, 26 to 35 . . . 95 to 100) and total percent cover were recorded in deer exclosures, deer-and-rabbit exclosures, and control plots. During 1990 and 1991 total cover of grasses and sedges were recorded in place of each separate species, except for cane [*Arundinaria gigantea* (Walter) Muhl.], because of the difficulty of identifying these species when they were not fruiting or flowering; *Smilax* and *Vitis* totals also were recorded. During 1992 all herbaceous species were recorded separately. Duplicates of plant species in the plots were collected from areas nearby and identified; species not present in the exclosures were also collected.

During each visit the number and species of shrub and tree seedlings in each plot were recorded. All oak seedlings were recorded as *Quercus* spp. during 1990 and 1991, but the oaks were recorded by species during 1992. Oak seedling leaves can be quite variable so a few hard-to-determine seedlings were counted as red oak group. We were not able to distinguish separate hickory or blueberry (*Vaccinium* spp.) seedlings because of the difficulty of classifying seedlings and small nonfruiting specimens of these species, so these were recorded as *Carya* or *Vaccinium* spp. Plants were collected and identified, using Radford and others (1968), Little (1978), Steyermark (1963), Allen (1980), and Chabreck and Condrey (1979). "An Atlas and Annotated List of the Vascular Plants of Arkansas" (Smith 1988) was consulted to verify that the species identified occurred in Arkansas.

During the summer of 1991, exclosure and control plots 16 and 20 were destroyed by tree falls; exclosures 31 and 32 with controls were subsequently constructed to replace them. During the summer of 1992, falling trees destroyed plots 9 and 30.

We assumed a priori there would be seasonal differences and reasonably expected to have yearly differences, so we dispensed testing for these effects. The most expedient analyses for comparing treatments at each measuring period were, therefore, simple paired t-tests. Hence, paired t-tests were used to analyze the percent-cover data with the following comparisons: deer exclusion versus control and deer and rabbit exclusion versus control. Due to the nested nature of rabbit exclosures with deer exclosures, no statistically independent test could be constructed for comparing the effects of rabbit exclosures versus deer exclosures. Nonparametric analysis of variance (Kruskal-Wallis test) was employed to evaluate the seedling data. A probability of < 0.05 was accepted as statistical justification for rejecting a null hypothesis.

RESULTS

One hundred and fifty-six vascular plant species were present in the plots. Thirty-eight of these were tree or shrub species. Twelve grass (*Graminae* spp.) species, 10 sedge (*Cyperaceae* spp.) species, and 73 other herbaceous species were recorded in the plots. Also, there were 13 woody vines (*Vitaceae* spp.), 8 nonwoody vines, and 2 ferns.

The number of plant species encountered varied considerably among treatments. There was no clear pattern of treatment effects across sampling periods on plant diversity as reflected by species richness (mean number of species per unit area), cumulative species (total number of species across all plots in a treatment category), or number of unique species (species that occurred in only one treatment category) (fig. 1A–C).

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[2] Peacock, Lance. 1983. Moro Bottoms site (preserve) summary. Little Rock, AR: Arkansas Nature Conservancy. 7 p. Unpublished report. On file with: The Nature Conservancy, Arkansas Field Office, 601 N. University Avenue, Little Rock, AR 72205.

[3] Devall, Margaret S. 1998. Dendroecological study of Moro Bottoms Natural Area. 10 p. Unpublished data. On file with: U.S. Department of Agriculture, Forest Service, Southern Research Station, Center for Bottomland Hardwoods Research, P.O. Box 227, Stoneville, MS 38776.

[4] Smith, Winston P.; Toliver, John R.; Devall, Margaret S.; Parresol, Bernard R. 1990. Windthrow gaps in an old-growth bottomland hardwood forest: wildlife use and consequent influence on forest composition. 16 p. Study plan. On file with: U.S. Department of Agriculture, Forest Service, Southern Research Station, Center for Bottomland Hardwoods Research, P.O. Box 227, Stoneville, MS 38776.

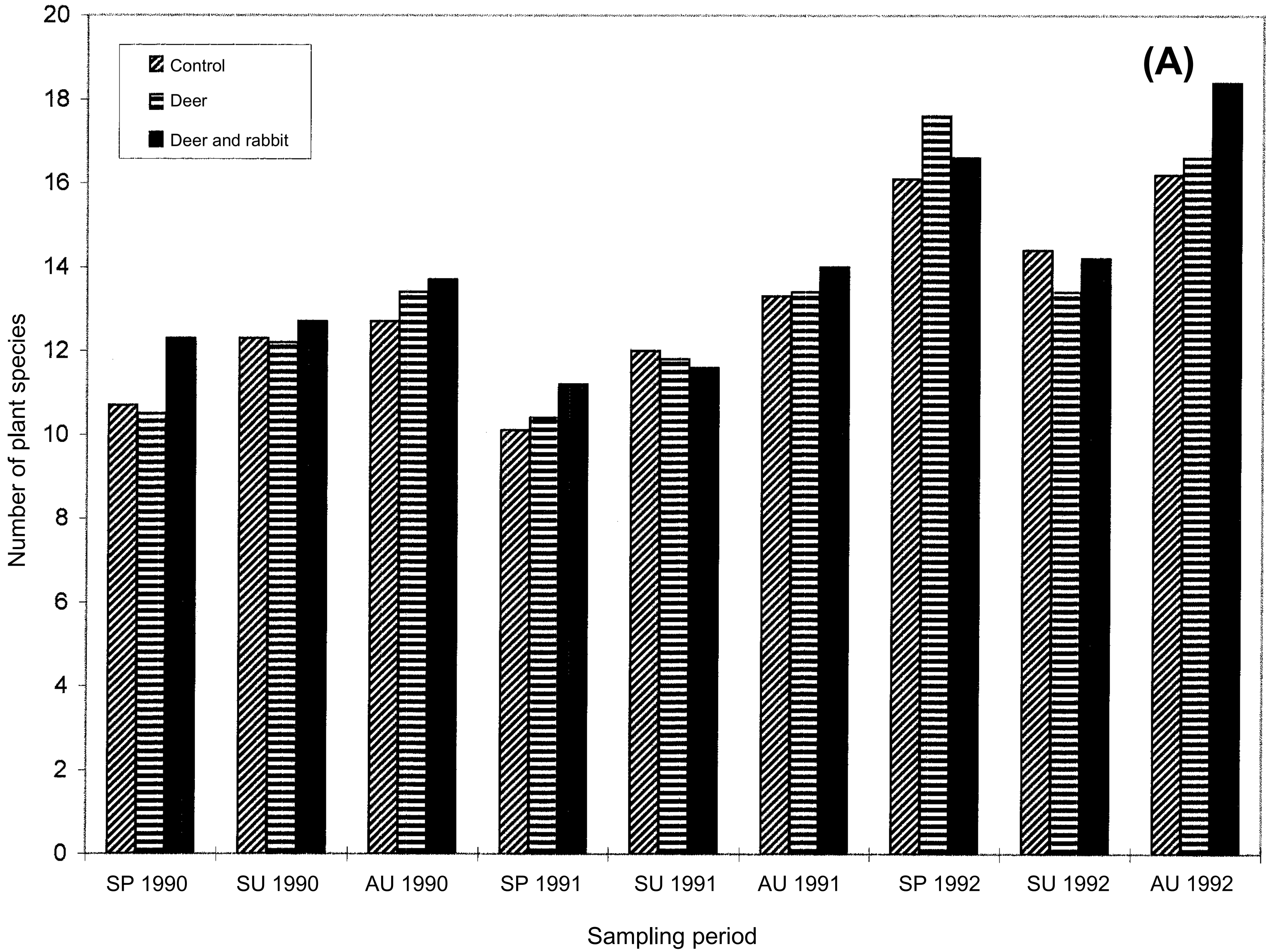

Figure 1A—Mean number of species per plot recorded seasonally in 5-m^2 plots (species richnness). Moro Bottoms Natural Area (SP = spring, SU = summer, AU = autumn).

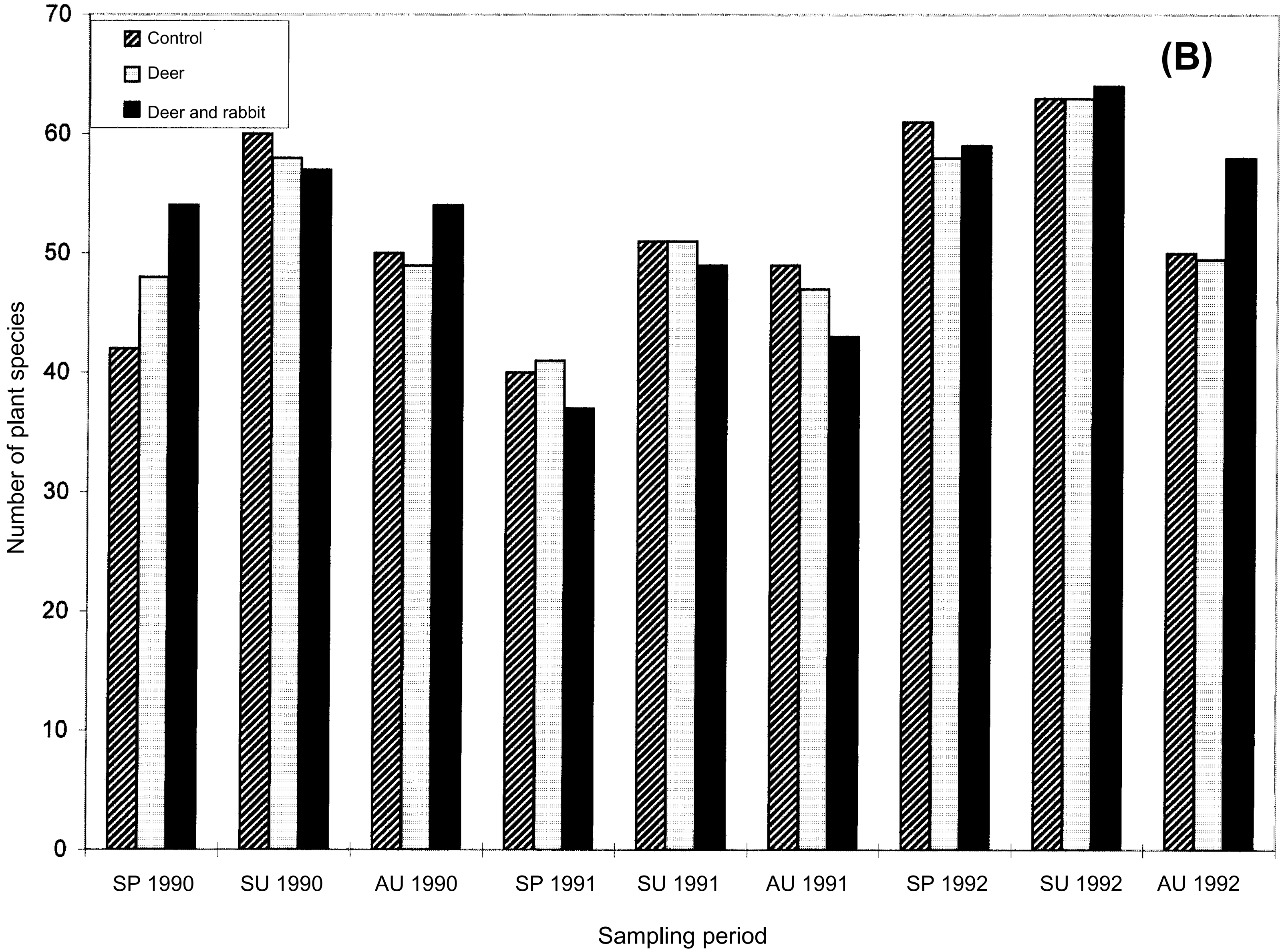

Figure 1B—Number of species across all plots within a treatment category for each period (cumulative species). Moro Bottoms Natural Area (SP = spring, SU = summer, AU = autumn).

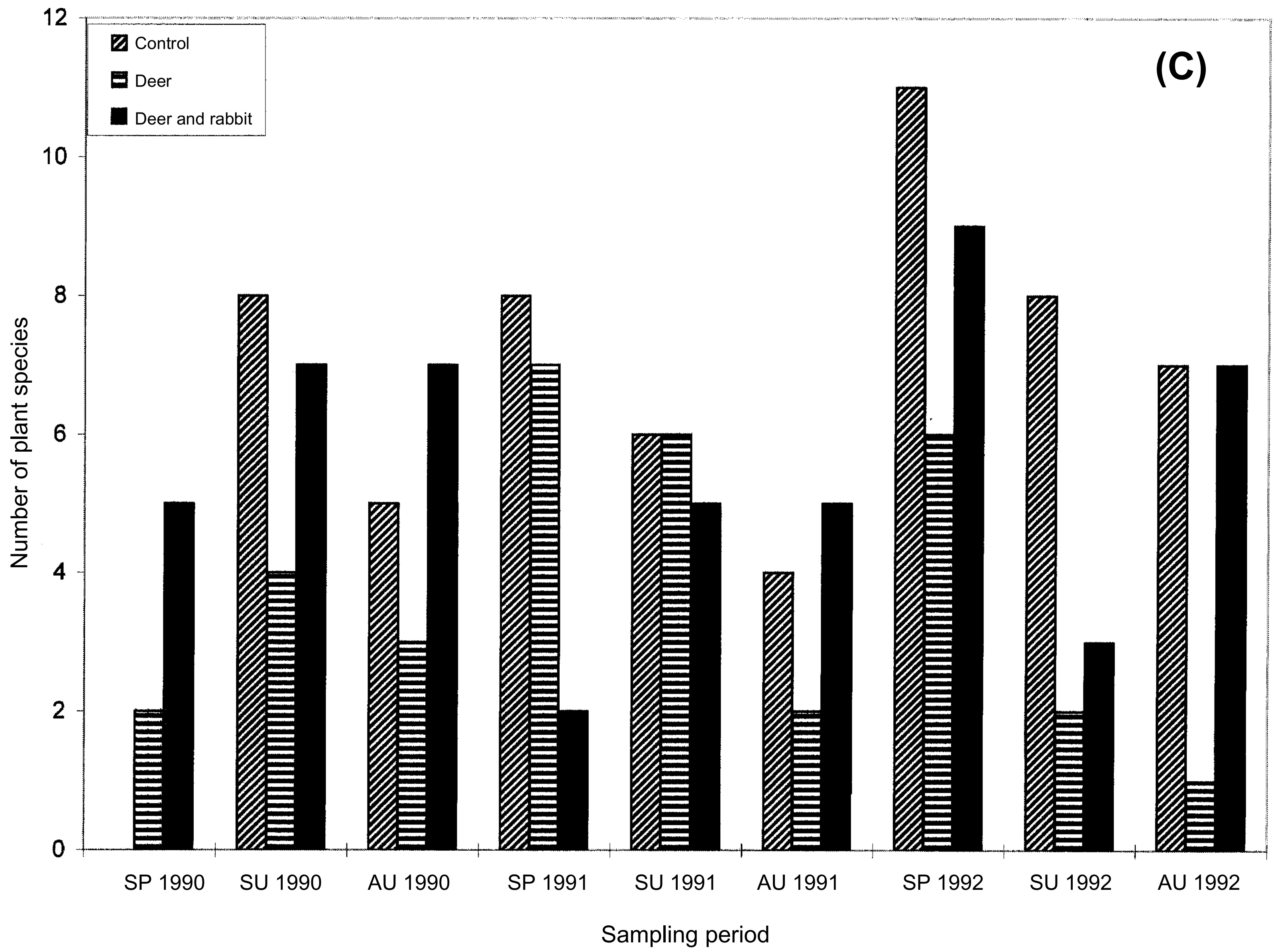

Figure 1C—Number of species found only in one treatment category for each period (unique species). Moro Bottoms Natural Area (SP = spring, SU = summer, AU = autumn).

Eighty plant species were present in the deer and in the deer-and-swamp-rabbit exclosures in 1992, and 82 in the controls. The number of species occurring in a plot ranged from 9 to 25 in the deer exclosures, 9 to 31 in the deer-and-swamp-rabbit exclosures, and 9 to 23 in the controls.

Percent cover of herbaceous vegetation recorded among treatment and control plots during 1990–92 is summarized in figure 2. Percent cover in the controls ranged from 15 to 100 with standard deviations ranging from 16 to 25; in the deer exclusion plots, cover ranged from 5 to 100 with standard deviations of 16 to 26; cover in the deer-and-rabbit plots varied from 5 to 100 with standard deviations of 18 to 28. Percent cover of vegetation in the deer and in the deer-and-rabbit exclosures was significantly less than that in the control plots in the spring of 1990 (table 1). The control versus deer comparison also was significant in the summer of 1990. Significant differences did not occur again until the summer of 1992, and in the fall of 1992 control versus deer exclusion and control versus deer-and-rabbit exclusion were both highly significant.

Means of percent cover of grasses, sedges, and other herbaceous vegetation are presented in figure 3 A–C. In general, percent cover of grasses and sedges was higher in control plots than in deer or in deer-and-rabbit plots, while coverage of other herbaceous species was higher in deer and in deer-and-rabbit plots. Paired comparisons (t statistic) of percent cover of grasses, sedges, and other herbaceous vegetation between control and treatment plots demonstrated that the observed pattern often reflected significant variation among treatments (table 2).

Table 1—Paired comparisons of percent cover of herbaceous vegetation in the Moro Bottoms exclosures

Date	Variable	Mean	Standard error	T	Prob > |T|
Spring 1990	C vs. D	.08	.03	2.64	.01[a]
	C vs. DR	.11	.03	3.17	0[a]
Summer 1990	C vs. D	.08	.03	2.53	.02[b]
	C vs. DR	.04	.03	1.61	.12
Fall 1990	C vs. D	.05	.03	1.61	.12
	C vs. DR	.02	.02	1.02	.32
Spring 1991	C vs. D	.01	.03	.29	.78
	C vs. DR	-0	.02	-.15	.88
Summer 1991	C vs. D	-0	.02	-.15	.88
	C vs. DR	.01	.03	.38	.70
Fall 1991	C vs. D	.04	.02	1.83	.08
	C vs. DR	.02	.02	.82	.42
Spring 1992	C vs. D	.04	.02	1.69	.10
	C vs. DR	.04	.02	1.73	.09
Summer 1992	C vs. D	.06	.02	3.04	.01[a]
	C vs. DR	.08	.02	3.47	0[a]
Fall 1992	C vs. D	.11	.22	4.67	0[a]
	C vs. DR	.08	.02	3.47	0[a]

Vs. = versus; mean and standard error = standard error of differences in percent cover; T = student's t statistic; Prob >|T| = associated probability from paired t-test; C vs. D = control versus deer; C vs. DR = control versus deer-and-swamp rabbit.

[a] P = 0.01.

[b] P = 0.05

The sum of woody seedlings of all species ranged from a low of 138 in the deer exclosures in spring 1991 to a high of 761 in the deer-and-swamp-rabbit exclosures in 1992 (table 3). The total numbers of woody seedlings were similar ($P > 0.05$) among treatments during the 3 years of the study (table 4). Although not significant, 1992 results showed smaller probability values than the 1990 and 1991 data.

Significant differences among deer and deer-and-swamp-rabbit exclosures and controls were not demonstrated during spring, summer, or fall of any year for selected species that were thought to be favorite deer foods: sweetgum, greenbriars, red maple (*Acer rubrum* L.), and oak species, and for ironwood, which is eaten by deer, but is low choice (Halls 1977).

Diversity of the stands was investigated using the Shannon diversity index. Values of the Shannon index ranged from a low of 3.15 to a high of 3.70 (fig. 4).

DISCUSSION

We studied the vegetation occurring in forest gaps, but did not collect quantitative data beyond the gaps. Nevertheless, some comparisons to other older bottomland hardwood forests can be made. Moro Bottoms is in the west gulf Coastal Plain. Other sites located in the Mississippi River alluvial floodplain have different soils, stand origin, and possible disturbance history. Robertson and others (1978) studied woody species in two stands on Horseshoe Lake Island in Alexander County, IL, one relatively undisturbed and one recovering from disturbance in the late 1800's or early l900's. Trees with the highest importance value in the 35-ha old-growth stand were sweetgum, red maple, and green ash (*F. pennsylvanica* Marsh.). Sugar maple (*A. saccharum* Marsh.), sweetgum, tupelo gum (*Nyssa aquatica* L.), bitternut hickory, American elm (*Ulmus americana* L.), northern red oak (*Q. rubra* L.), and sassafras [*Sassafras albidum* (Nutt.) Nees] were dominants in the secondary stand. In the old-growth shrub-sapling stratum, 22 woody species were encountered, with pawpaw [*Asimina triloba* (L.) Dunal], red buckeye (*Aesculus pavia* L.), buttonbush (*Cephalanthus occidentalis* L.), grapes (*Vitis* spp.), and silver maple (*A. saccharinum* L.) the dominant species. There were 20 species in the secondary forest. In the seedling stratum, 46 and 45 species of trees, shrubs, and vines occurred in the old growth and secondary areas, respectively, compared to 51 at Moro Bottoms. Pawpaw, red buckeye, green ash, tupelo gum, and bitternut hickory dominated seedlings in the secondary forest. The forests seem similar to that at Moro Bottoms, except that the secondary forest at Horseshoe Lake Island contained more fast-growing, short-lived species.

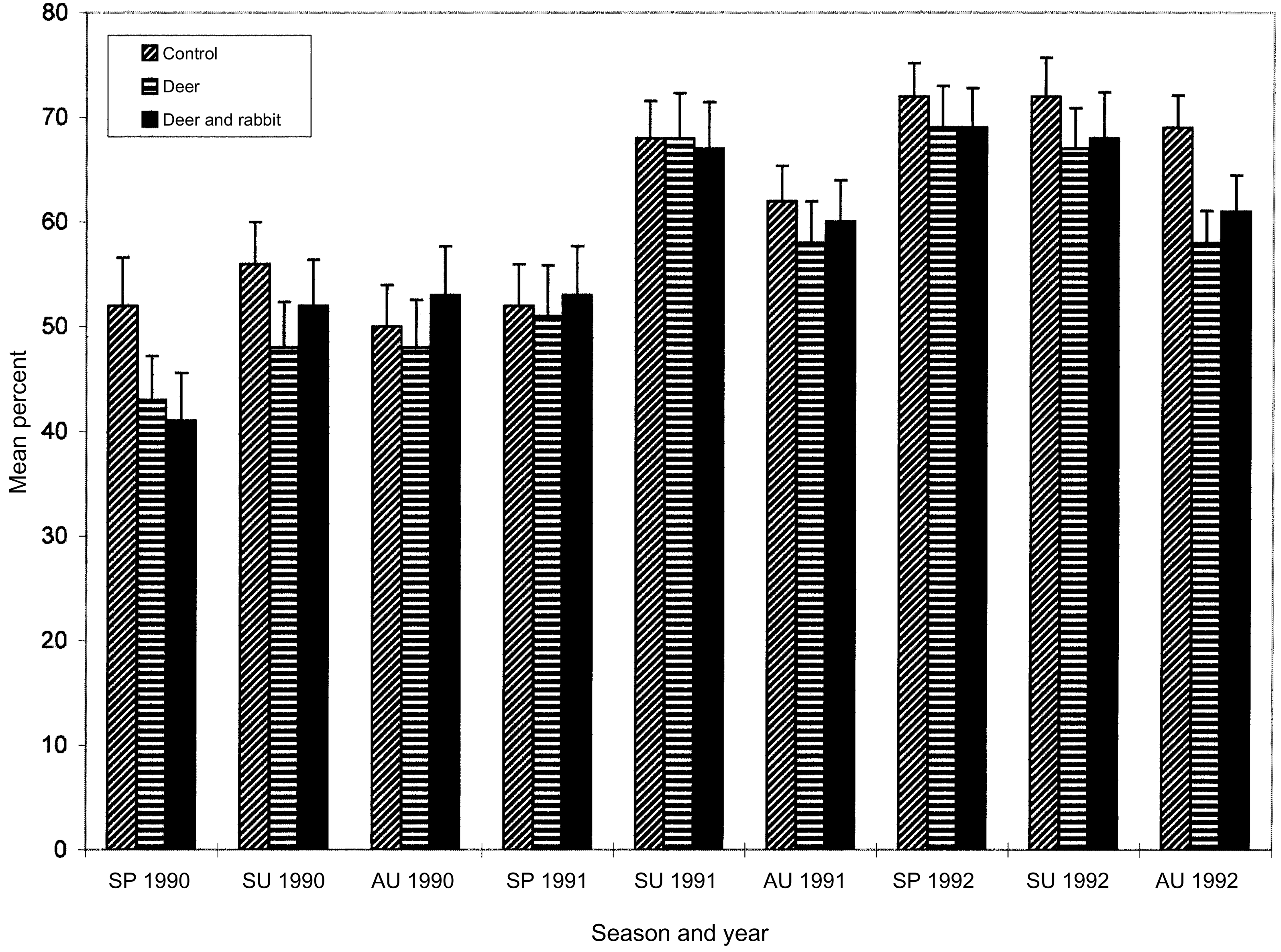

Figure 2—Mean of percent ground cover of herbaceous vegetation within control, deer exclusion, and deer-and-rabbit exclusion plots, Moro Bottoms Natural Area. (SP = spring, SU = summer, AU = autumn).

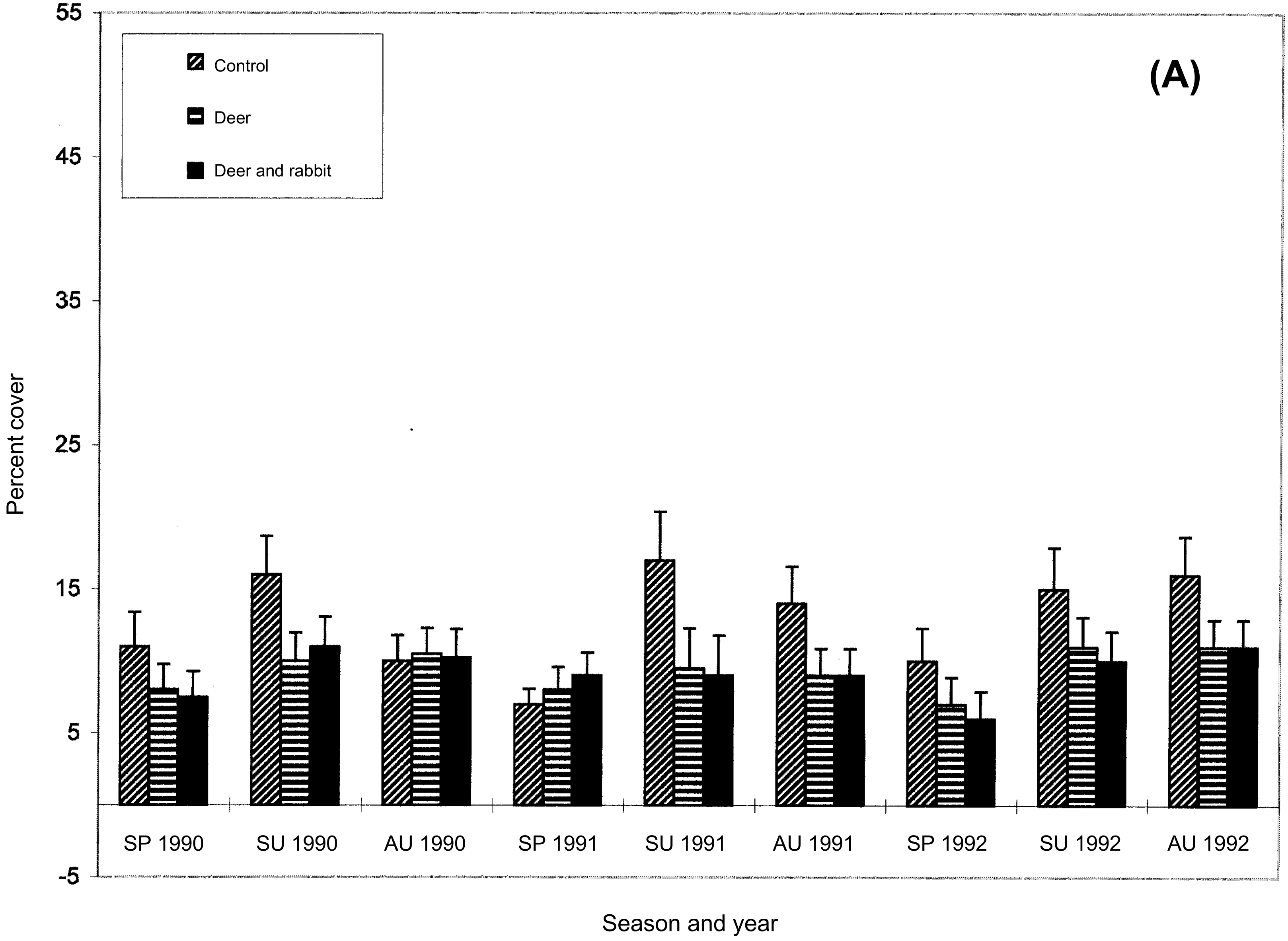

Figure 3A—Mean of percent ground cover of grasses and sedges at Moro Bottoms Natural area. (SP = spring, SU = summer, AU = autumn).

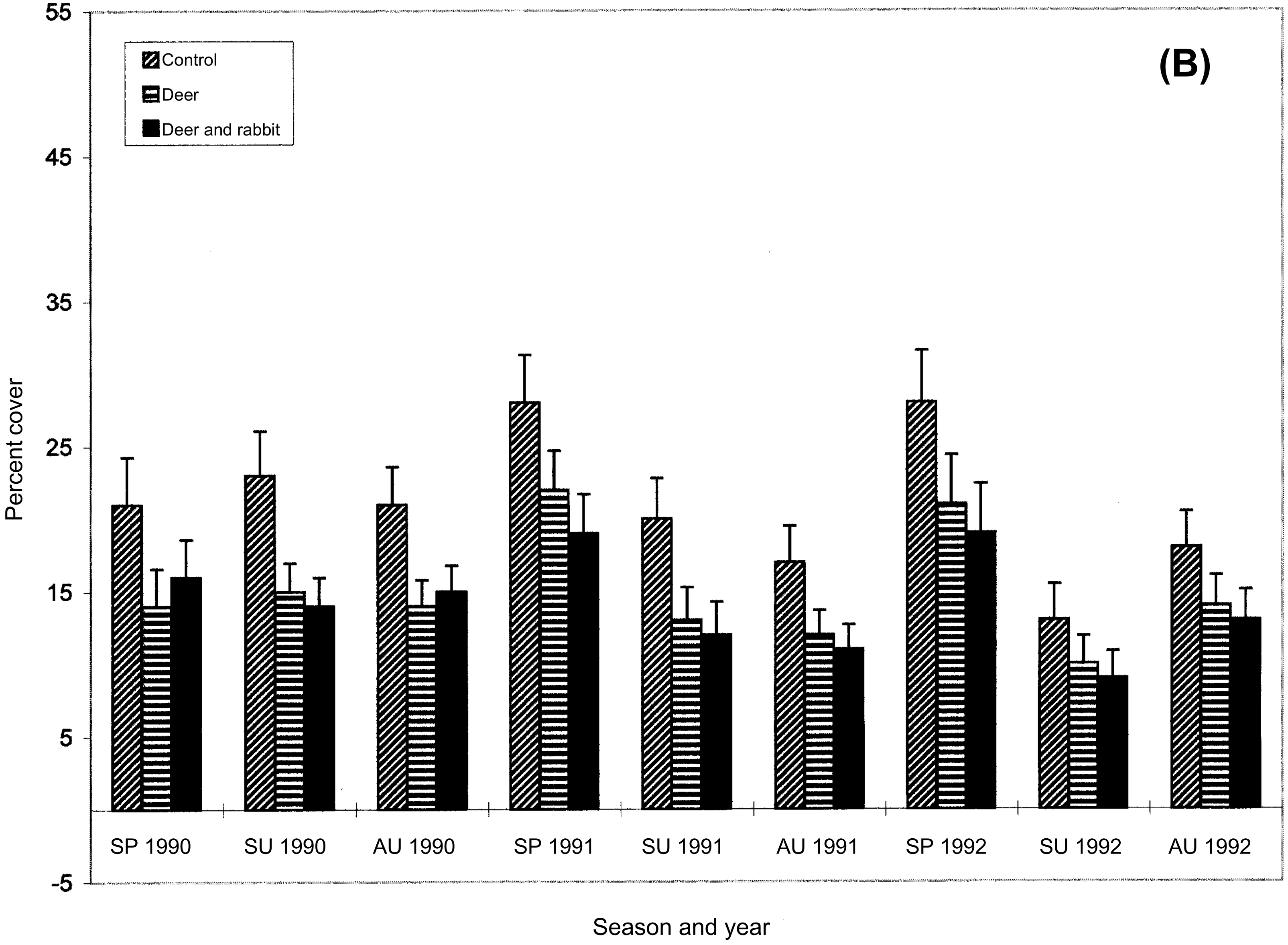

Figure 3B—Mean of percent ground cover of grasses and other herbaceous vegetation at Moro Bottoms Natural Area. (SP = spring, SU = summer, AU = autumn).

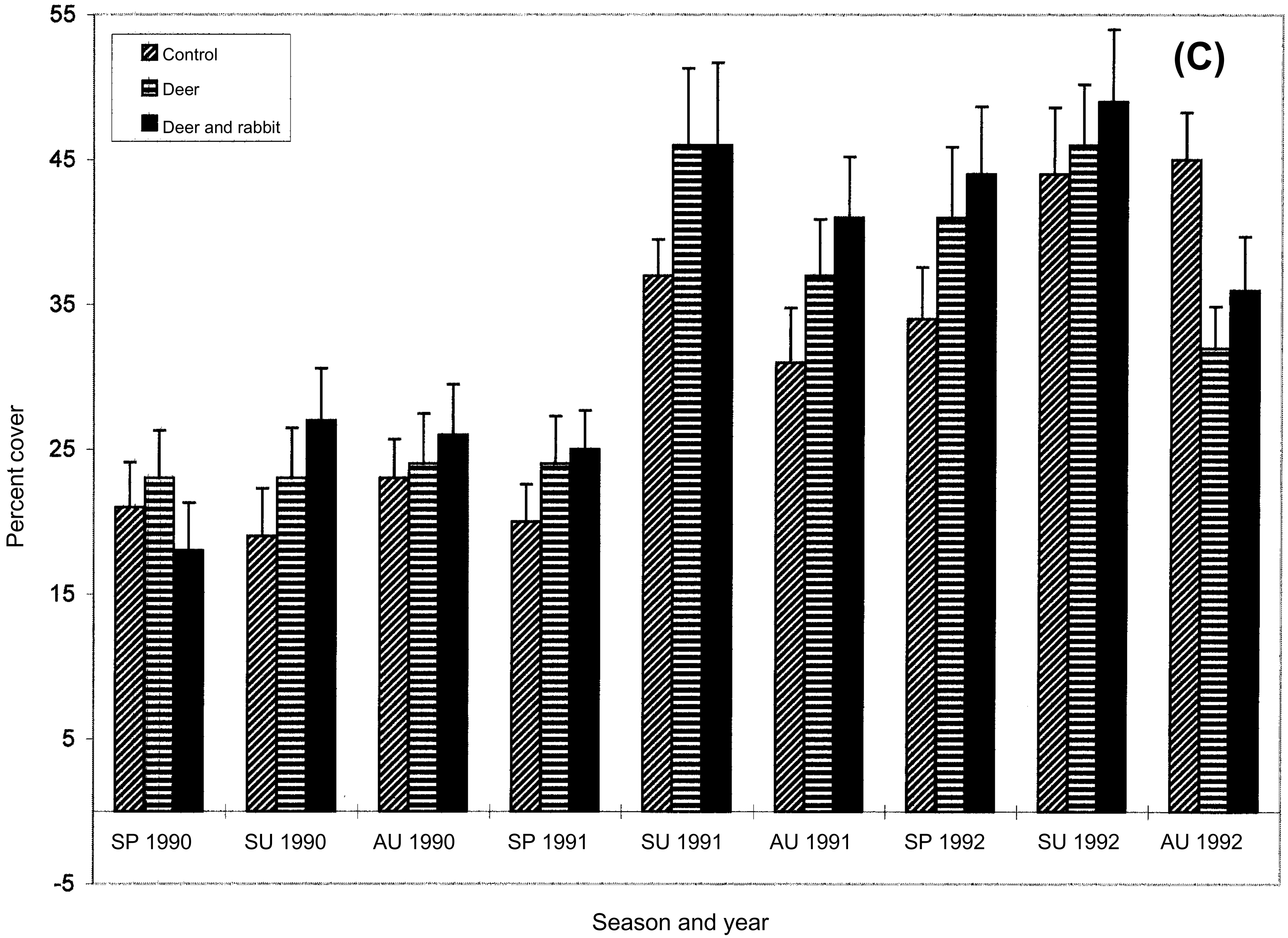

Figure 3C—Mean of percent ground cover of grasses within control, deer exclusion, and deer-and-rabbit exclusion plots at Moro Bottoms Natural Area. (SP = spring, SU = summer, AU = autumn).

Table 2—Mean and standard error of differences in percent cover of grasses, sedges, and other herbaceous vegetation between control and deer exclusion and between control and deer-and-rabbit exclusion, Moro Bottoms Natural Area

Date	Plant group	Sample size	Variable	Mean	Standard error	T	Prob > |t|
Spring 1990	Grasses	30	C vs. D	2.33	2.44	.96	.35
			C vs. DR	2.83	2.42	1.17	.25
	Sedges	30	C vs. D	7.17	2.68	2.68	.01[a]
		30	C vs. DR	4.67	1.74	2.68	.01[a]
	Other	30	C vs. D	-1.38	3.15	-.44	.66
		30	C vs. DR	1.55	3.20	.49	.63
Summer 1990	Grasses	30	C vs. D	4.83	2.80	1.72	.09
		30	C vs. DR	4.16	2.65	1.57	.13
	Sedges	30	C vs. D	7.33	2.09	3.52	0[a]
		30	C vs. DR	8.33	1.92	4.33	0[a]
	Other	30	C vs. D	-3.50	2.67	-1.31	.20
		30	C vs. DR	-7.50	3.28	-2.29	.03[b]
Fall 1990	Grasses	30	C vs. D	-.83	1.78	-.47	.64
		30	C vs. DR	-.66	1.85	-.36	.72
	Sedges	30	C vs. D	7.33	2.21	3.32	0[a]
		30	C vs. DR	6.17	1.31	4.72	0[a]
	Other	30	C vs. D	-2.17	2.42	-.90	.38
		30	C vs. DR	-4.31	2.48	-1.74	.09
Spring 1991	Grasses	30	C vs. D	-1.50	1.68	-.89	.38
		30	C vs. DR	-2.50	1.90	-1.32	.20
	Sedges	30	C vs. D	6.67	3.16	2.11	.04[b]
		30	C vs. DR	9.00	2.63	3.42	0[a]
	Other	30	C vs. D	-4.50	2.94	-1.53	.14
		30	C vs. DR	-6.67	2.63	-2.94	.01[a]
Summer 1991	Grasses	28	C vs. D	7.68	3.38	2.27	.03[b]
		28	C vs. DR	7.86	3.21	2.45	.02[b]
	Sedges	28	C vs. D	7.14	2.46	2.90	.01[a]
		28	C vs. DR	8.21	2.52	3.26	0[a]
	Other	28	C vs. D	-15.18	4.55	-3.34	0[a]
		28	C vs. DR	-15.18	4.38	-3.47	0[a]
Fall 1991	Grasses	28	C vs. D	5.00	2.04	2.45	.02[b]
		28	C vs. DR	5.18	2.42	2.14	.04[b]
	Sedges	28	C vs. D	5.18	2.25	2.30	.03[b]
		28	C vs. DR	6.07	2.48	2.44	.02[b]
	Other	28	C vs. D	-6.25	2.72	-2.30	.03[b]
		28	C vs. DR	-9.46	3.68	-2.57	.02[b]
Spring 1992	Grasses	29	C vs. D	3.28	1.89	1.73	.09
		29	C vs. DR	4.31	1.93	2.23	.03[b]
	Sedges	29	C vs. D	7.59	3.40	2.23	.03[b]
		29	C vs. DR	11.38	3.24	3.51	0[a]
	Other	29	C vs. D	-7.07	3.36	-2.10	.04[b]
		29	C vs. DR	-11.90	3.80	-3.13	0[a]
Summer 1992	Grasses	27	C vs. D	4.44	1.65	2.69	.01[a]
		27	C vs. DR	5.37	2.05	2.62	.01[a]
	Sedges	27	C vs. D	3.52	1.92	1.83	.08
		27	C vs. DR	4.44	2.02	2.20	.04[b]
	Other	27	C vs. D	-2.04	2.79	-.73	.47
		27	C vs. DR	-5.74	3.23	-1.78	.09
Fall 1992	Grasses	28	C vs. D	5.18	1.95	2.66	.01[a]
		28	C vs. DR	5.18	2.28	2.27	.03[b]
	Sedges	28	C vs. D	2.68	1.77	1.51	.14
		28	C vs. DR	3.39	1.76	1.92	.07
	Other	28	C vs. D	2.86	2.32	1.23	.23
		28	C vs. DR	-.71	2.89	-.25	.80

SE = standard error; T = student's t statistic; Prob > |t| = associated probability from paired t-test of means; C vs. D = control versus deer exclusion; C vs. DR = control versus deer-and-rabbit exclusion.

[a] P=0.01.

[b] P=0.05.

Table 3—Density values of woody seedlings occurring in the plots at Moro Bottoms

Species	Plot type	1990 SP	1990 SU	1990 F	1991 SP	1991 SU	1991 F	1992 SP	1992 SU	1992 F
		Number of seedlings								
All species	D	281	485	356	138	287	307	548	500	540
	DR	358	392	431	197	369	370	720	683	761
	C	309	526	473	159	400	360	493	609	697
Oaks[a]	D	178	240	232	48	160	173	336	295	333
	DR	220	288	253	73	202	225	417	402	443
	C	197	318	312	27	222	211	320	393	484
Red maple	D	26	19	3	5	5	2	25	12	14
	DR	14	27	10	5	1	4	92	35	35
	C	7	11	10	2	3	2	24	25	18
Sweetgum	D	11	18	11	12	12	12	10	18	15
	DR	13	21	23	10	19	18	18	25	24
	C	12	20	15	11	18	14	15	19	16
Ironwood	D	36	56	52	16	31	32	82	76	90
	DR	60	67	69	59	42	25	106	101	134
	C	40	78	68	59	55	29	63	86	78

SP = spring; SU = summer; F = fall; D = deer exclusion plots, DR = deer-and-swamp rabbit plots; C = control.

[a] Oaks = water oak, overcup oak, white oak, willow oak, black oak, cherrybark oak.

Table 4—Kruskal-Wallis test of number of woody seedlings present in the Moro Bottoms deer, deer-and-swamp rabbit, and control exclosures

Date	Chi-square	Degrees of freedom	Prob. > chi-square
Spring 1990	2.85	2	0.24
Summer 1990	1.34	2	.51
Fall 1990	1.38	2	.50
Spring 1991	1.20	2	.55
Summer 1991	.83	2	.66
Fall 1991	.92	2	.63
Spring 1992	4.36	2	.11
Summer 1992	1.56	2	.46
Fall 1992	4.92	2	.09

Devall (1982) studied the Beauvais tract (42 ha) at Cat Island, a bottomland swamp in West Feliciana Parish, LA, where timber has been selectively cut, but old trees are also present (oldest 450 years), and there is some gap regeneration. Twenty-two tree species occurred in this forest. Sugarberry (*Celtis laevigata* Willd.) had the highest importance value, followed by cypress and green ash. Many of the trees and woody vines occurring at Moro Bottoms were also present at Cat Island. The midstories were dissimilar, with sugarberry, green ash, and American elm common at Cat Island. Fifty-one species (herbs and woody seedlings) occurred in 1-m quadrats (not located in gaps), 18 of which were present at Moro Bottoms, and 75 species were collected outside of quadrats, 13 of these at Moro Bottoms. Grass and sedge species were much more important at Moro Bottoms, and herbaceous diversity was greater.

There are few exotic species present in Moro Bottoms. In addition to Mariana maiden fern [*Thelypteris torresiana (Gaud.*) Alston] reported by Orzell and Bridges,[5] Japanese

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[5] Orzell, Steve; Bridges, Edwin. 1990. Moro Creek Bottoms, Arkansas. 4 p. Unpublished report. On file with: Arkansas Natural Heritage Commission, 1500 Tower Building, 323 Center Street, Little Rock, AR 72201.

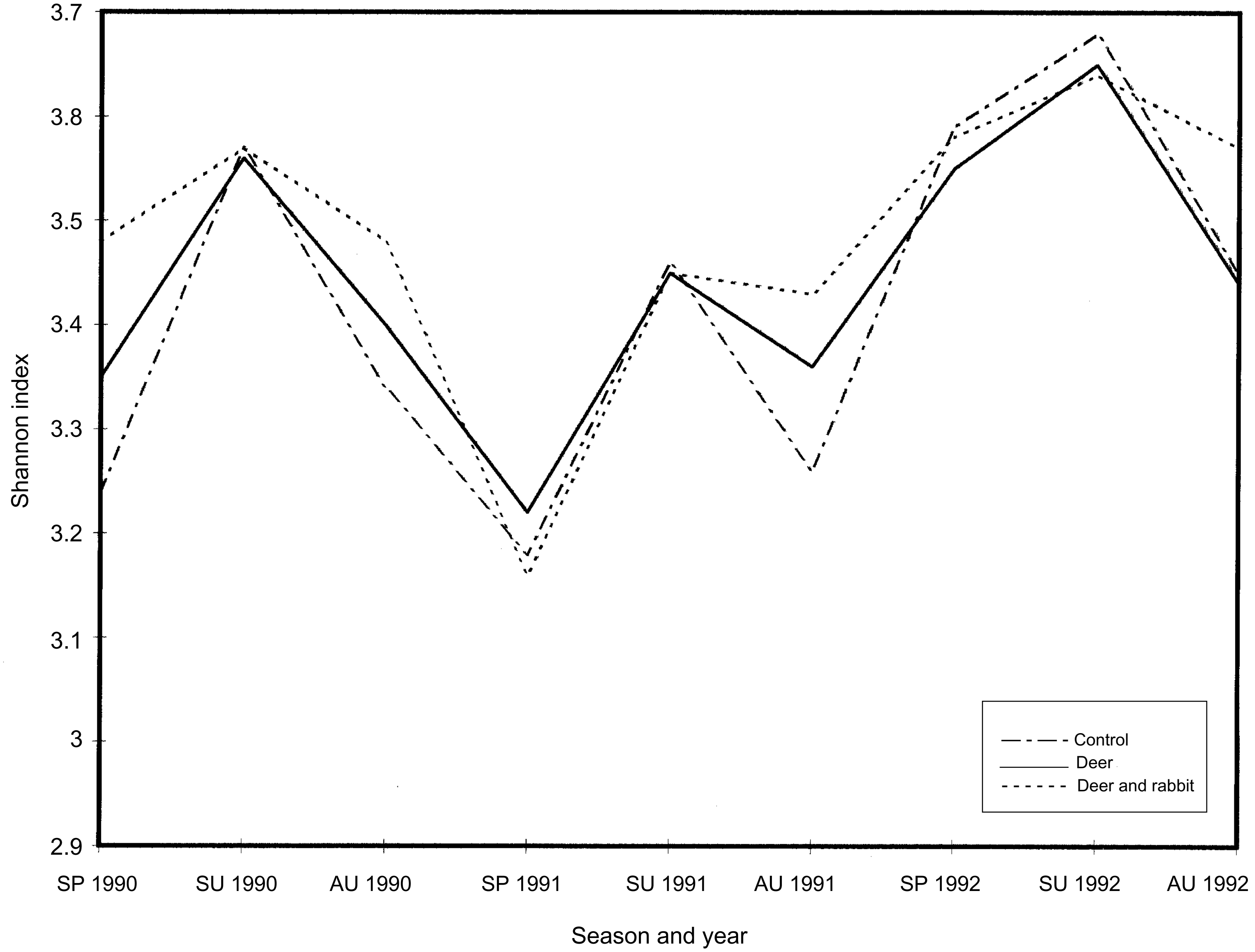

Figure 4—Values of the Shannon diversity index for herbaceous vegetation within control, deer exclusion, and deer-and-rabbit exclusion plots at Moro Bottoms Natural Area. (SP = spring, SU = summer, AU = autumn).

honeysuckle (*Lonicera japonica* Thunb.) was noted in and near plot 21. Although Orzell and Bridges (see footnote 5) mentioned damage by feral pigs, we did not note evidence of feral pigs during the study.

It was somewhat surprising that species richness, total cumulative species, and number of unique species were apparently not affected by herbivory of white-tailed deer or swamp rabbits (fig. 1A–C). Deer density varied considerably in different seasons, from < 1 deer per square kilometer in spring to 21.8 deer per square kilometer in autumn.[6] Alverson and others (1988) reported that herbivory prevented regeneration of common woody species such as Canada yew (*Taxus Canadensis* Marsh.), eastern hemlock [*Tsuga Canadensis* (L.) Carr.], and white cedar (*Thuja occidentalis* L.) even at deer densities as low as four deer per square kilometer, reduced reproductive success, or caused local extirpation of several herbaceous species indigenous to northern hemlock-hardwood forests. Tilghman (1989) reported analogous results for comparable deer densities in Pennsylvania. In other cases, comparable deer populations have caused severe damage to the understory (Hough 1965). Similar to our results, Balgooyen and Waller (1995) found that percent cover of several herbaceous species declined significantly in areas with higher historic and recent deer densities. In spite of these effects, deer densities did not seem to be directly related to the overall number of herbaceous species, the Shannon-Weaver index of diversity, or vegetative cover.

Perhaps the initial shock of exclusion accounted for the differences in percent cover of herbaceous vegetation in 1990, because all evidence of treatment effects disappeared by autumn 1990. It seems that the intensity of browsing pressure was not sufficient to cause apparent impacts until the end of the third year of exclusion of deer and rabbits. At that time we began to detect differences in the percent cover of total vegetation in the control versus deer exclosures, and by the fall of 1992 there were differences between the control versus deer and control versus deer and swamp rabbits, although not in the direction one might expect. The control plots had greater percent cover of vegetation than the exclosure plots. Perhaps deer and swamp rabbits kept the vegetation trimmed, so some species did not grow large and shade others, or grazing stimulated growth.

We observed that the percent cover of grasses and sedges was consistently greater and the percent cover of other herbaceous vegetation regularly less in control plots than in exclusion plots. Although there was some variation, sedges were clearly more abundant in control plots than in deer-exclusion plots, and the effect was even more pronounced in the deer-and-rabbit plots. Deer rarely eat sedges and grasses (Harlow and Hooper 1972, Murphy and Noble 1973, Newsom 1984); deer in bottomland forests prefer herbs such as *Aster* spp. (Murphy and Noble 1973). Little published information exists regarding the food preferences of swamp rabbits, but such features as digestability that are attractive to ungulates are also important to rabbits (Hjaltén 1991). Thus, the pattern of cover that we observed was probably a consequence of deer and/or rabbits avoiding grasses and sedges and selectively browsing other herbs.

Deer browsing has been shown to reduce plant biodiversity (Dzieciolowski 1980, Strole and Anderson 1992) and can bring about inconspicuous changes in species composition, even when deer are not very abundant (Anderson and Loucks 1979, Stewart and Burrows 1989, Strole and Anderson 1992). Treatment effects may occur slowly; recovery, if deer are excluded, can require several growing seasons (Ross and others 1970). Neither deer nor swamp rabbits appeared to be very numerous at Moro Bottoms, but by the third year of deer and swamp rabbit exclusion (summer 1992), the effects of herbivory became apparent. Many of the previous studies mentioned recount vegetation responses after five or more growing seasons; the effects of herbivory at Moro Bottoms may become more pronounced with time. The long-term consequences of herbivory on the biological diversity of this old-growth bottomland hardwood forest can only be determined through further study.

Few cypress, hickory, or holly seedlings occurred in the plots. Although acorns are a favorite deer food (Halls 1977), oak seedlings were not scarce (fig. 3). Ironwood and red maple seedlings were also numerous (fig. 3). It was apparent from the larger number of seedlings present in spring and fall that many seedlings did not survive the summer (evidently new seedlings germinated after rains). We did not monitor survival of particular seedlings, but few of the oaks, ironwood, red maple, cypress, and hickory appeared to be more than 1 year old until 1992, when more older oak seedlings were present, especially willow oak (*Q. phellos* L.) and water oak. Sweetgum seedlings were not as numerous as the oak species, but appeared to survive the summers better (dead willow oak and water oak seedlings were present in the fall, although new oak seedlings had germinated).

Balgooyen and Waller (1995) noted differences in the effects of deer grazing on herbaceous and woody plants. The gaps at Moro Bottoms were created by a windstorm in late summer of 1989, thus most of the vegetation we measured germinated no earlier than the spring of 1990, when the study began. Delayed oak germination can occur in the fall, as well. Perhaps herbaceous species are affected sooner by grazing than woody species, and the effects of herbivory by deer and rabbits on woody species will become apparent later.

The gaps are at different elevations, but all are covered with 1 m or more of water most years for varying periods during spring, and they may be flooded briefly after hard rains at other times of the year. While inundation no doubt had an effect on the vegetation at Moro Bottoms, periodic flooding occurred during the time that herbs and woody species growing at Moro Bottoms became adapted to conditions there, thus they should have adapted to withstand submersion (Noble and Murphy 1975).

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[6] Smith, Winston P.; Devall, Margaret S.; Parresol, Bernard R. 1995. Windthrow gaps, mammalian herbivores, and diversity of old-growth bottomland hardwood forests. 122 p. Completion report. On file with: U.S. Department of Agriculture, Forest Service, Southern Research Station, Center for Bottomland Hardwoods Research, P.O. Box 227, Stoneville, MS 38776.

Except as noted above, seedlings occurring in the exclosures reflected the composition of the overstory, suggesting that gap processes could have been operating when the existing canopy developed (Runkle 1991). This also suggests that without outside influence, the forest will remain stable in the near future and will not change in composition. Succession to a different forest type does not appear to be occurring. During the time the study was conducted, occasional trees fell, creating new gaps or increasing the size of existing ones; Runkle (1991) states that repeated death of canopy trees in eastern old-growth forests is common. In older forests, crown sizes are large enough to provide opportunities for seedling and sapling growth.

ACKNOWLEDGMENTS

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A COMPARISON OF BREEDING BIRD COMMUNITIES AND HABITAT FEATURES BETWEEN OLD-GROWTH AND SECOND-GROWTH BOTTOMLAND HARDWOOD FOREST

Winston P. Smith, Howard E. Hunt, and W. Kent Townley[1]

Abstract—To characterize bird species composition, relative abundance, and habitat affinities, spot-mapping and strip-count censuses were conducted in an old-growth stand and adjacent second-growth tracts in Moro Bottoms Natural Area, Arkansas, during 1991 and 1992. More species were recorded on the old-growth site (S = 35) as compared to the second-growth grid (S = 32). Similarly, the old-growth grid had a larger Shannon-Weaver diversity index than the second-growth site. Territories of several species coincided with specific habitat features: white-eyed vireo (*Vireo griseus*), Carolina wren (*Thryothorus ludovicianus*), Kentucky warbler (*Oporornis formusus*), and prothonotary warbler (*Protonotaria citrea*) were associated with treefall canopy gaps; Acadian flycatcher (*Empidonax virescens*) and prothonotary warbler were affiliated with standing water; and the American redstart (*Setophoga ruticilla*) showed a strong affinity for swamp chestnut oak (*Quercus michauxii*). Small forest openings ($\leq$ 0.26 ha) comprising $\leq$ 22 percent of the total area of old growth bottomland forest do not appear to adversely affect and may enhance breeding bird diversity.

INTRODUCTION

Southern bottomland hardwood forests are critical as breeding, wintering, and en-route habitat during migration, contributing significantly to continental avifaunal diversity of Eastern North America (Smith and others 1993a). Alarming is the rate of loss of this unique resource, especially during the recent half-century, with a conversion of 80 percent of the Mississippi River Valley (Creasman and others 1992, Turner and others 1981) and 52 percent of all southern bottomland forests (Smith and others 1993a) to agriculture or cleared for development (MacDonald and others 1978, Rudis and Birdsey 1986). Moreover, remaining forests occur as fragments (Rudis and Birdsey 1986) and have undergone a variety of timber harvests. Indeed, all but an estimated 0.01 percent of presettlement old-growth bottomland forests has experienced significant anthropogenic disturbance (Smith and others 1993a). Furthermore, future management imposed on remaining bottomland forests will necessarily intensify to meet increasing demands on hardwood products (Barton 1986, Murphy 1975), especially with the recent surge in markets for hardwood pulp.

Arkansas was no exception to the pattern that occurred across Eastern North America, especially in southern forests (Sharitz and others 1992). Before European arrival, Arkansas landscapes were largely vast acreages of continuous, upland and bottomland deciduous forests; early settlement and agriculture, and more recently silviculture, dramatically modified forest habitats (James and Neal 1986).

Conversion and alteration of remaining bottomland hardwood forests have been so extensive that its continued existence as a functioning ecological system is uncertain (Creasman and others 1992, Ernst and Brown 1989). Because songbirds (Passeriformes) and other forest landbirds occupy a broad spectrum of habitats encompassing the full vertical forest profile, i.e., forest floor to canopy, and use a diverse array of resources as food (e.g., plant material, soil and plant invertebrates) and as other necessary components of their life history, this vertebrate group represents an excellent barometer of forest ecosystem integrity and function.

Thus, a comparison of avifaunal species composition and abundance between undisturbed and second-growth forest should provide some insights regarding how well managed forests function as habitat for their indigenous biota; quantifying features associated with use of forest habitat by individual species would presumably identify essential stand-level components (or ecological correlates) necessary for successful reproduction. Moreover, the relationships between vegetative characteristics and avian distribution and abundance in southern bottomland hardwood forests are poorly documented. The purpose of this paper is to compare the bird community of a second-growth bottomland hardwood forest to a “paired” old-growth stand. Specific objectives were to: 1) determine whether breeding bird abundance and diversity were similar between old-growth and second-growth forests; 2) identify and quantify habitat features that were associated with distribution of bird species in old-growth and second-growth bottomland hardwood forests; and 3) determine whether these habitat attributes differed between old-growth and second-growth forests.

STUDY SITES

The study area was located approximately 8 km east of Fordyce, AR, along Moro Creek on the Moro Bottoms Natural Area (fig. 1). The Natural Area is a 70-ha tract of primarily old growth under the joint stewardship of the Arkansas Nature Conservancy and the Arkansas Natural Heritage Commission. The area is located in the upper West Gulf Coastal Plain (Hoiberg 1957 as cited in James and Neal 1986). The climate is hot and humid during the breeding season with a mean summer temperature of 27 °C. Mean annual rainfall is 123.4 cm, with much of the rain occurring in the spring.

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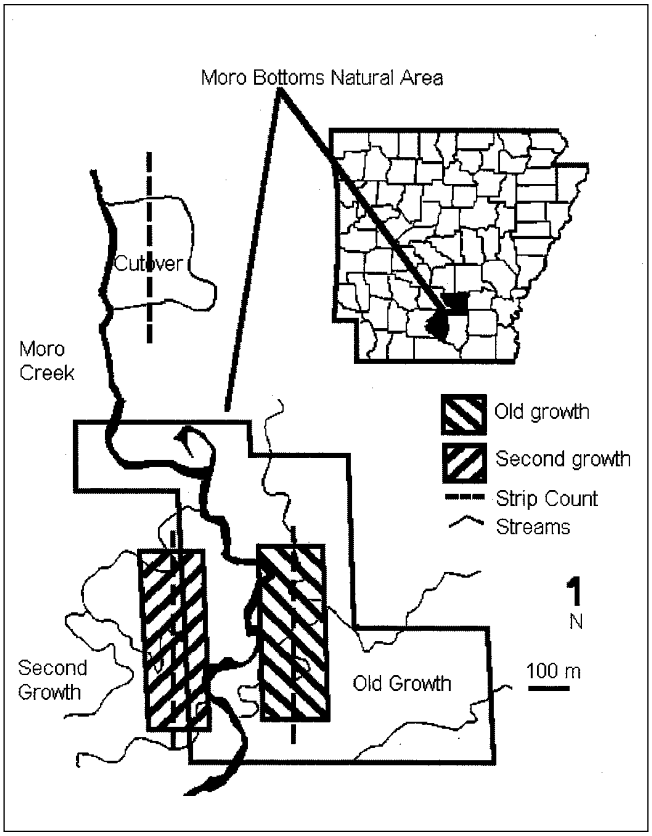

Figure 1—The study area, including Moro Bottoms Natural Area (large irregular shaped polygon) and adjacent private lands, Cleveland and Calhoun counties, AR, 1991 and 1992. (Hatched rectangles represent old-growth and second-growth spot-mapping grids.)

Portions of the study area adjacent to the creek are inundated periodically during the early part of the breeding season, but water usually does not persist for more than a week at a time. Several sloughs and creeks join the main channel of the stream such that water is abundant throughout the study area. The elevation of the site ranges 48 to 51 m above mean sea level.

The census areas consisted of two adjacent tracts of oak-gum-cypress (*Quercus* spp.-*Liquidambar styraciflua-Taxodium distichum*) bottomland hardwood forests located along Moro Creek. The first study site was a 12-ha tract of old growth east of Moro Creek in Cleveland County (fig. 1). Overstory on the old-growth site was dominated by sweetgum, black gum (*Nyssa sylvatica*), overcup oak (*Quercus lyrata*), and bald cypress. The understory was composed primarily of eastern hornbeam (*Carpinus caroliniana*) and American hop hornbeam (*Ostrya virginiana*). The herbaceous layer was poorly developed in areas of closed canopy. Dewberry (*Rubus* spp.) is common in areas of canopy gaps.

The second study site was a 12-ha second-growth stand of bottomland located to the west of Moro Creek in Calhoun County (fig. 1). This site experienced a high-grade harvest about 30 years before the study. Overstory dominants were similar to the old-growth site. The understory was composed primarily of saplings of overstory trees and eastern hornbeam. The herbaceous layer was denser than in the old-growth study area and was comprised mostly of dewberry and grasses (Gramineae).

During August 1989, Moro Bottoms experienced a severe windstorm. Numerous windthrows occurred creating gaps in the overstory ranging in size from a single stem to about 0.3 ha). Because of these natural disturbances within the old growth and the proximity to managed second-growth forests, the Natural Area presented an excellent setting to examine the effects of recent natural and anthropogenic disturbances on habitat for forest landbirds.

PROCEDURES

Detailed maps of the old-growth and second-growth study sites were made that included major habitat features like Moro Creek and branching sloughs as well as all downed trees. All treefall canopy gaps were delineated by drawing lines connecting the trunks of mature trees at the gap edge. Maps of streams and canopy gaps were digitized into a Geographic Information System (GIS).

Habitat Sampling

A stratified, random-sampling procedure was used to locate an equal number of random points in the old-growth and second-growth study sites. The point-center quarter method (Cottam and Curtis 1956) was used to sample the overstory; tree height was included with tree species and d.b.h. measurements. Distance to the nearest snag, water, and gap also were measured. Together these data served as a null model of habitat features "available" within study sites for comparisons with measurements recorded where birds were seen and between study grids.

For singing male birds detected visually during spot-map censuses, several habitat variables were measured. Each bird's height from the ground was recorded using a clinometer; also its position in the vegetation (e.g., trunk, interior canopy, exterior canopy) was noted. In addition, tree species and height, diameter at breast height (d.b.h.), distance to the nearest snag, and distance to the nearest water were measured. A snag was defined as a dead tree >1.8 m tall with a d.b.h. of >10.2 cm (Thomas 1979). Diameter at breast height was measured only in 1992. On the old-growth site, distance from each singing male to the nearest gap was recorded. Canopy closure was quantified using a spherical densiometer (Lemmon 1956).

To quantify vegetation regrowth in canopy gaps, visual obstruction was measured using a density board (Nudds 1977). The board was 4 m high and marked off in 10-cm increments. The board was placed in the center of the longest axis of the gap. Readings were made at 5-m intervals from the board along the axis and along an axis perpendicular to it.

Avifaunal Sampling

The spot-map technique (International Bird Census Committee 1970) was employed to map the territories of breeding males in a 12-ha grid (600 m x 200 m) within both the old-growth and second-growth sites during the breeding season in 1991 and 1992. Grid boundaries were located at least 50 m from any external edge. Numbered stakes were placed at 25-m intervals throughout the grid to facilitate locating each singing male's position on the grid. Weekly censuses were conducted on each grid. Locations of all male birds seen or heard were plotted on a map. Maps from each season were compiled by species and entered into the ARC/INFO GIS. Territories were derived as the minimum convex polygon that included all of the locations of a singing male (Mohr 1947). The area of each territory and the area covered by water and by gaps (old-growth site only) were calculated.

Strip count censuses were conducted weekly during the breeding season in 1991 and 1992. Strip count transects 50 m wide and 600 m long were established through the center of the old-growth and second-growth spot-map grids. All male birds seen or heard within the 50-m wide strip were recorded to provide an estimate of avian abundance for each study site. The time of each census was alternated weekly between morning and evening.

Statistical Analysis

All statistical analyses were performed using SAS 6.03 on an IBM personal computer. We used the Shapiro-Wilk test for normality (Shapiro and Wilk 1965) to examine the distribution of variables. When distributions departed from normality, or when variances were unstable or heterogeneous, we used nonparametric counterparts to test our ecological hypotheses. Statistical analyses almost invariably addressed common null hypotheses that were examined through multiple comparisons. Therefore, we followed the recommendations of Chandler (1995) and used sequential Bonferroni adjustments of *P*-values (Wright 1992). For a "family" (Chandler 1995:525) of multiple statistical tests, we selected an experiment-wise error rate of 10 percent; that is, the probability of a type I error for all individual comparisons collectively was < 0.1. We selected 10 percent, rather than the conventional 5 percent error rate, to mitigate a reduction in statistical power so that individual comparisons were not too conservative (Chandler 1995). Thus, corresponding individual, comparison-wise error rates varied according to the number of individual tests conducted and followed the general procedures for Bonferroni adjustments outlined by Wright (1992).

For example, multiple comparisons of habitat use were conducted in each habitat type to test the general hypothesis that distribution of birds was nonrandom. The general hypothesis was rejected with a 10 percent error rate if any of the underlying specific hypotheses was rejected. Individual comparisons were used to test underlying specific hypotheses, i.e., determine whether distribution in old growth or second growth was associated with any of a set of specific habitat features (e.g., snags). In this example, we made 13 comparisons of use against the same underlying availability distribution. In the most conservative scenario (i.e., where the adjusted comparison-wise *P*-value equals the experiment-wise error divided by the number of individual comparisons, Chandler 1995), the comparison-wise error rate of individual tests was 0.10/13, or 0.0077. That is, each comparison of use of a specific habitat feature in old growth or second growth to its corresponding availability occurred with an error rate of 0.77 percent. In some circumstances, we reduced the total number of individual tests and increased statistical power by conducting comparisons sequentially according to *P*-values (Wright 1992:1009).

We used nonparametric test statistics for all univariate comparisons of habitat features between bird use (visual observations) and availability (random points). Distance to the nearest water, snag, and treefall canopy gap were tested for correlation using the Pearson correlation statistic (Kleinbaum and others 1988). No significant correlation occurred among any of the variables, so all variables were treated as independent variables in subsequent analyses. Because no significant difference existed in habitat distribution between years, 1991 and 1992 data from each habitat were combined to increase sample size and statistical power. Only birds with at least five visual records in each habitat type were included in analyses. Habitat use patterns of American redstart were analyzed although they were recorded only in second-growth habitat.

Tree species used by each bird species and corresponding height and d.b.h. values were compared to trees available (as estimated from a random sample of points) with a Kolmogorov-Smirnov Goodness-of-Fit (one-sample) test for continuous data (Zar 1984:55). Canopy closure and distance to nearest water, snag, and treefall canopy gap were compared to the same measures from random sites using a Wilcoxon signed rank test (Zar 1984).

Species composition and structure of avian communities were characterized with the Shannon-Weaver diversity index (Shannon and Weaver 1949). A Student's *t* test (Zar 1984) was used to test for significant differences between old-growth and second-growth habitats with spot-mapping and strip census results.

RESULTS

Bird Species Distribution, Density, and Diversity

Twelve spot-mapping censuses were conducted between May 26 and August 13, 1991, and 15 spot-mapping censuses were conducted between May 12 and August 15, 1992, on the old-growth and second-growth sites. In 1991 and 1992, there were 486 and 651 individuals and 543 and 591 individuals recorded in the old-growth and second-growth, respectively. Twelve and 15 strip-count censuses also were conducted in the old-growth and second-growth sites during the same time periods in 1991 and 1992, respectively.

A total of 38 species was detected in old growth, whereas 34 species were detected in second-growth habitat (table 1). The ten most common species recorded each in old-growth and second-growth habitats (according to weighted estimates of density from 1991 and 1992) are presented in table 2. For comparison, we include ranks of bird species recorded in four previous studies of bottomland hardwood forests. In our study, 12 warbler species (Parulinae) were detected in old growth, whereas nine warblers were detected in second-growth habitat. The white-eyed vireo (*Vireo griseus*) was the most common bird in both habitats in 1991 and in second-growth habitat in 1992 along with the Carolina wren (*Thryothorus ludovicianus*). The red-eyed

Table 1—Breeding bird density (pairs per 100 ha) derived from spot-mapping censuses by habitat and year on Moro Bottoms Natural Area, Arkansas, 1991 and 1992.

Table 1—Breeding bird density (pairs per 100 ha) derived from spot-mapping censuses by habitat and year on Moro Bottoms Natural Area, Arkansas, 1991 and 1992.

	Old growth		Second growth	
Species	1991	1992	1991	1992
Great blue heron (*Ardea herodias*)	*	*		
Yellow-crowned night-heron (*Nycticorax violaceus*)	*	*	*	*
Wood duck (*Aix sponsa*)	*	*	*	*
Red-shouldered hawk (*Buteo lineatus*)	*	*	*	*
Wild turkey (*Meleagris gallopavo*)	*	*	*	*
Yellow-billed cuckoo (*Coccyzus americanus*)			*	*
Barred owl (*Strix varia*)	*	*	*	*
Chimney swift (*Chaetura pelagica*)	*	*	*	*
Ruby-throated hummingbird (*Archilochus colubris*)	*	*	*	*
Red-bellied woodpecker (*Melanerpes carolinus*)	20	20	10	20
Downy woodpecker (*Picoides pubescens*)	20	20	10	10
Northern flicker (*Colaptes auratus*)	*			
Pileated woodpecker (*Dryocopus pileatus*)	*	10	*	
Eastern wood-peewee (*Contopus virens*)	10			
Acadian flycatcher (*Empidonax virescens*)	30	40	30	30
Great crested flycatcher (*Myiarchus crinitus*)	20	20	10	10
American crow (*Corvus brachyrhynchos*)	*	*	*	*
Carolina chickadee (*Parus carolinensis*)	20	20	30	30
Tufted titmouse (*Parus bicolor*)	30	30	30	30
White-breasted nuthatch (*Sitta carolinensis*)	10	10	10	10
Carolina wren (*Thryothorus ludovicianus*)	30	40	40	61
Blue-gray gnatcatcher (*Polioptila caerulea*)	*	*	10	10
White-eyed vireo (*Vireo griseus*)	51	51	71	61
Yellow-throated vireo (*Vireo flavifrons*)	10	10	*	*
Red-eyed vireo (*Vireo olivaceus*)	30	60	40	30
Northern parula (*Parula americana*)	30	51	40	31
Black-and-white warbler (*Mniotilta varia*)	*	10	*	*
Yellow-throated warbler (*Dendroica dominica*)	10	10	10	10
Pine Warbler (*Dendroica pinus*)	10	10		
American redstart (*Setophoga ruticilla*)	*		40	40
Prothonotary warbler (*Protonotaria citrea*)	40	51	30	30
Swainson's warbler (*Limnothlypis swainsonii*)	*		10	10
Louisiana waterthrush (*Seiurus motacilla*)	*	10		
Kentucky warbler (*Oporornis formusus*)	20	40	20	40
Common yellowthroat (*Geothlypis trichas*)		10		20
Hooded warbler (*Wilsonia citrina*)	*	10	30	10
Worm-eating warbler (*Helmitheros vermivorus*)	*			
Summer tanager (*Piranga rubra*)	20	20	10	10
Northern cardinal (*Cardinalis cardinalis*)	40	30	51	40
Indigo bunting (*Passerina cyanea*)				10
Total density	451	584	522	542

* = species with too few sightings to delineate a breeding territory, or the species was too mobile to map accurately.

Table 2—Rank of 10 most abundant bird species in old-growth (OG) and second-growth (SG) habitats from Moro Bottoms Natural Area, Arkansas and from previous avifaunal studies in bottomland hardwood forest

	Moro Bottoms					
Species	OG	SG	Hoiberg[a]	Dickson[b]	Ford[c]	Hamel[d]
White-eyed vireo (*Vireo griseus*)	1	1	8	1	+	6
Red-eyed vireo (*Vireo olivaceus*)	2	3	1	7	+	5
Prothonotary warbler (*Protonotaria citrea*)	3	5	10	10	5	+
Northern parula (*Parula americana*)	4	4	–	+	+	1
Carolina wren (*Thryothorus ludovicianus*)	5	2	2	2	+	9
Acadian flycatcher (*Empidonax virescens*)	5	7	5	6	3	2
Northern cardinal (*Cardinalis cardinalis*)	7	6	4	5	2	4
Kentucky warbler (*Oporornis formosus*)	8	8	6	+	+	+
Tufted titmouse (*Parus bicolor*)	9	9	3	3	7	3
Red-bellied woodpecker (*Melanerpes carolinus*)	10	+	+	8	+	10
Downy woodpecker (*Picoides pubescens*)	10	+	+	+	8	+
Carolina chickadee (*Parus carolinensis*)	10	10	+	+	4	7
American redstart (*Setophaga ruticilla*)	+	+	9	–	–	+
Hooded warbler (*Wilsonia citrina*)	–	+	7	+	–	+
Yellow-billed cuckoo (*Coccyzus americanus*)	+	+	–	4	+	+
Swainson's warbler (*Limnothlypsis swainsonii*)	+	+	–	9	–	+
Blue-gray gnatcatcher (*Polioptila caerulea*)	+	+	+	–	1	8
Indigo bunting (*Passerina cyanea*)	+	+	–	–	6	+
Ruby-throated hummingbird (*Archilochus colubris*)	–	+	–	–	9	+
Common grackle (*Quiscalus quiscula*)	–	+	–	+	10	+

+ = species was recorded; – = species was not reported.

[a] Adapted from Hoiberg 1957, cited in James and Neal (1986).

[b] Adapted from Dickson (1978b).

[c] Adapted from Ford (1990).

[d] Adapted from birds recorded in old-growth bottomland hardwoods (Hamel 1989).

vireo (*Vireo olivaceus*) was the most common bird in old growth in 1992. The American redstart (*Setophaga ruticilla*) was a common bird in second-growth habitat, yet was only recorded once in old growth. The greatest density of breeding birds occurred in 1992 in old growth, whereas the lowest density was in old growth in 1991 (table 1).

Shannon-Weaver diversity indices derived from spot-mapping and strip-count censuses of old-growth forest were consistently greater, but not significantly different, than indices computed for second-growth habitat (table 3). Species richness also was not statistically different between habitats, but trends (table 3) were similar to diversity with a larger number of species recorded in old growth (29) as compared to second growth (27). Within a habitat type, no significant differences were detected either within years or between years for either sampling technique (e.g., spot-mapping in old growth between 1991 and 1992). We consistently recorded more species with the spot-mapping method, but spot-mapping and strip-count censuses produced similar species richness and diversity estimates.

The old-growth spot-mapping grid contained 24 gaps that ranged in size from 127.5 to 2685.5 m^2. Number of species and total number of birds recorded in gaps ranged 0 to 12 and 0 to 45, respectively. According to Spearman rank correlation analysis, species richness was positively correlated with area of treefall canopy gaps in 1991 ($r_s = 0.83$, $P < 0.001$) and 1992 ($r_s = 0.73$ $P < 0.001$). Total registrations also was positively correlated with gap area in 1991 ($r_s = 0.83$, $P < 0.001$) and 1992 ($r_s = 0.80$, $P < 0.001$). The highest values for species richness and total birds occurred in the largest gap.

Habitat Availability and Use

Habitat features—Comparison of distances measured from random points to various habitat features revealed significant differences between habitats. Average distance from random points to nearest snags and to surface water was significantly greater in old-growth than in second-growth habitat (table 4). Mean distance to the nearest tree was significantly greater in second-growth habitat than in old growth. No significant difference in d.b.h. distribution or tree height distribution existed between habitats.

Table 3—Shannon-Weaver diversity indices (H') and species richness (S) for spot-mapping and strip-count censuses among three forest habitats, Moro Bottoms Natural Area, Arkansas, 1991 and 1992

	Spot-mapping technique		Strip-count technique	
Habitat	H'	S	H'	S
Old growth				
1991	3.106	35	3.014	28
1992	3.099	33	3.095	30
Second growth				
1991	2.961	32	2.947	26
1992	3.021	32	3.037	28

Table 4—Means (x) and standard errors (SE) for all variables measured in random plots across old-growth and second-growth habitat, Moro Bottoms Natural Area, Arkansas, 1991 and 1992 (comparison-wise *P*-value: $P < 0.0167$)

	Old growth		Second growth	
Variable	x	SE	x	SE
Distance to water (m)	41.8	4.1	20.5	1.3[a]
Distance to snag (m)	14.0	0.7	11.1	0.7[b]
Distance to gap (m)	23.4	1.4	—	—
Canopy openness (percent)	24.1	1.1	27.3	1.3
Distance to tree (m)	3.5	.1	4.4	.2[c]
D.b.h. (cm)	17.8	1.5	17.1	1.2
Tree height (m)	11.3	.7	11.0	.6
Basal area (m^2/ha)	20.4		11.9	
Stem density (trees/ha)	816.3		516.5	

[a] Significant difference between old-growth and second-growth study sites, $P < 0.0001$.

[b] Significant difference between old-growth and second-growth study areas, $P < 0.003$.

[c] Significant difference between old-growth and second-growth study areas, $P < 0.001$.

Tree species composition (fig. 2) was similar in old-growth and second growth forests. Eastern hornbeam was the most common tree in both habitats, comprising 49 percent of stem density in old-growth and 23 percent in second-growth habitat. Oaks had a relative density of 20 percent in second-growth study habitat compared to 8 percent in old growth.

Species habitat distribution—Perch heights varied among species and were significantly different between habitat types for the downy woodpecker (table 5). Acadian flycatchers occurred closer to water than expected, i.e., as compared to random points, in both old growth and second growth; this was true of prothonotary warblers in old growth (table 6). Acadian flycatchers were sighted directly over water in 68.0 percent of the observations. In second growth, Carolina wrens, tufted titmice, and white-eyed vireos all occurred farther from water than expected. Carolina wrens and Kentucky warblers also occurred farther from water than expected in old growth.

Snags were abundant across both study sites, occurring primarily in canopy openings. Carolina wrens in both habitats, and Kentucky warblers in old growth, were recorded closer to snags than were random sites (table 7). Carolina wrens and Kentucky warblers used snags as singing perches in 50 percent of our observations.

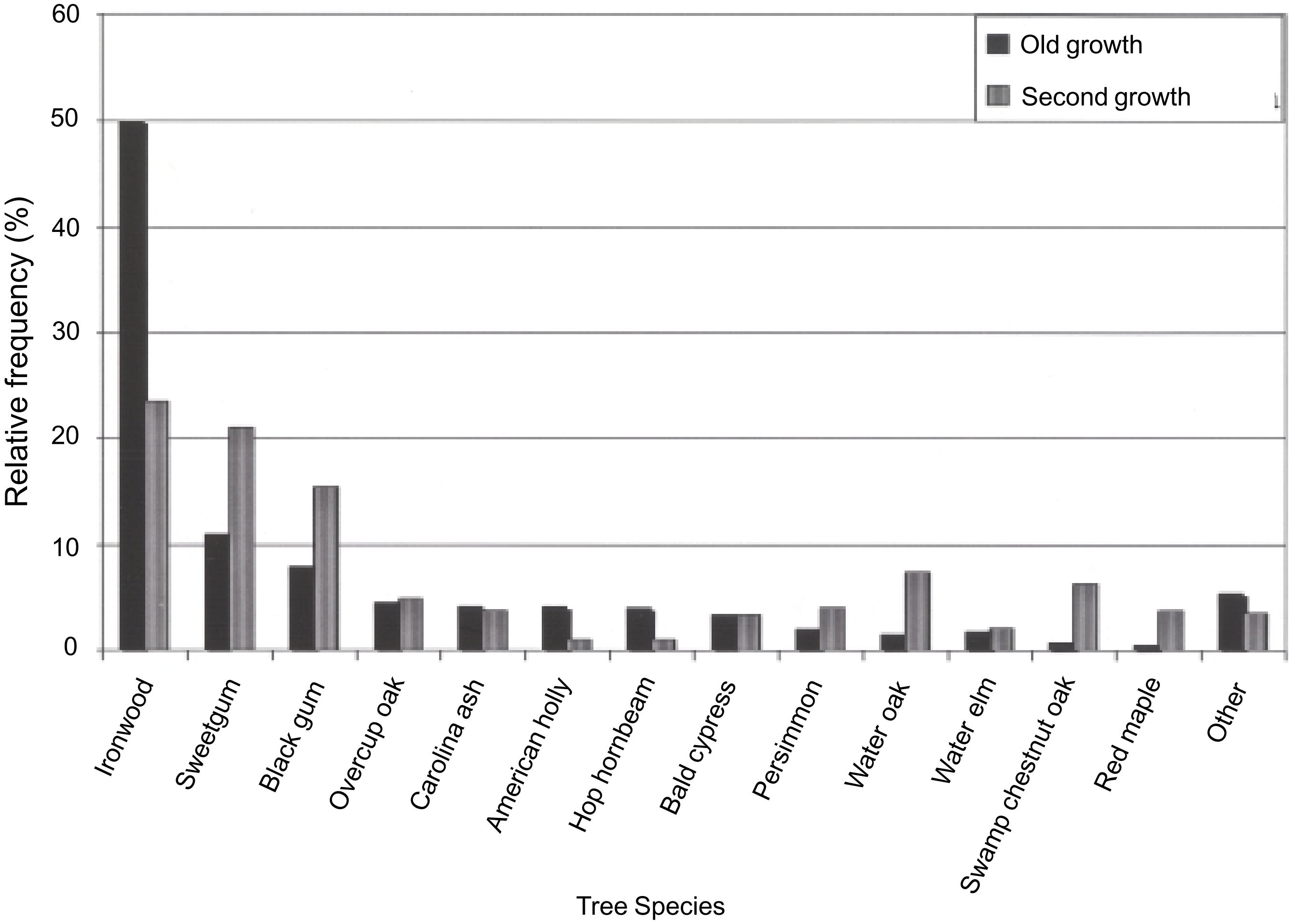

Figure 2—Relative frequency distribution (percent) of tree species in the old-growth and second growth study sites, Moro Bottoms Natural Area, Cleveland and Calhoun Counties, AR, 1991 and 1992.

Table 5—Sample size (N), mean perch height (x) and standard error (SE) of perch sites in meters for bird species in old-growth and second-growth habitat Moro Bottoms Natural Area, Arkansas, 1991 and 1992 (comparison-wise *P*-value: *P* <0.01)

	Old growth			Second growth		
Species	N	x	SE	N	x	SE
Acadian flycatcher	25	5.5	0.5	15	4.1	0.3
American redstart	—	—	—	29	15.4	1.3
Carolina chickadee	6	9.3	1.9	9	8.4	.9
Carolina wren	14	2.6	.4	26	3.0	.4
Downy woodpecker	5	7.2	.9	5	14.8	2.4[a]
Kentucky warbler	10	1.8	.4	12	1.5	.2
Northern cardinal	13	11.3	2.0	17	10.2	1.6
Prothonotary warbler	34	5.4	.5	19	5.2	.6
Red-bellied woodpecker	11	16.5	1.3	7	19.3	1.9
Tufted titmouse	11	10.8	1.3	9	9.9	1.8
White-eyed vireo	28	5.5	.3	30	5.9	.5

[a] Significant difference (*P* < 0.01) in mean perch height between old-growth and second-growth study areas.

Table 6—Sample size (N), mean (x), standard error (SE), Wilcoxon test statistic (Z), and significance level (Prob >|Z|) for each species for distance to the nearest surface water (m) for each habitat, Moro Bottoms Natural Area, Arkansas, 1991 and 1992 (comparison-wise *P*-value: $P < 0.0077$)

Species/ random variable	N	x	SE	$Z^{a\ b}$	Prob>|Z|
			Old growth		
Acadian flycatcher	25	5.2	3.0	-6.485	0.0001
Carolina chickadee	6	45.2	13.1	1.331	.1833
Carolina wren	14	81.8	14.2	3.766	.0002
Downy woodpecker	5	33.0	15.1	-0.298	.7652
Kentucky warbler	10	88.1	24.1	2.708	.0068
Northern cardinal	13	28.5	5.0	.510	.6098
Prothonotary warbler	34	27.6	7.8	-3.240	.0012
Red-bellied woodpecker	11	60.0	14.3	1.799	.0716
Tufted titmouse	11	54.7	16.1	.662	.5079
White-eyed vireo	28	58.1	12.4	1.474	.1404
Distance to water (m)	93	41.8	4.1		
			Second growth		
Acadian flycatcher	15	3.3	1.1	-4.871	.0001
American redstart	29	36.1	7.6	.511	.6013
Carolina chickadee	9	44.3	18.8	.792	.4282
Carolina wren	26	52.8	13.0	2.153	.0313
Downy woodpecker	52	3.0	3.3	.783	.4335
Kentucky warbler	12	40.0	17.9	.671	.5023
Northern cardinal	17	48.7	13.6	2.349	.0188
Prothonotary warbler	19	20.6	7.5	-1.496	.1345
Red-bellied woodpecker	7	27.3	10.4	.435	.6638
Tufted titmouse	9	87.3	27.9	3.039	.0024
White-eyed vireo	30	42.9	8.2	2.688	.0072
Distance to water (m)	96	20.5	1.3		

[a] Calculated from use sites and 93 random sites in the old-growth study site using the Wilcoxon signed rank test.

[b] Calculated from use sites and 96 random sites in the second-growth study site using the Wilcoxon signed rank test.

Carolina wrens, Kentucky warblers, prothonotary warblers, and white-eyed vireos were sighted closer to treefall canopy gaps than random points (table 8). Moreover, perch sites of the Carolina wren, Kentucky warbler, and white-eyed vireo had a greater mean percentage of canopy openness (table 9). The white-eyed vireo appeared to locate its territory around single canopy gaps >500 m^2. Although gaps composed only 22.0 percent of the old-growth study area, 38.0 percent and 35.4 percent of spot-mapping records occurred within treefall canopy gaps in 1991 and 1992, respectively. The reason for this positive association with canopy gaps is unclear, but occupied gaps had greater understory density (53.2 percent ± 5.56) from forest floor to a height of four meters than gaps where birds had not been recorded (31.1 percent ± 3.96). Only the Acadian flycatcher appeared to avoid canopy gaps. In second-growth habitat they used areas with greater closed canopy (table 9), and in old-growth forest, Acadian flycatchers were sighted at greater distances than expected from canopy gaps (table 8).

Red-bellied woodpeckers in old-growth and American redstarts in second-growth habitat used trees that had greater d.b.h. than was generally available (table 10). These species and the Carolina chickadee preferred trees of greater height in both habitats than was generally available (table 11). Carolina wrens in old growth and Kentucky warblers in both habitats, used shorter trees than expected. Unfortunately, because d.b.h. was only measured in 1992, some species were omitted from the analysis due to insufficient sample size.

Table 7—Sample size (N), mean (x), standard error (SE), Wilcoxon test statistic (Z), and significance level (Prob >|Z|) of distance to the nearest snag (m) for each bird species in old-growth and second-growth habitat, Moro Bottoms Natural Area, Arkansas, 1991 and 1992 (comparison-wise *P*-value: $P < 0.0077$)

Species/ random variable	N	x	SE	Z[a b]	Prob>|Z|
			Old growth		
Acadian flycatcher	25	15.6	2.2	0.681	0.4957
Carolina chickadee	6	22.3	6.2	1.817	.0708
Carolina wren	14	7.0	1.8	-3.591	.0003
Downy woodpecker	5	8.8	4.1	-1.171	.2414
Kentucky warbler	10	5.3	1.8	-3.210	.0013
Northern cardinal	13	13.8	2.0	.410	.6818
Prothonotary warbler	34	10.5	1.3	-1.923	.0544
Red-bellied woodpecker	11	15.5	3.5	.346	.7293
Tufted titmouse	11	13.4	2.8	- .410	.6815
White-eyed vireo	28	10.6	1.3	-1.826	.0680
Distance to snag (m)	93	14.0	0.7		
			Second growth		
Acadian flycatcher	15	13.7	2.1	1.892	.0585
American redstart	29	13.4	1.8	1.186	.1871
Carolina chickadee	9	10.0	2.1	.285	.7757
Carolina wren	26	4.0	1.1	-4.771	.0001
Downy woodpecker	5	5.4	2.0	-1.401	.1612
Kentucky warbler	12	8.1	1.2	- .303	.7619
Northern cardinal	17	12.3	2.8	.046	.9632
Prothonotary warbler	19	10.8	1.5	.682	.4948
Red-bellied woodpecker	7	12.6	2.4	.937	.3487
Tufted titmouse	9	8.9	1.7	- .129	.8972
White-eyed vireo	30	11.2	1.6	.827	.3973
Distance to snag (m)	96	11.1	.7		

[a] Calculated from use sites and 93 random sites in the old-growth study site using the Wilcoxon signed rank test.

[b] Calculated from use sites and 96 random sites in the second-growth study site using the Wilcoxon signed rank test.

Finally, we compared use of tree species by birds to corresponding estimates of availability with a Kolmogorov-Smirnov (KS) goodness-of-fit test (Appendix 1). We discourage drawing inferences about tree species preferences, however, because of the small sample of observations obtained for each bird species, and because the KS goodness-of-fit test was not developed for use with nominal data. Still, the relative frequency distributions and computed statistics suggest nonrandom use of trees by most bird species. The American redstart showed the largest bias toward use of a single species with 65 percent of its use occurring in swamp chestnut oak (*Quercus michauxii*). Perch sites selected by other bird species were more evenly distributed across a variety of tree species (Appendix 1).

DISCUSSION

Assumptions and Implications

Moro Bottoms Natural Area was an excellent natural laboratory for examining birds of old-growth and second-growth habitats. Because this was not a replicated experiment, however, we caution generalizing results of our study to other southern bottomland hardwood forests. Moreover, there were several assumptions inherent in procedures used in this study, some of which bear significant implications on results and conclusions. For example, we assumed that our sample of species distributions across habitats reflected the variability that existed in each of the habitats. Most of the visual observations of birds were distributed among species that

Table 8—Sample size (N), mean (x), standard error (SE), Wilcoxon test statistic (Z), and significance level (Prob >|Z|) of recorded distances to the nearest canopy gap (m) for each bird species in old growth, Moro Bottoms Natural Area, Arkansas, 1991 and 1992 (comparison-wise *P*-value: *P* <0.01)

Species/ random variable	N	x	SE	Z[a]	Prob>|Z|
Acadian flycatcher	25	37.7	5.4	2.734	0.0063
Carolina chickadee	6	21.5	4.4	.107	.9150
Carolina wren	14	6.4	2.9	-4.688	.0001
Downy woodpecker	5	15.2	5.6	- .865	.3873
Kentucky warbler	10	5.4	2.5	-3.555	.0004
Northern cardinal	13	17.5	3.0	- .864	.3874
Prothonotary warbler	34	10.9	1.6	-4.688	.0001
Red-bellied woodpecker	11	19.5	3.0	- .250	.8030
Tufted titmouse	11	39.9	12.1	.934	.3505
White-eyed vireo	28	5.2	1.1	-5.914	.0001
Distance to gap (m)	93	23.4	1.4		

[a] Calculated from use sites and 93 random sites using the Wilcoxon signed rank test.

typically frequent the midstory or understory strata. Dense foliage and low light conditions in bottomland hardwood forests made it difficult to observe birds in the upper canopy. Canopy species commonly sighted tended to be those that were more active (e.g., American redstart) or more vocal (e.g., red-bellied woodpecker). Consequently, our results were probably biased toward species or individuals of a species that were more easily detected and observed. Also, spherical densiometers yield biased estimates of forest canopy cover (Cook and others 1995). Cover may be overestimated and spherical densiometers may be insensitive to variation in forest cover, especially in the mid-range of canopy closure.

In addition, microhabitat features important for successful reproduction among forest landbirds are numerous and include food, foraging substrate, water, singing perches, and nest sites. Because we only obtained direct observations of singing perches, limited conclusions can be drawn about bird habitat needs and microhabitat segregation among species.

Finally, there were numerous comparisons of habitat features between habitats and between used and available sites within each habitat. In one such comparison, we used the KS one-sample test to compare tree species distributions (i.e., use versus available) when our data did not strictly meet an important assumption of this analysis, namely that observations are continuous data from a ratio, interval, or ordinal scale of measurement (Zar 1984:55).

Also, because we did not apply a Bonferroni correction to each set of analyses (e.g., Neu and others 1974), there was an average of one chance in 20 (for *P* < 0.05) that a statistical analysis could yield a spurious significant conclusion.

Forest Composition

Vegetation at Moro Bottoms appeared typical of bottomland hardwood forests of minor stream floodplains across the Southern United States. Clairain and Kleiss (1988) reported a similar assemblage of tree species for the Cache River Basin in eastern Arkansas. At Cache River and Moro Bottoms, forest types and corresponding overstory dominants were distributed according to a moisture gradient with cypress-tupelo inhabiting more hydric sites and overcup oak (*Quercus lyrata*) and swamp chestnut oak occurring on somewhat drier, mesic sites. Understory diversity was limited under closed canopy at both sites, a feature probably related to frequent and periodic prolonged inundation, as well as limited sunlight across the forest floor (Smith and others 1995).

Bird Species Distribution and Diversity

Moist bottomland hardwood forests of the Southern United States often support an abundant and diverse breeding bird community (Smith and others 1993a). James and Wamer (1982) reported that mature deciduous forests supported the highest avian diversity and density of all North American forest types. Similar results were reported for Arkansas where mature, moist forests had the highest breeding species diversities (Shannon-Weaver index = 2.91) of any habitat in the State (Shugart and James 1973). In our study, diversity indices computed from spot-mapping censuses of old growth averaged 3.10 (table 2).

It is generally recognized that there is a correlation between foliage height diversity and bird species diversity in several

Table 9—Sample size (N), mean (x), standard error (SE), Wilcoxon test statistic (Z), and significance level (Prob >|Z|) of canopy openness (percent) for each bird species in old growth and second-growth habitat, Moro Bottoms Natural Area, Arkansas, 1991 and 1992 (comparison-wise *P*-value: *P* < 0.0077)

Species/ random variable	N	x	SE	Z^{ab}	Prob>|Z|
			Old growth		
Acadian flycatcher	25	18.4	1.5	-1.554	0.1200
Carolina chickadee	6	15.7	3.4	-1.662	.0966
Carolina wren	14	57.5	2.8	6.077	.0001
Downy woodpecker	5	36.6	11.6	.751	.4527
Kentucky warbler	10	52.8	4.9	4.257	.0001
Northern cardinal	13	23.3	2.7	.687	.4920
Prothonotary warbler	34	31.6	3.0	2.554	.0107
Red-bellied woodpecker	11	22.3	1.6	1.518	.1291
Tufted titmouse	11	24.6	1.6	1.518	.1291
White-eyed vireo	28	36.1	2.1	5.231	.0001
Canopy openness (%)	93	24.1	1.1		
			Second growth		
Acadian flycatcher	15	14.7	1.8	-2.823	.0048
American redstart	29	17.7	1.6	1.891	.0494
Carolina chickadee	9	30.8	3.4	1.440	.1499
Carolina wren	26	42.8	2.6	4.580	.0001
Downy woodpecker	5	25.2	4.4	.234	.8146
Kentucky warbler	12	53.5	4.9	4.137	.0001
Northern cardinal	17	26.6	3.1	.636	.5246
Prothonotary warbler	19	21.6	1.8	- .477	.6335
Red-bellied woodpecker	7	21.9	3.3	- .297	.7687
Tufted titmouse	9	30.8	3.4	.111	.9113
White-eyed vireo	30	31.0	1.5	2.663	.0077
Canopy openness (%)	96	27.3	1.3		

[a] Calculated from use sites and 93 random sites in the old-growth study site using the Wilcoxon signed rank test.

[b] Calculated from use sites and 96 random sites in the second-growth study site using the Wilcoxon signed rank test.

forests in the Eastern United States (MacArthur and MacArthur 1961). At Moro Bottoms, breeding bird diversity and richness increased with successional stage. In old growth, or mature forests in general, Dickson (1991) attributed high avian diversity to an increased number of canopy layers and tree age categories. As habitat complexity and heterogeneity increase, habitat requirements for a greater number of species can be met (Martin 1992). Similar results were reported for the Atchafalaya Basin by Kennedy (1977): bird species richness and diversity varied with foliage density, which increased from the earliest seral stage to the oldest seral stage.

In our study, old growth had a closed canopy interrupted by treefall canopy gaps, which provided several layers of herbaceous and woody vegetation. The understory was sparse except in canopy gaps where midstory and understory layers proliferated. This diverse canopy structure was not present in second-growth habitat where trees were generally spaced farther apart and where development of a dense low understory under a more open canopy was presumably facilitated.

Avian abundance also varies with forest habitat structure and complexity, which presumably facilitates partitioning of resources among conspecifics (Kennedy 1977), as well as

Table 10—Sample size (N), mean (x), standard error (SE), Kolmogrov-Smirnov test statistic (D), and significance level (Prob > KS) of perch site d.b.h. (cm) for each bird species in old-growth and second-growth habitat, Moro Bottoms Natural Area, Arkansas, 1991 and 1992 (comparison-wise *P*-value: *P* <0.0077)

Species/ random variable	N	x	SE	D[a b]	Prob>KS
			Old growth		
Acadian flycatcher	14	12.2	2.2	0.1935	0.7521
Carolina wren	12	7.8	2.0	.2769	.3891
Kentucky warbler	6	1.7	1.0	.5269	.0875
Northern cardinal	8	20.4	5.8	.2311	.8260
Prothonotary warbler	18	12.5	2.1	.1505	.8840
Red-bellied woodpecker	6	46.8	2.4	.8065	.0013
Tufted titmouse	6	41.6	12.1	.4731	.1603
White-eyed vireo	16	11.4	2.1	.1505	.9165
D.b.h. (cm)	93	17.8	1.5		
			Second growth		
Acadian flycatcher	11	16.1	2.7	.2794	.4244
American redstart	18	46.1	3.5	.7601	.0001
Carolina wren	16	9.4	2.0	.2038	.5911
Kentucky warbler	7	1.3	0.6	.4479	.1459
Northern cardinal	10	24.0	5.3	.3604	.1900
Prothonotary warbler	12	12.0	2.2	.2083	.7435
Tufted titmouse	6	40.5	5.8	.6250	.0243
White-eyed vireo	19	13.6	2.3	.2889	.1415
D.b.h. (cm)	96	17.1	1.2		

[a] Calculated from use sites and 93 random sites in the old-growth study site and using the Kolmogrov-Smirnov test.

[b] Calculated from use sites and 96 random sites in the second-growth study site using the Kolmogrov-Smirnov test.

among species (Mannan and others 1984). That is, the number of conspecifics occupying a habitat is not necessarily reduced as habitat complexity and species diversity increases. In the Atchafalaya Basin, Kennedy (1977) reported that the greatest avian abundance occurred in bottomland hardwood forest, the latest seral stage among an array of successional seres examined, and the habitat with the greatest foliage complexity. In the Congaree Swamp and Santee Swamp, Hamel (1989:624) reported considerable overlap in bird communities (similarity index = 0.9) between old-growth and selectively cut stands and between selectively cut and clearcut stands. Similarity between old growth and second growth was intermediate (0.7); the lowest similarity in bird communities (0.6) existed between old-growth and clearcut stands (Hamel 1989:624).

In this study, breeding bird density varied inconsistently between years and habitats with total old-growth densities exceeding those in second-growth habitat in 1992, but not in 1991 (table 3). Unfortunately, we did not estimate foliage complexity in either habitat (only understory density in gaps) and only measured five features related to forest structure. Of these only two differed between habitats (table 4). Second-growth habitat had greater snag density and showed greater spacing among stems >10 cm d.b.h., the latter of which may have reduced canopy cover in second growth habitat.

Avian density at Moro Bottoms was greater than that reported for a moist forest in the Ozark region of Arkansas (Shugart and James 1973). Average breeding bird density was 525 breeding pairs per 100 ha in Moro Bottoms, whereas 150 breeding pairs per 100 ha were observed in the Ozarks. However, total avian density at Moro Bottoms was appreciably lower than that reported for bottomland forests of western Tennessee (830 breeding pairs per 100

Table 11—Sample size (N), mean (x), standard error (SE), Kolmogrov-Smirnov test statistic (D), and significance level (Prob > KS) of perch site tree height (m) for each bird species in old-growth and second-growth habitat, Moro Bottoms Natural Area, Arkansas, 1991 and 1992 (comparison-wise *P*-value: *P* <0.0077)

Species/ random variable	N	x	SE	D[a] [b]	Prob>KS
		Old growth			
Acadian flycatcher	25	11.4	1.2	0.2433	0.1048
Carolina chickadee	6	16.8	2.7	.6984	.0069
Carolina wren	14	3.3	.4	.4770	.0008
Downy woodpecker	5	12.8	3.8	.2984	.7785
Kentucky warbler	10	2.1	.4	.6349	.0009
Northern cardinal	13	15.4	2.6	.2882	.2647
Prothonotary warbler	34	8.7	.8	.2011	.1945
Red-bellied woodpecker	11	26.5	2.2	.6984	.0001
Tufted titmouse	11	20.7	2.6	.6657	.0002
White-eyed vireo	28	8.8	.9	.1865	.3664
Tree height (m)	93	11.3	.7		
		Second growth			
Acadian flycatcher	15	13.9	1.7	.3895	.0293
American redstart	29	24.4	1.2	.6563	.0001
Carolina chickadee	9	21.8	2.5	.6337	.0020
Carolina wren	26	5.7	1.0	.2247	.1976
Downy woodpecker	5	20.8	2.1	.6563	.0301
Kentucky warbler	12	2.3	.4	.6093	.0005
Northern cardinal	17	16.1	2.3	.3621	.0333
Prothonotary warbler	19	8.5	1.0	.1801	.6291
Red-bellied woodpecker	7	27.6	1.1	.8281	.0002
Tufted titmouse	9	23.7	2.2	.6562	.0012
White-eyed vireo	30	9.1	1.0	.1573	.5422
Tree height (m)	96	11.0	.6		

[a] Calculated from use sites and 93 random sites in the old-growth study site using the Kolmogrov-Smirnov test.

[b] Calculated from use sites and 96 random sites in the second-growth study site using the Kolmogrov-Smirnov test.

ha; Ford 1990) or breeding bird densities reported among all habitats of the Congaree Swamp (range 818 to 1572 pairs per 100 ha; Hamel 1989). In contrast, pine forests of the west Gulf Coastal Plain had 2 to 4 times lower densities than mature bottomland hardwood forests (Dickson 1978a).

Species common to Moro Bottoms were similar to communities reported for bottomland hardwood forests elsewhere (table 2). Regrettably, there are few remaining examples of bird communities of old-growth bottomland forests (Dickson 1978a, Hamel 1989). Except for Hamel (1989), previous studies of southern bottomland bird communities mostly come from sites where logging or other land uses have influenced extent and composition of remaining forests (Dickson 1978b, Ford 1990). Fortunately, there was an earlier study from southern Arkansas (Hoiberg 1957, cited in James and Neal 1986) that could be included in our comparisons (table 2). The 10 most abundant species recorded in Moro Bottoms (pooled between habitats) almost completely overlapped (one exception from each study) the 10 most common species reported by Hoiberg (James and Neal 1986). Northern parula, the sixth most frequently observed species in our study, was the only species not ranked among Hoiberg's 10 most common species. In contrast, the hooded warbler (*Wilsonia citrina*) was the seventh most common species in the Hoiberg study, but was not among the 10 most common species at Moro Bottoms. There also was substantial overlap between Moro Bottoms and the Atchafalaya Basin (Dickson 1978b) and between Moro Bottoms and the old-growth habitat of the Congaree Swamp (Hamel 1989) with eight and nine species, respectively, common to those communities (table 2). In west Tennessee bottomlands (Ford 1990), however, only six of the top ten species made the Moro Bottoms list.

At least some of the variation among studies can be explained as sampling error. For example, the 12-ha old-growth grid encompassed about 30 percent of the entire stand, but it did not include the complete range of elevation or microtopographic variation that existed throughout the stand (Zollner 1993). Alternatively, differences in species composition (or density) of ≥1 species across bottomland sites may reflect some habitat differences, albeit subtle, or even ephemeral. Hamel (1989) noted several species whose occurrence was limited to only one of the six forest habitats sampled in South Carolina. In our study, we noted variation across Moro Bottoms Natural Area in specific habitat features such as the presence of canebrakes. Canebrakes and other dense undergrowth are a favorite nesting habitat for Swainson's warblers.

Also, wood thrush may have been absent from our grids because those sites often were still flooded during spring when breeding males arrived. Indeed, it was not uncommon to have the Natural Area almost completed flooded for a few days in late June (Zollner 1993). Because of their dependence on soil invertebrates as a food base, wood thrush establishment of territories on our study grids may have been precluded by the extent and duration of flooding. Ford (1990:35) noted that the wood thrush had the lowest density (5 pairs per 100 ha) of widespread species in west Tennessee bottomlands where almost all of what remains is the lower elevation habitat, which was presumably too wet for clearing and conversion to agriculture.

Finally, some of the variation was almost certainly related to species-specific breeding ranges or because of the area-sensitive nature of some species (Robbins and others 1989). The American redstart, for example, was probably absent from south-central Louisiana (Dickson 1978b) because rarely (if ever) does this species breed that far south in Louisiana. Moro Bottoms Natural Area is part of a narrow, frequently interrupted, riparian system largely surrounded by pine plantations. The hairy woodpecker (*Picoides villosus*) may be precluded from occurring within small bottomland fragments; the cerulean warbler (*Dendroica cerulea*) was probably absent because of either of the aforementioned reasons.

Habitat Use

Water—Water is a dominant feature of bottomland hardwood forests (Smith 1977). Ford (1990) reported that the highest densities of birds in west Tennessee occurred in bottomland forests along an unchannelized river. Swift and others (1984) found the highest bird densities in Connecticut were associated with plots that included streams. They also reported a positive correlation between surface water coverage and species richness and density in both the foliage gleaning and ground foraging avian guilds. Shugart and James (1973) classified the Acadian flycatcher, northern parula, Kentucky warbler, and American redstart as moist forest specialists in Arkansas. However, Shugart and James (1973) did not specifically examine the effects of surface water on singing perch site selection. All four of these moist forest specialists were abundant at Moro Bottoms; only the Acadian flycatcher, however, was closely associated with surface water. Somewhat surprising, the prothonotary warbler was not listed as a moist forest specialist (Shugart and James 1973), but also showed a strong affinity for water at Moro Bottoms. The importance of water to these two species also was reflected by the large proportion of Acadian flycatcher and prothonotary warbler territories that were comprised of water (Smith and others 1993b).

The Kentucky warbler, another moist forest specialist (Shugart and James 1973), surprisingly occurred farther from water than expected in Moro Bottoms (table 6). Thus, surface water alone may not be critical to some moist forest species; rather, it may be an ecological correlate of the moisture regime, such as invertebrate abundance. For Acadian flycatchers and prothonotary warblers, standing water may provide direct and indirect benefits as both species were often seen perching over or adjacent to streams. They seemed to use these areas as flyways along which they foraged. Conversely, the Kentucky warbler was not observed using these flyways and probably prefers the moist forest because of increased food associated with these habitats. Indeed, Smith (1977) noted the high abundance of insects and soil invertebrates in moist forests as compared to an upland post oak forest (*Quercus stellata*) in Arkansas.

The Carolina wren and the Kentucky warbler were the only species that occurred in drier sites of both old-growth and second-growth habitats. This may be related to the flood regimes in Moro Bottoms. These two species both feed on or near the ground and nest on the ground or in cavities (Carolina wren only) or low shrubs (Ehrlich and others 1988). In our study, foraging substrate within territories that were too close to streams would frequently have been unavailable because of flooding, which occurred several times throughout the 1991 and 1992 breeding seasons.

Snags—Snags were very abundant in both habitats. In second-growth habitat, this was to some extent a result of "habitat improvement" by a local hunting club; in old growth, stubs created by wind (i.e., snapped tops) and mortality from windthrow damage of adjacent trees probably contributed to snag abundance. Flooding and associated stress-induced mortality was probably common in both habitats. Thus, snags at Moro Bottoms were probably not a limiting resource as reported elsewhere (e.g., Dickson and others 1983). Most cavity nesters at Moro Bottoms showed no significant affinity for snags (table 7). Only the Carolina wren, which occasionally nests in cavities, and the Kentucky warbler showed an affinity for snags, especially snags created by treefalls. These snags were generally located in the center of canopy gaps where Carolina wrens and Kentucky warblers were frequently observed foraging and singing. In many circumstances, snags were the only elevated singing and display perches in the interior of gaps.

Gap Size—Internal patchiness in the form of treefall canopy gaps attracted a large number of bird species and individuals in Moro Bottoms. Openings created by treefalls lead to a high degree of habitat structural diversity (Urban and Smith 1989). This diversity is similar to that at the forest edge, but might be considered internal edge that operates at a finer scale (Noss 1988). Noss (1988) reported that the proportion of gaps in a forest was the best predictor of bird density in Florida. At Moro Bottoms, gaps represented 22 percent of the old-growth habitat, which was greater than the 3.4 percent reported by Noss (1988).

Birds concentrated in gaps presumably because of increased food resources (Noss 1988) and abundant favorable nest sites (Morse 1985). The dense shrub layer that develops in gaps offers concealment for nests, as well as an increased fruit and seed production over nongap areas of the forest. Blake and Hoppes (1986), in a mist net study of gaps in Illinois, reported more migratory frugivores, granivore-omnivores, and foliage gleaning insectivores in gap areas than in nongap areas.

Of the 10 species intensively studied in old growth at Moro Bottoms, four species showed a significant association with gaps (table 8): Carolina wren, Kentucky warbler, prothonotary warbler, and white-eyed vireo. As expected, these same species preferred areas with a more open canopy (table 9). Freemark and Collins (1992) included tufted titmouse and northern cardinal in a list of interior edge species, but excluded the Kentucky warbler. Noss (1991) also listed Carolina chickadee and red-bellied woodpecker as edge attracted species in Florida. Variation in affinities shown by species (Freemark and Collins 1992, Noss 1991) may be a result of differences in habitat across studies. Abundance and availability of gaps at Moro Bottoms may have made it difficult to discern the importance of internal patchiness by simply measuring distances to the nearest gap. Only those birds that spent most of the time in the gap interior showed statistically significant use. For the Kentucky warbler, included among forest interior species by Freemark and Collins (1992), the difference may be only in semantics. Kroodsma (1984) reported that the Kentucky warbler avoided edge, but there was no apparent reference as to whether canopy gaps were considered edge.

The white-eyed vireo was the only species that clearly selected individual gaps based on the amount of vegetative cover in the understory and midstory. Emlen and others (1986) listed the absence of dense low shrubs as the main environmental constraint on white-eyed vireos. Ford (1990) reported that white-eyed vireo density in Tennessee increased with increasing height of the herbaceous layer and increasing stem density. Outline drawings of the “niche-gestalt” for this species (James 1971) seemed to show that they preferred areas of open canopy with a dense low shrub cover. The white-eyed vireo was the only species whose territory contained a significantly greater proportion of canopy gaps (65 percent) than expected in Moro Bottoms (22 percent) (Smith and others 1993b). In contrast, the Acadian flycatcher appeared to avoid gaps by using areas with a closed canopy. Ford (1990) found Acadian flycatchers to be negatively correlated with shrub cover. Noss (1988) and Kroodsma (1984) also listed this species as avoiding edge.

Tree species, d.b.h., and height—The frequency distribution of tree species used by birds was significantly different from the available distribution for all avian species (table 12). This difference may be related to height of various tree species; for example, the white-eyed vireo perched most often in eastern hornbeam which rarely (if ever) reaches a height of 15 m. Acadian flycatchers seemed to prefer Carolina ash (*Fraxinus caroliniana*) and water elm (*Planera aquatica*). This preference may be site specific, associated with perching over water, which is where these tree species grow, rather than because of the attributes of the trees. One probable example of a strict preference for tree species in our study was the frequent use of swamp chestnut oak by the American redstart. Sweetgum and black gum were much more abundant in second-growth habitat (fig. 2), yet the American redstart was nearly always seen in swamp chestnut oak. Large leaves and dense foliage, which are typical of the swamp chestnut oak, presumably provide abundant foraging substrate, an attractive feature for insectivorous leaf-gleaning specialists such as the American redstart.

Ecological and Management Implications

The high avian diversity associated with undisturbed mature deciduous hardwood forests may be related to small, naturally occurring canopy openings, <2 ha, created by windstorms and fire. These canopy gaps are responsible for much of the foliage and structural variation within these forests (Urban and Smith 1989). Large logs and snags remaining after disturbance provide foraging and nesting substrate for numerous bird species of old-growth forests (Juday 1988, Thomas and others 1988). Approximately 14 species of Arkansas’ birds are associated with edge habitat created by canopy gaps (Shugart and James 1973).

In contrast, anthropogenic disturbances, such as timber management, typically occur more frequently, create larger forest canopy openings, and result in more extensive cumulative disturbance across landscapes than natural disturbance regimes (Runkle 1982, 1991). Larger gaps (i.e., >2 ha) created by most regeneration and some thinning operations may reduce species diversity by displacing canopy or area-sensitive species and allowing invasion of common early succession and edge species (Urban and Smith 1989). Clearcutting, the harvest method generally practiced in Arkansas, creates larger canopy openings with harder, external edges (Noss 1988) than natural disturbance processes. Consequently, breeding forest interior species that depend on larger expanses of continuous mature forests have declined in many portions of their historical range (Freemark and Collins 1992, Hamel and others 1998).

The potential exists to modify timber harvest practices to promote avian diversity (Thompson and others 1992). Uneven-aged stands resembling presettlement forests could perhaps be achieved with silviculture prescriptions such as single tree or small group selection, which produce relatively small canopy gaps. However, additional research is needed on the effects of gap size and interspersion across landscapes on bird habitat use, especially as it relates to

Table 12—Sample size (N), Kolmogrov-Smirnov test statistic (D), significance level (Prob > KS) and relative frequency (percent) of tree species[a] used by birds perching in old-growth and second-growth bottomland hardwoods, Moro Bottoms Natural Area, Arkansas, 1991 and 1992

Species	N	D[b c]	Prob >KS	CC	FC	LS	NS	QL	QM	TD	Other
Old growth											
Acadian flycatcher	25	0.9000	0.0031	21	24	—	6	—	—	12	12
Carolina chickadee	6	.9500	.0015	34	—	17	—	—	17	—	34
Downy woodpecker	5	.9500	.0180	20	—	40	—	—	—	—	40
Northern cardinal	13	.9000	.0004	45	—	15	8	8	—	8	16
Prothonotary warbler	34	.6272	.0075	42	15	3	—	6	—	3	30
Red-bellied woodpecker	11	.9000	.0011	9	—	36	9	9	27	—	9
Tufted titmouse	11	.9000	.0002	—	9	27	9	18	—	9	27
White-eyed vireo	28	.7000	.0124	34	5	5	—	—	—	—	57
Second growth											
Acadian flycatcher	15	.6875	.0200	19	13	13	—	—	—	25	31
American redstart	29	.6625	.0118	—	—	—	4	18	65	—	18
Carolina chickadee	9	.8125	.0032	—	—	22	22	—	—	11	44
Downy woodpecker	5	.9375	.0236	—	—	40	40	—	—	—	20
Northern cardinal	17	.6875	.0200	8	—	8	32	40	—	—	48
Prothonotary warbler	19	.6250	.0222	21	11	—	11	—	—	—	57
Red-bellied woodpecker	7	.9999	.0128	—	—	43	29	—	—	29	—
Tufted titmouse	9	.8125	.0131	22	—	11	33	22	11	—	—
White-eyed vireo	30	.5625	.0918	40	—	23	—	—	—	—	36

[a] CC = *Carpinus caroliniana;* FC = *Fraxinus caroliniana;* LS = *Liquidambar styraciflua;* NS = *Nyssa sylvatica;* QL = *Quercus lyrata;* QM = *Quercus michauxii;* TD = *Taxodium distichum;* O = other.

[b] Calculated from use sites and 93 random sites in the old-growth study site using the Kolmogrov-Smirnov test.

[c] Calculated from use sites and 96 random sites in the second-growth study area using the Kolmogrov-Smirnov test.

reproductive success. Only then can prescriptions be developed to minimize negative impacts of forest management on indigenous avifauna.

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SEASONAL HABITAT DISTRIBUTION OF SWAMP RABBITS, WHITE-TAILED DEER, AND SMALL MAMMALS IN OLD GROWTH AND MANAGED BOTTOMLAND HARDWOOD FORESTS

Winston P. Smith and Patrick A. Zollner[1]

Abstract—We studied swamp rabbits, white-tailed deer, and small mammals in an old-growth and adjacent second-growth and young-growth bottomland hardwood forest stands in southern Arkansas, August 1991–February 1993. Based on average home range size and degree of overlap, minimum and maximum density estimates of swamp rabbits were 31 per km^2 (no overlap) and 52 per km^2 (overlap), respectively. Pellet group estimates of white-tailed deer suggested that density varied from virtually zero in spring to 22 per km^2 during autumn. With 29,436 trap nights of total effort during winter, spring, and summer seasons, we captured 939 small mammals that were distributed among 14 species. There were more individuals (n = 445) of more species (S = 11) in old-growth forest than other habitats; more new animals were captured during spring (n = 378). *Peromyscus gossypinus* was clearly the most abundant species in all habitats during all seasons; but it was always more abundant in old growth than other habitats. *Ochrotomys nuttalli* was the only species that was notably more abundant in habitat other than old growth.

INTRODUCTION

European settlement and associated development during the last three centuries were responsible for dramatic alteration of forested landscapes. Some of the greatest losses occurred in forested wetlands, presumably because of an early dependence on waterways and the readily available rich and productive soils of associated floodplains. Within the Mississippi River floodplain alone, 80 percent of the historical forested acreage (8.5 million ha, Creasman and others 1992) was converted to agriculture or cleared for urban development (MacDonald and others 1979, Rudis and Birdsey 1986). So extensive has been the transformation that southern bottomland forests are viewed as an "endangered ecosystem" (Ernst and Brown 1989). Remaining forests occur as fragments (Rudis 1993) that have experienced a variety of timber harvests. Thus, all but an estimated 0.1 percent of presettlement old-growth bottomland hardwood forests have experienced significant anthropogenic disturbance (Smith and others 1993).

There are attributes of old-growth forests (Thomas and others 1988) largely absent from second-growth forests (Runkle 1981, 1991). In bottomland forests, appreciable differences are apparent between old-growth stands and old (ca. 100 year-old) second-growth forests (Robertson and others 1978). These include substantial differences in forest structure such as the presence of large, decadent trees, stem density and volume, canopy height and cover, understory herb and shrub cover, and coarse woody debris (Bailey 1993). These and other differences are important to the relative success of different plant species (Runkle 1991) and ultimately the diversity of habitats available within a hardwood forest community (Sherman 1978). Continued disturbance of old-growth deciduous forests alters species composition and structure and generally reduces species richness and habitat diversity (Sherman 1978).

Biological investigations of floodplain forests of North America have been limited to game species such as white-tailed deer (*Odocoileus virginianus*; see Halls 1984), swamp rabbit (*Sylvilagus aquaticus*; see Whitaker and Abrell 1986; Zollner and others 1996), or waterfowl (see Reinecke and others 1989). Nongame wildlife received little attention from researchers or land managers until recently (Burdick and others 1989, Wigley and Roberts 1994). Invertebrates, plants, and other indigenous biota contribute significantly to local and regional biological diversity, yet have been virtually ignored (Harris 1989, Sharitz and others 1992).

To adequately assess and credibly project future, additional (and probable cumulative) adverse impacts of land management on the biological diversity of this unique resource, baseline information on species distribution, relative abundance, life history characteristics, and habitat requirements is essential. Moreover, these baseline studies should include previously unmanaged and relatively undisturbed environments to ensure that "the entire ecological arena within which our biota evolved" (Smith and Hamel 1991:4) is represented, even though all that remains are fragments of old-growth southern bottomland hardwood forests.

This paper presents a community profile of mammals in southern bottomland hardwood forests. Specifically, we describe seasonal habitat distribution and relative abundance of several mammal species along an age gradient of old growth, intermediate second growth, and young growth (i.e., recent high-grade harvest) from two successive years of intensive sampling. Although this study was an unreplicated retrospective study, it effectively represents a substantial portion of the quantitative information available on the mammal fauna of southern bottomland hardwood forests.

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STUDY AREA

The study area was Moro Bottoms Natural Area, approximately 8 km east of Fordyce, AR (fig. 1). Moro Bottoms Natural Area is in the upper West Gulf Coastal Plain (James and Neal 1986) and contains a 40-ha old-growth bottomland hardwood forest along Moro Creek, in Section 10, T11S, R12W, Cleveland County, AR. The old-growth stand was part of a larger tract (ca. 70 ha) in Cleveland and Calhoun counties, under the joint stewardship of the Arkansas Natural Heritage Commission and the Arkansas Nature Conservancy.

The climate is typical of the Coastal Plain with hot and humid summers and a mean summer temperature of 27 °C. Mean annual rainfall is 123.4 cm with much of the rain occurring during spring. Portions of the study area adjacent to the creek are inundated periodically during spring and early summer, but water usually does not persist for more than a week at a time. Several sloughs and creeks join the main channel of the stream such that water is abundant throughout the study area. Elevation of the site ranges 48–51 m above mean sea level.

The Moro Bottoms site is an excellent example of an old-growth bottomland hardwood forest. Trees, especially sweetgum (*Liquidambar styraciflua*) and cherrybark oak (*Quercus falcata* var. *pagodifolia*), are quite large with exceptionally good form. Average density for overstory trees was 31 stems per ha, and average basal area was 35.0 m^2 per ha (153 ft^2 per acre; Smith and others 1995, Zollner 1993). Sweetgum, cherrybark oak, and willow oak (*Q. phellos*) are the three most common overstory species (Smith and others 1995, Zollner 1993).

Moro Bottoms provided an ideal opportunity to study mammals of unmanaged bottomland hardwood forest. Also, during August 1989 Moro Bottoms experienced a severe windstorm. Numerous windthrows occurred creating gaps in the overstory ranging in size from a single stem (0.01 ha) to about 0.3 ha. Because of these natural disturbances within old growth and the proximity to managed second-growth forests, the Natural Area presented an excellent setting to examine the effects of recent natural and anthropogenic disturbances on mammalian species habitat distribution and relative abundance.

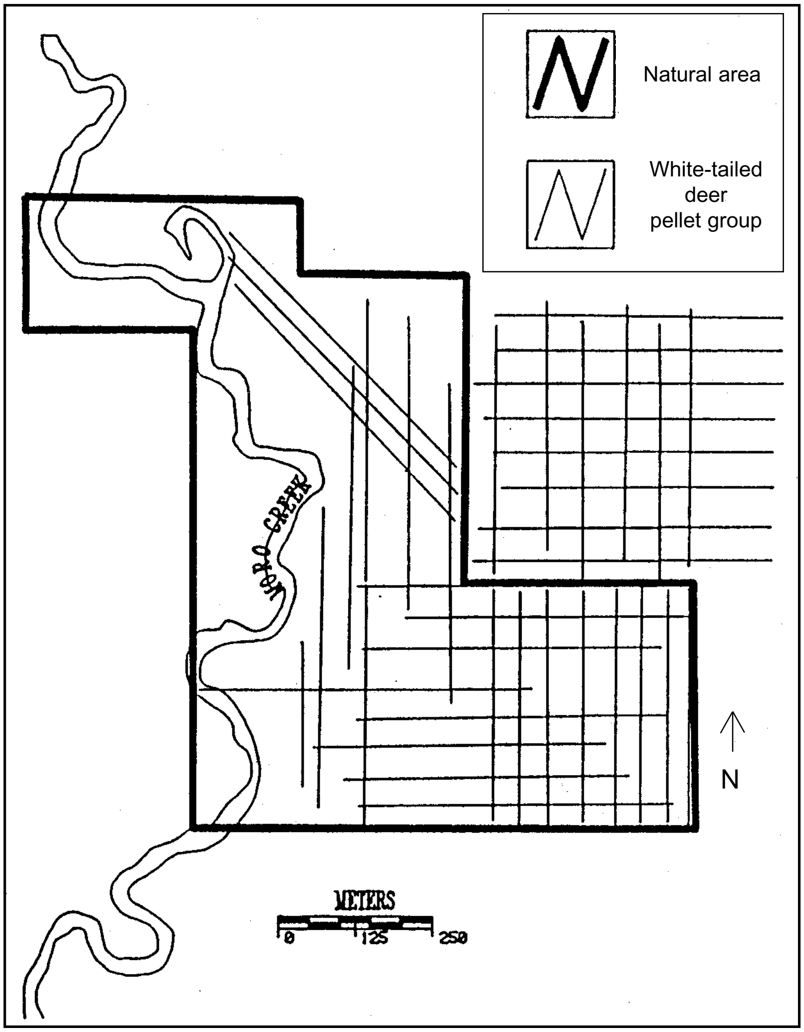

Figure 1—Distribution and orientation of deer pellet group transects, Moro Bottoms Natural Area, Cleveland County, AR.

METHODS

Swamp Rabbits

Capture and handling—Beginning on 12 January 1991, and continuing through 2 June 1991, from 60 to 145 traps were maintained and checked daily. These included 20 wire-mesh traps covered in shade cloth and 125 wooden box traps (20 X 20 X 60 cm). Eight drift fences were constructed and installed near clusters of box traps to enhance trapping success (Smith and others 1993, Zollner 1993).

Following capture, rabbits were weighed, identified to age (i.e., juvenile or adult) and sex, fitted with a 350-g radio-collar, and released. Each rabbit was allowed 1 week to adjust to its collar and recover from the stress of capture. Thus, observations of movements and habitat use began during the second week post-capture (Smith and others 1993, Zollner 1993).

Animal movements—It is important to monitor movements during all activity periods to accurately reflect habitat selection. However, it is difficult to determine the particular time when activity begins during different times of the year. Using the results of a detailed behavioral study as our basis (Marsden and Holler 1964), we selected 1830 as a conservative estimate of when evening activity should commence during any month of the year. Likewise, 0630 was selected as a time when rabbits continued to be active during all times of the year. Accordingly, the period between 0800 and 1700 was designated as the period during which rabbits would most likely be resting during all times of the year (Smith and others 1993, Zollner 1993).

Each rabbit was monitored daily between 0630 and 1830. Because the initial response of swamp rabbits to perceived threat is to remain motionless (Hamilton, 1955), we were often able to approach within a few meters of individuals and locate specific brush piles or thickets where the animal was resting. This procedure facilitated our locating rabbits consistently within an area defined by a 5–m radius. The difficulty of moving through the study area in the dark limited our ability to monitor rabbits at night. Twice each week, rabbits were located between 1830 and 0630.

Microhabitat use—During June and October of 1991, 36 quadrats in each of three study grids (fig. 2) were randomly selected and searched for signs of swamp rabbit browse. This sample size was calculated based upon variance (Stein 1945) in the density of browseable stems found during a pilot study (Zollner 1993). Quadrats were searched for browse by dividing them into quarters that correspond to the corners of the quadrat. Inside each quarter 15 0.5 X 0.5-m plots were placed systematically at 2-m intervals along three rows, 5 m apart. Inside each plot, number of browseable (available) stems and browsed (used) stems of each plant species were recorded. Browseable stems were defined as

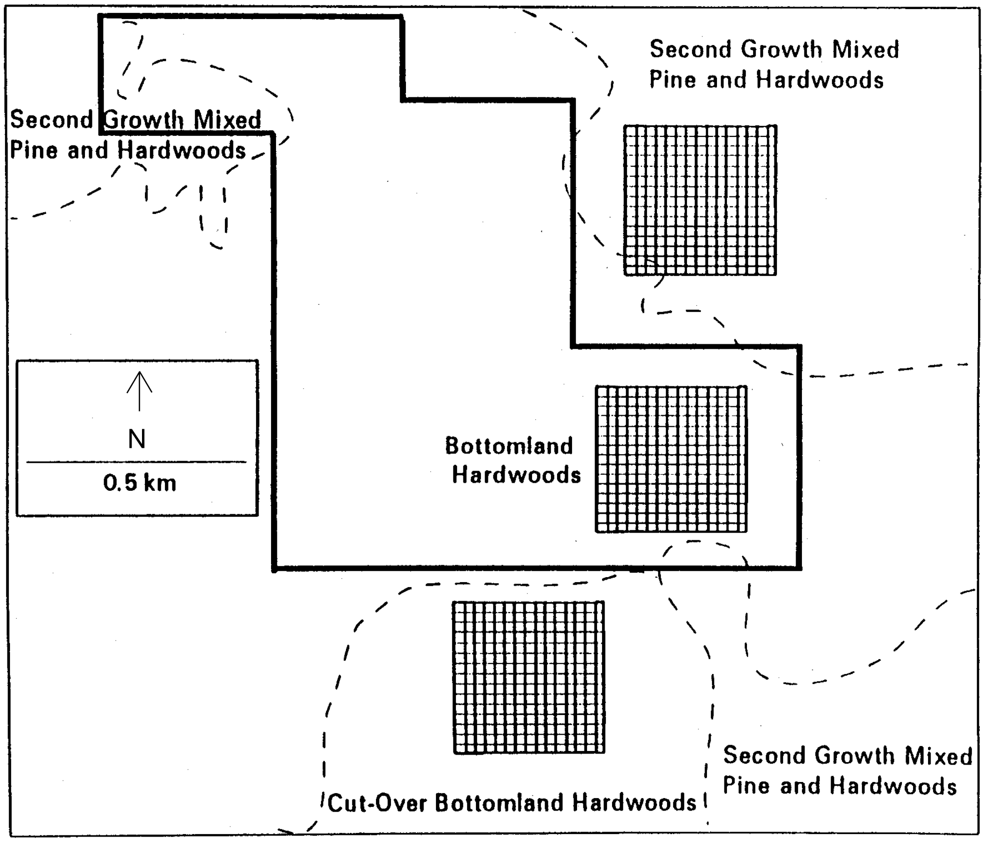

Figure 2—Location of old growth, second growth, and recently harvested (cut-over) bottomland hardwood small mammal trapping grids, Moro Bottoms Natural Area, Cleveland County, AR.

all vegetation less than 0.8 m above the ground and <1 cm in diameter. Stems were considered browsed by rabbits if they were cut off cleanly and not torn as is typical of white-tailed deer (Strole and Anderson 1990). All quarter sections where browse was observed in any plot were considered browsed for that survey and their locations were noted. During July and November of 1991, microhabitat characteristics were measured in each quadrat quarter where evidence of browsing was observed. Six characteristics were measured at each site where swamp rabbit browsing was observed and at randomly selected points in each habitat type. A 10-m north-south line transect intercepted the center of each habitat point, and was used to estimate the percent composition of herbaceous vegetation, shrub coverage, down treetops, and fallen logs at each site. The average value of spherical densiometer measurements (Vora 1988) at the center of each plot and 5 m from the center of each plot at 0, 90, 180, 270 degrees was used to estimate percent canopy closure at each site. A point-center-quarter method of habitat evaluation was used to approximate overstory basal area (Gysel and Lyon 1980). Trees >5 cm diameter at breast height (d.b.h.) with no branches from other trees over their crowns were considered in the overstory.

Density—Because of the small number of new captures and recaptures, we were not able to use a ratio-estimator to estimate population size and density. Instead, we present minimum population estimates that were derived from the average core area (i.e., maximum area where observed utilization distribution exceeds a uniform utilization distribution, Dixon and Chapman 1980) occupied by each adult female, adult male, and juvenile. In addition, we estimated density under the following assumptions: an average home range overlap of 25 percent among females and 50 percent between females and juveniles; and the entire study area was suitable swamp rabbit habitat.

White-Tailed Deer

Habitat use—We estimated seasonal use of gaps and forested habitats by white-tailed deer from counts of fecal pellet groups (Eberhardt and Van Etten 1956). This technique requires that observers remove or mark (e.g., spray paint) all pellets encountered along a predefined transect. The observer then returns to the transect after a predetermined period of time has elapsed and records the number of pellet groups that are encountered. Typically, the sequence of transects traversed during the marking or clearing phase is maintained during the enumeration phase so that the "elapsed time," i.e., time period between clearing and counting, is approximately the same for all transects (Neff 1968). Total number of pellet groups recorded among all transects provides an estimate of deer density according to the premise that white-tailed deer on the average defecate at a predictable rate. We used the summer (24 groups per day) and autumn-winter (31 groups per day) estimates for southern white-tailed deer (Sawyer and others 1990).

In this study, we conducted bimonthly censuses; months were alternated between years so that a 2–year period provided seasonal estimates that included every month. Also, transects were established in such a fashion as to incorporate forested habitats and gaps in proportion to their occurrence across the study area. We initially (December 1990) established 17 transects: four transects were 4 m X 0.25 km; the remaining transects were 4 m X 0.5 km (fig. 1). In July 1992, we added one 4 m X 325 m transect and eight 4 m X 350 m transects. Figure 1 illustrates the spatial distribution and orientation of transects across the study area. Chi-square was used to test the null hypothesis that occurrence of deer within habitats was according to availability (i.e., proportion of study area) of gaps and forested habitats (Byers and others 1984). We used an experiment-wide error rate of 0.05; comparison-wide error rate varied according to the number of comparisons and followed the procedures of Bonferroni adjustments (Byers and others 1984).

Small Mammals

Habitat distribution—We estimated seasonal species distribution and abundance across three bottomland hardwood habitats by live trapping for 2 years during spring, summer, and winter. Trapping began August 1991 and continued through February 1993. We established three 300 m X 300 m (9 ha) trapping grids, one each in old-growth, second-growth, and recently logged (cutover) bottomland hardwood forest habitats (fig. 2). A 15 X 15 array (i.e., 20–m spacing between traps) of Sherman (H.B. Sherman Traps Inc., P.O. Box 20267, Tallahassee, FL 32316) live traps (7.6 X 8.9 X 22.9 cm) was established on the forest floor of each grid. Superimposed on the existing grid in each habitat, we established a 3 X 3 array (100–m spacing) of elevated platforms (1.8 m) and a 5 X 5 array (60–m spacing) of wooden box traps on the forest floor. On each elevated platform, we placed a Sherman live trap and a wooden box trap (20 X 20 X 60 cm). All wooden box traps were equipped with a predator guard (Zollner, 1993)

Also, four "triad" arrays of 10 pitfall traps were installed, one midway on each of three sides (north, south, east), and one in the approximate center of each grid. Each triad array included a center pitfall trap and three drift fence "arms" radiating at about 120° angles from the center. Each triad arm was comprised of a center pitfall trap and a trap on each end, between which were two 10–m X 60–cm aluminum drift fences. Each pitfall trap was made of two No. 10 aluminum cans taped end-to-end; concrete "anchors" were bolted to the bottom of each pitfall trap to prevent water table pressure from expelling the cans.

Thus, each habitat grid contained 408 traps: 234 Sherman live traps, 34 wooden box traps, and 40 pitfall traps. General sampling protocol included the operation of all grids simultaneously during each season. On each grid, traps were checked once in the morning; Sherman and box live traps were baited with a mixture of rolled oats and vanilla extract. Each trapping session began during the approximate middle of each calendar season and continued continuously until we approached 100 percent recapture, or for a period not exceeding 10 days. Individuals were identified to species and sex, weighed, measured, uniquely marked, and released at the trap site. Small mammals (e.g. *Peromyscus* sp.) were toe-clipped using a standard procedure (Blair 1941); larger mammals (e.g., *Didelphis virginiana*) were marked with a numbered, self-piercing ear tag (National Band and Tag Company, Newport, KY) in both ears.

Species abundance was estimated seasonally as the number of individuals of each species captured on a habitat grid. Although total area contained within each grid was similar, number of captures was not an estimate of density because of movements of individuals from and to the grid during the sampling period (Van Horne 1982). For the purpose of estimating relative abundance, however, we assumed that the effective sampling area, i.e., total area supporting animals captured on a grid, did not vary across habitats.

RESULTS

An initial survey of the study area revealed that at the beginning of the study, about 25 percent of the old-growth tract was in windthrow gaps. Canopy openings ranged in size from 500 m^2 to 5000 m^2 with most of the gaps being less than 1500 m^2; about a third of the gaps were larger than 2500 m^2 (Smith and others 1995).

Swamp Rabbits

Density—From 12 January through 26 June 1991, 13,520 trap nights of effort were used to capture 13 swamp rabbits. Seven individuals, four adult females, one adult male, and two juveniles were large enough to carry a radio-transmitter for monitoring. A total of 107 nocturnal, 809 diurnal, and 308 crepuscular locations were recorded; 862 locations were recorded during spring-summer (summer) and 362 locations were recorded during fall-winter (winter).

Mean home range for adult females during the growing season (spring-summer) was 11.9 ha (29.3 acres), whereas the adult male had a summer home range of 19.9 ha (49.2 acres) and a juvenile home range was 5.6 ha (13.8 acres). Assuming no home range overlap among females or among males, nor between juveniles and males or females, with complete overlap of male and female home ranges, our minimum density estimate during the growing season was 8.4 adult females per km^2 (21.8 per mi^2), 5.0 adult males per km^2 (13 per mi^2), and 17.9 juveniles per km^2 (46.4 per mi^2).

With 25 percent overlap, the average exclusive area occupied by females becomes 8.9 ha (22.0 acres); for juveniles averaging 50 percent overlap, their exclusive core area is 2.8 ha (6.9 acres). Corresponding density estimates become 11.2 adult females per km^2 (29.1 per mi^2) and 35.7 juveniles per km^2 (92.8 per mi^2); adult male density estimates remain unchanged. Thus, minimum population size on the study area (40 ha) during the growing season was 13 swamp rabbits with perhaps as many as 21, if our estimates of home range overlap were reasonable.

Habitat use and microhabitat characteristics—The initial survey of the study area classified 27 percent of the quadrats as gaps with the remaining portion categorized as closed-canopy forest. All but five of 1,117 diurnal and crepuscular locations occurred in gaps. When compared to that expected according to the relative abundance of gaps (i.e., 27 percent of 1,117, or 302 locations) with a goodness-of-fit test (Zar 1984), we found that the probability of this occurring by random chance was very small ($\chi^2 = 2{,}978$, $P < 0.0001$). In some circumstances, mostly during crepuscular time periods, rabbits were first encountered in open, grassy areas; the vast majority of diurnal and crepuscular locations, however, were within resting/hiding places such as in large brushpiles or woody debris from windthrown trees, or inside a cavity in the bole of a down tree. Unfortunately, we were unable to classify nocturnal locations because of having to use triangulation rather than direct observations.

Microhabitat features of browsing sites used by rabbits during summer and winter are summarized in table 1 along with features measured at random sites. During the summer, stand density of the overstory at sites used by rabbits for browsing (42.0 stems per ha) was greater ($\chi^2 = 7.51$, d.f. = 1, $P < 0.01$) than at random sites (23.0 stems per ha). Understory basal area at browse sites (0.13 m^2 per ha) was less ($\chi^2 = 6.21$, d.f. = 1, $P < 0.025$) than that available across the study area (0.22 m^2 per ha). Also, midstory basal area at browse sites (2.35 m^2 per ha) was less ($\chi^2 = 4.28$, d.f. = 1, $P < 0.05$) than that recorded at random sites (2.78 m^2 per ha).

White-Tailed Deer

During the period December 1990—April 1992, 17 transects were sampled in the old-growth stand (48.4 ha) bimonthly; 14 transects were sampled in adjacent second-growth stands (26.4 ha). Beginning July 1992 and continuing through November, an additional nine transects were surveyed in the old-growth stand. The elapsed time (i.e., period between cleaning a transect and enumerating pellet groups) varied from 3 to 8 days across bimonthly sampling periods according to number of investigators and amount of flooding, but was similar among transects within a sampling period (fig. 3).

Density of white-tailed deer across the old-growth and second-growth stands varied considerably among bimonthly sampling periods (fig. 3). Throughout the study period, the study area (i.e., old-growth stand) received much more use during autumn-winter (x = 13.5 deer per km^2 [35.0 deer per mi^2]) than during spring-summer (x = 1.1 deer per km^2 [2.8 deer per mi^2]). Unfortunately, estimates were not available from March or April 1991 because >90 percent of the transects were flooded. Deer densities in the adjacent second-growth stand (fig. 2) showed the same seasonal patterns as that recorded in the old-growth stand (fig. 3). Deer densities recorded during March and April in the second-growth stand (of which <25 percent was inundated) were typical of spring-summer values in the old-growth habitat (fig. 3).

Frequency of occurrence of white-tailed deer in gaps or closed-canopy forest in the old-growth stand or in an adjacent second-growth stand is summarized in table 2. In table 3, frequency of occurrence of white-tailed deer in canopy gaps or closed-canopy forest across old-growth and adjacent second-growth stands is presented. The latter provides insight into how deer used the old-growth stand relative to surrounding available forest habitat.

Table 1—Mean (×) and standard error ($\times_s$) of microhabitat features of random sites and sites where rabbits were observed browsing, Moro Bottoms Natural Area, AR, February 1991–March 1992 (χ^2 statistic is from a non-parametric analysis of variance.)

Variable	Random site		Browse site			
	×	$\times_s$	×	$\times_s$	χ^2	$P > \chi^2$
			Summer			
	(n = 46)		(n = 30)			
Percent cover dead						
Wood <5 cm	3.13	1.21	8.37	2.55	2.13	0.250
Wood >5 cm	3.01	1.79	3.36	1.88	0.09	.750
Shrub cover %	9.83	2.91	8.19	1.68	.01	.900
Bare ground %	68.23	5.74	73.85	3.13	.01	.900
Herbaceous cover %	28.77	5.29	26.11	3.13	.23	.750
Basal area (m^2 per ha)						
Overstory	34.66	2.36	37.16	2.17	.36	.750
Midstory	2.78	0.45	2.35	0.31	4.28	.050
Understory	0.22	.40	0.13	.03	6.21	.025
Density (stems per ha)						
Overstory	23.0	2.03	42.0	5.74	7.51	.010
Midstory	137.0	38.65	118.0	13.31	.26	.750
Understory	397.0	67.21	483.0	131.07	.61	.750
Canopy closure	75.9	2.63	80.8	1.94	3.45	.100
Herbaceous density (stems per m^2	9.2	1.36	10.9	1.09	.87	.750
			Winter			
	(n = 53)		(n = 48)			
Percent cover dead						
Wood <5 cm	5.31	1.75	3.78	2.06	.41	.500
Wood >5 cm	1.77	.62	1.59	.66	.03	.750
Shrub cover %	4.86	1.65	9.50	4.63	.09	.750
Bare ground %	80.96	3.83	79.73	5.24	1.19	.250
Herbaceous cover %	11.83	2.14	13.82	3.48	.06	.750
Basal area (m^2 per ha)						
Overstory	35.34	1.82	36.00	2.58	.11	.500
Midstory	1.86	.23	1.40	.22	.74	.250
Understory	.09	.02	.10	.03	.04	.750
Density (stems per ha)						
Overstory	31.0	6.70	23.0	3.23	.03	.750
Midstory	234.0	49.22	147.0	20.32	.73	.250
Understory	418.0	143.03	240.0	42.59	.71	.250
Canopy closure	28.5	1.84	32.7	3.72	1.08	.250
Herbaceous density (stems per m^2)	5.3	.77	8.3	1.78	1.36	.750

Generally, white-tailed deer used gaps and closed-canopy forest in proportion to availability ($\chi^2 < 3.84$, d.f. = 1 $P > 0.05$) across the old-growth study area and in an adjacent second-growth stand   Notable exceptions occurred in the old-growth stand during April 1992 ($\chi^2 = 6.4$, $P < 0.025$) and June 1992 ($\chi^2 = 4.3$, $P < 0.05$) when deer used gaps more frequently and closed-canopy forest habitat less frequently than expected from availability. Also, percent use of canopy-gaps in the second-growth stand during February 1992 was greater ($\chi^2 = 6.9$, $P < 0.01$) than expected. Although a similar pattern occurred in the old-growth stand, it was not quite significant ($\chi^2 = 2.9$, $0.05 < P < 0.10$), probably because of the effect that inundation had on area sampled (table 2) and the sample size of pellet groups.

When examined from the perspective of bimonthly distributions in habitats across both stands, deer appeared to depart (i.e., $\chi^2 > 7.82$ $P < 0.05$) more from the expected

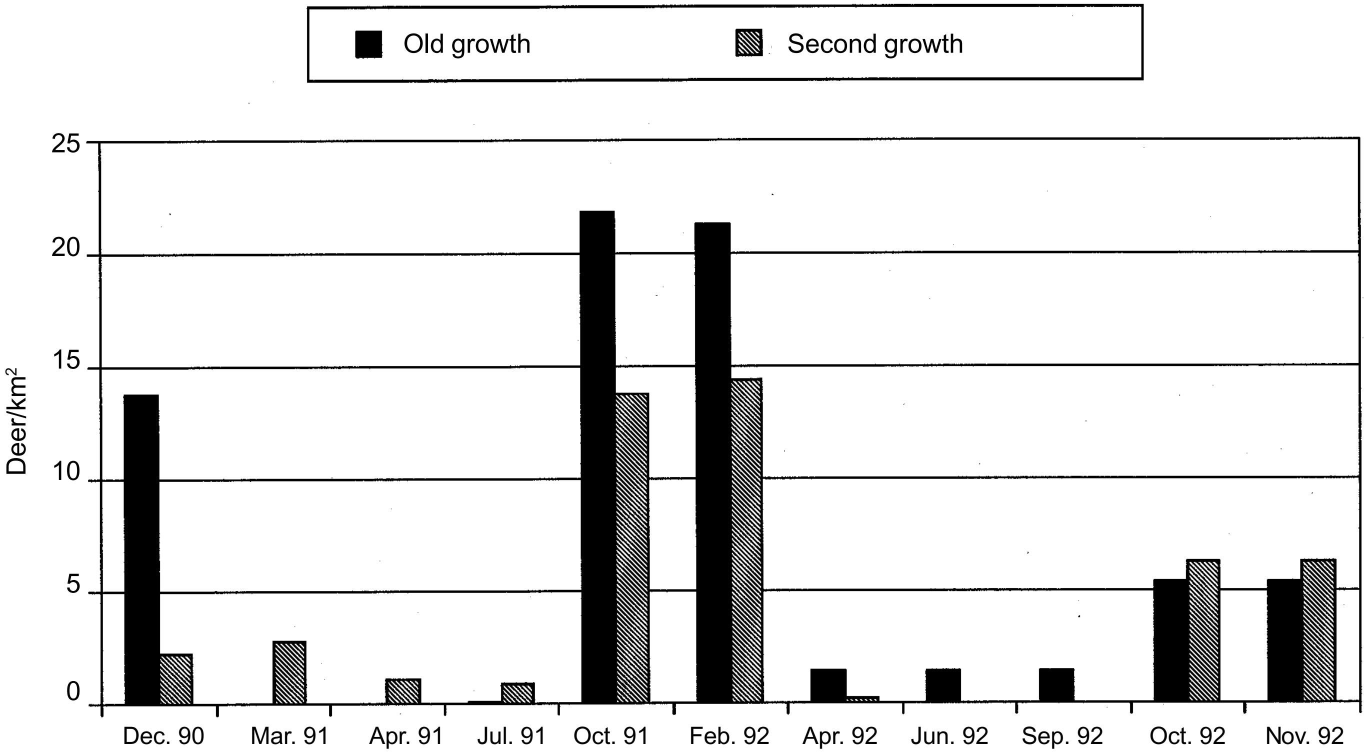

Figure 3—White-tailed deer density from bimonthly pellet group counts in bottomland hardwood forest, Moro Bottom Natural Area, AR, December 1990–November 1992.

Table 2—Relative abundance (percent occurrence) of white-tailed deer in closed-canopy forest and canopy openings (gaps) in bottomland forest, Moro Bottoms Natural Area, AR, December 1990–November 1992 (percentages computed for within habitat totals; Chi-square statistic [χ^2] computed for goodness-of-fit test, d.f. = 1)

	Old growth					Second growth				
	Availability		Use			Availability		Use		
Month per year	Gaps	Forest	Gaps	Forest	χ^2	Gaps	Forest	Gaps	Forest	χ^2
December 1990	8.5	91.5	12.0	88.0	0.2	10.3	89.7	0.0	100.0	0.4
March 1991	—	—	—	—	—	10.3	89.7	23.0	77.0	.2
April 1991	—	—	—	—	—	10.3	89.7	.0	100.0	.6
July 1991	18.8	81.2	0.0	100.0	.1	10.3	89.7	.0	100.0	.6
October 1991	18.8	81.2	17.3	82.7	.2	10.3	89.7	11.5	88.5	.3
February 1992	18.8	81.2	32.0	68.0	2.9	10.3	89.7	22.2	77.8	6.9
April 1992	18.8	81.2	50.0	50.0	6.4	10.3	89.7	.0	100.0	.1
June 1992	18.8	81.2	100.0	0.0	4.3	10.3	89.7	.0	0.0	.0
September 1992	18.8	81.2	50.0	50.0	1.3	10.3	89.7	33.3	66.7	1.7
October 1992	18.8	81.2	16.7	83.3	.1	10.3	89.7	7.1	92.9	.3
November 1992	18.8	81.2	12.0	88.0	.8	10.3	89.7	3.6	96.4	1.3

Table 3—Relative abundance (percent occurrence) of white-tailed deer in closed-canopy forest and canopy openings (gaps) in bottomland forest, Moro Bottoms Natural Area, AR, December 1990–November 1992 (percentages computed for across habitat totals; Chi-square statistic [χ^2] computed for goodness-of-fit test, d.f. = 3)

	Old growth				Second growth				
	Availability		Use		Availability		Use		
	Gaps	Forest	Gaps	Forest	Gaps	Forest	Gaps	Forest	χ^2
December 1990	4.6	49.4	6.0	78.6	1.4	44.7	0.0	15.4	32.0
March 1991	—	—	—	—	10.3	89.7	23.0	77.0	4.3
April 1991	—	—	—	—	10.3	89.7	.0	100.0	.6
July 1991	12.0	52.0	0	20.0	3.7	32.3	.0	80.0	4.5
October 1991	12.0	52.0	15.1	71.9	3.7	32.3	1.5	11.5	45.6
February 1992	12.0	52.0	11.4	24.3	3.7	32.3	14.3	50.0	38.4
April 1992	12.0	52.0	45.5	45.5	3.7	32.3	.0	9.0	12.6
June 1992	12.0	52.0	100.0	0.0	3.7	32.3	.0	0	7.3
September 1992	12.0	52.0	20.0	20.0	3.7	32.3	20.0	40.0	6.9
October 1992	12.0	52.0	10.0	2.9	3.7	32.3	50.0	37.1	1.0
November 1992	12.0	52.0	5.7	41.5	3.7	32.3	1.9	50.9	9.2

null model (table 2). In particular, deer used closed-canopy, old-growth forest more often (χ^2 = 14.5, d.f. = 1, $P < 0.001$) and closed-canopy, second-growth forest less often (χ^2 = 16.0, d.f. = 1, $P < 0.001$) than expected in December 1990. This pattern occurred again during early autumn (October) 1991 (old-growth: χ^2 = 15.1, d.f. = 1, $P < 0.001$; second-growth: χ^2 = 26.4, d.f. - 1, $P < 0.001$). Conversely, deer used closed-canopy second-growth forest more often during autumn (November) of 1992 (χ^2 = 5.8, d.f. = 1, $P < 0.01$) while showing proportional use among other habitats. During February 1992, deer mostly occurred in the second-growth stand with greater than expected use of both gaps (χ^2 = 21.2, d.f. = 1, $P < 0.001$) and closed-canopy forests (χ^2 = 6.8, d.f. = 1, $P < 0.01$). This pattern was reversed in the following spring (April) when deer occurred almost exclusively within the old-growth stand (table 4), with a significant preference for canopy gaps (χ^2 = 10.2, d.f. = 1, $P < 0.01$).

Small Mammals

During the study, 29,436 trap nights of effort were equally distributed across habitats as follows: summer—2,396 trap nights; winter—8,520 trap nights, and spring—8,520 trap nights. We captured a total of 871 terrestrial small mammals distributed among 9 species (table 4); we also captured 2 southern flying squirrels (*Glaucomys volans*), 6 gray squirrels (*Sciurus carolinensis*), 1 fox squirrel (*S. niger*), 51 opossum (*Didelphis virginiana*), and 8 raccoons (*Procyon lotor*). More animals were captured during spring (n = 378) than either winter (n = 330) or summer (n = 231). Old growth produced the largest number of new captures (n = 445) and species (S = 11), whereas second growth produced the fewest new captures (n = 183).

Mammal species composition of habitats varied across seasons and years. The cotton mouse (*Peromyscus gossypinus*) was clearly the predominant species during all seasons and across all habitats (table 4); it was more abundant in old-growth habitat during all seasons. The only other small mammals that were consistently captured across habitats and seasons were hispid cotton rat (*Sigmodon hispidus*) and golden mouse (*Ochrotomys nuttalli*). The golden mouse was the only small mammal species that was notably less common in old growth as compared to the other habitats (table 4).

There were limited data, but some interesting variation in platform captures of terrestrial small mammals was apparent. During spring 1992, relatively heavy rainfall occurred at the end of the trapping session. During the initial 4 days of trapping, when there was no measurable precipitation, we captured 11 *Peromyscus gossypinus* in elevated platform traps; no other species were recorded. Results from one night of trapping following and during rainfall yielded 19 *P. gossypinus* and 2 *Ochrotomys nuttalli*. Nine *P. gossypinus* were recaptures of individuals previously caught in forest floor traps; the other 10 platform captures were unmarked *P. gossypinus*. When we examined data from the 9 nearest forest floor traps (i.e., surrounding 3 X 3 array), in only one instance did we find >1 trap occupied. In that one instance, there were four occupied traps.

Another interesting anecdote was a dramatic increase in the number of gray squirrels captured during April—May 1991. While trapping swamp rabbits with wooden box traps on the forest floor, we captured squirrels at a rate that was an order of magnitude greater than previously observed during this study. Typically, efforts to capture swamp rabbits during this study averaged 1 to 2 gray squirrels per week. After 2 to 3 weeks of catching notably more gray squirrels, comparable trapping efforts again yielded about 1 to 2 gray squirrels per week. A relatively large proportion of the gray squirrels was represented by juveniles, suggesting perhaps that the sudden increase in number of captures was related to dispersal.

DISCUSSION

Assumptions and Limitations

The Moro Bottoms Natural Area and adjacent private lands represented a natural laboratory and unique opportunity to examine small mammal communities across a variation of unmanaged and managed bottomland hardwood forests. Unfortunately, this was not a replicated experiment and thus one should be cautious about drawing general inferences beyond our study.

Sources of error in this study included escape of captured individuals before confirming whether they were new captures. Unconfirmed small mammal captures occurred infrequently (≤1 per grid per season). We recorded them as new animals and thus may have over-estimated relative abundance of some species. Another potential source of error was misidentification of *Peromyscus gossypinus* and *P. leucopus*, which are extremely difficult to differentiate in the field (Lowery 1974, St. Romain 1976). Adult *P. gossypinus* were relatively easy to recognize in this study because their weights clearly exceeded the maximum reported for *P. leucopus* (36 g; Sealander and Heidt 1990). The primary difficulty was determining whether smaller (<35 g) individuals were juvenile *P. gossypinus* or adult *P. leucopus*. Pelage of juvenile and adult *Peromyscus* typically differ, but variation exists and opportunities for confusion are not uncommon (St. Romain 1976, Lowery 1974). Consequently, we likely misclassified some individual *Peromyscus*.

Swamp Rabbit

Density—The swamp rabbit is confined to southern bottomland forests of the Southeastern United States (Chapman and others 1982). Historically, its range extended from east Texas to extreme northeast South Carolina, and from southern Illinois and extreme southwestern Indiana, to the coast of the Gulf of Mexico. The lower Mississippi Alluvial Valley (MAV) likely was a center of abundance for

Table 4—Seasonal abundance of small mammals in old-growth (OG), second-growth (SG), and young-growth (YG) bottomland hardwood forest, Moro Bottoms Natural Area, AR, during the period August 1991–February 1993

	Summer			Winter			Spring		
Species	OG	SG	YG	OG	SG	YG	OG	SG	YG
					1991–92				
Peromyscus gossypinus cotton mouse	42	21	24	56	24	28	48	23	25
Peromyscus leucopus white-footed mouse	0	0	1	0	0	0	3	2	0
Sigmodon hispidus hispid cotton rat	3	0	2	0	0	0	2	0	3
Ochrotomys nuttalli golden mouse	0	8	0	0	2	2	0	10	0
Reithrodontomys fulvescens fulvous harvest mouse	1	1	3	0	1	4	0	0	0
Microtus pinetorum woodland vole	0	0	1	0	0	0	0	0	0
Cryptotis parva least shrew	1	0	0	0	0	0	0	0	0
Blarina carolinensis southern short-tailed shrew	2	1	0	0	0	0	0	0	0
Sciurus carolinensis gray squirrel	0	0	0	0	0	0	0	0	0
Sciurus niger fox squirrel	0	0	0	0	0	0	0	0	0
Glaucomys volans southern flying squirrel	0	0	0	0	0	0	0	2	0
Didelphis virginiana opossum	4	9	1	1	1	0	2	1	0
Procyon lotor raccoon	1	0	0	0	0	0	0	0	0
Rattus rattus black rat	1	0	0	0	0	0	0	0	0
Totals	55	40	31	57	28	34	55	38	28

continued

Table 4—Seasonal abundance of small mammals in old-growth (OG), second-growth (SG), and young-growth (YG) bottomland hardwood forest, Moro Bottoms Natural Area, AR, during the period August 1991–February 1993 (continued)

	Summer			Winter			Spring		
Species	OG	SG	YG	OG	SG	YG	OG	SG	YG
				1992–93					
Peromyscus gossypinus cotton mouse	33	17	16	74	15	71	118	14	79
Peromyscus leucopus white-footed mouse	1	0	0	0	0	0	6	0	3
Sigmodon hispidus hispid cotton rat	4	0	7	8	4	6	10	0	10
Ochrotomys nuttalli golden mouse	1	0	0	2	6	9	0	4	2
Reithrodontomys fulvescens fulvous harvest mouse	0	0	2	0	0	0	0	0	1
Microtus pinetorum woodland vole	0	0	0	0	1	0	0	0	0
Cryptotis parva least shrew	0	0	0	0	0	0	0	0	0
Blarina carolinensis southern short-tailed shrew	2	0	0	0	0	0	0	0	0
Sciurus carolinensis grey squirrel	1	2	0	0	0	0	1	2	0
Sciurus niger fox squirrel	0	0	0	0	0	0	1	0	0
Glaucomys volans southern flying squirrel	0	0	0	0	0	0	0	0	0
Didelphis virginiana opossum	3	6	5	7	4	2	3	1	1
Procyon lotor raccoon	2	1	2	1	0	0	0	0	1
Rattus rattus black rat	0	0	0	0	0	0	0	0	0
Totals	47	26	32	92	30	89	139	21	97

this species; indeed, the MAV historically included 65 percent of all southern bottomland forests (Smith and others 1993) and perhaps as much as 80 percent of the bottomland forests in the range of Sylvilagus aquaticus.

In recent years, the distribution of the swamp rabbit has diminished southward (Chapman and others 1982) and population levels have decreased (Korte and Fredrickson 1977), presumably because of habitat loss and fragmentation. In Missouri, Korte and Fredrickson (1977) reported a decrease in distribution and abundance of this species that coincided with the reduction of potential habitat from 850,000 ha in 1870 to fewer than 40,000 ha in 1973. Conversion of bottomland forests to row crops and urbanization continued on into the mid–1980's (Rudis and Birdsey 1986); recall, 80 percent of the bottomland forests in the lower MAV has been lost since European settlement. Comparable loss of potential habitat was reported for other portions of the range of this species (Whitaker and Abrell 1986). Consequently, the swamp rabbit is listed as a species of special concern in Illinois, Indiana, Kentucky, and Missouri.

In Indiana, Whitaker and Abrell (1986) attributed the decline of swamp rabbits to four factors: (1) loss of available habitat, (2) hunting pressure, (3) flooding, and (4) predator pressure. Also, landscape context was listed as an important factor determining long-term viability of swamp rabbit populations. Apparently, populations occupying prime habitat nearby are important as sources for marginal, less suitable habitat, which may support swamp rabbits in good years.

Little information exists regarding historical or current densities of swamp rabbit populations across its geographical range. Terrel (1972) reported an autumn density of 0.4 per ha (40 per km^2) in Indiana, with individuals typically requiring a home range of 4.4 ha. More recently, Whitaker and Abrell (1986) reported that an estimated 80 rabbits were distributed across 10 sites totaling 700 acres (283.4 ha), which represents an average density of 0.28

rabbits per ha (28.2 per km^2). In this study, the minimum density estimate during the growing season was 31.3 per km^2 (0.31 per ha); average home range (100 percent) during this period was 19.8 ha (Smith and others 1993, Zollner 1993). Our less conservative estimate (i.e., assuming 25 percent overlap in home range among females and 50 percent overlap between females and juveniles) of swamp rabbit density approached 52 rabbits per km^2 (0.52 per ha). Given the observed overlap in home ranges among females, and between females and juveniles (Smith and others 1993, Zollner 1993), we suspect that swamp rabbit density during our study was greater than the minimum 0.31 per ha; and perhaps was not very different from that reported for Indiana (Terrel 1972).

Nevertheless, it is difficult to ascertain whether densities observed in this study (or reported in the literature) represented low, intermediate, or high population levels. If frequency of encountering pellet groups or incidental direct observations are indicative of population levels, Moro Bottoms Natural Area supported a conspicuously lower density of swamp rabbits than Delta Experimental Forest, an essentially contiguous 1050–ha tract of secondary bottomland forests within the Mississippi River floodplain, near Stoneville, Washington County, MS (W.P. Smith, personal observation). Behavioral experiments and other observations conducted during this study support the hypothesis that swamp rabbit latrines (i.e., pellet groups) represent territorial markers (Zollner and others, in press) and thus, are probably a fair indication of relative abundance.

Habitat use—One of the earliest investigations of this species (Harrison and Hickie 1931) concluded that *S. aquaticus* was associated with canebrakes, hence the common name “cane cutter.” Whitaker and Abrell (1986) later reported that good swamp rabbit habitat included cane (*Arundinaria gigantea*), or elderberry (*Sambucus canadensis*) on elevated areas with sufficient cover and protected from most flooding. They noted that several tree species were common among these sites: sugarberry (*Celtis laevigata*), hackberry (*C. occidentalis*), silver maple (*Acer saccharinum*), hickories and pecan (*Carya laciniosa*, *C. cordiformis*, *C. p*ecan [*illinoensis*]) elms (*Ulmus* spp.), ashes, (*Fraxinus* spp.), sweetgum, cottonwood (*Populus deltoides*), sycamore (*Platanus occidentalis*), oaks, and boxelder (*Acer negundo*).

Although it varied considerably, giant cane was common in portions of Moro Bottoms, especially where the canopy previously had been interrupted. Generally, swamp rabbits were observed more often where cane occurred than expected; but it is unclear as to whether this was a causal relationship, or if the co-occurrence of swamp rabbits and cane are ecological correlates of some other phenomenon, i.e., response to an interruption of the forest canopy. Clearly, swamp rabbits occurred in canopy gaps much more frequently than would be predicted from availability; but many gaps did not have cane. The close association of swamp rabbits with cane in Indiana (Harrison and Hickie 1931, Whitaker and Abrell 1986) was also likely a circumstance where two bottomland hardwood endemics with similar ecological requirements occupied the same habitat rather than an obligate, or even facultative, relationship.

Similar to Whitaker and Abrell (1986), we observed greater than expected occurrence of certain tree species at sites used by swamp rabbits, especially at browsing sites (Zollner 1993). Many of the species were similar to those reported by Whitaker and Abrell (1986), notably elms, hickories, and oaks. Since swamp rabbits typically do not use soft or hard fruit, nor do they have any known needs affiliated with certain tree species, we suspect that these associations are reflecting common favorable environmental circumstances rather than any life history need. One notable exception is the predisposition that certain tree species have for forming bole or buttress cavities, which may offer ideal refuge against predation or inclement weather. Red maple was identified in lowland sites as a cavity-prone species (W.P. Smith, unpublished data).

Some tree species were observed less often at browse sites than random sites, notably black gum, Carolina ash, shellbark hickory, and Nuttall oak (Zollner 1993). But again, this is probably a coincidence related to specific habitat needs. Microsite distribution of many bottomland tree species is often influenced greatly by smal1 (10–20 cm) variations in elevation (Castleberry and others 1996, Pauley and others 1996, Putnam and others 1960). Many of the tree species that occurred less frequently at sites where rabbits were observed foraging (as compared to random sites) typically occur at lower elevations (e.g., Nuttall oak vs. water oak, Zollner 1993) where flooding occurs more frequently and for longer periods. Conversely, loblolly pine was three times more likely to occur at sites used by rabbits for foraging as compared to random sites. Loblolly pine typically occurs on the highest sites within a floodplain, usually on a small, elevated knoll.

Thus, it may be that the seasonal schedule of inundation to a large extent dictates habitat use by swamp rabbits by limiting the availability of the more hydric habitat types, especially during winter and early spring. Strole and Anderson (1992) clearly demonstrated that use of browse resources by a mammalian herbivore is directly related to the availability of those resources. That flooding in Moro Bottoms Natural Area restricted access to portions of individual home ranges, or availability of resources, was supported by the behavioral response of swamp rabbits to inundation (Zollner 1993). During periods of prolonged flooding, swamp rabbits with home ranges near the adjacent, upland pine per hardwood forest moved into the uplands until the water receded. Individuals on the western portion of the study area restricted their movements, remaining on patches of small, elevated ridges.

If inundation frequently imposes restrictions on the use of resources within a floodplain, such as often happened in Moro Bottoms Natural Area, then the quality of swamp rabbit habitat may be as much dependent on the nature of adjacent upland sites as the species composition and structure of the more hydric forest associations. Moreover, when these ecological bottlenecks occur during periods of resource impoverishment, such as in winter and early spring, short-term carrying capacity and long-term population viability are directly linked to frequency and duration of perennial flooding and the quality of adjacent elevated habitat, respectively. Whitaker and Abrell (1986) reported that elevated areas that were protected from most flooding represented an important feature of good swamp rabbit habitat. It appears that the landscape context of bottomland forests may be an equally important feature of swamp rabbit habitat, especially where minor bottoms (i.e., bottomland forests of relatively narrow streams and floodplains) occur in an agriculture-dominated landscape or matrix of upland, even-aged pine forests.

White-Tailed Deer

Natural history—The white-tailed deer has an almost ubiquitous distribution in the coterminous United States with a geographic range that extends into southern Canada and south to northern South America (Smith 1991). Among forest biomes, the density of white-tailed deer generally is directly related to the number of forest openings. In the Southeast, bottomland hardwood forests of the Coastal Plain produce some of the highest quality food for white-tailed deer, which attain densities of 25 deer per km^2. Bottomland forests adjacent to agricultural row crops, such as soybean, can support substantially higher densities of white-tailed deer. Where agricultural crops add significant amounts of nutrients to their diet, deer are much larger and local populations can be more than twice the density of comparable areas without row crops nearby (Smith 1991). Although early regeneration stands offer much variety and biomass of herbaceous and woody forage, the lowest quality foods in the Southeast occur in homogeneous loblolly pine and slash pine (*Pinus elliottii*) forests (Newsom 1984).

White-tailed deer allocate more time to feeding than any other activity. Significant seasonal shifts in center of activity often occur in response to local changes in food availability. Generally, grasses and forbs dominate the diet during spring and early summer; as herbs mature, deer switch to succulent, new-growth leaves and twigs. During autumn, soft and hard fruit (e.g., berries and acorns, respectively) predominate in the diet, including fruits of beech, *Smilax* spp., *Crataegus* spp., *Vaccinium* spp. *Rhus* spp., *Vitis* spp., *Rubus* spp., and *Pyrus* spp. Winter diets are determined largely by availability. Dried leaves of deciduous trees, sedges, grasses, mushrooms and other fungi, and woody browse comprise a large proportion of the diet (Smith 1991).

Habitat distribution and density—In this study, use of old-growth bottomland hardwoods by deer varied seasonally with the greatest use occurring during autumn (table 2). Even then, densities were about one-half the average reported for southern bottomland forests (Smith 1991). Although it is uncertain why deer density in the old-growth stand was less than expected, we suspect it was at least in part related to the landscape context of Moro Bottoms Natural Area (Castleberry and others, in press). Moro Bottoms is a segment of a relatively narrow, riparian corridor that dissects a landscape of intensively managed timberland, mostly even-aged stands of loblolly pine. This habitat represents one of the poorest quality environments for white-tailed deer, typically supporting from one-third to one-fifth the density of deer that can be sustained in bottomland forests (Newsom 1984).

The pattern of seasonal use observed in our study (table 2) is probably typical of deer inhabiting minor bottoms (Castleberry and others, in press). White-tailed deer of the Coastal Plain will often make short-distant movements (as opposed to migrations elsewhere) in response to changes in the abundance of local food resources. Because of the importance of acorns as a high-energy food item during autumn, deer in this study were probably attracted to the bottoms during October 1991 to exploit a va1uable but ephemeral resource. That deer did not concentrate in the bottoms in November 1992 (table 2) may have been related to early, prolonged periods of inundation. When prolonged flooding occurs in early autumn, acorns that otherwise would be easily accessible are either submerged or washed away. Alternatively, acorns may not have been readily available because 1992 was a poor year for acorn production.

Few deer used the old-growth or second-growth bottomland hardwood stands during spring or summer (table 2). Again, this was probably related to food availability. Although even-aged loblolly pine stands offer little in the way of palatable forage, nearby (<1 km) young regeneration stands probably provided a greater abundance of better quality forage than was available in the bottomland forests. Indeed, deer use of the bottoms was in early succession habitat of forest gaps where one would expect to find more palatable herbaceous and woody new-growth during this period.

Small Mammals

Species habitat distribution and abundance—According to season, Peromyscus gossypinus comprised 50–98 percent of new captures across habitat grids (fig. 2). In 12 of 18 samples (3 habitats X 3 seasons X 2 years), $\geq$70 percent of new captures were *P. gossypinus*. Its prevalence was most apparent in old-growth habitat, especially during winter and spring (table 4). Its abundance in second-growth habitat was less than in old growth with new captures often less than 50 percent of that recorded on the old-growth grid. The cut-over site supported comparable (1991–1992) or greater numbers (winter and spring 1992–1993) of *P. gossypinus* than did second-growth habitat (Table 4).

Peromyscus gossypinus is primarily an inhabitant of moist forest habitats, especially common within dense underbrush along streams and throughout bottomland hardwood forest (Sealander and Heidt 1990). Where *P. gossypinus* and *P. leucopus* are sympatric, *P. gossypinus* typically diminishes in abundance along a mesic-xeric gradient (St. Romain 1976); it is absent from drier upland forest types (Sealander and Heidt 1990). *Peromyscus gossypinus* nests in hollow stumps, tree cavities, or beneath logs.

Old-growth forests possess many characteristics that are absent in second-growth forest (Runkle 1991). In bottomland forests, even older (ca. 100 year-old) second-growth stands lack many of the features typical of their old-growth counterparts (Robertson and others 1978). Abundant snags, dead or dying tree limbs, and coarse woody debris, typical of old-growth forest (Harmon and others 1986, Thomas and others 1988), contribute critical nesting microhabitat components and provide an array of substrates within which a plethora of invertebrates proliferate (Bailey 1993, Savely 1939). Moreover, natural disturbances and regeneration typical of old-growth gap dynamics (Runkle 1991) contribute significantly to habitat diversity (Sherman 1978).

Variation between old-growth and second growth bottomland hardwood forest in abundance of *P. gossypinus* can probably be explained by many of the habitat differences outlined above. However, the second-growth grid also included some drier, upland forest habitat components. Elevational differences between adjacent lowland habitats were probably important during periods of inundation as the second-growth grid rarely became flooded. Although *P. gossypinus* is arboreal and apparently can move vertically in response to heavy rainfall, many individuals may be forced to move to higher sites during periods of prolonged flooding (Andrzejewski 1963). Temporary immigrants may be more susceptible to live capture as they are presumably pressed to search for food. The lowest capture rates in second growth occurred during spring 1993 when lower elevation habitat was not flooded and old growth experienced its highest number of new captures of *P. gossypinus* (table 4). Conversely, water was common across lowland sites during spring 1992, and we captured more new *Peromyscus* spp. and more new *Ochrotomys nuttalli* than in spring 1993. But, there was not a clear inverse relationship between new captures on old-growth and second-growth grids during the entire study.

In addition to differences in elevation and moisture, there were apparent differences between old-growth and second-growth habitat in soil and vegetation; loblolly pine, for example, was a significant component of the overstory (Zollner 1993). Some of the variation we observed in *P. gossypinus* habitat distribution was likely attributable to upland habitat features that were common across the second-growth grid. Afterall, *P. gossypinus* is reported to be less abundant or absent in drier, upland woodlands where *P. leucopus* is apparently more abundant (Sealander and Heidt 1990).

The recently harvested (cut-over) site was high graded during 1989–1990 and had some habitat features that were similar to old growth. In particular, the remaining slash was an abundant source of coarse woody debris. Also, many portions of the cutover were not different in habitat structure to windthrow gaps that occurred across the old-growth site. An obvious difference was the absence of large, old trees and associated canopy cover and standing basal area. Whether these similarities in habitat contributed to *P. gossypinus* abundance more closely resembling old-growth habitat than second-growth habitat is unclear. Indeed, it is uncertain whether variation in *P. gossypinus* abundance between second-growth and recently harvested sites (table 4) reflected real differences associated with habitat quality, or as with old-growth habitat, represented an influence of seasonal flooding.

Features of the second-growth grid probably contributed to variation in habitat distribution of other species. In particular, *Ochrotomys nuttalli* was captured more frequently than predicted from random chance; 65 percent (30 per 46) of its captures occurred in second-growth habitat (table 4). *Ochrotomys nuttalli*, like *P. gossypinus*, is common in moist, lowland forests with dense underbrush and is arboreal, often building nests in vine thickets as high as 5 m above the forest floor (Sealander and Heidt 1990). Both *O. nuttalli* and *P. gossypinus* readily move vertically in bottomland forest; in our study, they were the only species that were regularly captured in elevated platform traps. Food items of *O. nuttalli* are apparently similar, but contain less animal matter than *P. gossypinus* (Sealander and Heidt 1990).

Given its reputed preference for bottomland forests, it is unclear why we caught so few *O. nuttalli*. Overall, *P. gossypinus* was nearly 16 times more abundant than *O. nuttalli*; in old-growth habitat, the disparity in abundance between the two species was much greater (table 4). Perhaps the variation we recorded reflected differences in habitat preference. Although both species occur in moist, lowland forests, *O. nuttalli* also occurs in drier, upland forests of pine and cedar (Sealander and Heidt 1990). Thus, although both habitats may be generally suitable, each species may find microhabitat features common to one habitat more attractive; or, each may be behaviorally or physiologically predisposed to successfully responding to peculiar ecological scales.

Regular and frequent inundation, typical of the old-growth grid, may have had a greater influence on the distribution and abundance of *O. nuttalli* as compared to *P. gossypinus*. Some small mammals, notably shrews (Soricidae), are not predisposed to moving vertically in forested habitats. In circumstances where lowland forests become flooded for prolonged periods, terrestrial small mammals presumably must seek higher elevation, suitable habitat as refugia. Voles (*Clethrionomys* spp.) of European bottomland forests typically moved from lowland forest into surrounding habitat during flooding episodes (Andrzejewski 1963).

Alternatively, interspecific interactions may have contributed to the variation in distribution of *O. nuttalli. Peromyscus gossypinus* is very aggressive, whereas *O. nuttalli* is notably docile (Sealander and Heidt 1990). Perhaps the abundance and aggressive nature of *P. gossypinus* influenced the occurrence of *O. nuttalli* on the old-growth grid. It is not uncommon for competitive interactions to influence the structure of rodent communities (Brown 1975, Grant 1972). Moreover, interspecific aggression is a common mechanism mediating competitive exclusion, indeed, “the machinery of competition” (MacArthur 1972). This conclusion also is supported by the more frequent occurrence of *O. nuttalli* in second-growth habitat where abundance of *P. gossypinus* was 30 percent of that in old growth, and less than 4 times more abundant than *O. nuttalli* on the second-growth grid (table 4).

The remaining species were captured in too few numbers to detect response to habitat variation. There were many species, shrews in particular, whose scarcity or absence in our samples remains confusing. Shrews are difficult to capture and typically are under-represented with Sherman live traps (Kirkland 1977), but we totaled over 1,300 trap nights of effort with pitfall traps. Further study of bottomland forest is necessary to determine whether shrews are an insignificant component of the mammal fauna, or whether more innovative or intensive measures of sampling are needed to adequately include this guild.

Didelphis virginiana appeared to be more abundant on the second-growth grid with 22 of 51 captures (table 4), but we suspect that this result could have just as easily occurred because of unrelated factors. *Didelphis virginiana* prefers riparian woodlands and typically to a lesser extent, occurs in drier upland forest (Sealander and Heidt 1990). In this study, the second-growth grid had elements of both lowland deciduous woodlands and upland mixed forests. If its more frequent capture was a response to habitat condition, occurrence on the second-growth grid may have been a reflection of habitat heterogeneity rather than specific microhabitat features.

Managed Versus Unmanaged Forest

The effect of forest management on indigenous vertebrate populations has gained prominence in recent years and is probably one of the most pressing questions of applied ecologists (Smith, in press). There are notable limitations (e.g., unreplicated study design) to what general conclusions can be drawn from direct comparisons of the three habitats studied in our experiment. Still, examining the results of this study in the context of a disturbance and forest stand age gradient may provide some useful insights regarding the impacts of logging on the mammal fauna of bottomland forest.

In a retrospective study of managed and unmanaged stands, McComb and Noble (1980) reported that densities of some small mammals typical of bottomland hardwood forests (e.g., *Peromyscus leucopus*) can decline following intensive timber harvesting. However, they reported more captures for most species in harvested stands than in unmanaged stands. In our study, there was no consistent disparity in abundance between the old-growth and cutover grids. However, we did not sample the cutover site until two growing seasons following harvest.

Studies of upland hardwood forests in the Eastern United States have produced somewhat ambiguous and inconclusive results. Healy and Brooks (1988) reported no differences in small mammal community composition across seedling, sapling, sawtimber, and mature hardwood forest habitats. These were somewhat surprising results as clearcutting Appalachian hardwood forests is usually followed by a dramatic increase in small mammal abundance (Kirkland 1977).

In northern hardwoods, Degraaf and others (1991) reported striking differences in the abundance of some mammals between poletimber and sawtimber stands. Overall, shrews occurred in somewhat higher numbers in poletimber stands, but primarily because of the response of a single species. The remaining three shrew species had comparable captures in both habitats. Other species, such as the woodland jumping mouse (*Napeozapus insignis*), showed a similar preference for poletimber stands. In contrast, *Peromyscus maniculatus* was nearly twice as abundant in sawtimber than poletimber stands.

According to Kirkland (1977), small mammal communities increase in abundance following harvest, but decrease in abundance and diversity to below preharvest levels by the time a stand reaches the pole stage. Subsequently, both abundance and diversity of small mammal communities tend to increase as northern Appalachian hardwood forests mature. This same pattern was generally observed in our study with the fewest number of individuals and species recorded in the second-growth stand (table 4). The old-growth grid typically had the greatest species richness and abundance of mammals, whereas the recently harvested stand was intermediate between old-growth and second-growth habitats (table 4).

The general pattern of small mammal distribution observed in this study and reported by Kirkland (1977) parallels changes that occur in understory vegetation structure in response to disturbance. Old-growth forests show considerable spatial heterogeneity because of the interspersion of canopy gaps. Where the canopy has been interrupted because of windthrow, a dense herbaceous and woody understory develops and existing regeneration surges into the midstory. Anthropogenic disturbance, such as diameter-limit logging, also creates considerable spatial heterogeneity within a forest with uniform canopy. In recent cutovers, understory vegetation increases dramatically and young-growth stands in many ways resemble canopy gaps found within old-growth forests. Conversely, poletimber and young sawtimber second-growth stands can have relatively homogeneous horizontal and vertical structure as compared to old-growth forests or young-growth stands, particularly cutovers with some sort of legacy. This is especially true of second-growth stands that have not undergone intermediate stand management and the canopy closes in, becomes fairly dense, and very little sunlight reaches the forest floor.

Maintaining spatial heterogeneity, especially vertical and horizontal structure, may be the single most important feature of habitat management of bottomland forests for indigenous small mammal communities. Considerations of scale of disturbance, both temporal and spatial, also may be important (Hayward and others 1999) to sustain populations of forest habitat specialists. This is especially true of species, such as *Peromyscus gossypinus*, that apparently require moist forest habitat. Single tree or group selection harvests of late seral forests will likely create the understory and midstory structure typical of gap-phase old growth without overly exposing these stands to drying and other detrimental consequences that arise when the entire forest canopy is removed through clearcutting (Hayward and others 1999).

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CHAINSAWS, CANEBRAKES, AND COTTON FIELDS: SOBER THOUGHTS ON SILVICULTURE FOR SONGBIRDS IN BOTTOMLAND FORESTS

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Abstract—Forested wetlands of the Mississippi Alluvial Valley (MAV) are the most productive of birds, including neotropical migratory birds, of all land uses there. Forest land uses are difficult to maintain in economic competition with annual crops. We compare perspectives of a bird biologist, a wildlife manager, a production forester, and an economic pragmatist to the issue: How can we manage bottomland forests for products, like birds, in addition to economically viable commodities? Our thesis assumes: (a) private lands are the major land ownership category, (b) economically successful timber production generally is prerequisite to existence of forest on private lands, and (c) traditional silvicultural tools can produce bird habitats. Principles for production of specific bird communities in bottomland hardwoods remain to be articulated. We assert that the future of neotropical migratory birds in bottomlands depends upon communication between avian biologists and silviculturists and the innovative capacity of land managers.

INTRODUCTION

The forested wetlands and seasonally inundated bottomland hardwood forests of the Lower Mississippi Alluvial Valley (MAV), growing as they do on soils deposited as erosional products of the major portion of the North American continent, are very productive as bird habitats. The soils here are also productive for a number of warm-season agricultural crops, from cotton to catfish, and forest products including short-rotation fiber and long-rotation high-quality wood products. Land use in the region is a competitive result of potential for cash production, constrained by hydrological uncertainties. For a century, public policy at the Federal, State, and local level has emphasized control of water flow (Barry 1997) which has produced outstanding opportunities for agriculture, seriously reduced forestry activities, and eliminated many wildlife species, including some song and other birds. Still, however, MAV forests are the primary contributors of certain birds to the nation's avifaunal estate (Hunter and others 1993).

In this paper, we address the question: How can we afford to manage bottomland forests for products, like birds, in addition to economically viable commodities? To explore this question, we review current knowledge and practice of silviculture for forest birds in MAV forests, we illustrate the intensity of potential conflicts over land use with several different management viewpoints, and we provide case histories of consequences of past and of potential land management actions. Our role is to highlight the difficulties involved in attempting to produce commodities, like neotropical migratory birds (NTMB), that have low direct economic return, in an environment where the burgeoning population of the nation has created a very great demand for food and fiber. We conclude by pointing out the importance of cooperation among people with differing interests in land use to the future persistence of the current avifauna. We contend that only by collaboration among the variety of viewpoints represented among land owners, land managers, and interested citizens can this rich environment succeed in producing the desired economic, ecological, and aesthetic commodities of which it is capable.

CURRENT ENVIRONMENT

For illustrative purposes, we use the lands of the MAV. The 2193 400 ha (5,417,700 ac) of the Delta, as it is called, were formerly primarily covered by forest (Hamel and Buckner 1998, MacDonald and others 1979), on which grew truly vast volumes of high-quality timber of a number of species. These forests and their history have been described thoroughly (Foti 2001, Rudis 2001, Tingle and others 2001). At the present time, < 30 percent of the landscape is forested (Faulkner and others 1995). The great majority of the remaining land in the Delta is devoted to cash crop production, primarily of cotton, soybeans, rice, corn, catfish, wheat, and other crops. The entire Delta is separated from the floodwaters of the Mississippi River by an extensive levee system, which extends from near Memphis, TN, in the north to the mouth of the Yazoo River near Vicksburg, MS, nearly 320 airline kilometers south.

Much of the forest land is located in the batture, the area between the levees and the Mississippi River. In this area, flooding usually occurs on at least an annual basis. Major remaining patches of forest on the protected side of levees in the Delta include the Delta National Forest in Sharkey and Issaquena Counties; Mahannah Wildlife Management Area in Issaquena County; as well as Yazoo, Panther Swamp, and Dahomey National Wildlife Refuges in Washington, Sharkey, Issaquena, and Bolivar Counties. The remaining forests primarily are confined to relatively low-lying sites, sites formerly flooded for extensive periods each growing season. Because of this, the full range of bottomland forest types currently is not represented in proportion to its past occurrence. Extent of flooding creates limits for forest production on sites; additionally, the use of revetments and dikes for water control limits the creation of new land and hence the sites for some species like eastern cottonwood (*Populus deltoides*). A reasonable correspondence exists

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between the bottomland hardwood zones of Wharton and others (1982) and the agricultural crop potential of sites (table 1). Drainage and flood protection make possible the cultivation of crops on relatively lower sites. Much of the remaining forest land is too low to support tree species typical of sites flooded only briefly each year, such as cherrybark oak (*Quercus falcata* var. *pagodaefolia*). Thus, the forest of the remaining landscape lies on a highly skewed subset of the original presettlement situation, as well as a relatively skewed subset of the forested lands before the most recent episode of land clearing during the soybean era subsequent to 1968. This lack of high sites restricts opportunities for silviculture, both for timber and for songbirds.

THE PEOPLE

Land use conflicts can be intense because individuals with a stake in decisions about land have separate, valid, seemingly non-overlapping views of the most appropriate uses of the land. The different perspectives lead to different sets of objectives in management. Until the advocates of different perspectives understand (Covey 1989) and respect the objectives of others, achievement of objectives of several different perspectives is not likely.

We here offer thoughts on four separate perspectives on the use of MAV lands—perspectives that represent a wide range, albeit not the full range, of potential views. We present them to stimulate the reader to identify not only with their particular favorite but also to appreciate the consistency of the others. We invite readers to see this situation as one in which a greater success will be achieved when proponents of different perspectives draw circles to include additional ideas rather than draw lines in the sand to separate themselves from their supposed opponents.

The perspectives we identify are those of a bird biologist, intended to reflect a strong protectionist position; a wildlife manager, intended to reflect an intense interest in successful hunting of game; a production forester, intended to reflect a focused attention on maximizing fiber production; and an economic pragmatist, intended to reflect a sincere concern with the bottom line of profit. To the bird biologist, any forest land use is preferable to agricultural cropland; those land management activities are gauged as profitable which increase the extent of bird habitat for species otherwise in limited supply. Often, the older the forest the better it is perceived to be. To the wildlife manager, any land use or practice that improves the quality of the hunting experience is useful; substantial manipulations are often necessary. The wildlife manager is interested in producing habitat that supports high populations of certain desirable species. To the production forester, maintenance of sufficient land in forest to assure a steady supply of top-quality wood of desired species is paramount. Foresters appreciate the change that occurs with time in any forest stand, and are prepared to groom the forest as it changes. To the economic pragmatist, any land use or practice is reasonable, as long as no other is available to produce a higher profit; this usually implies an agricultural or development land use. In this perspective lands that do not pay for themselves are of questionable use.

Each of these perspectives, as a sole determinant of objectives, leads to single-minded attachment to a particular set of objectives that may exclude the others, i.e., produces

Table 1—Correspondence between capacity of sites to support forest and agricultural crops

Hydrologic situation	Wharton zone	Forest type	Agricultural crop
Permanently inundated	I: Open water	None	None
Seasonal flooding			
>6 months per year	II	Baldcypress-water tupelo	Catfish, rice
3 to 6 months/year	III	Overcup oak-water hickory, Nuttall oak	Rice, soybeans (marginally)
1 to 2 months/year	IV	Mixed hardwoods: water oak, sweetgum, green ash	Soybeans, corn, cotton
<1 month/year	V	Mixed hardwoods: cherrybark oak, sweet pecan, swamp chestnut oak	Cotton primarily
Wet years only	VI	Mixed hardwoods: including upland species	Cotton primarily

conflict with them. Such conflict is unavoidable. The important issue is how the conflict is resolved, and whether resolution represents a loss of opportunity to achieve objectives of other perspectives in the aggregate. Relative costs and benefits of seeking to achieve different combinations of objectives have not frequently been evaluated on the broad scale of such varying perspectives. Unless such a broad approach can be pursued, however, the prognosis for the future of NTMBs in the MAV is grim. These birds are representative of the apparently most dispensable elements in the ecological and or economic puzzle. The cost of dispensing with them is unknown.

Two useful examples of approaches to bringing different perspectives into discussion with each other are the Black Bear Conservation Committee (BBCC) and the Southeast Management Working Group Partners in Flight. The experience of these two groups that began as ad hoc partnerships suggests that successful achievement of objectives to maintain populations of species like bears and migratory birds need not interfere with objectives to maintain productive forest management in the landscape. These two partnerships have constructively drawn a circle to include the views of the perspectives above. The BBCC, in particular, has usefully engaged all four of them in dialogue.

CURRENT SILVICULTURAL PRACTICE

Silviculture, the theory and practice of controlling forest establishment, composition, structure, and growth (Spurr 1979) provides forest managers with practical methods designed to manipulate current stand conditions in order to achieve desirable future stand conditions. Similarly, forest management is the process of making and executing decisions that direct the long-term development of forests on any particular tract of land. Ideally, both silviculture and management can be used to manipulate the forest to provide a particular vegetative structure at a specified time in the future. The following principles may be obvious but are nonetheless worthy of recognition:

1. “It ain’t management unless you do it on purpose.” Management requires the statement of objectives, indicated as desired future conditions or outputs.
2. Manipulation of survivorship of trees is the primary silvicultural activity currently used, i.e., the chainsaw is the primary management tool of silviculture; corollary to this is that cutting trees is a necessary part of managing forest lands.
3. Hydrological manipulations have profoundly affected the remaining patches of forest, such that site characteristics today may reflect the hydrological manipulations as much as or more than the historical development of the site.
4. Management options are limited by the site characteristics, which reflect history of hydroperiod and land use.
5. Management must be cost effective, or alternative land uses will take precedence.
6. Within the context created by the previous five principles, we can learn from old-growth stands about the productive capacities of sites.

In a useful, nontechnical review of silvicultural systems for ornithologists, Thompson and others (1995) identify the four regeneration methods commonly used in North America as selection, shelterwood, seed tree, and clearcutting. They compare the use of these methods in terms of the age-class distribution they produce in even-aged (shelterwood, seed tree, clearcutting) or uneven-aged silvicultural systems (selection). They identify silvicultural practices as regeneration practices or intermediate treatments. Regeneration practices include the method of establishing the new stand (natural or artificial) and the site preparation activities that may be employed to do so. Intermediate treatments include release cuttings of saplings, thinnings of older stands, and salvage and sanitation cuttings to remove dead or dying trees. Additional aspects of forest management operations, such as road building and maintenance, fire control and management, and use of pesticides and herbicides, as well as fuel wood harvest can have effects on stand structure and composition, and hence on the bird community that inhabits the stands. A more technical review of silvicultural systems for bottomland hardwoods is presented by Meadows and Stanturf (1997).

In MAV habitats where extensive conversion of forest to croplands has occurred, reforestation involving natural or artificial establishment of stands of trees on former agricultural lands is an important forest management technique. Often, stand establishment is difficult. Intercropping cottonwoods and oaks is a possible silvicultural manipulation to address the situation in which land use changes have reduced the rate of development of sites necessary for natural regeneration of cottonwood (Schweitzer and others 1997, Twedt and Portwood 1997).

GENERAL PRINCIPLES FOR MANAGEMENT OF NEOTROPICAL MIGRATORY BIRDS

The bird communities of the bottomland hardwood forests are quite diverse (Smith and others 1996), and include numerous species in both the spring and summer breeding season and in the winter nonbreeding season (Hamel 1992). Many of these birds are NTMB species whose declining populations make them of particular concern at the present time (Hunter and others 1993, Smith and others 1996).

Our thesis is that profitable silviculture is the primary hope for NTMB in the MAV. We believe this because most of the birds of interest in the MAV are forest birds, for which maintenance of forest cover in the landscape is critical. Competition among land uses, i.e., agriculture and forestry, is intense, and extensive set-asides of forest land, either through purchase or regulation, are unlikely to provide sufficient tracts to assure the persistence of all bird species. Furthermore, manipulation of forests will be necessary to assure the persistence of early successional habitats and the birds that require them.

Our thesis depends upon three premises:

1. private lands are the major land ownership category in the MAV,
2. economically successful timber production is generally a prerequisite for the existence of forest on private lands, and

3. traditional tools of silviculture can effectively be used to produce habitats for NTMB.

From these premises, we argue that the future of NTMB in bottomlands depends upon:

1. improved inventory of bird communities,
2. communication between avian biologists and silviculturists, and
3. the innovative capacity of land managers.

All of the management activities aimed at producing suitable habitat for birds assume that:

1. satisfactory bird habitat can be described in primarily structural terms;
2. production of woody vegetation cover is not only necessary but sufficient for production of insect foods as well as fruits of forest trees, and that this cover is sufficient to accord appropriate cover for roosting and breeding purposes of the birds;
3. corollary to the first two, if woody cover is produced, insect populations will follow, and they will in turn support bird populations, i.e. secondary consumers;
4. bird occurrence is synonymous with successful bird reproduction and survival.

These assumptions appear reasonable. However, they are not validated, particularly in bottomland systems (Wigley and Roberts 1994, 1997). They also oversimplify a complex reality, e.g., Hamel 1992, Sherry and Holmes 1995, Thompson and others 1995. They do form a starting place for adaptive management, in which as actions are taken, managers are enabled to learn from the consequences of their actions and improve the desirability of the consequences as time goes on. The work of Twedt and others (1999), Mueller and others (1999), and Loesch and others (1999) is illustrative of the process by which assumptions such as those above serve to structure management decision-making and lead to useful improvements. The process is similar to that advocated by Starfield (1997).

Our major theory of habitat utilization assumes that vegetation structure, rather than its species composition, is the driving force behind bird species occurrence. We assume that where appropriate structure occurs, the birds will be present. Especially do we see this as a question of choice on the part of the birds, where by some mechanism dispersing individuals locate and choose to settle in habitats of appropriate structure. We focus on structure because extensive theory exists that relates bird occurrence to vegetation structure, based upon the work of James (1971), Shugart (1984), DeGraaf (1987), and well illustrated by the works of Verner and others (1986), and Morrison and others (1992). Additional extensive theory assumes that the conditions of land use surrounding a particular patch, that is, the landscape position of the tract of appropriate vegetation, is a key feature limiting the occurrence of birds (Robbins and others 1989). A major, little-tested assumption embedded in the focus on structure is its linkage to appropriate foods and to appropriate sites for nesting, roosting, and escape cover.

Because we are not sure of the specific responses of individual bird species to particular manipulations, management activities have inherent risks of failure. Individual managers, as reasonable humans, exhibit a range of tolerance toward risk-taking in their management decisionmaking. Pukkala and Kangas (1996) note that measuring attitude toward risk is probably more difficult than measuring risk itself. They state, “In a situation involving risk, the optimum plan may be different for a risk-avoiding, a risk-neutral, and a risk-seeking decision-maker.” Uncertainties of outcomes in land management thus may be caused by deficiencies in the information base on which decisions are taken as well as on the decision style of the manager.

Specific considerations for the management of individual bird species are not likely to be developed soon (Martin and Finch 1995). Earlier workers (Dickson and others 1995, Hamel 1992, Pashley and Barrow 1993, Wigley and Roberts 1994,) have provided information on the occurrence of species in stands of different ages. We lack a long-term data set indicating how individual species respond to particular treatments applied to bottomland hardwood stands and followed over time. Wigley and Roberts (1997) and Hamel (1992) provide hypotheses of landscape-scale interactions of songbirds and forest management, but these too have not been subjected to sufficient experimental testing.

Several principles seem appropriate as guidelines for management of NTMBs in bottomland hardwood forests, however, they need to be tested (Dickson and others 1995, Wigley and Roberts 1997).

1. Bigger patches of forest are always better for forest birds than smaller ones. Pashley and Barrow (1993) recommend the optimal condition at the local scale to be a very large, forested tract managed under a natural disturbance regime. Large patches of forest buffer the effects of increased brood parasitism, predation, and other demographic consequences attendant on small populations inhabiting small tracts. The data of Robbins and others (1989) provide a strong rationale for maintenance of large tracts.
2. Reforestation will be a most important part of the future potential for birds in bottomland hardwoods. Particularly in the MAV where only a modest proportion of the landscape is forested, primarily in small, scattered patches, only specific reforestation activities will provide for the establishment of forests on lands far from seed sources (Mueller and others 1999).
3. We can learn from old-growth stands about the future composition and structure of stands left without intervention. The works by Devall and others (2001) and Smith and others (2001) as well as Hamel (1989) provide information on the use of old-growth stands as controls for comparison with second-growth bottomland forests.
4. Fragmentation of habitats has profound effects that local managers may be helpless to control, mitigate, or otherwise affect. Robinson and others (1995) provide a

> chilling review of the effects of forces operating at the landscape scale on bird community dynamics within stands at the local scale. Readers uncertain of the consequences to local populations of such landscape-scale factors would do well to read that work.

Several recent papers provide some guidance to land managers concerning silviculture for songbirds in bottomland hardwoods (Dickson and others 1995; Hamel 1992; Pashley and Barrow 1993; Wigley and Roberts 1994, 1997). Hamel (1992) related individual species to particular layers of vegetation in the forest, assuming that manipulations which eliminate or favor particular layers of forest will similarly destroy or improve habitats for the species that use those layers. Pashley and Barrow (1993) provide a set of recommendations that involves local level management as well as regional scale management. Wigley and Roberts (1994) review results of 17 studies that indicate associations or dissociations between individual bird species and particular management treatments. Most of these studies involve descriptions of bird communities in stands of different ages, although some reflect experimental work. Few of the studies were long-term examinations of community changes in response to application of treatments. Dickson and others (1995) identify species that have been shown to increase or to decrease in response to particular treatments in bottomland hardwood forests. They note that little specific information on such effects has been developed in bottomland hardwood ecosystems. They recommend maintaining current forests and preventing further conversion to other uses, as well as reclamation of some previously converted land to forest. They suggest protection of existing old growth, existing corridors between existing stands, and the development of more old-growth stands. Wigley and Roberts (1997) review the modest literature on landscape correlates of species occurrence and abundance in bottomlands, noting that much of the theory is intuitively sound, but that it lacks empirical and experimental testing.

Among issues for which scant information currently exists are the role of fire and long-term annual variation in population levels of species. Unlike other southern ecosystems, very little is known about the utility of fire in wetlands as a management or ecological tool. Likewise, few long-term data sets are available to evaluate the variability of bird use of particular stands.

Management for NTMBs in bottomland hardwood forests is only part of the management picture, even of birds, for more than many other forests. Southern forests, particularly bottomland hardwood forests, are winter destinations for migrants from the north as well as summer destinations for migrants from the south, and stopover habitat for migrants in transit both spring and fall. Concentration on management of breeding habitats only will overlook the importance of these habitats in other seasons.

CASE STUDIES: SILVICULTURE FOR SEVERAL RARE BIRDS IN THE MAV

Two bird species, one a resident and the other a NTMB, have been effectively lost from the MAV fauna. One of them is probably extinct, the other possibly so; each was a regular, if not common, member of the MAV fauna. They provide an opportunity to review the possible silvicultural treatments that might have been employed to keep them from becoming so rare. A third species provides an example of an unintended benefit of silviculture designed strictly to produce fiber.

Ivory-billed woodpecker—In bottomland hardwoods, ivory-billed woodpeckers (*Campephilus principalis*) utilized stands of big, old trees. The apparent habitat requirements were for extensive stands with dying or senescent trees. An approach to producing this habitat silviculturally is the use of thinnings on moderate-to-good sites to accelerate the production of large trees with substantial crowns, eventually creating the conditions in which dead and dying limbs can supply the insect foods for the birds. Such senescent trees are not usually retained in stands managed for economic objectives. Unfortunately, needed information on the possible density of birds and their energetic requirements is unavailable, hindering the process of modeling how to do produces their habitat. Our point, nevertheless, is that active management possibly could produce the desired conditions faster than could passive.

Bachman's warbler—The Bachman's warbler (*Vermivora bachmanii*) was a species of openings in the canopy and areas with dense shrub cover interspersed with larger trees. They have long been associated with canebrakes (*Arundinaria gigantea*), and may have been obligate users of them (Remsen 1986). In the MAV, canebrakes likely occurred most prominently on relatively high ground, land now devoted to production of cotton. Serious gaps exist in our knowledge of the ecophysiology of cane: Does the species require full sunlight, partial sunlight, or full shade? Can canebrakes be developed on relatively wetter sites? Assuming that cane requires relatively open conditions, thinning a stand heavily would probably produce the light conditions in which woody understory vegetation, such as cane, could thrive in a forested environment, thereby producing habitat for the species (Platt and Brantley 1997). Such manipulative intervention may be a more direct method for creating habitat for the birds than passively waiting for a natural disturbance such as an ice storm, tornado, or hurricane. Unfortunately, the extreme rarity of the birds has prevented the implementation of such an experiment.

Warbling vireo—A third case involves another species rare in the MAV, the warbling vireo (*Vireo gilvus*). Its habitat is relatively long, narrow tracts of willows or other early successional trees growing along a watercourse or a slough. In such conditions, the species is exposed to potentially severe pressure from brown-headed cowbirds (*Molothrus ater*), birds that lay their eggs in other birds' nests. Reforestation treatments involving cottonwood plantations, with and without intercropping with other species, have produced habitats in which warbling vireos do very well.[2]

RESEARCH AND MANAGEMENT NEEDS

Virtually all authors commenting on land management for birds in bottomland hardwood forests note that information

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[2] Personal observation. 1997. Paul Hamel, Research Wildlife Biologist, USDA Forest Service, Southern Research Station, P.O. Box 227, Stoneville, MS 38776.

on the basic biology and silviculture for birds is scanty, that landscape effects may be as or more profoundly influential on populations as stand-level vegetation structure, and that currently existing monitoring data, comprised mostly of relative abundance information, do not give as detailed a picture as will data on survivorship and reproductive success. These latter data are, however, expensive to gather; they may be virtually impossible to gather outside the research context for some forest canopy dwelling species like the cerulean warbler (*Dendroica cerulea*) (Hamel 2000, Mueller and others 1999).

CONCLUSIONS

Conflicts between different interests in the use of the land can and perhaps may produce serious potential problems in the future. We believe that such conflicts can best be avoided by active dialogue between perspectives. When the debate relates to objectives of management, rather than to a decision to manage or not to manage, each of the outlined perspectives will be able to contribute to a vision of a landscape containing a rich mix of chainsaws, canebrakes, and cotton fields. Where bird biologists and wildlife managers do not attempt to incorporate their objectives into production forestry, many opportunities will be missed. When production foresters fail to incorporate bird management objectives and wildlife habitat goals into their silvicultural practice, opportunities for improved silviculture will be foregone. In such cases, all dependents on the bottomland forest landscape may become losers, especially the NTMBs and other species that depend on forest habitats.

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A LONG-TERM VIEW OF OLD-GROWTH DECIDUOUS FORESTS

James T. Tanner and Paul B. Hamel[1 2]

Abstract—Lowland old-growth forests in the Southeastern United States and Eastern Europe (Poland) survived because of accidents of history, topography, and ownership until they came under governmental protection. Such old-growth stands are the similar the world over; they have trees of many ages, patchy distribution of habitats, and a variety of microhabitats, all of which result from the death and fall of trees. Species diversity is high for both plants and animals. Old-growth forests constitute important habitat for many carnivores and for some endangered species; they are places for ecological research and for recreation and enjoyment. Science has shown that management, as well as protection, is necessary and can improve conditions.

INTRODUCTION

These remarks primarily concern old-growth deciduous forests in the lowlands of two areas: the Southeastern United States and Poland. My own experience in old growth has been in bottomland forests of the Southeastern States (Tanner 1942, 1986).

LOCATIONS OF OLD-GROWTH FORESTS

Where are old-growth deciduous forests today, particularly in the Southeastern United States, and why are they there? The answer lies partly in the history of the logging industry, the events of which did not occur uniformly over all areas. For example, logging interests grew faster in Georgia than in South Carolina. In the former, no old-growth bottomland forests survived, but in the latter two areas are now preserved, largely as a result of the action of conservationists: one in the Congaree Swamp National Monument, of Richland County, and the other in Four Holes Swamp, of Berkeley and Dorchester Counties. Four Holes Swamp is now the Francis Beidler Forest. In the Mississippi Delta, logging began in Missouri and progressed southward. Later, it started in southern Louisiana and moved northward. The two movements met in northern Louisiana at the Singer Tract, Madison Parish, then the largest tract of remaining bottomland forest (Tanner 1942). This occurred unfortunately at the beginning of World War II, when hardwood timber was in high demand and funds for conservation were reduced. The Singer Tract was logged, but some similar old-growth bottomland forest was preserved several kilometers to the east in the Delta National Forest in Mississippi; Devall and Ramp (1992) describe three Research Natural Areas there.

Old-growth forests persisted in other areas because of stand inaccessibility and the difficulties of logging. For example, old-growth forest remains in the remote Great Smoky Mountains. In both the Okefenokee Swamp and the Everglades, hardwood or cypress stand as islands in vast expanses of marshland that have kept loggers at bay. These two areas now are preserved as a National Wildlife Refuge and a National Park, respectively. Noss (1991) described a somewhat similar situation where a hardwood forest in a Florida hammock persisted because it was isolated in a pine forest. In the Southeast larger old-growth forests remain because of accidents of history and topography that delayed and eventually prevented logging. Many small stands, albeit not forests, have survived because family-owned farms have brought protection, notably in the upper Mississippi valley (Parker 1989).

In Poland, however, as Tomiałojc (1991) describes, an old-growth forest survives today because it once was a hunting preserve for royalty. The same is true of Denmark’s forests; and in Japan I visited old forests that remained only because they were Shinto shrines.

CHARACTERISTICS OF OLD-GROWTH

Old-growth forests have survived in two ways. One is by history of not having been changed by human action nor destroyed by natural accident. This implies that an old-growth forest is the terminal stage of a plant succession (Barnes 1989). Because almost no forest has been unaffected by human activity (Tomiałojc 1991), we need a definition based on observable forest characteristics of the forest.

Participants at the 1989 symposium, “Characteristics, management, and restoration of old-growth temperate deciduous forests in the Southern United States,” 16th

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[2] Editors note: This contribution originally was prepared for a 1989 Natural Areas Conference symposium on old-growth deciduous forests. Dr. Tanner’s untimely death in early 1991 prevented publication of the manuscript with others in that symposium (Natural Areas Journal in volume 11, 1991, and volume 12, 1992). It is presented here in abridged form as a tribute to Dr. Tanner whose work on old-growth bottomland hardwoods in the Mississippi Alluvial Valley stands as a tribute to the persistence of the man and the value of biodiversity in the Mississippi Alluvial Valley.

Natural Areas Conference, 18 October 1989, Knoxville, TN, and the authors of notable publications (Barnes 1989, Parker 1989) generally agree on the characteristics of old-growth forests. They contain trees of all ages, from saplings to large individuals. These trees form at least a two-layered canopy. Tree distribution is patchy; and there are openings where trees have fallen. Standing-dead and dead-topped trees are present, and on the ground are large and small logs and exposed root masses. Details of these characteristics as observed in the Polish Białowieża Forest are described by Tomiałojc (1991).

Old-growth forest characteristics result from the death of individual trees and from small-scale disturbance. Tree death produces the standing dead trees, fallen logs, upturned root masses, and small canopy gaps. Small-scale disturbance events (a very relative term) include windfalls or blow-downs, mortality from insects and disease, flooding, and fire (Dickson 1991, Runkle 1991). All such natural processes produce patchiness and the microhabitats so important to species inhabiting old-growth forests.

A general characteristic of old-growth forests (Dickson 1991, Tomiałojc 1991) is that they contain a high diversity of species, both plant and animal, but often with a low number of individuals of each species. Much more has been written about the diversity of animals than of plants. Important to animals is the typical horizontal patchiness resulting from a mixture of habitats, each with a relatively small area. Noss (1991) discusses in detail the relation between patchiness and the well-known “edge effect,” where adjacent habitats may provide different animal necessities. Noss (1991) also points out that patchiness can produce a variety of microclimates within a small area.

Several kinds of microhabitats are more abundant in old-growth than in young forests, e.g., hollow, standing snags and prostrate logs, broken and tangled limbs of fallen trees, and upturned roots of fallen trees. Animal groups that use such microhabitats are woodpeckers, other hole-nesting birds, flying squirrels (*Glaucomys* Thomas sp.), bats, and carnivores that need dens for sleeping or reproduction. Especially important to woodpeckers are dead and dying trees that provide habitat for wood-boring insects. These are all examples of how tree death is such a significant process in old-growth. Details of these relations are reinforced by Dickson (1991), Hamel and Ford,[3] Pelton (personal communication. 1989. M.R. Pelton. Professor Emeritus. Dept. of Forestry, Wildlife & Fisheries, University of Tennessee, P.O. Box 1071, Knoxville, TN 37901–1071), and Tomialojc (1991); other examples are given by Carey (1989).

Authors who remark on the abundance of carnivores in old-growth forests are Dickson (1991), Hamel and Ford 1989 (see footnote 3), and Tomiałojc (1991). Higher abundance probably results from a combination of the microhabitats that provide dens and the greater diversity of animal species that may constitute prey.

Old-growth forests have a greater supply of some foods than young forests. In deciduous forests large oaks (*Quercus* L. sp.), hickories (*Carya* Nuttall sp.), and other mast-producing trees are heavier producers than younger trees; and in an evergreen forests the old conifers produce more seed than younger ones (Carey 1989).

Some outstanding exceptions exist to the proposition that old-growth forests are characterized by a diversity of species and patchiness. For example, pine forests (*Pinus* L. sp.) of the Southeastern United States (Dickson 1991) and the pine and other coniferous forests of the Rocky Mountain region (Moir and Dieterich 1988) present an almost monotonous scene because of the few tree species, and the often unbroken extent of forest. Animal diversity also is low. In some respects, however, such forests of old trees are the best producers of seed, which is food for several animal species. Their dying and dead trees provide food for woodpeckers and nesting or denning places for several kinds of birds and mammals. Indeed, in longleaf pine (*Pinus palustris* Miller)-wiregrass (*Aristida stricta* Michaux) communities regularly disturbed by fire, the diversity of herbaceous plants and of fauna dependent on burrows of gopher tortoises [*Gopherus polyphemus* (Daudin)] is especially high (Wharton 1978).

In both the Southeastern and Rocky Mountain coniferous forests, fire has been vital in establishing and maintaining evergreen forests. This raises an interesting question: Are these coniferous stands true “old-growth,” or are they patches created by disturbance within a larger forest? Any answer will depend on definitions and interpretations of scale, but I [Dr. Tanner] believe that such forests should be considered old-growth because they provide important habitat for some animal and plant species.

PRESERVATION OF OLD-GROWTH

A compelling reason for preserving old-growth forests is to prevent the extinction of endangered species. In North America, examples of rare species that lived in mature forests are the ivory-billed woodpecker [*Campephilus principalis* (Linnaeus), which now may be extinct], red-cockaded woodpecker [*Picoides borealis* (Vieillot); Dickson 1991], red wolf (*Canis niger* Bartram; now extinct in its original range), Florida cougar (*Felis concolor* Linnaeus), and northern spotted owl [*Strix occidentalis* (Xantus)]. Rare species surviving in the primeval Białowieża forest of Poland are listed by Tomiałojc (1991). However, there is danger in discussing forest preservation only in terms of endangered species and not the entire habitat. Our objective should be to preserve the whole forest, which in its diversity is the habitat of many species, including some that may be rare.

Some old-growth stands are now being preserved in the Research Natural Areas (RNA’s) program of the USDA Forest Service, described by Devall and Ramp (1992), who explain the objectives of the program and describe three established areas in Mississippi. Greene (1988) describes this program as it operates in Washington and Oregon. Within RNA’s, old-growth forests are the focus for ecological research. We know that woodland species evolved in mature forests long before humans entered their habitat. We need

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[3] Hamel, P.B.; Ford, Robert P. 1989. Unpublished report on file with: Research Wildlife Biologist. USDA Forest Service, P.O. Box 227, Stoneville, MS 38776.

examples of the original habitat if we are to understand the evolution and ecology of the native species.

Tomiałojc (1991) lists a number of research projects conducted in the Białowieża Forest. In one such study, Walankiewicz (1991) found that the conclusions about nesting in highly modified forest habitats, including the addition of nesting boxes, are not supported by results of studies in the old-growth forest of Poland. There are differences between the two habitats other than the nature and number of nesting cavities.

Moore and Swank (personal communication. 1989. Wayne T. Swank. Scientist Emeritus. Coweeta Hydrologic Laboratory, 3160 Coweeta Lab Rd., Otto, NC 28763) report on the movement of plant nutrients through precipitation, soil, biomass, and streams in old-growth forests of the Great Smoky Mountains. Their work is highly relevant to our understanding old-growth hardwood forest ecology. The insight from their work may have its greatest application in understanding differences between the nutrient dynamics of temperate forests and those of less-studied tropical rain forests such as are found in the Amazon Basin. We do not know enough to understand the ecology of rain forests and not nearly enough to plan intelligently for the tremendous human changes occurring in tropical regions.

Although one definition of old growth is “climax forest,” which implies a steady state, Tomiałojc (1991) has observed changes in the Białowieża Forest and Barnes (1989) in mature forests of the Great Lakes region of the United States. Possible and widely different causes of such changes are (1) a protracted plant succession, (2) effects of browsing mammals or of insects, (3) climatic change, and (4) air pollution (including acid rain). Each possible cause is both a very interesting ecological problem and a process significant to humankind. We submit that old-growth forests are needed as places for studying vital problems.

A final reason for preservation of old-growth forests, and to some the most important, is their aesthetic beauty. The inherent worth of them is difficult to put into words, but its reality is proven by the number of visitors to the Białowieża Forest (Tomiałojc 1991), to trails of the Great Smoky Mountains, and to the Congaree Swamp in South Carolina and Mahogany Hammock in the Everglades National Park.

MANAGEMENT OF OLD-GROWTH FORESTS

The two most often discussed subjects concerning old-growth forests are their characteristics and their management. Management goals and practices are discussed by Devall and Ramp (1992), Noss (1991), Runkle (1991), Tomiałojc (1991), and Wellbaum and Doyle (personal communication. 1989. Wellbaum, E.M. Forester. Tennessee Valley Authority. Land Between the Lakes, Golden Pond, KY 42211-9001). Earlier discussions were published by Thomas and others (1988), Barnes (1989), and Parker (1989). At one extreme is the hands-off policy, holding that old-growth forests should be preserved and not managed. This approach has proven to be impractical; experience has shown that such forests benefit from procedures such as selective cutting, control of non-native species, and the re-introduction of extirpated species. To accomplish the goal that old-growth forests should be used for research and education requires management, as described for the Polish forest by Tomiałojc (1991). For years the U.S. Department of Interior’s National Park Service (NPS) has been charged with conflicting responsibilities: to preserve and protect natural areas while, at the same time, making them open to the public. Almost every management decision the NPS makes is a compromise.

A most troubling problem concerning conservation of old-growth has to do with size. Old-growth forests constitute a variety of habitats resulting from random storms, floods, and other disturbances. To realize the ecological benefits of such incidental events, large areas are needed. Large areas reduce the effects on habitat wrought by boundaries with cut-over or cultivated lands, mitigating the encroachment of invasive plant species. Also, some animals, especially carnivores, need large home ranges or territories. Unfortunately, many, if not most, old-growth forests in the United States and similarly developed regions are only remnants, too small to foster successful conservation. This has led several ecologists to apply principles of island biogeography (MacArthur and Wilson 1967) to the planning and management of forest preserves (Frankel and Soulé 1981, Harris 1984).

Finally, another question remains: Can management produce the many characteristics by which we recognize an old-growth forest, thereby effectively reconstructing an old-growth ecosystem? During the planning process we must know what we are trying to restore. Preservation of existing old-growth stands will be necessary to provide the model. Papers (from the 1989 Symposium; Smith and Hamel 1991) that address the question of reconstruction include that by Runkle (1991) and the unpublished remarks of Wellbaum and Doyle (personal communication. 1989. Wellbaum, E.M. Forester. Tennessee Valley Authority. Land Between the Lakes, Golden Pond, KY 42211-9001). On the Tensas River National Wildlife Refuge, which is the old Singer Tract in Louisiana, managers have begun to restore some areas to at least resemble an old stand of bottomland timber. Whether such efforts succeed remains to be seen.

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Dr. Tanner’s final words are prophetic; they presage the current work by a dozen years, and the current symposium by 6 years. His contributions to our understanding of the ecology of old-growth stands, particularly in bottomland hardwoods, will not diminish with time. His junior author thanks Margaret Devall and Wayne Swank for their thoughtful reviews.

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Hamel, Paul B.; Foti, Thomas L., tech. eds. 2001. Bottomland hardwoods of the Mississippi Alluvial Valley: Characteristics and management of natural function, structure, and composition. 1995 October 28. Fayetteville, AR. Gen. Tech. Rep. SRS–42. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 109 p.

A symposium entitled “Bottomland hardwoods of the Mississippi Alluvial Valley: characteristics and management of natural function, structure, and composition” convened on October 28, 1995, as part of the Natural Areas Conference, October 25–28, 1995, in Fayetteville, AR. The symposium’s goal was to provide information that managers need to begin restoring the composition, structure, and function of forest ecosystems in the Mississippi Alluvial Valley. Included in the proceedings from that symposium are 8 of 13 presentations. These peer-reviewed contributions address historical conditions of forests in the Mississippi Alluvial Valley (two papers), historical changes that are reflected in today’s forests (one paper), the effect of historic and prehistoric rainfall patterns (one paper), forest fauna in the region (two papers), the effect of herbivory on forest vegetation (one paper), and management of bottomland hardwood forests for multiple outputs (one paper). A ninth paper, concerning characteristics of old-growth forests, is a posthumous submission authored by Dr. James T. Tanner; and the tenth paper was published in another venue. The intended audience of these proceedings includes managers of private, State, and Federal lands, as well as land management planners from a range of jurisdictions.

Keywords: Bottomland hardwoods, forest history, mammals, Mississippi Alluvial Valley, old growth, songbirds, wetland restoration.