

**PROCEEDINGS OF THE CONTRIBUTED PAPERS SESSIONS
OF THE FOURTH ANNUAL SYMPOSIUM ON THE
NATURAL HISTORY OF LOWER TENNESSEE AND
CUMBERLAND RIVER VALLEYS**

Held at Brandon Spring Group Camp
Land Between The Lakes
March 2, 1991

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PREFACE

On 1 and 2 March 1991 the Fourth Annual Symposium on the Natural History of Lower Tennessee and Cumberland River Valleys was held at Brandon Spring Group Camp in Land Between The Lakes. The symposium was sponsored by Austin Peay State University's Center for Field Biology, the Tennessee Valley Authority's Land Between The Lakes, and the Tennessee Academy of Science.

Presentations on the first day of the symposium constituted a special invited papers session treating the vertebrates of Tennessee and Kentucky. Twenty papers from that session, edited by A. Floyd Scott and David H. Snyder, were published as a special issue of the Journal of the Tennessee Academy of Science in October 1991 (Vol. 66, No. 4).

On the second day, 16 contributed papers, concerning a broader range of topics, were presented. Speakers at the contributed papers sessions had the option of submitting for publication either a manuscript (with abstract) or an abstract only. Six manuscripts with abstracts (each refereed by at least one reviewer), and 9 abstracts only, from that session are published here.

The style and format used in this volume follow generally the conventions established in earlier versions of the proceedings of this symposium. Journal abbreviations used in the literature cited sections follow the recommendations of the *Serial Sources for the BIOSIS Previews Database*, Vol. 1990 (published in 1991 by BIOSIS, Philadelphia, Penn.). In the paper by Gildrie—because Gildrie is a historian by training and is dealing with a piece of historical research—the style of literature citation used follows conventions which are standard in historical journals.

ACKNOWLEDGMENTS

An editor's job is simultaneously frustrating, time-consuming, and rewarding. But with the task complete, the final product in hand, and reflections in order, my first thought is of all the help I got along the way. The authors, of course—without their efforts and cooperation there would be nothing here. Referees of the manuscripts provided suggestions that materially improved the quality of those manuscripts; though the referees must remain anonymous, they should know that their efforts are appreciated, by me and by the authors. When wrestling with some issue in a botany paper I often found myself running next door to Wayne Chester's office for advice, which he always gave authoritatively and graciously; Wayne is a handy guy to have around when you're editing a botany paper. Julie Brash was my right arm throughout; her intelligence, reliability, initiative, and candor made for a better product, with substantially less effort and frustration on my part than would have been the case had she not been involved.

I have done enough editing to know that I am apparently incapable of producing an errorless document; therefore I herewith apologize and accept responsibility for the errors in this one.

David H. Snyder
June 1992

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Following, in alphabetical order, is a list of those individuals who registered at the 1991 symposium. Institutional affiliation (when available), city (of the person's institution or home), and state are also given.

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SYMPOSIUM PARTICIPANTS



Contributed Papers Session I: Botany - (from left) Hal DeSelm, Scott Franklin, Carol Baskin, Richard Jensen, Kristin Snyder, Wayne Chester, and Xiaoying Nan.



Contributed Papers Session II: Zoology - (row 1, from left) Pete Wyatt, Wayne Davis, Rosanna Mattingly, Richard Gildrie, David Pitts, Fred Busroe, James Fralish, and David Sharpe.

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CONTRIBUTED PAPERS

SESSION I: BOTANY

Moderated by:

Richard J. Jensen
St. Mary's College

BARRENS OF THE CENTRAL BASIN OF TENNESSEE

HAL R. DESELM

The University of Tennessee, Knoxville

ABSTRACT. Four barren (grassland) areas in the Central Basin of Tennessee have been examined floristically; three areas were plot sampled. The sites lie on Lebanon and Ridley limestones and are on shallow, stoney, droughty soils. Of 307 native taxa found, 13 are listed in various Federal and State levels of endangerment. Floristic element percentages approximate those found in other Tennessee barrens areas except that here the western and local intraneous (endemic) elements are higher. This vegetation is perennial grass-perennial forb vegetation; the most important grass is *Schizachyrium scoparium*, little bluestem. Environmentally and vegetationally these barrens "fit" between cedar glades and cedar or oak forests with deeper soils. The possible times of migration of the barrens flora might have been in late Tertiary, Pleistocene, or Holocene times.

INTRODUCTION

Over much of the southeastern United States, prescientific-age observers, as well as observers of modern times, have seen stands of native grasses which resemble midwestern Tallgrass Prairie. These openings in the forest, although extensive in the Black Belt of Alabama and Mississippi and on the Kentucky Barrens, are elsewhere usually small and have often, since the early explorers and hunters, been called barrens (Michaux 1793-96, Safford 1869, Killebrew et al. 1874).

This paper characterizes floristically and vegetationally the barrens of the Central Basin of Tennessee. These areas are of interest because of their floristic and physiognomic relationships to midwestern and southern grasslands, their various floristic elements, and the factors which have operated to cause and maintain them. Other studies of barrens are those of DeSelm (1988; 1989a,b; 1990), DeSelm and Murdock (in press), Chester (1988), Bryant (1977, 1981), and Jones and Patton (1966).

THE STUDY AREA

Geology-Topography

The Central Basin is an elliptical depression 120-215 m below the Highland Rim of Tennessee, within the Interior Low Plateau Physiographic Province (Fenneman 1938) (Fig. 1). It is thought to be a breached and eroded dome structure, the top (center) once located a few kilometers north of Murfreesboro. Bedrocks exposed are chiefly Ordovician limestones and calcareous shales which slope gently down from the center (Safford 1869; Galloway 1919; Bassler 1932; Wilson 1948, 1949).

The Highland Rim had been reduced to a rolling surface by Miocene or early Pliocene time. Uplift and downcutting of the Nashville dome began in late Pliocene or early Pleistocene

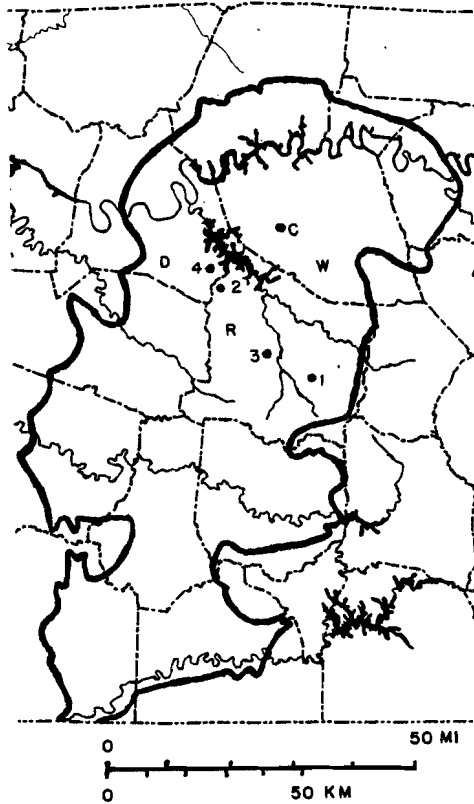


Figure 1. Outline map of the Central Basin of Tennessee (modified from DeSelm 1959). Barrens locations are: 1 - Gladeview, 2 - La Vergne, 3 - Stones River, 4 - Couchville. C is location of Cedars of Lebanon State Forest. Counties are: D - Davidson, R - Rutherford, and W - Wilson.

and the basin floor was excavated by mid-Pleistocene. This was followed by late Pleistocene and Holocene uplift and river entrenchment (Thornbury 1965).

The basin floor, of flat to gently rolling topography, is developed on various Ordovician limestones--this is the inner basin. It is surrounded by a rolling outer basin on other limestone strata (DeSelm 1959). Outcrops of limestone, especially the Lebanon Limestone, occur widely in the inner basin and near the inner-outer basin contact (Hardeman 1966). Cedar glades and their usually nearby community, the barrens, occur on the Lebanon and adjacent Ridley limestones. Both bedrocks are high carbonate, low silicate rock, and are soluble enough that cracks, tubes, caves, springs, and sinkholes form; underground drainage is common (Galloway 1919, Maher and Milici 1975, Piper 1932, Theis 1936).

Soils

The sample sites occur on variously named county soil associations: Davidson County-Talbott-Rock Outcrop, and Rutherford County-Rock Outcrop-Talbott-Barfield. The Talbott series is a Typic Hapludalf (Alfisol). The Barfield, and associated Gladeville series, are both Mollisols; the Barfield is a Lithic Hapludoll, and the Gladeville is a Lithic Rendoll. The grassy sample sites occur on soils about 10 cm to bedrock; this puts them in the Rock Outcrop class. If the soils are 25-50 cm to bedrock, Gladeville is the series. Gladeville is a flaggy, silty clay loam with 40-60 percent of the profile occupied by limestone fragments. The subsoil is clayey. The profile is mildly alkaline with medium to high natural fertility, but because of the shallow depth and high rock content, the available water capacity is very low. Rock Outcrops generally have shallower and stonier soils than Gladeville. Talbott and Barfield generally are deeper, less stony, and more acid soils than Gladeville (Edwards et al. 1974, True et al. 1977, North 1981).

Climate

The Central Basin lies within the moist, humid climates of Thornthwaite (1948). However, Vaiksnoras and Palmer (1973) note that in the period 1929-1969, 15.9 percent of the months of May through August experienced moderate, severe, or extreme droughts in the central part of the state. Safley and Parks (1974) calculate that on a 2.5 cm average water holding capacity soil at Murfreesboro (May through September), one-week droughts have probabilities of occurrence as high as 26 percent. Probabilities decrease on deeper soils and for periods longer than one week.

Mean annual precipitation is 125 cm at Murfreesboro and varies from a winter high of 14.4 to an autumn low of 5.9 cm per month. January temperatures average 5.4°C; July temperatures average 26.4°C (1931-1955 data, Dickson 1960).

Paleoecology

Emiliani (1972) believes that the Caribbean Sea surface water temperature has fluctuated during the past 425,000 years in response to climatic oscillation and North American glaciation. Eight cool-warm oscillations are recorded in the data. The Basin was already excavated and its surfaces available to the biota moving in response to these climatic changes. The Wordfordian (Wisconsinan) substage at Nonconnah Creek (near Memphis) at 30,000 to 24,000 YBP had graminoid communities amid the forest cover. This was followed, at Nonconnah Creek and at Anderson Pond on the eastern Rim, by full glacial spruce-pine pollen rain. Northern and persistent Pleistocene animal remains have been found in caves (Corgan 1975; Guilday 1977; Parmalee and Klippel 1981a, 1982; Klippel and Parmalee 1982). Dominance by hardwood trees began about 10,000 YBP. The warm/dry Hypsithermal is recorded at both fossil sites (Delcourt 1979, Delcourt et al. 1980) and by animal fossil evidence (Klippel and Parmalee 1982, Parmalee and Klippel 1981b).

Flora and Vegetation

The total flora of the Central Basin is not known, but will be included in the flora of Middle Tennessee and Alabama in preparation (Kral 1989). A flora characteristic of the Basin was noted by Gattinger (1901), and the woody plants were enumerated by Shanks (1958). The cedar glade herb flora is well-known (Quarterman 1950, Baskin et al. 1968, Baskin and Baskin 1975). Endemics of southeastern cedar glades total 29 taxa, of which 20 occur on Basin glades (Baskin and Baskin 1986). Extraneous floristic elements include disjunct taxa with centers of distribution to the west, south, east, and north (Bridges and Orzell 1986b).

Vegetation of the Basin has not been treated completely, but that of the cedar stands adjacent to glades and barrens has been examined by Quarterman (1950). The glades themselves were last examined in detail by Somers et al. (1986). Barrens have been noted by DeSelm and Murdock (in press) and Baskin and Baskin (1977).

Early Scientific Study

Michaux (1793-96) mentions various forest species but no cedar glades or barrens in the Basin. Safford (1869), who studied the whole state intensively, notes cedar stands and describes the general location of them and the associated glades. Killebrew et al. (1874) takes measure of the forest openings in describing Rutherford County: "At the early settlement of the county, the prairie portion was covered with buffalo grass [*Bouteloua*], clover [various legume species], peavines [*Amphicarpa*], strawberries [*Fragaria*], black and white berries [?], raspberries [*Rubus*], dewberries [*Rubus*], wild oats [*Danthonia*], and wild rye [*Elymus*]...." Gattinger (1901) distinguished both cedar glades and cedar barrens among the various types of Basin vegetation; he considered such taxa as *Meibomia (Desmodium) marilandica* and *Euphorbia commutata* as characteristic of cedar barrens.

HUMAN HISTORY

The Central Basin was the hunting or living area of a succession of native American cultures, beginning in the late Pleistocene. Evidence of Paleoindian, Archaic, Woodland, and Mississippian cultures occurs (Swanton 1946, Lewis and Kneberg 1958, Hudson 1976, Hofman 1984, Dowd 1989). The last known native American village in the Basin, the Shawnee at Nashville, disbanded and left the area about 1714 (Williams 1937). For subsequent decades the area was under the control of the Cherokees, who hunted there. Long hunters entered the area in the 1760s and began removing many of the big game animals. Settlement began at and near Nashville in 1780. The northern part of the Basin was made available for settlement by treaties with native Americans between 1770 and 1791; the southern section of the Basin was opened to settlement by treaties of 1805 and 1806 (Haywood 1823, Folmsbee et al. 1969). The area, as described by long hunters and early settlers, was summarized by the administrator William Blount as "generally covered with thick and high cane, and a heavy growth of large timber, and where there happens to be no cane, with a thick underwood ..." (Sims 1947). Mentioned in histories of the area are cane, cedar and a few other kinds of trees, and glade privet. Buffalo, elk, and deer were

numerous, at least at first, especially near springs. Openings of this region were noted in the Hutchins survey of 1768 as the "Shawanoë town," and buffalo licks (Williams 1928). Settlers cleared the forest, drained the lowlands, and cultivated crops on lowland and deep upland soils. Forest trees were harvested for local use and items such as barrel staves and cedar boards were exported. The forests and cedar glades were grazed (Carr 1857, Putnam 1859, Haywood 1823, Goodspeed 1887, Williams 1937, journal of DeSchweinitz in Williams 1928).

The widespread forest dominant or associate, eastern red cedar, has been widely identified with the Basin. By 1834, five local place names included the word "cedar" (Morris 1834); now, nearly four dozen place names in the Basin include that word (U.S. Geological Survey 1980).

METHODS

General

During the periods 1955-1960 and 1985-1988, parts of the Central Basin were road reconnoissanced for barrens vegetation. Knowledgeable people were consulted who might know of such stands. In 1977 TENN (Herbarium of the Botany Department, the University of Tennessee, Knoxville) collection records from one site were found and incorporated into my database. Floristic lists were compiled for each site and ranges of native taxa were determined using Fernald (1950), Little (1971, 1977), Pennell (1935), and Cronquist (1980). Nomenclature, for the most part, follows Gleason and Cronquist (1963) and Cronquist (1980). Specimens are at the Herbarium of the Botany Department, the University of Tennessee, Knoxville, or at Eastern Kentucky University. The four sites used here to represent these barrens are described below.

Barrens Sites

- 62 Gladeview. Rutherford County, Dillton Quad. This approximately 1.2 ha site is characterized by Lebanon and Ridley limestones (Wilson 1964a), and soils mapped chiefly as Gladeview-Rock Outcrop-Talbott and some Talbott-Barfield-Rock Outcrop (True et al. 1977). The site is gently south-facing, has three sinkholes, and is being actively eroded along its eastern edge where it passes into old field vegetation. The vegetation types are *Schizachyrium* barren, *Juniperus* thicket and *Quercus-Juniperus* savanna with *Schizachyrium* understory. This site was found in 1955 and has been seen more than four dozen times since then. It had a surface fire about 1963.
- 63 La Vergne Barren. Rutherford County, La Vergne Quad. This approximately 0.8 ha site, now destroyed, was characterized by Lebanon limestone (Wilson 1966) and Gladeview-Rock Outcrop-Talbott soils (True et al. 1977). This site sloped gently to the north and lay along U.S. Route 41 and between that route and the railway, about 2.4 km east of La Vergne. The vegetation was dominated by *Schizachyrium* interspersed with *Quercus* and *Juniperus* thickets. This site was found in 1954 and was seen four times from 1954-1958.

- 64 Stones River. Rutherford County, Walter Hill Quad. This site is underlain by Ridley Limestone (Wilson 1964b) with soils mapped as Talbott-Rock Outcrop (True et al. 1977). This barrens lay along U.S. 41 opposite the entrance to Stones River National Military Park, but is now destroyed. The land surface was partly rock outcrop and partly the *Schizachyrium* community interspersed with hardwood thickets. The approximately 0.8 ha site was reported to me by A. J. Sharp, and visited by me 1956-60.
- 108 Couchville or Mt. Juliet Road Barren. Davidson County, La Vergne Quadrangle. This approximately 20 ha site is underlain by Lebanon and Ridley limestones (Wilson 1966) and has soils mapped as Talbott silt loam and Gladeville flaggy silty clay loam (North 1981). It includes a house and barn location and may be old field vegetation. Plant communities are dominated by *Schizachyrium* interspersed with *Juniperus* and hardwood thickets. It has a spring (which runs or seeps, depending upon rainfall), and had a surface fire in the summer of 1990. I learned of this site from Larry Smith and Paul Somers of the Tennessee Department of Conservation, and visited it six times from 1985-88.

In 1986 and 1987 three sites were quadrat sampled. Results from 1986 have already been published (DeSelm 1989). Sets of 20, 0.5 m square samples spaced one meter apart were placed on a line through the long axis of the opening. Cover was estimated for each vascular taxon present. Cover of rock, gravel, bare soil, lichens, bryophytes, and tree litter was also estimated. Frequency, mean cover, relative frequency, relative cover, and importance value to the base 200 (IV200; the sum of relative frequency and relative cover) were calculated. Relationships between sample sets were calculated using Jaccards coefficient of community similarity (Mueller-Dombois and Ellenberg 1974) as $2C/A+B \times 100$, where A is the number of taxa from one sample area, B is the number of taxa from the second sample area, and C is the number of taxa in common.

Samples were obtained in the barren at Mt. Juliet Road and in a glade border at Cedars of Lebanon State Forest. As part of another set, nine samples from Mt. Juliet Road proved to have less than 50 percent perennial grass cover, and have been called glade.

RESULTS

Flora

Three-hundred thirty-five vascular plant taxa occur on the four Central Basin barrens; 307 of them are native (see Appendix list). Sixty-seven plant families are represented. Among native plants, Asteraceae and Poaceae each include 14.3 percent of all taxa present, and Fabaceae includes 8.8 percent. These percentages are similar to those of the western Highland Rim (DeSelm 1988). Nearly 16 percent of the taxa are woody.

Thirteen taxa (listed below) appear in Somers et al. (1989), classified in various states of endangerment in Tennessee. In this list, E, T, and S are the Tennessee State categories--endangered, threatened, and of special concern. C2, 3C, and LE indicate Federal status; C2 taxa are appropriate for listing federally but data on abundance is still being collected, 3C

taxa are rare but more widespread than formerly believed, and LE taxa are formally listed as endangered (Somers 1989).

Astragalus tennesseensis, E, C2
Dalea candida, E
D. foliosa, E, C2
Echinacea pallida, T
E. tennesseensis, E, LE
Lobelia appendiculata var.
gattingeri, T, C2

Mirabilis albida, T
Onosmodium molle var. *molle*, S, 3C
Psoralea subacaulis, S, 3C
Schoenolirion croceum, T
Silphium pinnatifidum, T
Solidago gattingeri, E
Talinum calcaricum, T, C2

Eight of the taxa listed above are glade endemics (Baskin and Baskin 1986). The 13 rare taxa above are only 28 percent of the approximately 46 rare taxa known from Basin counties (Committee for Tennessee Rare Plants 1978). Three additional rare taxa, *Ammoselinum popei*, *Liatris cylindracea*, and *Oenothera missouriensis*, though not actually found on the barrens, were found on glades near the Gladeview Barren.

Of native taxa, 54.1 percent are intraneous--a slightly lower percentage than has been reported for other Tennessee barrens floras (DeSelm 1988, 1989a, 1990, 1992). The 24.1 percent southern taxa and 7.8 percent northern taxa are intermediate among percentages of southern and northern taxa seen on other barrens areas. Percentages higher than in other barrens areas are those of western taxa (8.8 percent) and local intraneous (including endemic taxa) at 4.3 percent. Over two-thirds of local intraneous taxa are cedar glade endemics as characterized by Baskin and Baskin (1986). Nearly 62 percent of the native herbs of barrens occur on the list of cedar glade native herbs of Baskin et al. (1968) and Baskin and Baskin (1975). Conversely, 58 percent of the native cedar glade herb list taxa also occur on the barrens sample areas.

Vegetation

The small remnants of barrens seen in the Basin are on shallow soil and occur as an alternative to the cedar forest which borders glades. Large glades often have a crescentic ring of barren-like vegetation between the glade and cedar thicket or forest. With clearing of the cedar or burning and grazing of this vegetation, the perennial grasses spread, forming the barren. Soils and treatment believed conducive to barrens maintenance are not always adjacent to glades, but may appear in any rocky part of the oak/cedar/glade vegetation mosaic.

The results from three sample sets--barren, glade border, and glade sites-- appear in Table 1. The coefficient of community similarity between sites (using the first nine samples in each set to make them all equivalent) vary from 0.19 to 0.20; thus, floristically these samples are about equally related at a low level. Although the number of glade plots is small, the number of perennial grass taxa in the series glade to glade border to barren community increases (in the nine plot samples) from two to three to seven, and in the full set of sample plots from two to eight to 11 (Table 1). Mean perennial grass cover changes from 21 to 162 to 143 in the same series, whereas total forb cover changes from 29 to 16 to 17 percent. Total woody plant cover changes from one to three to 13 percent. This suggests that on the soil depth gradient (from very shallow and rocky to deeper) numbers of total taxa

and perennial grass taxa rise, the number of forbs and their mean cover falls, and the number of woody plant taxa and their total cover increases. This environmental gradient behaves to some extent like a successional series (Oosting 1942).

Table 1. Floras with species frequency (F), mean cover ($\bar{X}C$), and Importance Value 200 (IV200) of three Central Basin sample sites. Frequency and mean cover are shown for five surface types.

| Surface Types | Sites | | |
|-------------------------------|----------------------------------|--|-----------------------------------|
| | Mt. Juliet Road <u>Barren</u> | Cedars of Lebanon <u>glade border</u> | Mt. Juliet Road <u>"glade"</u> |
| | F- $\bar{X}C$ | F- $\bar{X}C$ | F- $\bar{X}C$ |
| Bedrock/gravel | 15-20 | 35-10 | 100-47 |
| Bare soil | | 70-12 | 33-33 |
| Lichens | 5-1 | | |
| Bryophytes | | 40-6 | |
| Tree litter | 10-2 | 35-1 | 22-1 |
| Taxa | F- $\bar{X}C$ -IV200 | F- $\bar{X}C$ -IV200 | F- $\bar{X}C$ -IV200 |
| <i>Allium vineale</i> | 10- 1-019 | 5- 1-015 | |
| <i>Andropogon gyrans</i> | 5- 5-032 | | |
| <i>Aristida longispica</i> | 45-20-164 | 64- 2-122 | |
| <i>Asclepias verticillata</i> | | | 11- 1-032 |
| <i>Aster dumosus</i> | 30- 1-047 | | 33- 1-069 |
| <i>Bouteloua curtipendula</i> | | 5-60-307 | |
| <i>Carex</i> sp. | 15- 1-041 | | 11- 1-032 |
| <i>Cassia fasciculata</i> | 30- 1-047 | 5- 1-015 | |
| <i>Celtis</i> sp. | | | 5- 1-015 |
| <i>Croton capitatus</i> | | 45- 1-082 | 44- 1-088 |
| <i>C. monanthogynus</i> | | 10- 1-023 | |
| <i>Desmanthus illinoensis</i> | 10- 1-019 | | |
| <i>Desmodium ciliare</i> | 5- 1-012 | | |
| <i>Diodia teres</i> | 20- 1-033 | 5- 1-015 | |
| <i>Eragrostis spectabilis</i> | 10- 1-019 | 5-10-081 | |
| <i>Erigeron strigosus</i> | 5- 1-012 | 10- 1-023 | |
| <i>Euphorbia corollata</i> | | | 22- 1-050 |
| <i>E. dentata</i> | | 35- 1-065 | |

Table 1. (Continued)

| Taxa | Mt. Juliet Road <u>barren</u> | Cedars of Lebanon <u>glade border</u> | Mt. Juliet Road <u>"glade"</u> |
|--|----------------------------------|--|-----------------------------------|
| | F- \bar{X} C-IV200 | F- \bar{X} C-IV200 | F- \bar{X} C-IV200 |
| <i>E. preslei</i> | | 15- 1-032 | |
| <i>Galactia volubilis</i> | 30- 1-047 | 10- 1-023 | |
| <i>Gerardia tenuifolia</i> | | | 11- 1-032 |
| <i>Grindelia lanceolata</i> | 5- 1-012 | | 22- 1-050 |
| <i>Heliotropium tenellum</i> | | 25- 1-048 | 33- 1-069 |
| <i>Houstonia longifolia</i> | | 5- 1-015 | |
| <i>H. nigricans</i> | | | 100-19-420 |
| <i>Hypericum sphaerocarpon</i> | | | 11- 1-032 |
| <i>Ipomoea pandurata</i> | | 5- 1-015 | |
| <i>Isanthus brachiata</i> | | | 11- 1-032 |
| <i>Juniperus virginiana</i> | | 10- 1-023 | |
| Legume, unknown | 10- 2-019 | | |
| <i>Leptoloma cognatum</i> | 10- 2-019 | | |
| <i>Lespedeza procumbens</i> | 20- 1-033 | | |
| <i>L. repens</i> | 15- 1-026 | | |
| <i>L. stipulacea</i> | 5- 1-012 | | |
| <i>L. virginica</i> | 35- 1-054 | | |
| <i>Linum sulcatum</i> | | 10- 1-023 | |
| <i>Manfreda virginica</i> | | 20- 1-040 | |
| <i>Panicum anceps</i> | 25-23-151 | | |
| <i>P. flexile</i> | | 30- 1-057 | |
| <i>P. lanuginosum</i> | 20- 1-033 | 10- 1-023 | |
| <i>P. sphaeocarpon</i> | | 5- 1-015 | |
| <i>Panicum</i> sp. | 20- 1-033 | 5- 1-015 | |
| <i>Petalostemum gattingeri</i> | | | 33- 1-069 |
| <i>Polygala verticillata</i> var. <i>ambigua</i> | 5- 1-012 | | |
| <i>Potentilla simplex</i> | | 15- 1-032 | |
| <i>Rosa carolina</i> | 20- 1-033 | | |
| <i>R. setigera</i> | 5- 1-012 | | |
| <i>Ruellia humilis</i> | | 5- 1-015 | |
| <i>Schizachyrium scoparium</i> | 80-50-364 | 100-76-714 | 100-40-696 |

Table 1. (Continued)

| | Mt. Juliet Road <u>barren</u> | Cedars of Lebanon <u>glade border</u> | Mt. Juliet Road <u>"glade"</u> |
|--|----------------------------------|--|-----------------------------------|
| Taxa | F- \bar{X} C-IV200 | F- \bar{X} C-IV200 | F- \bar{X} C-IV200 |
| <i>Scirpus lineatus</i> | 5- 1-012 | | |
| <i>Scleria pauciflora</i> | 65- 1-095 | 5- 3-030 | |
| <i>Senecio anonymus</i> | 5- 1-012 | 5- 1-015 | |
| <i>Setaria geniculata</i> | 15- 1-026 | | |
| <i>Sisyrinchium albidum</i> | 5- 1-012 | 15- 1-032 | 11- 1-032 |
| <i>Smilax bona-nox</i> | 10-11-070 | 10- 2-023 | |
| <i>Sporobolus asper</i> | 80-44-333 | | |
| <i>S. clandestinus</i> | | 20- 6-073 | |
| <i>S. neglectus</i> | 5- 1-012 | | 78- 4-186 |
| <i>S. vaginiflorus</i> | | 70- 6-160 | |
| <i>Tridens flavus</i> | 20-12-089 | 5-10-081 | |
| Unknown forb | 15- 3-026 | 20-10-038 | 56- 1-108 |
| Number of sample plots | 20 | 20 | 9 |
| Numbers of taxa, all plots | 35 | 33 | 15 |
| Numbers of taxa, first 9 plots | 25 | 16 | 15 |
| Numbers of perennial grasses, all plots | 11 | 8 | 2 |
| Numbers of perennial grasses, first 9 plots | 7 | 3 | 2 |

DISCUSSION

The pattern of distribution found among cedar glade endemics is paralleled on the barrens. Most taxa are endemic to the southeast, two are disjunct to the midwest, one is disjunct to the Ozarks, and one (*Leavenworthia uniflora*) occurs in the southeast, the Ozarks, and in southern Indiana and southern Ohio (compare Floristic List at the end of this paper with Table 1 in Baskin and Baskin 1986). The fact that several families and genera are represented by Basin endemics suggests that these or progenitor species arrived during development of the Central Basin (which occurred during the late Tertiary or Pleistocene [Thornbury 1965]), occupying glady habitats as the Ordovician rocks were exposed. Rollins and Shaw (1973) show that most *Lesquerella* taxa related to Basin species occur in Texas and Oklahoma. Further, *Leavenworthia aurea* of Texas and Oklahoma is thought to be the progenitor of *L. crassa* of Alabama, which gave rise to the other Alabama and Tennessee

Leavenworthia (Rollins 1963). Eight other genera have similar western/southwestern affinities (Baskin and Baskin 1986). It is not known whether these founder species and the western element of the barrens (and glades) arrived during the Tertiary, during some warm/dry interglacial period such as the Sangamon (King and Saunders 1986), or during the post-glacial Hypsithermal when prairies spread eastward into the eastern midwest (Transeau 1935) and farther (Cain et al. 1937).

The western element, well-represented by 17 taxa on the barrens (Bridges and Orzell 1986a,b), has taxa ranging both to the northwest and to the southwest. Migration directly from the west is not suggested; these taxa are largely absent from Mississippi alluvial plain clay and loess prairies (Irving and Brenholts 1977). Migration seems possible across southern Illinois on Mississippian limestones south of the glacial boundary and just east of the loess-covered Jackson Purchase of western Kentucky (Skorepa 1973, Voigt and Mohlenbrock 1964, Mohlenbrock 1975, Baskin and Baskin 1986) to the Silurian limestones of the Tennessee River border and the Mississippian and Ordovician limestones of Middle Tennessee and the Central Basin. The distribution of *Carex oxylepis* Torr. and Hook. in Illinois, Kentucky, and Middle Tennessee, as it is presently known, suggests such a route (Beal and Thieret 1986, Mohlenbrock 1975, TENN records). Perhaps the evolution of *C. oxylepis* Torr. and Hook. var. *pubescens* J. K. Underwood (Underwood 1945) suggests a Pleistocene or earlier migration.

Migration from the north would have been facilitated by habitats along bluffs of the Cumberland River from the Cumberland Plateau of Kentucky and Tennessee, and from the highlands of East Tennessee and southwestern Virginia via the southern tributaries of the Tennessee River into the Basin. Migration from the south would have been facilitated by continuous Mississippian and Cretaceous geologic beds and landforms stretching from Alabama and Mississippi into Tennessee. The prairie-adorned Black Belt (Jones and Patton 1966) is on the Cretaceous Selma Chalk (Adams et al. 1926) and the Demopolis Chalk (Bicker 1969).

But one cannot rule out long-distance dispersal as a mechanism of arrival (Cain 1945); in fact, just such a mechanism is suggested by the presumed progenitor species of *Leavenworthia* and *Lesquerella*. Other possible examples include *Astragalus distortus* in the shale barrens (Keener 1983), *Sporobolus heterolepis* in the cedar barrens of north Georgia (Cronquist 1949), and *Agropyron trachycaulon* in the serpentine barrens of western North Carolina (Radford et al. 1968). The arrival of high-biomass dominant species, such as some perennial graminoids, may have been mediated by tornadic winds (cf. Ridley 1930) or animals such as buffalo whose ranges expanded in the late Holocene (Rostlund 1960). Propagules arriving at glade borders or lightning-caused burned areas may have found there sufficient light and enough surface soil fertility to allow their establishment. The arrival of propagules at field borders or on old fields where village-building Archaic, Woodland, or Mississippian native Americans were using fire to manage the landscape could have resulted in other sites of temporary establishment; such temporary populations may have subsequently spread into suitable natural environments in the vicinity, such as glade borders or open cedar woods where barren species now occur.

SUMMARY AND CONCLUSIONS

The earliest explorers, travelers, and settlers in Tennessee wrote little or nothing of glades and barrens in the Basin. But by the nineteenth century scientific writers of repute were writing of glades, and Killebrew called the open areas of Rutherford County "prairie." Barrens in the Basin occur on the soil thickness/available moisture gradient between cedar glades and cedar forests. Today they probably occur chiefly on sites where the cedar forest has been removed. Maintenance of such openings against cedar and hardwood successional pressure has been accomplished by grazing, fire, and today perhaps by bushhogging.

The mechanism of arrival and spread of barrens species, about two-thirds of which are the same as cedar glade species, is, as in the case of glades, conjectural. Some taxa may have arrived or evolved during the Tertiary to early-middle Pleistocene as the Basin was forming and the extensive Lebanon and Ridley limestones were being exposed and colonized. The well-known western element may have arrived then or during the Holocene Hypsithermal when midwestern prairie advanced eastward.

The Central Basin barrens are dominated by *Schizachyrium scoparium*, as are other dry barrens in Tennessee. They seem to grade aspectually and floristically into cedar glades. They are a perennial grass-perennial forb dominated community.

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APPENDIX
Floristic List^{1,2}

Thallophyta

Isoetaceae

Isoetes butleri Engelm.-L,63,64

Ophioglossaceae

Ophioglossum engelmannii Prantl-I,62,108

Pteridaceae

Cheilanthes lanosa (Michx.) DC. Eat.-S,108

Selaginellaceae

Selaginella apoda (L.) Spring.-I,69

Gymnospermae

Cupressaceae

Juniperus virginiana L.-I,62,63,64,108

Angiospermae

Acanthaceae

Ruellia caroliniensis (Walt.) Steud.-I,64

R. humilis Nutt.-I,62,64,108

Amaryllidaceae

Hypoxis hirsuta (L.) Cov.-I,62,64,108

Manfreda virginica Salisb.-S,62,63,108

Anacardiaceae

Rhus aromatica Aiton-I,62,64,108

R. copallina L.-I,62,63,108

R. glabra Britt.-I,62,64,108

R. radicans-I,108

Apiaceae

Bupleurum rotundifolium L.-X,62,108

Chaerophyllum tainturieri Hook.-S,64,108

Daucus carota L.-X,62,108

Eryngium yuccifolium Michx.-I,62

Sanicula canadensis L.-I,62

Torilis arvensis (Huds.) Link-X,62

Zizia aptera (Gray) Fern.-I,62

Apocynaceae

Apocynum cannabinum L.-I,108

¹Floristic elements are: I-intraneous regional; S-southern; W-western; N-northern; L-intraneous local; X-introduced.

²Sites are: 62-Gladeview; 63-La Vergne; 64-Stones River; 108-Couchville or Mt. Juliet Road

Asclepiadaceae

- Asclepias tuberosa* L.-I,108
- A. variegata* L.-I,108
- A. verticillata* L.-I,62,63,64,108
- A. viridiflora* Raf-W,62,63,64
- A. viridis* Walt.-W,62,63,64,108

Asteraceae

- Achillea millifolium* L.-X,108
- Ambrosia artimisiifolia* L.-I,64,108
- Antennaria plantaginifolia* (L.) Hook.-I,108
- Aster dumosus* L.-S,62,108
- A. hemisphericus* E. J. Alex.-S,62
- A. laevis* L.-I,62
- A. patens* Ait.-I,62,63
- A. pilosus* Willd.-I,62,63
- A. undulatus* L.-I,62
- Bidens polylepis* Blake-W,108
- Carduus nutans* L.-X,108
- Chrysanthemum leucanthemum* L.-X,108
- Coreopsis tripteris* L.-N,63,64
- Echinacea pallida* Nutt.-W,62
- E. tennesseensis* (Beadle) Small-L,108
- Erigeron strigosus* Muhl.-N,62,63,64,108
- Eupatorium altissimum* L.-S,62,63,64,108
- E. coelestinum* L.-I,63,64
- E. incarnatum* Walt.-S,62
- E. serotinum* Michx.-S,63,64
- Gnaphalium obtusifolium* L.-I,62,63,64,108
- Grindelia lanceolata* L.-W,62,63,108
- Helenium autumnale* L.-N,64,108
- Helianthus augustifolius* L.-S,62
- H. hirsutus* Raf.-I,62,63,108
- H. mollis* Lam.-I,63
- H. occidentalis* Riddell-W,62
- Krigia dandelion* (L.) Nutt.-S,64
- Kuhnia eupatorioides* L.-S,62,63,108
- Liatrix scariosa* (L.) Willd.-I,63
- Parthenium integrifolium* L. var. *henryanum* Mears-I?,62,63
- Polymnia canadensis* L.-I,108
- Pyrrhopappus carolinianus* (Walt.) DC.-S,63,108
- Ratibida pinnata* (Vent.) Barnh.-W,108
- Rudbeckia fulgida* Ait.-L,108
- R. hirta* L. var. *pulcherrima* Farw.-W,64
- R. triloba* L.-I,62,63,64

- Senecio anonymus* A. Wood-S,62,64,108
Silphium pinnatifidum Ell.-L,63
Solidago canadensis L. var. *scabra* (Muhl.) T. and G.-I,62,108
S. gattingeri Chapm.-L,62
S. nemoralis Ait.-I,62,108
S. odora Ait.-I,62
S. speciosa Nutt. var. *rigidiscula* T. and G.-W,62
S. ulmifolia Muhl.-N,62
Tragopogon pretensis L.-X,108
Verbesina helianthoides Michx.-S,63
V. virginica L.-S,62,63,108
Vernonia gigantea (Walt.) Trel.-S,62,63
- Bignoniaceae**
- Anisostichus capreolata* (L.) Bureau-S,62,63,108
Campsis radicans (L.) Seem.-S,62
- Boraginaceae**
- Heliotropium tenellum* Torr.-W,62,63,108
Lithospermum canescens (Michx.) Lehm.-I,62
Myosotis macrosperma Engelm.-S,63,64
Onosmodium molle Michx.-L,62,108
- Brassicaceae**
- Arabis canadensis* L.-I,62
Leavenworthia uniflora (Michx.) Britt.-L,62,63
- Cactaceae**
- Opuntia humifusa* Raf.-I,62,63,108
- Campanulaceae**
- Lobelia appendiculata* A. DC. var. *gattingeri* (A. Gray) McVaugh-L,62,63,64,108
L. spicata Lam.-N,62,108
Triodanis perfoliata (L.) Nieuwl.-I,62,64
- Caprifoliaceae**
- Lonicera japonica* Thunb.-X,62,108
L. sempervirens L.-I,62
Symphoricarpos orbiculatus Moench-I,62,63,108
Viburnum rufidulum Raf.-S,62,108
- Caryophyllaceae**
- Arenaria patula* Michx.-S,62,63,64,108
- Cistaceae**
- Lechea tenuifolia* Michx.-I,62
L. villosa Ell.-I,62
- Clusiaceae**
- Hypericum hypericoides* (L.) Crantz-S,64
H. frondosum Michx.-S,62,63,108
H. punctatum Lam.-I,63

- H. sphaerocarpum* Michx.-W,62,64,108
H. stragalum Adams and Robson.-I,62
- Convolvulaceae
Ipomoea pandurata (L.) G. F. W. Mey.-S,62,63
- Crassulaceae
Sedum pulchellum Michx.-W,64,108
- Cyperaceae
Carex blanda Dew.-I,62
C. bushii Mackenz.-I,64
C. cherokeensis Schwein.-S,108
C. complanata Torr. and Hook.-S,64
C. gravida Bailey-W,108
C. hirsutella Mackenz.-I,62,64,108
C. meadii Dew.-I,62,64
Cyperus inflexus Muhl.-I,64,108
Eleocharis compressa Sulliv.-I,62,64,108
E. tenuis (Willd.) Schultes-N,64
Scirpus lineatus Michx.-I,64,108
Scleria oligantha Michx.S,62,108
S. pauciflora Muhl.-S,62,108
- Ebenaceae
Diospyros virginiana L.-I,62,108
- Euphorbiaceae
Acalypha ostryaefolia Riddell-S,108
Croton capitatus Michx.-I,62,64,108
C. monanthogynus Michx.-S,64,108
Crotonopsis elliptica Willd.-I,64
Euphorbia chamaesyce L.-X,108
E. commutata Engelm.-I,108
E. corollata L.-I,62,63,64,108
E. dentata Michx.-I,62,108
E. maculata L. (incl. *E. preslii* Guss.)-I,62
- Fabaceae
Amphicarpa bracteata (L.) Fern.-I,62
Astragalus tennesseensis Gray-L,62,63,64,108
Baptisia australis (L.) R. Br.-W,62
Cassia fasciculata Michx.-I,63,64,108
Cercis canadensis L.-I,62,63,64,108
Desmanthus illinoensis (Michx.) MacMill.-W,62,63,64,108
Desmodium ciliare (Muhl.) DC.-I,62,63,108
D. marilandicum (L.) DC.-I,62
D. paniculatum (L.) DC.-I,62
D. paniculatum (L.) DC. var. *dillenii* (Darl.) Isley-I,62
D. rotundifolium DC.-I,62

- D. sessilifolium* (Torr.) T. and Gr.-I,108
Galactia volubilis (L.) Britt.-S,62,63,108
Gleditsia triacanthos L.-I,62,108
Lespedeza capitata Michx.-I,64
L. cuneata (Dumont) G. Don-X,108
L. intermedia (S. Wats.) Britt.-I,62
L. procumbens Michx.-I,62
L. repens (L.) Bart.-I,62,108
L. stipulacea Maxim.-X,62,108
L. virginica (L.) Britt.-I,62,63,64,108
Medicago sativa L.-X,108
Melilotus alba Desr.-X,63,108
M. officinalis (L.) Lam.-X,62,108
Petalostemum candidum (Willd.) Michx.-W,62,63
P. foliosum Gray-L,64
P. gattingeri Heller-L,62,63,64,108
Psoralea psoraloides (Walt.) Cory var. *eglandulosa* (Ell.) F. L. Freeman-S,62,63
P. subacaulis T. and G.-L,62,63,64,108
Strophostyles umbellata (Muhl.) Britt.-S,62
Stylosanthes biflora (L.) BSP.-I,62
Tephrosia virginiana (L.) Pers.-I,62
Vicia augustifolia Reichard-X,108
- Fagaceae
- Quercus falcata* Michx.-S,62
Q. imbricaria Michx.-N,62
Q. marilandica Muenchh.-S,62
Q. muhlenbergii Engelm.-I,62,108
Q. shumardii Buckl.-S,62,108
Q. stellata Wang.-I,62,63,108
Q. velutina Lam.-I,62
- Gentianaceae
- Frasera caroliniensis* Walt.-S,62
Sabatia angularis (L.) Pursh-I,62,108
- Geraniaceae
- Geranium carolinianum* L.-I,64,108
- Iridaceae
- Belamcanda chinensis* (L.) DC.-I,62,64,108
Iris cristata Ait.-S,62
Sisyrinchium albidum Raf.-I,62,63
- Juglandaceae
- Carya ovata* (Mill.) K. Koch var. *australis* (Ashe) Little-S,62,108
C. ovalis (Wang.) Sarg.-N,63
- Juncaceae
- Juncus dudleyi* Wieg.-N,64

- J. tenuis* Willd.-I,64
J. torreyi Coville-W,62
- Lamiaceae
Blephilia ciliata (L.) Benth.-I,62,108
Hedeoma pulegioides (L.) Pers.-I,62
Isanthus brachiatus (L.) BSP.-I,62,63,108
Monarda fistulosa L.-I,62,64
Physostegia virginiana (L.) Benth.-N,62
Prunella vulgaris L. var. *lanceolata* (Bart.) Fern.-I,62
Pycnanthemum tenuifolium Schrad.-I,64,108
Salvia lyrata L.-I,62,108
S. urticaefolia L.-S,62
Satureja arkansana-W,63,108
Scutellaria australis Epl.-S,62,63,64,108
S. incana Biehler-N,62
- Lauraceae
Sassafras albidum (Nutt.) Nees-I,62
- Liliaceae
Allium canadense L.-I,108
A. cernuum Roth-I,62,63,64,108
A. vineale L.-X,64,108
Muscari botryoides (L.) Mill.-X,62
Nothoscordum bivalve (L.) Britt.-S,62,63,64,108
Ornithogalum umbellatum L.-X,62,63
Polygonatum biflorum (Walt.) Ell.-I,62
Schoenolirion croceum (Michx.) Gray-S,64
Smilax bona-nox L.-S,108
S. glauca Walt.-S,108
Yucca filamentosa L.-I,62
Y. smalliana Fern.-S,62,64
- Linaceae
Linum medium (Planch.) Britt.-I,62,63
L. sulcatum Riddell-S,62,63,108
- Loganiaceae
Spigelia marilandica L.-S,64
- Lythraceae
Cuphea petiolata (L.) Koehne-I,108
- Menispermaceae
Cocculus carolinus (L.) DC.-S,62,63
- Moraceae
Maclura pomifera (Raf.) Schneid.-W,108
Morus rubra L.-I,62,108
- Nyctaginaceae
Mirabilis albidus (Walt.) Heimerl-W,62

Oleaceae

- Forestiera ligustrina* (Michx.) Poir.-S,62,64,108
Fraxinus americana L.-I,62,108
F. quadrangulata Michx.-N,108
Ligustrum vulgare L.-X,108

Onagraceae

- Gaura biennis* L.-N,108
G. filipes Spach-S,62,63,108
Ludwigia alternifolia L.-I,64
Oenothera biennis L.-I,64
O. speciosa Nutt.-W,62
O. triloba Nutt.-W,108

Orchidaceae

- Hexalectris spicata* (Walt.) Barnh.-S,62
Spiranthes cernua (L.) Richard-I,64
S. gracilis (Bigel.) Beck-I,62,63,108

Oxalidaceae

- Oxalis priceae* Small-S,62
O. stricta L.-I,62,64,108
O. violacea L.-I,62,108

Passifloraceae

- Passiflora incarnata* L.-S,64
P. lutea L.-S,62

Plantaginaceae

- Plantago aristata* Michx.-W,62,63,108
P. lanceolata L.-X,108
P. pusilla Nutt.-W,62
P. virginica L.-I,63,64

Poaceae

- Aegilops cylindrica* Host-X,108
Agrostis hyemalis (Walt.) BSP.-I,64
A. perennans (Walt.) Tuckerm.-I,62
A. stolonifera L.-X,108
Andropogon gerardii Vitman-I,62
A. gyrans Ashe-I,108
Aristida dichotoma Michx.-I,62,63,64,108
A. longispica Poir.-I,64,108
A. oligantha Michx.-I,62,63,108
Bouteloua curtipendula (Michx.) Torr.-W,62,64,108
Bromus japonicus Thunb.-X,108
B. pubescens L.-I,108
B. tectorum L.-X,108
Chasmanthium latifolium (Michx.) H. O. Yates-I,108
Dactylis glomerata L.-X,108

- Danthonia spicata* (L.) Beauv.-I,62,63,108
Elymus villosus Muhl.-I,108
E. virginicus var. *glabriflorus* (Vasey) Bush-I,62,63,64,108
Eragrostis frankii C. A. May.-I,62
E. spectabilis (Pursh) Steud.-I,62,63,64,108
Festuca arundinacea Schreb-X,108
Hordeum pusillum Nutt.-I,108
Hystrix patula Moench-N,108
Leptoloma cognata (Schult.) Chase-I,108
Melica mutica Walt.-S,62,64,108
Muhlenbergia capillaris (Lam.) Trin.-I,62
Panicum anceps Michx.-S,63,64,108
P. boscii Poir.-I,62
P. commutatum Schult.-I,62
P. depauperatum Muhl.-I,62
P. flexile (Gatt.) Scrib.-I,62,64,108
P. lanuginosum Ell.-I,62,63,64,108
P. laxiflorum Lam.-S,62
P. malacophyllum Nash-W,62,64
P. philadelphicum Bern. ssp. *campestre* D. F. Fairbr.-N,64
P. polyanthes Schult.-I,63
P. sphaerocarpon Ell.-62,64,108
P. villosissimum Nash-I,64
Paspalum setaceum Michx. var. *muhlenbergii* (Nash) D. Banks-I,64
Poa pretensis L.-X,62,63,64,108
Schizachyrium scoparium (Michx.) Nash-I,62,63,64,108
Setaria geniculata (Lam.) Beauv.-S,63,108
Sorghastrum nutans (L.) Nash-I,62
Sphenopholis nitida (Biehler) Scribn.-I,63,64
S. obtusata (Michx.) Scribn.-I,62
Sporobolus asper (Michx.) Kunth-I,62,63,64,108
S. clandestinus (Biehler) Hitchc.-I,62
S. neglectus Nash-I,108
S. ozarkanus Fern.-W,64
Tridens flavus (L.) Hitchc.-I,62,108
Vulpia octoflora Walt.-I,62
- Polemoniaceae
- Phlox bifida* Beck-W,62,108
P. pilosa L.-I,62
- Polygalaceae
- Polygala verticillata* L. var. *ambigua* (Nutt.) Wood-I,62,108
- Portulacaceae
- Talinum calcaricum* Ware-L,62,64
- Primulaceae
- Dodecatheon meadii* L.-S,62,64

- Lysimachia lanceolata* Walt.-I,62
- Ranunculaceae
- Anemone virginica* L.-N,62,63
- Delphinium virescens* Nutt. ssp. *penardii* (Huth) Ewan-W,62,64,108
- Rhamnaceae
- Berchemia scandens* (Hill) K. Koch-S,62
- Rhamnus carolinianus* Walt.-S,62,108
- R. lanceolata* Pursh-I,108
- Rosaceae
- Fragaria virginiana* Duchesne-N,62,63
- Geum canadensis* Jacq.-N,62
- G. virginianum* L.-N,62,108
- Potentilla recta* L.-X,108
- P. simplex* Michx.-N,62,64
- Prunus americana* Marsh.-I,108
- P. augustifolius* Marsh.-S,62,108
- P. serotina* Ehrh.-I,62,108
- Rosa carolina* L.-I,62,108
- R. multiflora* Thunb.-X,108
- R. setigera* Michx.-I,63,108
- Rubiaceae
- Diodea teres* Walt.-I,64,108
- Galium aparine* L.-I,108
- G. pilosum* Ait.-I,62
- Houstonia nigricans* (Lam.) Fern.-W,62,63,64,108
- H. purpurea* L. var. *calycosa* Gray-I,62,64,108
- H. pusilla* Schoepf.-S,62,63
- Santalaceae
- Commandra umbellata* (L.) Nutt.-I,62,108
- Sapotaceae
- Bumelia lycioides* (L.) Gaertn. f.-S,62,63,108
- Scrophulariaceae
- Buchnera americana* L.-S,62
- Gerardia gattingeri* Small-N,62
- G. pedicularia* L.-N,62
- G. tenuifolia* Vahl.-I,64,108
- Leucospora multifida* (Michx.) Nutt.-W,108
- Mecardonia acuminata* (Walt.) Small-S,64,108
- Penstemon brevisepalus* Pennell-L,108
- Solonaceae
- Physalis heterophylla* Nees.-I,108
- P. virginica* Mill.-I,62
- Ulmaceae
- Celtis laevigata* Willd.-S,62,108
- C. occidentalis* L.-N,63,108

- C. tenuifolia* Nutt.-S,62
Ulmus alata Michx.-S,62,108
U. rubra Muhl.-I,62,108
U. serotina Sarg.-L,108
- Valerianaceae
Valerianella radiata (L.) Dufr.-I,63,64,108
- Verbenaceae
Callicarpa americana L.-S,62
Verbena canadensis (L.) Britt.-S,62
V. simplex Lehm.-I,62,63,108
- Violaceae
Viola pedata L. var. *lineariloba* DC.-I,62
V. sororia Willd.-N,62,64
V. triloba Schwein.-I,62
- Vitaceae
Parthenocissus quinquefolia (L.) Planch.-I,108
Vitis vulpina L.-I,62

FLORA AND VEGETATION OF THE BARRENS OF THE CUMBERLAND PLATEAU OF TENNESSEE

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ABSTRACT. Twenty barrens (grassland) have been examined floristically on the Cumberland Plateau of Tennessee. The cumulative flora of these sites is 627 native taxa, including 10 Tennessee rare plants. Most of the flora is intraneous but there are significant northern and southern elements. There are also small western, Coastal Plain, and Appalachian endemic or near endemic percentages. Quadrat sampling of 12 stands in six sites revealed the *Panicum virgatum*, *Andropogon gerardii*, and *Schizachyrium* dominated communities of the Tallgrass prairie, but the first two of these communities are rare. Currently most stands are maintained as open, non-forest vegetation by mowing or bushhogging. Prior to the end of the open range period and prior to settlement of this area by Europeans, fire is believed to have been the factor that inhibited invasion by trees and maintained the barrens as distinctive vegetation.

INTRODUCTION

Like many other parts of the southeastern United States, Tennessee once had barrens vegetation as part of its landscape. Extensive openings lay to the north--the Kentucky Barrens, and to the south--the Black Belt. The small openings resembled Tallgrass prairie, but the term barrens was used locally for this and related vegetation (Michaux 1793-1796, Safford 1869, Killebrew et al. 1874).

This paper characterizes open barrens vegetation of the Cumberland Plateau of Tennessee. This vegetation is of interest because of its similarity to such vegetation in the Middle West and the Southeast, and because of questions about the maintenance of open vegetation under the pressure of forest succession. Regional studies of barrens are those of DeSelm and Murdock (in press), containing a review of southeastern barrens studies; Neel (1914); and studies on the flora of Daniel Boone National Forest where comparable flood zone, cliff edge, and road edge vegetation has been found (Palmer-Ball et al. 1988, Campbell et al. 1990).

THE STUDY AREA

General

The Cumberland Plateau occupies all or part of 22 counties, bisecting the east-central part of Tennessee (Fig. 1). It is elevated 150-425 m above the adjacent topography and is distinctive climatically, geologically (the surface has mainly sandstone and shales exposed), edaphically (with soils derived from these deposits), floristically, and vegetationally.

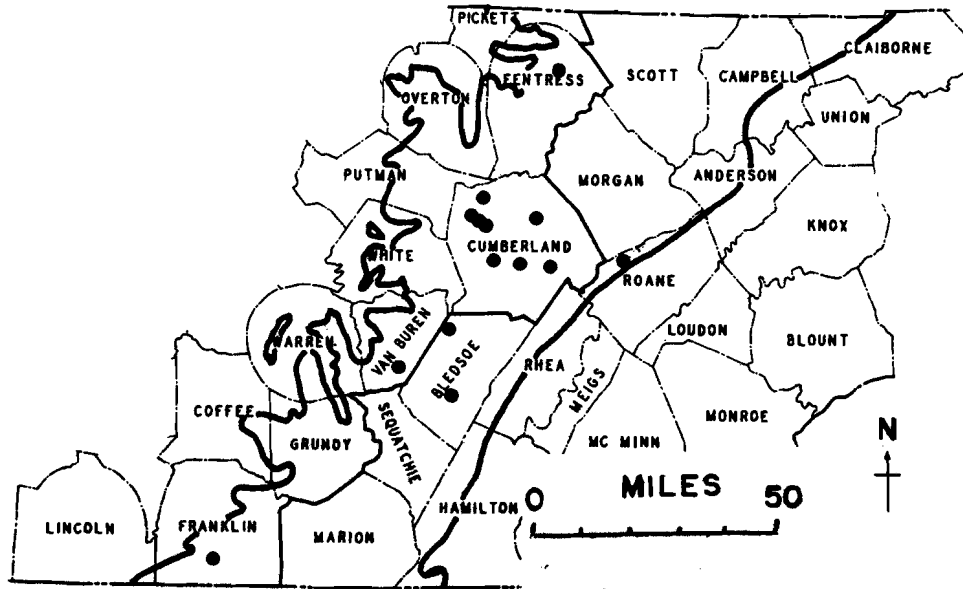


Figure 1. Location of the Cumberland Plateau (between the heavy lines) in Tennessee (after Elder and Springer 1978). Solid line following county boundaries separates East from Middle Tennessee. Dots are approximate locations of barrens and groups of barrens.

Climate

Temperatures on the Cumberland Plateau are somewhat lower than on the adjacent eastern Highland Rim and Ridge and Valley--July minima and maxima range from 17-21°C and 29-31°C. January minima and maxima range from -2 to -1°C and 9-10°C.

Annual precipitation varies from 122-152 cm (Dickson 1960). The moisture region, as mapped by Thornthwaite (1948), is B₄ humid. During the 1931-1969 period, 10 percent of the growing season months exhibited moderate, severe, or extreme meteorological droughts (Vaiksnoras and Palmer 1973). According to Safley and Parks (1974), on a one-inch average water-holding capacity soil at Crossville, whole week drought probabilities vary around 5.4 to 11.3 percent. Probabilities decline on deeper soils, but increase for periods shorter than one week.

Topography and Geology

The Cumberland Plateau, part of the Appalachian Plateau's Physiographic Province (Fenneman 1938), is capped by essentially flat-lying Pennsylvanian strata which include conglomerates, sandstones, siltstones, shales, and coals. Where not dissected by streams and where on the surface, these strata form a flat to rolling landscape. Underlying the Plateau are many meters of Mississippian limestones (chiefly Bangor limestone)--near the contact are beds of the Pennington formation of limestone, sandstone, and shale (Stearns 1954, Wilson et al.

1956, Hardeman 1966). Extensively exposed on the flat to rolling plateau surface is the Crab Orchard Mountain Group which includes the Rockcastle conglomerate (a conglomeritic sandstone including some shale and coal) and the Vandever Formation with conglomerate, sandstone, shale, and siltstone (Wilson 1956). Roosevelt Mountain is part of the faulted eastern edge of the Plateau; here strata may be nearly vertical. The bottom of the Sequatchie Valley has exposed limestone/dolomite strata considered part of the Knox group of the Ridge and Valley to the east (Hardeman 1966), or the Stones River Group of the Central Basin to the west (Milici 1967, 1969). The surface of the flat to rolling Plateau upland may be an erosion product of late Tertiary time (Fenneman 1938), although Hack (e.g., Hack 1966) attacks the idea of multiple erosion cycles.

Soils

Soils of the flat to rolling uplands (which include 13 of 19 areas sampled in this study) are the Hartsells-Lonewood-Ramsey-Gilpin state soil association. These soils are Typic Normudult, Typic Hapludult, Lythic Dystrocrept, and Typic Hapludult, respectively. They are moderately deep and sandy but are usually rocky, acid, and infertile. Four sampled sites are on the Bouldin-Rock outcrop-Ramsey state soil association. The Bouldin and Ramsey Series are Typic Paleudults and Lithic Dystrocrepts, respectively; these are also sandy, rocky, acid, infertile soils. Two sampled sites are on shallow or crevice soils of limestone/dolomite rockland (Elder and Springer 1978, Springer and Elder 1980, Hubbard et al. 1950, Swann et al. 1942, Fox et al. 1958, Moore et al. 1981).

Flora and Vegetation

While the size of the Plateau flora is not known, floras of individual study sites, such as Fall Creek Falls State Park (292 taxa, Caplenor 1955), Fiery Gizzard (604 taxa, Clark 1966), Savage Gulf (680 taxa, Wofford et al. 1979), and the Obed River area (734 taxa, Schmalzer et al. 1985) suggest that it may be 1500 species or more.

Gattinger (1901) and Shanks (1958) both point out the unusual species of the Plateau, including an Appalachian element with species that also occur in the Blue Ridge, and, to a lesser extent, in the Ridge and Valley. This element includes northern taxa. Gattinger (1901), Sharp (1937), and Kral (1976) have noted the Coastal Plain element.

Vegetation studies indicate that most of the upland is dominated by oak forests (Hinkle 1978, Schmalzer 1988). Barrens here are most common as alternatives to xeric oak forests, but also occur as replacements of swamps. They also occur on shallow soils over limestone and sandstone, and on boulder bars of major streams.

The presettlement vegetation developed from shifting vegetation patterns responding to climatic changes in the Pleistocene and Holocene. Many glacial periods have occurred and they may have been paralleled by vegetation change--the effects of the Wisconsinan are best known. Emiliani (1972) believes that there have been 17 major Caribbean surface water temperature shifts in the past 425 thousand years, suggesting eight glacial episodes. While climatic cooling and glaciation resulted from the lower temperatures, the interglacials were warm and may have

been dry (as the Sangamon and Hypsithermal) (King and Saunders 1986; Delcourt and Delcourt 1981; Delcourt 1979; Watts 1970, 1973, 1975).

HUMAN HISTORY

The Plateau was a hunting or living area of the sequential cultures of native Americans: Paleoindian, Archaic, Woodland, and Mississippian. The Paleoindians arrived late in the Pleistocene and were basically hunter-gatherers. Later groups cultivated crops. The details of the extent and intensity of use of the Plateau by these groups are little known but, except for hunting on the plateau surface, more intensive uses were probably confined to river valleys (Hudson 1976, Lewis and Kneberg 1958, Swanton 1946, Ferguson 1988). From the 1500s onward, the Cherokees were an important force in the area and by about 1714 had induced the last of the Shawnees to leave Middle Tennessee (Williams 1937). The Cherokee and other tribes used the area for hunting (Williams 1937). During the 1760s the long hunters began entering central Kentucky and Tennessee, and they eliminated most of the big game animals there (Haywood 1823, Williams 1937).

During the late 1700s, East Tennessee and the Nashville area were being settled, and in 1795 a wagon road was opened across the Plateau from Knoxville to Nashville (Putnam 1859). Squatters had claimed land on the Plateau by 1786 and held it by tomahawk rights (Wirt 1954). The area was released to white settlement in various treaties dating from 1805 to 1819 (Folmsbee et al. 1969). Settlement proceeded rapidly, and settlers cleared and farmed at least the deeper soils of gentle topography. Slope forests were logged for wood as needed. Forests were grazed and the understory burned in spring to increase forage growth (Killebrew et al. 1874).

BARRENS OBSERVATIONS

An early description of this general area in Kentucky and Tennessee is given by Imlay (1797): "The land on the waters of the Tanassee and Cumberland rivers is generally well timbered. In some places there are glades of rich land without timber; but these are not frequent nor large." Travelers on the road to Nashville saw, at Crab Orchard, "a plain or natural meadow" (Baily 1856), or "a great level plain for the most part denuded with wood and overgrown with grass" (report by Steiner and De Schweinitz, cited in Williams 1928). Krechniak and Krechniak (1956) state that when the early settlers first saw Grassy Cove, it too was covered with grass as high as the horses' heads. Doubtless there were other openings, but the following statement by Ramsey (1853), ascribed to early explorers, must apply to some specific place rather than the whole plateau surface: "The top of the mountain is described as being then a vast upland prairie, covered with the most luxuriant growth of native grasses...."

The full extent of the openings, both on the uplands and elsewhere, is now unknown. But certainly on disturbed sites (as burned), on shallow to deep soils, there were grassy openings. There were (and are now) also rock outcrop vegetation on cliff edges. There were numerous wet sites, from ponds to marshes and swamps (and bogs?) of which only the swamps were forested.

The institution of periodic burning to facilitate hunting by native American populations mediated the spread of the species of open vegetation. Frequently burned sites, burn borders, and adjacent burned forest understory became sites susceptible to invasion by barrens dominants. These grassy sites then became places where other invading taxa may have become established, e.g., those taxa from adjacent forests as well as extraneous elements (DeSelm 1989b).

The initiation of regular burning and grazing regimes with settlement resulted in the spread of non-forest vegetation, enlargement of marshes at the expense of swamps, and encroachment on adjacent xeric forest by grassy vegetation peripheral to flatrocks. This was reported by Killebrew et al. (1874) on soils with yellowish red subsoils, and dark soils along streams. In Cumberland and Van Buren counties they note areas as "small prairies, destitute of timber and covered with coarse, rank grass." The uplands of most Plateau counties were then pastured by cattle and sheep.

Place names have been given to sites on the Plateau which suggest early settlement openings. There are six "glade" or gladey places (three each used with "grassy" or "meadow"). Interestingly, the terms barren--used for grassy vegetation by early explorers, prairie--the French word used westward for grassland, and savanna--the word used by Spanish southward, do not appear among Plateau place names.

The open vegetation was seen by Gattinger (1901), who collected in "ponds" and "bogs," and later by A. J. Sharp and R. E. Shanks, whose place names such as "Duggans glady meadow," "bog near Clarkrange," and "Hugo Gernt pond near Allart" represent the wet end of this vegetation spectrum. The wetlands also were seen by Robinson (Robinson 1956, Robinson and Shanks 1959), by Patrick (1979), by Jones (1989), and by Dennis and Morgan (1987). Ditching and building of farm ponds on the wet soils, fire control, and the illegality of open range by about 1940 eliminated most of this vegetation on hydric to xeric sites. Remnant flatrock vegetation was examined by Perkins (1981).

METHODS

General

During some years from 1954-1960 and 1976-1990, parts of the Plateau were road reconnoissanced for barrens vegetation, and knowledgeable people were consulted for possible locations. Floristic lists were compiled at chosen sites. In 1977, barrens collection records of two sites from the Herbarium, Botany Department, The University of Tennessee, Knoxville, were incorporated into these lists. Ranges of native taxa were determined using Fernald (1950), Little (1971, 1977), Pennell (1935), and Cronquist (1980). Nomenclature, for the most part, follows Gleason and Cronquist (1963) and Cronquist (1980). Community floras were compared using the Sorensen coefficient of community similarity (Mueller-Dombois and Ellenberg 1974).

During the late summers of 1986-1989, 12 communities at six sites were sampled using sets of 15-35, 0.5 m square quadrats. Cover was estimated for each species. Species frequency (F), mean cover ($\bar{X}C$), and Importance Value 200 (IV200) based on the sum of relative frequency and relative cover were calculated.

Sample Sites

- 44 Jamestown. Fentress County, Stockton Quad. Along a gravel road and around rock outcrops on a peninsula of North White Oak Creek and Yellow Creek 6.9 airline km east of Jamestown. This site is a broad ridgetop sloping gently south, east, and north; bedrock Rockcastle, soils rocky. Found by Ross Hinkle, Larry Smith, and Gary Wade, summer 1979; examined 1979-1982.
- 45 Roosevelt Mountain (State Forest). Roane County, Rockwood Quad. This site consists of forest borders and rock outcrops of the upper 0.8 km of the road. Bedrock is the Crab Orchard Mountain Group; soils are stony, shallow, and sandy. The site was examined 1979-1987 but records include those of University Herbarium collectors for "mountain above Rockwood" in previous years.
- 46 Daddys Creek. Cumberland County, Ozone Quad. This is a boulder bar on the west creek edge below Antiock Bridge. Rocks are the Rockcastle; sandy fines occur between the rocks. The site floods one or more times per year. This site was found by Rogers and others (Rogers 1972). The site was examined 1972-1975.
- 47 Cox Barren. Cumberland County, Isoline Quad. This is a roadside (U.S. 127 and side road) site just north of Lickfork Creek. It is over the Rockcastle; the soil is Hartsells fine sandy loam. It is flat with small rock outcrops. The site was examined 1976-1978.
- 48 Isoline. Cumberland County, Isoline Quad. This is a site under a road edge power line parallel to U.S. 127 on the northwest edge of Lickfork Creek. It is on Hartsells fine sandy loam over the Rockcastle (Wilson 1956). It slopes gently to the south. The site was examined 1976-1978.
- 50 Crossville Barren. Cumberland County; Crossville Quad. This site lies between the railroad and U.S. 70 east of Crossville. It slopes gently to the south. It is underlain by the Vandever Formation; the soil is fine sandy loam. It was examined 10 times from 1955-1960.
- 51 Crab Orchard. Cumberland County; Dorton Quad. This site lies between the railroad and U.S. 70 near the west edge of Crab Orchard. It is flat, and underlain by the Vandever Formation and the Muskingum series. The ca. 0.04 ha site was seen three times from 1959-1960.
- 53 Glade Creek. Bledsoe County, Billingsley Gap Quad. This site was found by R. E. Shanks, E. H. Cooley, and F. N. Woods, 9 September 1949, and described as a "natural grassland glade." I was unable to relocate this site in 1958 and in subsequent attempts. Bedrock is the Crab Orchard Mountain Group with the Muskingum series soils.
- 88 Lee Station. Bledsoe County, Brockdell Quad. This flat site lies between the railroad and U.S. 127 north of the north crossing of Rocky Branch. It was found about 1980 by Tom Patrick and Bretta Perkins, and examined by me in 1980-82 and in 1988. It is underlain by the Stones River Group and has shallow, cherty, limestone or dolomite-derived soils. It is in the bottom of Sequatchie Valley.

- 106 U.S. 70 (south). Cumberland County, Crossville Quad. This site occurs as two roadside strips along U.S. 70 west of Crossville, near the Crossville Airport entrance. It features Hartsells soils over the Rockcastle, with both mowed upland and mesic little bluestem stands. This site was examined 1985-1987.
- 109-110-111 U.S. 70 N Swale. Cumberland County, Campbell Junction Quad. These sites are between U.S. 70 N and the railroad, centering at a small swale west of Campbell Junction. Bedrock is the Rockcastle; upland and slope soils are the Hartsells series. The soil of the swale bottom is the less well-drained Crossville loam. Uplands are mown, slopes and bottom are bushhogged periodically. The sites were examined 1985-1987.
- 112 Boulder Way. Cumberland County, Campbell Junction Quad. This is a strip of grass between U.S. 70 N and the railroad west of Crossville, near Mayland. Bedrock is the Rockcastle, which is exposed here; soils are the Hartsells series. This site was examined 1985-1987.
- 113 U.S. 70 N at I40. Cumberland County, Campbell Junction Quad. This is another partially mown strip of grass along the railroad at the intersection of U.S. 70 N and I-40, north of Dripping Springs Road. The bedrock is Rockcastle; the soil series is Hartsells. The site was examined 1985-1987.
- 114 Raceway. Cumberland County, Crossville Quad. This is a small site (ca. 0.08 ha) along U.S. 70 N, west of Dykes Crossroad. Part of it is mown, part is growing up to a *Pinus virginiana* thicket. Bedrock is Rockcastle; the soil series is a rocky Muskingum. The site was examined 1985-1987.
- 115 Experiment Station Entrance. Cumberland County, Campbell Junction Quad. This is a roadside and open thicket area between U.S. 70 N and an oak forest at the west station entrance. It is 3.7 km east of Campbell Junction and is of 0.20 ha extent. Bedrock is the Rockcastle; soils are the Hartsell series. The site was examined in 1985-1987.
- 138 Rowe Gap Barren. Franklin County, Beans Creek Quad. This small site (ca. 0.12 ha) is both between the old and new State Route 16 and east of the old road north of Rowe Gap. Fire damage on peripheral trees and snags is evident. The site is over Bangor limestone (Stearns and Ferguson 1967), on soil described as Rockland. The site was seen in September 1987 and July 1988.
- 141 Power line. Van Buren County, Smartt Mountain Quad. This is a strip of scrubby grassland extending from the intersection of the powerline with Brockdell Road east and west, making a 2.8 ha site. It was seen 14 times from 1988-1990, after I learned of its location from Dr. Ron Jones. The soils are the Gilpin, Lonewood, and Tilsit series (Moore et al. 1981) which have developed from the Crab Orchard Mountain Group.

RESULTS AND DISCUSSION

Flora

On the 20 Plateau barrens sample areas, 679 vascular plant taxa are known--627 are native taxa (see Appendix List). Eighty-six families are represented; the largest, and the percent of native plant species in each, are: Asteraceae (17.3), Poaceae (14.1), Cyperaceae (6.7), and Fabaceae (5.3). Trends are similar to those seen in other barrens floras (e.g., DeSelm 1989a). Native woody plants are at 16.9 percent.

Several taxa are listed in Tennessee in different states of endangerment (Somers et al. 1989). They are:

Aster pretensis - T

Calamovilfa arcuata - E, C1

Cotinus obovatus - S

Drosera capillaris - T

Helianthemum propinquum - S

Lilium michiganense - T

Lobelia canbyi - T

Marshallia grandiflora - E, C2

Panicum leucothrix - S

Poa languida - T

Here, the E, T, and S are endangered, threatened, and of special concern in Tennessee. The designations C1 and C2 are U.S. Fish and Wildlife Service designations for rare taxa on which data has been or is being collected. These 10 taxa compare to nine rare taxa on the barrens of the western Highland Rim (DeSelm 1988), an area of nearly equal size. The 10 taxa are only 15 percent of the estimated 67 rare taxa known from the entire area of the Plateau (Committee for Tennessee Rare Plants 1978).

This native flora, developed mainly on sandy soils, is related to the flora of the adjacent eastern Highland Rim, centered 56 km west and developed on loess-derived soils, by a coefficient of community similarity of 60.6 percent. It is related to the barrens flora of the western Highland Rim (centered 225 km west) at 59.1 percent, and to the barrens of West Tennessee (centered 346 km west) at 43.6 percent.

The native flora is largely intraneous (70.5 percent)--a fact not surprising considering that the axis of the Plateau, with its similar bedrocks and soils, extends from New York to Alabama. Basically northern (12.8 percent) and southern (14.2 percent) proportions occur. Disjunct coastal plain taxa (1.1 percent), western taxa (1.6 percent), and local intraneous taxa (1.8 percent) are all few. Compared to the flora of the barrens of the eastern Highland Rim (DeSelm 1990), the intraneous percent is large (the Plateau constitutes a large, homogenous evolution and migration surface compared to the Rim); the northern percent is larger (higher elevation, cooler climate; cf. Dickson 1960); the southern percentage is lower (climate cooler); and Coastal Plain and western percentages are slightly lower (Plateau sites are farther from the presumed western propagule source). Assuming that the Coastal Plain taxa are also southern, perhaps the cooler climate also operates here.

The limestone exposed on lower Plateau slopes supports the Route 16 barren near Winchester and, in Sequatchie Valley, the Lee Station barren (the Crab Orchard Valley site is on sandstone-derived Muskingum soils [Hubbard et al. 1950]). On the Route 16 and Lee Station sites, 106 taxa occur, 19 taxa occur only on both of these two calcareous-substrate barrens. Ten

of these 19 taxa are either weedy (as *Sida spinosa*) or also occur in natural areas on other substrates (as *Vitis vulpina*, TENN herbarium records). The nine apparent calciphiles (as *Helianthus occidentalis*, see Appendix List) are restricted to the limestone sites as they also are in the Central Basin and Ridge and Valley. Of the nine calciphiles, four are listed as cedar glade plants for Tennessee and adjacent areas (Baskin et al. 1968, Baskin and Baskin 1975).

Vegetation

Data from extensive plot sampling has been consolidated in Table 1 by including species present in three of four *Schizachyrium* dominated stands, two of three *Andropogon gerardii* stands, and *Panicum virgatum* dominated stands. The *A. gerardii*-*Schizachyrium* dominated boulder bar and *Schizachyrium* dominated limestone substrate community at Lee Station are of sufficient interest themselves to be included. The wet end of the gradient, the marsh dominated by *Carex glaucescens* (not *C. jorii*)-*Panicum longifolium*-*P. virgatum* has already been described (DeSelm 1989b).

By including plot-sampled taxa only, the list of 679 taxa has been reduced to 104. Species totals per community vary from 23 to 42. Coefficients of community similarity between stand types vary from 36.0 between the wet *Panicum* and mesic *Andropogon gerardii* communities, to 8.7 between the wet *Panicum* and xeric *Schizachyrium* communities. Others vary from 20.3 to 30.8, with causal mechanisms inapparent. Seventy-three percent of the taxa of the *Andropogon gerardii* community are shared by the *Panicum* stands downslope and the *Schizachyrium* stands upslope. The *Andropogon* community is certainly not distinctive floristically.

The distinctiveness of the limestone site (Lee Station) is only moderate; its coefficients vary from 21.7 to 24.3. Likewise the boulder bar on Daddys Creek, kept open by flooding, has coefficients which vary only from 20.3 to 30.8. These sites are neither the most nor the least closely related to other communities/sites, although I would have suspected that they would be least related to the others in view of the unique substrates underlying each.

Physical and thallophte character of the sites varies considerably (Table 1, top). The *Panicum* sites are winter and spring flooded, have little exposed soil, and may have the soil covered by bryophytes, e.g., *Sphagnum*. Tree litter decays during the extended hydroperiod. The upland, deep soil *Andropogon* community also has little exposed soil. However, the *Schizachyrium* stands, usually growing on shallow, stony soils, may have lichen cover as well as exposed soil and gravel. The boulder bar shares a bryophyte cover character with the *Panicum* stands and rock and soil exposure with xeric sites. The Lee Station limestone site had high rock and soil frequency with moderate cover. Soil exposure indicates incomplete plant cover because of low plant productivity (droughty site). Gravel in the soil is the main cause of that aridity (Brady 1974).

Fire is of little importance in barrens maintenance today, but it was important before settlement, through the open range period, and into the 1970s or 1980s along the railway (U.S. 70 sites) before train traffic ceased. Only the flooded boulder bar community is maintained by natural forces today. The *Panicum* stands are maintained by periodic bushhogging, and other stands by periodic mowing or bushhogging.

Table 1. Floristic composition of 5 communities from 12 barrens sites on the Cumberland Plateau of Tennessee. Data are frequency (F), mean cover ($\bar{X}C$), and Importance Value 200 (IV200).

| | Community or Site | | | | |
|-----------------|--|---|------------------------------|-----------------------------|---|
| | <i>Panicum virgatum</i> ^{1,5} | Upland <i>Andropogon gerardii</i> ^{2,5} | Daddys Creek ³ | Lee Station ³ | <i>Schizachyrium scoparium</i> ^{4,6} |
| Surface Types | F- $\bar{X}C$ | F- $\bar{X}C$ | F- $\bar{X}C$ | F- $\bar{X}C$ | F- $\bar{X}C$ |
| Lichens | 0-0 | 0-0 | 0-0 | 0-0 | 11-1 |
| Bryophytes | 23-10 | 0-0 | 35-7 | 0-0 | 0-0 |
| Tree Litter | 0-0 | 0-0 | 0-0 | 0-0 | 14-8 |
| Soil | 1-3 | 3-3 | 5-10 | 50-8 | 37-12 |
| Gravel and Rock | 0-0 | 0-0 | 85-34 | 40-7 | 15-17 |

| Taxa | Number of Sites/Plots | | | | |
|--------------------------------|-----------------------|----------------------|----------------------|----------------------|----------------------|
| | <u>3/60</u> | <u>3/70</u> | <u>1/20</u> | <u>1/25</u> | <u>4/98</u> |
| | F- $\bar{X}C$ -IV200 | F- $\bar{X}C$ -IV200 | F- $\bar{X}C$ -IV200 | F- $\bar{X}C$ -IV200 | F- $\bar{X}C$ -IV200 |
| <i>Acer rubrum</i> | 40-17-110 | | | | |
| <i>Alnus serrulata</i> | 1-10-049 | | 62-19-081 | | |
| <i>Ambrosia artemisiifolia</i> | 30- 3-048 | | | | 6- 2-018 |
| <i>Apios americana</i> | 45- 4-071 | 5- 3-028 | | | |
| <i>Angelica venenosa</i> | 20- 2-033 | | | | |
| <i>Aster dumosus</i> | 40- 1-042 | 17- 1-029 | 65- 1-065 | 28- 2-040 | 25- 1-026 |
| <i>A. umbellatus</i> | 24- 6-070 | | | | |
| <i>Eupatorium fistulosum</i> | 10- 3-027 | 15- 5-063 | | | |
| <i>E. perfoliatum</i> | 20- 1-023 | | | | |

Table 1. (Continued)

| Taxa | Panicum <i>virgatum</i> ^{1,5} | Upland <i>Andropogon</i> <i>gerardii</i> ^{2,5} | Daddys Creek ³ | Lee Station ³ | <i>Schizachyrium</i> <i>scoparium</i> ^{4,6} |
|---|---|---|------------------------------|-----------------------------|---|
| | F- \bar{X} C-IV200 | F- \bar{X} C-IV200 | F- \bar{X} C-IV200 | F- \bar{X} C-IV200 | F- \bar{X} C-IV200 |
| <i>E. rotundifolium</i> | 40- 1-051 | | | | |
| <i>Gerardia purpurea</i> | 40- 1-042 | | | | |
| <i>Helianthus angustifolius</i> | 10- 1-027 | | | | |
| <i>Nyssa sylvatica</i> | 13- 6-037 | | 10- 1-013 | | |
| <i>Panicum longifolium</i> | 4- 2-018 | | | | |
| <i>P. microcarpon</i> | 24-14-122 | | | | |
| <i>P. virgatum</i> | 100-64-440 | | | | |
| <i>Polygala cruciata</i> | 15- 1-023 | | | | |
| <i>Potentilla simplex</i> | 40- 1-052 | 20- 4-044 | 55- 1-056 | | |
| <i>Pycnanthemum muticum</i> | 35- 1-037 | 5- 1-018 | | | |
| <i>Pyrus melanocarpa</i> | 65- 7-111 | 15- 4-057 | | | |
| <i>Rhexia mariana</i> | 15- 3-023 | | | | |
| <i>Rubus</i> spp. | 35- 1-037 | 46- 4-088 | 20- 1-023 | | 11- 1-013 |
| <i>Smilax glauca</i> | 7- 1-011 | 80- 1-130 | 5- 1-009 | | |
| <i>Solidago canadensis</i> var. <i>scabra</i> | 35- 3-036 | 75- 5-219 | | | |
| <i>S. rugosa</i> var. <i>aspera</i> | 20- 4-046 | | | | |
| <i>Spirea tomentosa</i> | 27- 5-047 | | | | |
| <i>Vernonia noveboracensis</i> | 5-10-056 | | | | |
| <i>Andropogon gerardii</i> | | 100-55-364 | 40-43-216 | 16- 5-047 | 50-31-128 |
| <i>Chrysopsis camporum</i> | | 7- 1-014 | | | |
| <i>Desmodium marilandicum</i> | | 17- 1-029 | | | 39- 1-029 |

Table 1. (Continued)

| Taxa | Panicum | Upland | Daddys | Lee | Schizachyrium |
|---|--------------------------------|---|----------------------|----------------------|---------------------------------|
| | <i>virgatum</i> ^{1,5} | <i>Andropogon</i> <i>gerardii</i> ^{2,5} | Creek ³ | Station ³ | <i>scoparium</i> ^{4,6} |
| | F- \bar{X} C-IV200 | F- \bar{X} C-IV200 | F- \bar{X} C-IV200 | F- \bar{X} C-IV200 | F- \bar{X} C-IV200 |
| <i>Festuca pratensis</i> | | 30- 9-078 | | 4- 1-010 | 12-10-057 |
| <i>Galium pilosum</i> | | 7- 1-014 | | | 39- 1-029 |
| <i>Helianthus hirsutus</i> | | 10- 3-041 | | | 28- 1-023 |
| <i>Lespedeza repens</i> | | 3-10-038 | | | 11- 2-023 |
| <i>Lobelia siphilitica</i> | | 5- 1-011 | | | |
| <i>Rhus copallina</i> | | 3- 1-039 | | | |
| <i>Salix tristis</i> | | 10- 1-031 | | | |
| <i>Schizachyrium scoparium</i> | | 75-36-240 | 60-17-127 | 100-63-481 | 100-56-401 |
| <i>Scutellaria elliptica</i> | | 5- 1-011 | | | |
| <i>Setaria geniculata</i> | | 60- 1-098 | | | |
| <i>Sorghastrum nutans</i> | | 80-63-334 | 25-18-095 | 8-13-084 | 5-50-136 |
| <i>Aster linariifolius</i> | | | 35- 1-037 | | 10- 1-012 |
| <i>Clematis virginiana</i> | | | 20- 8-052 | | |
| <i>Coreopsis pubescens</i> | | | 20- 1-023 | | |
| <i>C. tripteris</i> | | | 70- 1-070 | | |
| <i>Elymus virginicus</i> var. <i>glabriflorus</i> | | | 20-18-094 | | |
| <i>Hypericum prolificum</i> | | | 20- 1-023 | | |
| <i>Ipomoea pandurata</i> | | | 20- 1-023 | | |
| <i>Liatris graminifolia</i> | | | 40- 1-042 | | |
| <i>Marshallia grandiflora</i> | | | 20- 1-023 | | |
| <i>Muhlenbergia tenuiflora</i> | | | 25- 1-028 | | |

Table 1. (Continued)

| | <i>Panicum virgatum</i> ^{1,5} | Upland <i>Andropogon gerardii</i> ^{2,5} | Daddys Creek ³ | Lee Station ³ | <i>Schizachyrium scoparium</i> ^{4,6} |
|---------------------------------|--|---|------------------------------|-----------------------------|---|
| Taxa | F- \bar{X} C-IV200 | F- \bar{X} C-IV200 | F- \bar{X} C-IV200 | F- \bar{X} C-IV200 | F- \bar{X} C-IV200 |
| <i>Prunella vulgaris</i> | | | 40- 1-042 | | |
| <i>Pteridium aquilinum</i> | | | 40-11-084 | | |
| <i>Pycnanthemum tenuifolium</i> | | | 50- 2-055 | 48- 5-079 | |
| <i>Rhododendron arborescens</i> | | | 30- 4-045 | | |
| <i>Salvia lyrata</i> | | | 30- 1-032 | | |
| <i>Solidago erecta</i> | | | 30- 1-032 | | |
| <i>Spigelia marilandica</i> | | | 25- 1-028 | | |
| <i>Thalictrum revolutum</i> | | | 25- 1-028 | | |
| <i>Vaccinium arboreum</i> | | | 5- 1-009 | | |
| <i>Danthonia spicata</i> | | | | 20- 7-060 | |
| <i>Galactia volubilis</i> | | | | 48- 1-060 | |
| <i>Gaura filipes</i> | | | | 20- 1-027 | |
| <i>Helianthus occidentalis</i> | | | | 76-13-157 | |
| <i>Hypericum dolabrifforme</i> | | | | 20- 2-032 | |
| <i>Juniperus virginiana</i> | | | | 24- 1-034 | |
| <i>Liatris aspera</i> | | | | 48- 3-072 | |
| <i>Lobelia spicata</i> | | | 5- 1-009 | 20- 1-027 | |
| <i>Physostegia virginiana</i> | | | | 24- 2-036 | |
| <i>Ruellia humilis</i> | | | | 20- 1-027 | |
| <i>Sisyrinchium albidum</i> | | | | 28- 1-036 | |
| <i>Solidago rigida</i> | | | | 68- 5-100 | |

Table 1. (Continued)

| | <i>Panicum virgatum</i> ^{1,5} | Upland <i>Andropogon gerardii</i> ^{2,5} | Daddys Creek ³ | Lee Station ³ | <i>Schizachyrium scoparium</i> ^{4,6} |
|--|--|---|------------------------------|-----------------------------|---|
| Taxa | F- \bar{X} C-IV200 | F- \bar{X} C-IV200 | F- \bar{X} C-IV200 | F- \bar{X} C-IV200 | F- \bar{X} C-IV200 |
| <i>Tomanthera auriculata</i> | | | | 20- 1-027 | |
| <i>Zizia aptera</i> | | | | 68- 5-102 | |
| <i>Antennaria plantaginifolia</i> | | | | | 12- 1-015 |
| <i>Aristida purpurea</i> | | | | | 5- 2-010 |
| <i>Aster patens</i> | | | | | 40- 1-041 |
| <i>A. undulatus</i> | | | | | 10- 1-012 |
| <i>Cassia nictitans</i> | | | | | 15- 1-017 |
| <i>Ceanothus americanus</i> | | | | | 3- 5-032 |
| <i>Chrysopsis mariana</i> | | | | | 17- 1-022 |
| <i>Coreopsis major</i> | | | | | 15- 1-017 |
| <i>Danthonia sericea</i> | | | | | 5-20-057 |
| <i>Daucus carota</i> | | | | 4- 1-010 | 25- 1-026 |
| <i>Desmodium ciliare</i> | | | | 4- 1-010 | 11- 1-013 |
| <i>D. paniculatum</i> var. <i>dillenii</i> | | | | | 9- 1-015 |
| <i>Diospyros virginiana</i> | | | | | 10- 1-012 |
| <i>Gnaphalium obtusifolium</i> | | | | | 5- 1-008 |
| <i>Helianthus atrorubens</i> | | | | | 11- 3-029 |
| <i>Lechea minor</i> | | | | | 3- 1-009 |
| <i>L. virginica</i> | | | | | 32- 1-032 |
| <i>Panicum commutatum</i> | | | | | 5- 1-008 |
| <i>P. depauperatum</i> | | | | | 16- 1-019 |
| <i>P. lanuginosum</i> | | | | | 3- 1-009 |
| <i>P. laxiflorum</i> | | | | | 3- 1-009 |

Table 1. (Continued)

| | <i>Panicum virgatum</i> ^{1,5} | Upland <i>Andropogon gerardii</i> ^{2,5} | Daddys Creek ³ | Lee Station ³ | <i>Schizachyrium scoparium</i> ^{4,6} |
|---------------------------------|--|---|------------------------------|-----------------------------|---|
| Taxa | F- \bar{X} C-IV200 | F- \bar{X} C-IV200 | F- \bar{X} C-IV200 | F- \bar{X} C-IV200 | F- \bar{X} C-IV200 |
| <i>P. sphaerocarpon</i> | | | | | 9- 1-015 |
| <i>Parthenium integrifolium</i> | | | | | 8- 1-012 |
| <i>Potentilla canadensis</i> | | | 5- 1-009 | | 25- 1-026 |
| <i>Senecio anonymus</i> | | | 15- 1-018 | | 33- 1-026 |
| <i>Solidago nemoralis</i> | | | | 16- 3-037 | 10- 1-012 |
| <i>Stylosanthes biflora</i> | | | 5- 1-009 | | 28- 1-023 |
| <i>Vaccinium vacillans</i> | | | | | 3- 1-009 |
| <i>Viola triloba</i> | | | | | 3- 1-009 |

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¹Species occurring in two of three stands at power line and US 70N.

²Species occurring in two of three stands at power line, US 70N, and US 70S.

³Only species included with > 20 percent frequency, unless occurring in another community.

⁴Species occurring in three of four stands at power line, Roosevelt Mountain, US 70N, and US 70S.

⁵Data used for each species present represent the middle IV200 if present at three stands, or the larger if only present at two.

⁶Data used for each species present represent the middle of three IV200; if present in all four stands, the datum is the larger of the middle-of-series pair.

The three basic vegetation types here--those dominated by *Panicum*, *Andropogon*, and *Schizachyrium* (Table 1)--are well-represented on the Tallgrass prairie to the west (Weaver 1954) and in Tennessee (DeSelm 1989b). The *Schizachyrium* type is particularly well-represented in West Tennessee and on the western Highland Rim (DeSelm 1989a, 1988). The boulder bar type is the open form of habitat type number 7 on the Obed River (Schmalzer et al. 1985), on the Cumberland and Rockcastle rivers in Kentucky (Palmer-Ball et al. 1988), and on the Big South Fork in Kentucky (Campbell et al. 1990). The type seen on shallow soil over limestone at Lee Station is also seen in the Central Basin and in the Ridge and Valley of Tennessee. The *Panicum* and *Andropogon* types were once more widespread but, because of agricultural land usage, are now confined to the Plateau and, for example, a few places on the eastern Highland Rim (DeSelm 1990).

SUMMARY AND CONCLUSIONS

Barrens communities are widely distributed on the Cumberland Plateau of Tennessee where they replace forests on wet, mesic, and xeric sites. At the wet end of the moisture gradient, hydric barrens intergrade with marshes and ponds; at the xeric end, they intergrade with rock outcrop "flatrock" communities. Communities along the moisture gradient are dominated by *Panicum virgatum* (wet mesic), *Andropogon gerardii* (mesic), and *Schizachyrium scoparium* (xeric); there are many associated taxa.

The vascular flora of the barrens exceeds 600 taxa and is believed to be mainly a forest flora taking advantage of periodic openings, as well as open or low density forest at the hydric and xeric ends of the moisture scale.

The flora is largely intraneous as would be expected on the north-south oriented physiographic surface which extends for hundreds of kilometers. The local intraneous taxa represent Plateau or Southern Appalachian endemism or persistence of taxa; our understanding of them would be increased by an analysis of the type conducted for the shale barrens endemics by Keener (1983). There is a moderate-sized northern floristic element which may have arrived here during a previous climatic cooling and persisted on the elevated surface. There is also a moderate-sized southern element which was either persistent during Pleistocene cooling, or is a Holocene arrival.

Fire may have been the main cause of barrens in preColumbian times, maintaining openings in the forest where barrens taxa thrived. Fires became more frequent after arrival of native Americans and after settlement by Europeans.

Most rare plant taxa of these barrens are extraneous, with ranges centered elsewhere; but *Marshallia* is chiefly an Appalachian endemic (Cronquist 1980), and *Calamovilfa* occurs also in Oklahoma (Rogers 1972) and may be some type of extraneous.

This barrens flora is related by the coefficient of community similarity to other Tennessee barrens floras to the west; as expected, the degree of relationship decreases away from the study area. Four of the nine calciphile taxa of limestone sites are herbs of cedar glades.

The *Panicum virgatum* and *Schizachyrium* communities are most distinct floristically. Woody plant cover is highest in the first; lichen, rock, gravel, and soil cover are highest in the second. The intermediate *Andropogon gerardii* community is not distinctive floristically. These three community types are well-represented in the Tallgrass prairie. The *Schizachyrium* type

is also well-represented in southeastern barrens, but the *Panicum* and *Andropogon* habitats have been converted to agricultural use and are now rare in Tennessee and in the Southeast.

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APPENDIX

Floristic List^{1,2}

Thallophyta

Aspidiaceae

Polystichum acrostichoides (Michx.) Schott-I,44,46

Thelypteris noveboracensis (L.) Nieuwland-I,46

Woodsia obtusa (Sprengel) Torrey-I,45

Aspleniaceae

Asplenium platyneuron (L.) Oakes-I,44,45

Lycopodiaceae

Lycopodium tristachyum Pursh-N,44

L. digitatum Dillen. ex A. Braun-I,141

Osmundaceae

Osmunda cinnamomea L.-I,44

O. regalis L. var. *spectabilis* (Willd.) Gray-I,45,46,109,141

Pteridaceae

Pteridium aquilinum (L.) Kuhn-I,45,46,47,50,106,109,110,111,115,141,158

Schizaeaceae

Lygodium palmatum (Bernh.) Swartz-I,44,46

Selaginellaceae

Selaginella apoda (L.) Spring-I,46

Gymnospermae

Cupressaceae

Juniperus virginiana L.-I,44,46,114,115,138

Pinaceae

Pinus echinata Mill.-I,44,45,48,113,115,158

P. strobus L.-N,46,115

P. virginiana Mill.-I,44,46,48,106,109,112,113,141,158

Tsuga canadensis (L.) Carr.-N,46

¹Floristic elements are: I-intraneous regional; S-southern; N-northern; W-western; L-intraneous local; CP-coastal plain disjunct; X-introduced.

²Sites are: 44-Jamestown barren; 45-Roosevelt Mountain; 46-Daddys Creek; 47-Cox barren; 48-Isoline; 50-Crossville barren; 51-Crab Orchard; 53-Bledsoe County; 88-Lee Station; 106-U.S. 70S, south of Crossville; 109-U.S. 70N, slopes of big swale; 110-U.S. 70N, bottom of big swale; 111-U.S. 70N, upland west of big swale; 112-U.S. 70N, Boulder Way; 113-U.S. 70N at I-40; 114-U.S. 70N at Raceway; 115-U.S. 70N at Experiment Station entrance; 138-Barren on Rt. 16 near Winchester; 141-Van Buren County power line; 158-Rt. 56 south of Altamont.

Angiospermae

Acanthaceae

Ruellia caroliniensis (Walt.) Steud.-I,44,45,46

R. humilis Nutt.-I,44,48,138

Aceraceae

Acer rubrum L.-I,44,45,46,47,48,50,51,106,109,110,112,113,114,115,141,158

Aizoaceae

Mollugo verticillata L.-S,44

Amaryllidaceae

Hypoxis hirsuta (L.) Cov.-I,45,46,48,115,141

Manfreda virginica (L.) Salis.-S,47,138,141

Anacardiaceae

Cotinus obovatus Raf.-S,138

Rhus aromatica Aiton-I,138

Rhus copallina L.-I,44,45,47,48,50,106,109,113,114,115,138,141

R. glabra Britt.-I,44

R. radicans L.-I,48,106,112

Apiaceae

Angelica venenosa (Greenway) Fern.-I,46,47,48,50,113,141

Chaerophyllum tainturieri Hook.-I,45,50,88

Daucus carota L.-X,44,45,47,48,50,51,106,109,111,112,113,114,115,141,158

Eryngium yuccifolium Michx.-I,45,50,141

Ligusticum canadense (L.) Britt.-I,45,46,48

Oxypolis rigidior (L.) C. and R.-I,46,50,53,109,110,113

Sanicula canadensis L.-I,50

S. marilandica L.-I,44

Thaspium trifoliatum (L.) Gray-I,46

Zizia aptera (Gray) Fern.-I,46,88,138

Z. trifoliata (Michx.) Fern.-L,46

Apocynaceae

Amsonia tabernaemontana Walter-I,46

Apocynum cannabinum L.-I,45,46,47,88,112,113,141

Aquifoliaceae

Ilex montana T. and G.-N,46

I. opaca Ait.-I,113

I. verticillata (L.) Gray-N,46

I. verticillata (L.) Gray var. *padifolia* (Willd.) T. and G.-N,113

Araliaceae

Aralia spinosa L.-I,47

Asclepiadaceae

Asclepias amplexicaulis Sm.-I,45,141

A. tuberosa L.-I,45,46,47,48,50,88,112,114,141

A. variegata L.-I,44

A. verticillata L.-I,44,45,50,138

A. viridiflora Raf.-I,88,113,138

Asteraceae

Achillea millifolium L.-X,44,47,48,50,106,109,111,112,113,114,115,141

Ambrosia artemisiifolia L.-I,44,45,47,48,106,110,112,113,114,115,138, 141,158

A. trifida L.-I,158

Antennaria plantaginifolia (L.) Hook.-I,44,45,47,48,50,106,109,112,113,
114,115,138,141

Artemisia vulgaris L.-X,45

Aster concolor L.-I,44,45,47,141

A. divaricatus L.-I,46

A. dumosus L.-I,44,45,46,47,48,50,53,88,106,109,110,111,112,113,114, 115,141,158

A. hemisphericus E.J. Alex.-S,138,158

A. laevis L.-I,138

A. lateriflorus (L.) Britton-N,46

A. linariifolius L.-I,44,45,46,47,106,109,111,141

A. novae-angliae L.-I,141

A. oblongifolius Nutt.-I,138

A. patens Ait.-I,44,45,46,47,48,50,51,88,106,138,141,158

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THE VASCULAR FLORA OF LAKE BARKLEY (LOWER CUMBERLAND RIVER) SEASONALLY DEWATERED FLATS

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ABSTRACT. A floristic survey of seasonally dewatered flats (mudflats) along Lake Barkley (the lower Cumberland River impounded in 1966) in western Kentucky and Tennessee was made from 1983-1989. Sixty-five vascular taxa were encountered, dominated by annual species of Asteraceae, Cyperaceae, Lythraceae, and Poaceae. Taxa are listed, categorized, and compared with published lists of reservoir mudflats indicator species for the Tennessee Valley region and for the nearby Kentucky Lake (the lower Tennessee River impounded in 1944).

INTRODUCTION

The Tennessee Valley Authority and U.S. Army Corps of Engineers have constructed a series of dams along the Tennessee and Cumberland rivers and their major tributaries. Although most of the resulting impoundments have multipurpose uses, flood control is a primary function. Therefore reservoir levels are normally lowered (drawn down) during seasons of low precipitation (late summer-fall) to provide storage capacity for runoff during normally heavy rainfall seasons (winter-spring). At some sites the drawdown exposes nearly level expanses of reservoir bottom. Such areas are referred to as seasonally dewatered flats, or mudflats, and an ephemeral flora develops if sufficient time exists between dewatering and freezing weather.

The purpose of this paper is to catalog, and in some cases to characterize, the flora of mudflats along Lake Barkley (the lower Cumberland River) in western Kentucky and Tennessee. The results are compared with a list of mudflats indicator species developed by Carter and Burbank (1978) for the entire Tennessee Valley, and with lists of mudflat species found by Webb et al. (1988) and Webb and Bates (1989) along Kentucky Lake (the lower Tennessee River), also in western Kentucky and Tennessee.

LITERATURE REVIEW

The environmental effects of dams and impoundments were discussed by Baxter (1977). Recent wetland classification systems include habitat types associated with reservoirs (Cowardin et al. 1979, Cowardin 1982, Carter et al. 1977, Carter and Burbank 1978). Several studies relate specifically to the Tennessee River, including those of Wiebe and Hess (1944), Wiebe (1946, 1958), and Givens and Atkeson (1957), who studied impoundments in relation to wildlife management. Hess and Kiker (1944), Hess and Hall (1945), and Hall et al. (1946) related changes in shoreline vegetation of reservoirs to mosquito and malarial control. Hess and Hall

(1945) included a classification of vegetation, and Hall and Smith (1955) studied the effects of flooding on woody species.

Attempts to seed mudflats along the Tennessee River for wildlife were reported by Fowler and Maddox (1974), Fowler and Hammer (1976), and Fowler and Whelan (1980). Efforts to establish tree species along reservoir shorelines were discussed by Silker (1948), Smith et al. (1969), and Bates et al. (1978). Several Tennessee River mudflat species were reported as state records from Tennessee or Kentucky by Browne and Athey (1978), Cranfill and Medley (1981), Dennis et al. (1980), Patrick et al. (1983), Webb and Dennis (1981), and Webb et al. (1981).

THE STUDY AREA

Barkley Dam is located on the lower Cumberland River near the border of Lyon and Livingston counties, Kentucky, at river mile (RM) 30.6, southeast of the confluence of the Cumberland and Ohio rivers. The U.S. Army Corps of Engineers completed the dam in 1966, thus forming Lake Barkley which extends upstream to RM 148.7 at Cheatham Dam near Ashland City, Tennessee (U.S. Dept. Army 1981). The reservoir lies within three Kentucky and four Tennessee counties and covers, at maximum pool, more than 37 811 surface ha. Normal summer pool covers 23 440 ha at an elevation of 109.45 m above sea level while winter pool, at normal maximum drawdown, covers 18 296 ha at an elevation of 107.93 m above sea level (U.S. Dept. Army 1981). Many of the flats exposed by drawdown were cultivated fields prior to impoundment and are mostly downstream of RM 110, which is just east of the Montgomery-Stewart County line. Few flats occur upstream of RM 110 because there the reservoir is largely confined to original river banks.

Typical flats are nearly level (less than 5 percent slope), and covered with alluvium, silt, scattered anthropogenic debris, and transient driftwood. Deposits of gravel and sand, dead stumps remaining from preimpoundment clearing, and slightly elevated islands supporting permanent vegetation are not uncommon. The landward boundary of flats may be any of several wetland community types or even footslopes of upland forests or fields. A distinct demarcation between flats and adjacent community types is usually evident except in areas where emergent communities occur along low-gradient shorelines; in these areas, an ecotone may occur where mudflat and emergent species intergrade.

METHODS

From early September to mid-November of 1983-1989, 37 Lake Barkley mudflats were surveyed between RM 34.5 just south of Barkley Dam and RM 116.5 near Clarksville. Each was examined at least twice during the study period. Sites along the 82 river miles were selected primarily because of land accessibility, determined by examining Lake Barkley navigation charts (U.S. Dept. Army 1983). Study sites ranged in size from a few square meters to several hectares. Four sites were studied in Montgomery County, 12 in Stewart, 10 in Trigg, and 11 in Lyon.

A floristic survey was made at each site and representative vouchers collected for accession into the Austin Peay State University Herbarium. Identifications were made from, and

nomenclature follows, Cronquist (1980) and Fernald (1950), except for three genera: *Amaranthus* follows Sauer (1972), *Lindernia* follows Cooperrider and McCready (1975), and *Sagittaria* follows Gleason and Cronquist (1991). Other parameters determined include: (1) the number of sites with the species; (2) presence (percent of sites with the species), and presence classes based on standard groupings (Oosting 1956); (3) percent of total presence for each species and genus; (4) life form, i.e., annual, perennial, or a perennial functioning as an annual; and (5) status, i.e., native or introduced. Life form and status are based on data in Fernald (1950) and Gleason and Cronquist (1991).

RESULTS AND DISCUSSION

The 65 vascular species encountered on Lake Barkley mudflats are listed in Appendix 1, in descending order of the number of site occurrences, and alphabetical order when several species occurred at the same number of sites. Other data in Appendix 1 indicate the number of flats with the species, presence, percent of total presence, life form (A = annual, P = perennial, P/A = a perennial functioning as an annual), and status (N = native, I = introduced).

Presence, a quantifier of the degree of regularity with which a species occurs in different examples (stands) of a community type regardless of example size, is an important indicator of stand diversity-similarity (Cain and Castro 1969, Oosting 1956). Presence data are especially meaningful when grouped into the five-degree scale of presence classes of Oosting (1956). In a typical community spectrum, 55 percent of the species occur in 1-20 percent of the community examples (stands)—this is Presence Class (PC) 1. Presence Class 2, encompassing 21-40 percent of the stands, normally includes 15 percent of the community's species. Presence Class 3 (41-60 percent of stands), PC-4 (61-80 percent of stands), and PC-5 (81-100 percent of stands), each normally include 10 percent of the species. The occurrence of one presence class (PC-1) distinctly larger than any other is a significant feature of a typical community spectrum. The Lake Barkley mudflat flora is atypical in that classes 2, 3, and 4 include fewer species than normal, and class 5 includes more species than normal, resulting in a second maximum (Figure 1). This atypical bimodality indicates a greater regularity of occurrence in examples of this community type than is normally found in other communities.

All families, with the number of genera, the number of native and introduced species, and percent of total presence, are listed in Table 1. Although 25 families occur on Lake Barkley mudflats, just three—the Cyperaceae (12 species, 18.5 percent of the species), Poaceae (10 species, 15.4 percent), and Asteraceae (9 species, 13.8 percent)—account for nearly half of all taxa. *Cyperus*, with seven species, is the largest genus represented, and two or more species occur at each site. *Bidens* and *Jussiaea* are each represented by three species, eight other genera by two species each, and 36 genera include only one species (Table 2).

Data on life form (Appendix 1; Table 3) show that annuals make up the majority of this flora (about 68 percent). Of the perennials present, such species as *Alisma subcordatum*, *Boltonia diffusa*, *Cyperus esculentus*, *Diodia virginiana*, *Helenium flexuosum*, *Jussiaea repens*, *Sagittaria calycina*, and *Solanum carolinense* flower during their first year of growth and on the mudflats do not function as true perennials. This characteristic of mudflat perennials behaving as annuals also was observed by Salisbury (1970) in Great Britain and by van der Valk (1981) in Iowa. Herbaceous perennials whose below-ground parts survive inundation include *Aster*

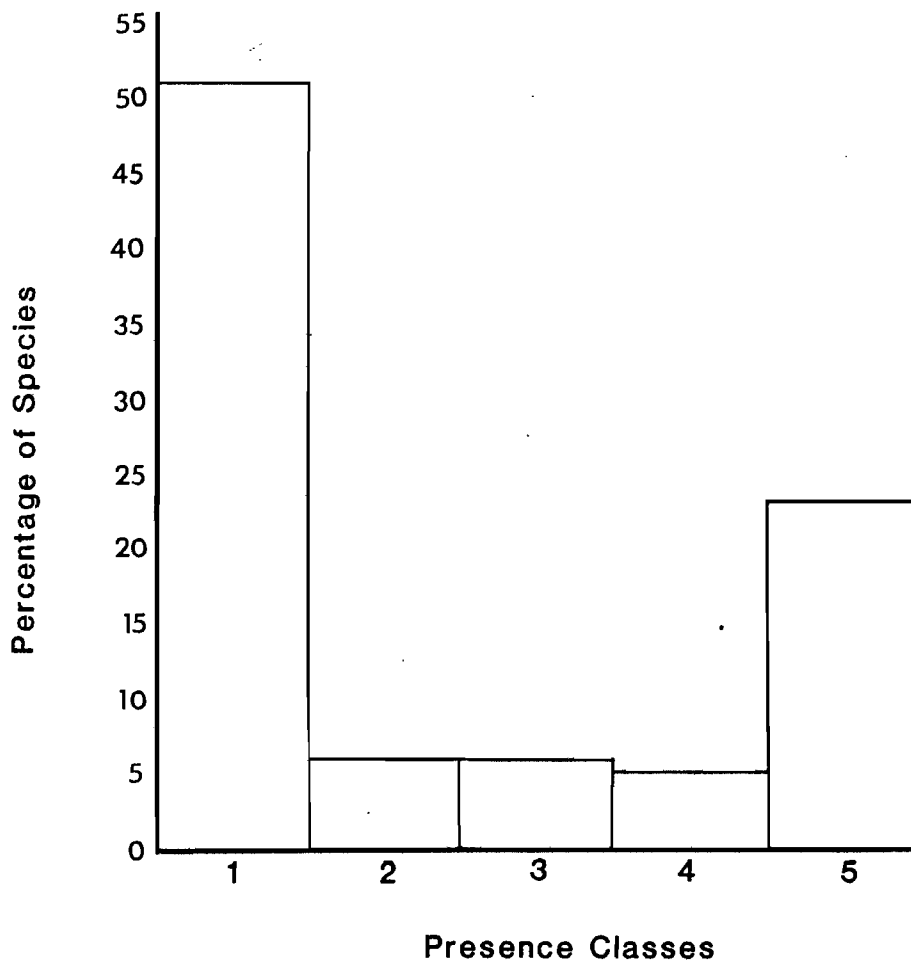


Figure 1. Distribution of species of the Lake Barkley mudflat flora among the five standard presence classes of Oosting (1956).

simplex, *Cyperus strigosus*, *Eleocharis acicularis*, *Panicum agrostoides*, *Hibiscus militaris*, *H. moscheutos*, and *Justicia americana*. However, these taxa are not abundant and with one exception, succession toward perennial dominance, as Wilson (1973) found in some Iowa fluctuation zones, is not evident. *Eleocharis acicularis* is the exception and dominates some flats toward the northern portion of Lake Barkley.

Five woody species were observed. *Campsis radicans* occurs mostly as short, new runners from stumps sheared of previous growth. Both *Cephalanthus occidentalis* and *Salix nigra* occur as seedlings, as prostrate transient individuals, and sometimes as permanent invaders, especially in ecotones and in upstream flats where water levels are not as deep and flooding is of shorter duration. *Acer saccharinum* and *Fraxinus pennsylvanica* occur very rarely as germlings.

Table 1. Families of the Lake Barkley mudflat flora.

| Family | Number of genera | Number of species | | | Percent of total presence |
|---------------------|------------------|-------------------|--------|-------|---------------------------|
| | | Native | Intr.* | Total | |
| Cyperaceae | 4 | 11 | 1 | 12 | 29.35 |
| Poaceae | 7 | 5 | 5 | 10 | 16.05 |
| Asteraceae | 7 | 7 | 2 | 9 | 14.05 |
| Lythraceae | 2 | 2 | 0 | 2 | 7.82 |
| Scrophulariaceae | 2 | 2 | 0 | 2 | 7.04 |
| Polygonaceae | 1 | 2 | 0 | 2 | 4.14 |
| Onagraceae | 1 | 3 | 0 | 3 | 3.21 |
| Amaranthaceae | 1 | 1 | 0 | 1 | 3.05 |
| Convolvulaceae | 2 | 2 | 1 | 3 | 2.86 |
| Euphorbiaceae | 2 | 2 | 0 | 2 | 1.92 |
| Alismataceae | 3 | 3 | 0 | 3 | 1.81 |
| Malvaceae | 2 | 2 | 1 | 3 | 1.68 |
| Caprifoliaceae | 1 | 1 | 0 | 1 | 1.68 |
| Brassicaceae | 1 | 1 | 0 | 1 | 0.94 |
| Rubiaceae | 1 | 1 | 0 | 1 | 0.74 |
| Salicaceae | 1 | 1 | 0 | 1 | 0.74 |
| Aizoaceae | 1 | 0 | 1 | 1 | 0.63 |
| Boraginaceae | 1 | 0 | 1 | 1 | 0.63 |
| Bignoniaceae | 1 | 1 | 0 | 1 | 0.43 |
| Potamogetonaceae | 1 | 1 | 0 | 1 | 0.43 |
| Acanthaceae | 1 | 1 | 0 | 1 | 0.31 |
| Aceraceae | 1 | 1 | 0 | 1 | 0.12 |
| Oleaceae | 1 | 1 | 0 | 1 | 0.12 |
| Sapindaceae | 1 | 0 | 1 | 1 | 0.12 |
| Solanaceae | 1 | 1 | 0 | 1 | 0.12 |
| Totals: 25 families | 47 | 52 | 13 | 65 | 100.00 |

*Intr. = Introduced

Thirteen species (20 percent) are not native. This percentage is about the same as reported for the area by Carpenter and Chester (1987). All introductions are annuals, and mostly composites and grasses (Appendix 1; Tables 1, 2). Though mudflats provide an apparently ideal habitat for the expansion of non-native (and native) species (Webb et al. 1988, Webb and Bates 1989), *Cyperus iria* was the only non-native species that increased in abundance during the years of observation. This introduced sedge was first observed on Trigg County mudflats during October of 1989. The few previous reports of this species from the Cumberland drainage were from wetlands adjacent to mudflats.

Table 2. Major genera of the Lake Barkley mudflat flora.

| Genera | Number of species | | | Percent of total presence |
|---------------------|-------------------|------------|----------|---------------------------|
| | Native | Introduced | Total | |
| <i>Cyperus</i> | 6 | 1 | 7 | 13.50 |
| <i>Fimbristylis</i> | 2 | 0 | 2 | 7.04 |
| <i>Bidens</i> | 2 | 1 | 3 | 6.34 |
| <i>Eleocharis</i> | 2 | 0 | 2 | 5.52 |
| <i>Eragrostis</i> | 1 | 1 | 2 | 5.91 |
| <i>Polygonum</i> | 2 | 0 | 2 | 4.14 |
| <i>Jussiaea</i> | 3 | 0 | 3 | 3.21 |
| <i>Ipomoea</i> | 1 | 1 | 2 | 2.66 |
| <i>Panicum</i> | 2 | 0 | 2 | 1.57 |
| <i>Hibiscus</i> | 2 | 0 | 2 | 1.48 |
| <i>Digitaria</i> | <u>0</u> | <u>2</u> | <u>2</u> | <u>0.63</u> |
| Subtotals: 11 | 23 | 6 | 29 | 52.00 |
| Others: 36 | 29 | 7 | 36 | 48.00 |
| Totals: 47 | 52 | 13 | 65 | 100.00 |

The dense and low-growing flora of mudflats was aptly described as the "carpet zone" by Hess and Hall (1945). Such growth, often not exceeding 10 cm in height, is normal for such species as *Eragrostis hypnoides* and *Hemicarpha micrantha*. Others (e.g., *Bidens*, *Xanthium*) mature at greatly reduced heights on flats, where the growing season may be only a few weeks, while normal-sized individuals occur in nearby wetlands. Some species express a developmental continuum ranging from seedling stages near the water to mature fruit stages at the shoreward periphery of the flat. Some areas nearest the water may not be exposed long enough for rooted vegetation to develop. Dense but ephemeral stands of the thalloid liverwort *Ricciocarpus* and mats of dead *Potamogeton* spp. are commonly found on recently exposed portions of flats.

Some groups presented taxonomic problems. Although many *Lindernia* specimens express leaf and pedicel characteristics of *L. anagallidea* and may be this species, the treatment of Cooperrider and McCready (1975) was followed and all material placed under *L. dubia*. Also, the dioecious amaranths are morphologically diverse and difficult to identify. Dr. J. D. Sauer, who kindly examined representative material, noted that introgression had occurred and that the common Cumberland River mudflat species is *Amaranthus tuberculatus*. Specimens of *Cuscuta* were always vegetative and specific determinations impossible.

Reservoir dewatered zones are apparently vegetated by those species whose germination requirements are met, or at least not hindered, by inundation. Van der Valk (1981) notes that at the majority of mudflat representatives are S-species, or those with long-lived propagules that

Table 3. Life-form statistics for the Lake Barkley mudflat flora.

| Life-form category | Number of species | Percent |
|--------------------------------------|-------------------|------------|
| Annuals | 44 | 67.7 |
| Perennials functioning as annuals | 8 | 12.3 |
| True perennials | | |
| Herbaceous species | 8 | 12.3 |
| Woody species | <u>5</u> | <u>7.7</u> |
| Totals: | 65 | 100.0 |

may accumulate over many years and become established whenever favorable circumstances occur. These species must then be able to grow in muddy or boggy soil that is usually anaerobic, and to flower and fruit under a brief, short-day growing season. While a myriad of residual and newly deposited seeds must be present, all except *Eleocharis* require dewatering for germination, and most terrestrial herbs fail to develop on sites inundated until June or later (Hall et al. 1946).

Though presence or dominance is influenced by such physical factors as substrate and current and wave action (Gill and Bradshaw 1971), further studies are required to determine the germination ecology and life histories of mudflat species.

Comparisons

Wetland communities and their indicator species in the Tennessee Valley (a diverse region including parts of seven states) were listed by Carter and Burbank (1978). As expected, both similarities and differences were found between the 13 mudflat indicators for the Tennessee Valley (Carter and Burbank 1978) and the taxa listed here for the lower Cumberland River. Four species are in common: *Ammannia coccinea*, *Eragrostis hypnoides*, *Fimbristylis autumnalis*, and *Rotala ramosior*. Three other Tennessee Valley indicators--*Diodia virginiana*, *Panicum agrostoides*, and *Polygonum pensylvanicum*--occur regularly on lower Cumberland River flats but are never common and cannot be considered indicators there. None of the other six Tennessee Valley indicator species assumed that role on Lake Barkley mudflats: *Justicia americana* was observed on only three Lake Barkley mudflats and the plants were transients that had lodged against stumps; *Eleocharis acicularis* was quite rare on upstream flats and became significant only in Trigg and Lyon counties; *Carex* and *Juncus* were not found, even though several species of both these genera are regularly abundant in adjacent emergent wetland communities; and *Polygonum*

hydropiperoides and *P. coccineum*, though often found nearby, were not found on Lake Barkley flats.

The most comprehensive description of area mudflats is that of Webb et al. (1988), who studied TVA mainstream and tributary reservoirs from 1978-1987. Similarities between Kentucky Lake and Lake Barkley flats are apparent when numerical results are compared (Table 4). A comparison of species, also using only Kentucky Reservoir data, likewise shows close affinities. This is unsurprising since these two reservoirs (Kentucky and Barkley) are connected by a man-made canal at their downstream ends and are less than 15 km apart for a distance of about 65 km. However, these great rivers are the result of different and diverse drainage patterns, and the potential for floristic differences is great. Of the 31 species listed by Webb et al. (1988) from Kentucky Reservoir flats, only *Bacopa rotundifolia*, *Cyperus tenuifolius*, *Fimbristylis miliacea*, *Oldenlandia boscii*, and *O. uniflora* are not known from the Cumberland flats. All Lake Barkley species have been reported from or observed by the author on Kentucky Reservoir flats.

Table 4. Numerical comparison between the Lake Barkley and Kentucky Lake mudflat flora (Kentucky Lake data from Webb et al. 1988).

| Characteristics | Kentucky Lake | Lake Barkley |
|---------------------------------|---------------|--------------|
| Number of families | 16 | 25 |
| Number of genera | 32 | 47 |
| Number of species | 51 | 65 |
| Number (and percent) annuals | 35(68) | 44(68) |
| Number (and percent) perennials | 16(32) | 21(32) |
| Number (and percent) native | 43(84) | 52(80) |
| Number (and percent) introduced | 8(16) | 13(20) |
| Species of Cyperaceae | 17 | 12 |
| Species of Poaceae | 8 | 10 |
| Species of <i>Cyperus</i> | 11 | 7 |

Vegetational studies on seasonally dewatered lands have been conducted in several other areas, including Iowa (Wilson 1973), Louisiana (Brown 1943), Ohio (Kadlec 1962, Mandossian and McIntosh 1960), Oklahoma (Ware and Penfound 1949), and Ontario (Burma and Day 1975). Although physical parameters of flooding and dewatering in these areas are often similar to those of Lake Barkley, vegetational patterns are so dissimilar that floristic comparisons between these areas and Lake Barkley are not appropriate.

SUMMARY

Although seasonally dewatered flats along Lake Barkley in Kentucky and Tennessee are dominated by annual species of Asteraceae, Cyperaceae, Lythraceae, and Poaceae, several other families are represented. The 65 documented taxa also include a few perennial herbs functioning as annuals, some perennials whose below-ground parts survive inundation, one woody vine, and four shrubs-trees. A number of casual or incidental species occur, but their percentages of occurrence at sites (presence) is not high. As a whole, the flora is not diverse, and plants often develop flowers-fruits quickly and when small. The floristic list shows some similarities and some major differences with a previously published regional list of mudflat indicators; closer affinities are shown with flats of the lower Tennessee River (Kentucky Lake).

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Appendix 1. Vascular flora of Lake Barkley mudflats.

| Species | No. & % of flats with this species | Presence ¹ | Form ² | Status ³ |
|--|---------------------------------------|-----------------------|-------------------|---------------------|
| <i>Ammannia coccinea</i> Rottb. | 37 (100) | 3.91 | A | N |
| <i>Cyperus erythrorhizos</i> Muhl. | 37 (100) | 3.91 | A | N |
| <i>Cyperus esculentus</i> L. | 37 (100) | 3.91 | P/A | N |
| <i>Echinochloa crusgalli</i> (L.) Beauv. | 37 (100) | 3.91 | A | I |
| <i>Eragrostis hypnoides</i> (Lam.) BSP. | 37 (100) | 3.91 | A | N |
| <i>Fimbristylis autumnalis</i> (L.) R.&S. | 37 (100) | 3.91 | A | N |
| <i>Lindernia dubia</i> (L.) Pennell | 37 (100) | 3.91 | A | N |
| <i>Rotala ramosior</i> (L.) Koehne | 37 (100) | 3.91 | A | N |
| <i>Cyperus aristatus</i> Rottb. | 36 (97) | 3.80 | A | N |
| <i>Xanthium strumarium</i> L. | 36 (97) | 3.80 | A | I |
| <i>Leptochloa panicoides</i> (Presl) Hitchc. | 34 (92) | 3.60 | A | N |
| <i>Eleocharis obtusa</i> (Willd.) Schlt. | 34 (92) | 3.60 | A | N |
| <i>Hemicarpha micrantha</i> (Vahl) Pax | 31 (84) | 3.29 | A | N |
| <i>Conohea multifida</i> L. | 30 (80) | 3.13 | A | N |
| <i>Fimbristylis vahlii</i> (Lam.) Link | 30 (80) | 3.13 | A | N |
| <i>Amaranthus tuberculatus</i> (Moq.) Sauer | 29 (78) | 3.05 | A | N |
| <i>Bidens tripartita</i> L. | 29 (78) | 3.05 | A | I |
| <i>Jussiaea decurrens</i> (Walt.) DC. | 28 (76) | 2.97 | A | N |
| <i>Polygonum pennsylvanicum</i> L. | 28 (76) | 2.97 | A | N |
| <i>Bidens frondosa</i> L. | 25 (68) | 2.66 | A | N |
| <i>Ipomoea lacunosa</i> L. | 21 (57) | 2.23 | A | N |
| <i>Eragrostis pilosa</i> (L.) Beauv. | 19 (51) | 2.00 | A | I |
| <i>Eleocharis acicularis</i> (L.) R.&S. | 18 (49) | 1.92 | P | N |
| <i>Euphorbia supina</i> Raf. | 17 (46) | 1.80 | A | N |
| <i>Cephalanthus occidentalis</i> L. | 16 (43) | 1.68 | P | N |
| <i>Aster simplex</i> Willd. | 15 (41) | 1.60 | P | N |
| <i>Eclipta alba</i> (L.) Hassk. | 14 (38) | 1.49 | A | N |
| <i>Sagittaria calycina</i> Engelm. | 14 (38) | 1.49 | P/A | N |
| <i>Polygonum lapathifolium</i> L. | 11 (30) | 1.17 | A | N |
| <i>Panicum agrostoides</i> Spreng. | 9 (24) | 0.94 | P | N |
| <i>Cyperus albomarginatus</i> Mart. & Sch. | 9 (24) | 0.94 | A | N |
| <i>Rorippa sessiliflora</i> (Nutt.) Hitchc. | 9 (24) | 0.94 | A | N |
| <i>Diodia virginiana</i> L. | 7 (19) | 0.74 | P/A | N |
| <i>Hibiscus militaris</i> Cav. | 7 (19) | 0.74 | P | N |
| <i>Hibiscus moscheutos</i> L. | 7 (19) | 0.74 | P | N |
| <i>Salix nigra</i> Marsh. | 7 (19) | 0.74 | P | N |
| <i>Bidens cernua</i> L. | 6 (16) | 0.63 | A | N |
| <i>Heliotropium indicum</i> L. | 6 (16) | 0.63 | A | I |

Appendix 1, continued

| | | | | | |
|---|---|------|------|-----|---|
| <i>Mollugo verticillata</i> L. | 6 | (16) | 0.63 | A | I |
| <i>Panicum dichotomiflorum</i> Michx. | 6 | (16) | 0.63 | A | N |
| <i>Cyperus strigosus</i> L. | 5 | (13) | 0.51 | P | N |
| <i>Campsis radicans</i> (L.) Seem. | 4 | (11) | 0.43 | P | N |
| <i>Digitaria ischaemum</i> (Schl.) Muhl. | 4 | (11) | 0.43 | A | I |
| <i>Ipomoea hederacea</i> (L.) Jacq. | 4 | (11) | 0.43 | A | I |
| <i>Potamogeton nodosus</i> Poir. | 4 | (11) | 0.43 | P | N |
| <i>Boltonia diffusa</i> (L.) L'Her | 3 | (8) | 0.31 | P/A | N |
| <i>Cyperus ferruginescens</i> Boeckl. | 3 | (8) | 0.31 | A | N |
| <i>Helenium flexuosum</i> Raf. | 3 | (8) | 0.31 | P/A | N |
| <i>Justicia americana</i> (L.) Vahl. | 3 | (8) | 0.31 | P | N |
| <i>Paspalum fluitans</i> (Ell.) Kunth | 3 | (8) | 0.31 | A | N |
| <i>Cuscuta</i> spp. | 2 | (5) | 0.20 | A | N |
| <i>Digitaria sanguinalis</i> (L.) Scop. | 2 | (5) | 0.20 | A | I |
| <i>Echinodorus cordifolius</i> (L.) Griseb. | 2 | (5) | 0.20 | A | N |
| <i>Iva annua</i> L. | 2 | (5) | 0.20 | A | N |
| <i>Sida spinosa</i> L. | 2 | (5) | 0.20 | A | I |
| <i>Acer saccharinum</i> L. | 1 | (3) | 0.12 | P | N |
| <i>Alisma subcordatum</i> Raf. | 1 | (3) | 0.12 | P/A | N |
| <i>Cardiospermum halicacabum</i> L. | 1 | (3) | 0.12 | A | I |
| <i>Cyperus iria</i> L. | 1 | (3) | 0.12 | A | I |
| <i>Eleusine indica</i> (L.) Gaertn. | 1 | (3) | 0.12 | A | I |
| <i>Fraxinus pennsylvanica</i> Marsh. | 1 | (3) | 0.12 | P | N |
| <i>Jussiaea leptocarpa</i> Nutt. | 1 | (3) | 0.12 | A | N |
| <i>Jussiaea repens</i> L. | 1 | (3) | 0.12 | P/A | N |
| <i>Phyllanthus caroliniensis</i> Walt. | 1 | (3) | 0.12 | A | N |
| <i>Solanum carolinense</i> L. | 1 | (3) | 0.12 | P/A | N |

¹Expressed as percentage of total presence.

²A = annual, P = perennial, P/A = perennial functioning as an annual.

³N = native, I = introduced.

SOME ASPECTS OF THE GERMINATION ECOPHYSIOLOGY OF MUDFLAT SPECIES

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ABSTRACT. Extensive mudflats develop each summer as water levels of impoundments on the Cumberland River are lowered. A plant community consisting of various species of summer annuals that germinate from temporary and/or persistent seed banks develops soon after drawdown, the time of which may vary from year to year and from one mudflat to another. The purpose of our research is to identify the seed/environmental factors controlling the timing of germination in these species. Large quantities of seeds of *Ammannia coccinea*, *Cyperus albomarginatus*, *C. erythrorhizos*, *Eragrostis hypnoides*, *Fimbristylis autumnalis*, *F. vahlii*, *Leptochloa panicoides*, *Leucospora multifida*, and *Rotala ramosior* were collected, placed in fine-mesh nylon bags, and buried in flooded and nonflooded soil at near-natural temperatures. At monthly intervals, seeds are exhumed and tested in light (14-hr photoperiod) and constant darkness at 12/12 hr daily thermoperiods of 15/6, 20/10, 25/15, 30/15, and 35/20°C.

Seeds are dormant or conditionally dormant at maturity. With the exception of *Leptochloa panicoides*, seeds of all nine species become nondormant during winter and germinate to high percentages at simulated spring/summer temperatures; nondormant seeds require light for germination. Seeds of *L. panicoides* come out of dormancy in late spring-early summer. In the laboratory, *L. panicoides* seeds became nondormant during burial at 25/15 and 30/15°C, but not at 5, 15/6, or 20/10°C. Flooding does not inhibit loss of dormancy in any of the species. In fact, higher percentages of the seeds of *Rotala ramosior* and *Eragrostis hypnoides* come out of dormancy during burial in flooded than in nonflooded soil.

Seeds can germinate at any time during the growing season, whenever the water recedes, because they do not re-enter dormancy (secondary dormancy). This is in contrast to *Ambrosia artemisiifolia* and *Bidens polylepis*, two summer annual weeds of cultivated fields in LBL, whose seeds go back into dormancy as habitat temperatures increase in late spring.

These germination responses are an important ecophysiological adaptation of mudflat species to their temporally unpredictable habitat, and a knowledge of them is a key to understanding the dynamics of the mudflat community.

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**ECOLOGICAL ASPECTS OF SEED GERMINATION AND
FLOWERING IN A PERENNIAL AND AN ANNUAL
SPECIES OF *Senna* (Leguminosae:
Section *Chamaefistula*)**

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ABSTRACT. This study investigated the ecological aspects of seed dormancy, germination, and flowering in *Senna obtusifolia* (L.) Irwin and Barneby and *Senna marilandica* (L.) Link (Fabaceae). *Senna obtusifolia* is a summer annual weed of cultivated fields and other ruderal habitats, whereas *S. marilandica* is a polycarpic perennial that grows in open habitats, such as roadsides and pastures, that are less severely disturbed than cultivated fields.

Seed dormancy in both species is due to a hard (impermeable to water) seed coat which can be overcome by mechanical scarification, boiling in water, treatment with concentrated sulfuric acid, or soaking in ethanol. However, seeds of *S. obtusifolia* are less dormant than those of *S. marilandica*. While intact (untreated) seeds of *S. obtusifolia* germinated to a high percentage at 40/20°C, but not at lower daily thermoperiods (15/6-35/20°C), those of *S. marilandica* did not germinate at any of the above temperature regimes. Further, a longer treatment period with concentrated sulfuric acid or boiling water was required to break dormancy in seeds of *S. marilandica* than in those of *S. obtusifolia*. Nondormant seeds of both species germinated to high percentages over a wide range of thermoperiods (15/6-40/25°C) in light (14 h daily photoperiod) and in constant darkness. Neither dry heat nor freezing and thawing overcame dormancy in either species. Preliminary studies of water entry into seeds made nondormant by boiling in water suggest that seeds of *S. obtusifolia* become permeable in the micropyle-hilum-strophiole region, whereas in *S. marilandica* the peripheral zone is the region that becomes permeable.

In a germination phenology study carried out in a nonheated greenhouse, 71 percent of the seeds of *S. obtusifolia* planted in autumn 1989, but only 8.5 percent of those of *S. marilandica*, also planted in autumn 1989, had germinated by autumn 1990. Seeds of both species germinated throughout the growing season, with peaks occurring in late spring/early summer.

Senna obtusifolia is a quantitative short-day plant. Under a 10 h daily photoperiod in a growth chamber, flowering began 40 days after (scarified) seeds were planted, whereas under a daily photoperiod of 8 h plus a 2 h light interruption of the dark period, flowering did not begin until 153 days after planting. On the other hand, *S. marilandica* is a long-day plant. Even under long days, flowering did not begin until 170 days after the (scarified) seeds were planted, and only three of 15 plants flowered in their first year. Further, since only 24 of 197 plants grown under greenhouse conditions flowered in their first year, plants in the field probably do not reach flowering size until the second year or later.

These differences in life cycle characteristics of *S. obtusifolia* and *S. marilandica* help explain why the former can be a weed in cultivated fields, whereas the latter requires a more stable habitat.

A COMPARATIVE STUDY OF GROWTH AND RELATIVE
COMPETITIVE ABILITY OF *Echinacea angustifolia*,
E. pallida, AND *E. tenesseeensis* (Asteraceae)
UNDER GREENHOUSE CONDITIONS

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ABSTRACT. Competitive relationships among *Echinacea angustifolia* DC. var. *angustifolia*, *E. pallida* (Nutt.) Nutt., and *E. tenesseeensis* (Beadle) Small were investigated under greenhouse conditions by de Wit replacement series experiments at multiple densities (addition series). When each species was paired with the other two species in three proportions at total densities of 8, 12, and 16 plants per 1750 ml pot, the relative yield (RY, dry weight in mixture/dry weight in monoculture) of *E. pallida* significantly increased in four and decreased in none of 18 mixtures with the other two species (78 percent overall increase in yield), while that of *E. angustifolia* significantly decreased in three and increased in none of nine mixtures with *E. tenesseeensis* (89 percent overall decrease in yield). In mixtures with each of the other two species, the RY of *E. tenesseeensis* neither increased nor decreased significantly. Thus, the competitive hierarchy was *E. pallida* > *E. tenesseeensis* > *E. angustifolia*.

Competitive relationships of each of the three *Echinacea* species with the grass, *Andropogon scoparius* Michx. (little bluestem), were investigated under greenhouse conditions by de Wit replacement series experiments at one density. Little bluestem was grown with each of the three *Echinacea* species in three proportions at a total density of six plants per 1750 ml pot. Relative yield of *A. scoparius* significantly increased in three and decreased in none of nine mixtures with the other species (89 percent overall increase in yield). In mixtures with *A. scoparius*, the RY of *E. tenesseeensis* significantly decreased in one and increased in none of three mixtures (67 percent overall reduction in yield), whereas *E. angustifolia* and *E. pallida* neither increased nor decreased significantly. Thus, the competitive hierarchy of the three *Echinacea* species against *A. scoparius* was *E. pallida* > *E. angustifolia* > *E. tenesseeensis*.

In a classical growth analysis of the three *Echinacea* species carried out simultaneously in the greenhouse with the competition experiments in 1990 (plants started in March), neither final dry weight, leaf area ratio (LAR), net assimilation rate (NAR), nor relative growth rate (RGR, LAR x NAR, g/g/day) differed significantly among the three species. Thus, RGR was not related to competitive ability. In a 1989 growth analysis (plants started in May), RGR differed significantly among the three species, with *E. tenesseeensis* > *E. angustifolia* > *E. pallida*. The higher RGR of *E. tenesseeensis* was related to a higher average NAR for this species. Maximum dry weight and leaf area also differed significantly among the three species, with *E. pallida* > *E. tenesseeensis* > *E. angustifolia*.

Weights of seeds from which plants of the three species were grown differed significantly in 1989 and 1990. In 1989, *E. tenesseeensis* > *E. pallida* > *E. angustifolia*, whereas in 1990 *E. angustifolia* > *E. tenesseeensis* > *E. pallida*. Thus, initial seed size was not related to RGR or competitive ability.

We conclude that lack of competitive ability *per se* does not limit the establishment of *E. tennesseensis* outside its cedar glade environment, and thus does not account for the narrow geographic range or restriction of this species to cedar glades. Based on its relative competitive ability under greenhouse conditions, we predict that *E. tennesseensis* could compete successfully in habitats occupied by the geographically widespread *E. angustifolia* var. *angustifolia*, and perhaps also with *E. pallida*.

MORPHOMETRIC VARIATION IN ACORNS FROM TWO RED OAK COMMUNITIES IN LAND BETWEEN THE LAKES: HYBRIDIZATION OR NORMAL VARIATION?

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ABSTRACT. Acorns from oaks (*Quercus* subgenus *Erythrobalanus*) in two communities containing putative hybrids were collected in the fall of 1987. A set of eight morphometric characters was used to evaluate patterns of variation among trees in each community. Tree-tree taxonomic distances were calculated from (1) standardized raw data, (2) log-transformed raw data, (3) size-adjusted log-transformed data, and (4) F-weighted raw data. Phenograms were produced for each distance matrix and a consensus tree was prepared for each community. A third community, in which tree-tree relationships had been evaluated based on an independent set of leaf variables, was used as a frame of reference. In general, distance matrices 1, 2, and 4 yield very similar clustering patterns while distance matrix 3 provides a quite different view of among-tree relationships in each community. The degree of consensus among the four analyses, coupled with patterns for three qualitative characters, suggests that there may be extensive hybridization in one community and limited evidence of hybridization in the other.

INTRODUCTION

The study reported here had its origin during 1986-87 as I was analyzing specimens collected for two other studies (Jensen 1988a, 1988b, 1989). In both of those studies, morphometric comparisons among species of oaks were based on two sets of data: leaves versus fruits/buds. The rationale for recognizing these two sets of data was that they reflect the primary sources of taxonomic characters for summer versus fall/winter collections. I was interested in determining whether or not species differences could be recognized without access to a full set of characters. After all, many collections (1) are made in the summer when mature buds and fruits are not available, (2) are from sterile individuals, (3) are made in years when fruit production is minimal (a non-mast year), or (4) are made in the late fall or winter when leaves are not available. I was interested in testing the hypothesis that the results of a numerical taxonomic analysis would yield the same clusters regardless of the source of data.

The results of those earlier studies (Jensen 1988a, 1988b, 1989) failed to confirm the above hypothesis. In the first instance (Jensen 1988a, 1988b) I found that in some communities clustering patterns based on the two sets of data were quite congruent, whereas in others that was not true. Evidence of hybridization was seen in unstable OTU-OTU phenetic relationships and in patterns of among-character correlation. Furthermore, the fruit/bud data seemed to be less variable in the face of hybridization than did the leaf data. The last was not surprising in that hybrids invariably are first suspected on the basis of aberrant leaf morphologies, and a general tenet in plant systematics is that reproductive characters are more conservative--hence

less variable--than vegetative characters (e.g., Lawrence 1951). In the second instance (Jensen 1989), among-tree relationships based on fruit/bud characters were found to be significantly different from among-tree relationships based on leaf characters.

While conducting field work in 1986, I noted evidence of hybridization in two additional communities in Land Between The Lakes, each community containing at least four species of *Quercus* subg. *Erythrobalanus*: *Q. coccinea* Muenchh., *Q. falcata* Michx., *Q. imbricaria* Michx., and *Q. velutina* Lam. The evidence of hybridization was the presence of at least one tree with distinctly asymmetrical leaf outlines, suggesting that *Q. imbricaria*, which has entire leaves, may have hybridized with a species having lobed leaves. Such hybrids are well-known and their leaves invariably show a wide range of two-dimensional forms, from almost entire to conspicuously asymmetrical lobed.

Hybridization among oaks is well-documented, but poorly understood. As with most cases of putative hybridization, the primary evidence has been the discovery of individuals with morphologies intermediate between those of species known to occur in the same locality. But there has not always been agreement that such apparently atypical variants indicate hybrid origin. For example, Muller (1951) argued that many cases of putative hybridization represent misidentified juvenile or sterile specimens. The implication is that if one examined adults, or concentrated on reproductive structures, there would be fewer cases of suspected hybridization.

My own view is that hybridization may be common locally and the frequency of hybridization may, in fact, be underestimated. The open pollination systems of oaks literally ensure inter-specific pollination events that could lead to the production of hybrid offspring. Although some sympatric oaks flower asynchronously (e.g., Johnson and Abrahamson [1982], Duncan and Duncan [1988]), some others do not (Hunt 1989). When hybridization occurs, our ability to detect it will depend upon the analytical approach used and the degree to which the parental species differ.

As noted above, one of the best indicators of hybridization in oaks is the presence of individual trees with leaves that are rather uniformly asymmetrical in outline and have both quantitative and qualitative characters that reflect either intermediacy between, or a mixture of, the characters of the putative parents. A few well-documented cases of controlled hybridization have confirmed the morphological intermediacy of known hybrids (e.g., Burk 1965). Extrapolating from cases of known hybridization to cases of putative hybridization is common, and most reports of interspecific hybrids in oaks are based on that practice.

It is not that other forms of evidence are without merit. Knops and Jensen (1980) demonstrated congruence between patterns of variation in phenolic compounds and morphology among three sympatric species of oak. The patterns they found supported previously constructed hypotheses as to which species were hybridizing. Because all of their data came from reproductively mature and fertile trees, it is not possible that those patterns were due to immaturity or sterility of the individual trees in their sample.

The analyses reported by Knops and Jensen (1980) suggest that not all of the three possible interspecific crosses had occurred. But, as they pointed out, the absence of apparent hybrids as mature, fertile trees does not necessarily mean that hybridization is not occurring; perhaps some hybrids do not survive to maturity, or are reproductively sterile. Notwithstanding the lack of evidence for one of the crosses, the fact that morphologically intermediate trees were also biochemically intermediate provided good evidence for the existence of hybrid trees.

Attempts to use gel-electrophoresis as a tool for identifying genetically intermediate trees have met with limited success. Though there are "marker" alleles which can be used to differentiate the subgenera, any allele occurring in one species within a subgenus apparently also occurs in other species of that subgenus (Guttman and Weigt 1989, Manos and Fairbrothers 1987). Differences among species of a subgenus appear to be a function of allele frequencies, not allele presence or absence. And allelic frequencies can only be determined in those cases where species are recognizable a priori. If trees are assigned to species based on their morphological features, and the groups thus recognized are then examined to determine allele frequencies, obviously the genetic profile of a species is a function of the accuracy of the initial assignment of individual trees to species.

In a sense, we have come full circle. Though biochemical studies can be used to develop species profiles, we cannot assign individual trees to species based on their biochemical profiles until such profiles have been developed. We begin by assigning trees to species based on their morphology, and we then establish the biochemical profiles for those groups. The validity of those biochemical profiles thus obviously depends upon the validity of the morphological characters as species discriminators. If hybrid individuals in a population confound our efforts to delimit well-defined species on the basis of morphology, then we should not expect the biochemical profiles to work any better (or even as well) in differentiating species. Therefore we must exclude from our initial biochemical surveys those trees that appear, based on their morphological characters, to be hybrids. So the trick is to be able to identify hybrids at the outset.

In this paper I report the results of studies of fruit variation in three communities of *Quercus* subg. *Erythrobalanus*. I have reported on one of these communities earlier (Jensen 1988b). In that report I concluded that, based on both leaf and fruit/bud data sets, there was little evidence of hybridization. That same community is used in the present study as a frame of reference for evaluating data from the other two communities. For these other two communities there are no leaf or bud characters to examine, and conclusions regarding the taxonomic status of individual trees in these two communities are based solely on characters derived from mature fruits.

METHODS AND MATERIALS

In each of three communities, mature fruits were collected (either directly from the tree or from the ground immediately beneath) from randomly selected trees. When possible, 10-20 fruits were collected from each tree, but in many instances only 3-5 fruits were available.

Community 1, adjacent to Mulberry Flat Road, was sampled in the fall of 1986 (Jensen 1988b). Although in that study no attempt was made to ensure that cups and nuts could be measured as matched pairs, it is nevertheless possible to estimate both within- and between-tree variation for each character. Communities 2 (Craven's Bay) and 3 (Wrangler's Camp) were sampled in the fall of 1987. If five or fewer fruits were available from a tree, all were used in the statistical analysis; if more than five were available, five were selected at random. In no case were fewer than three fruits available. These sample sizes may seem small, but previous experience (e.g., Knops and Jensen [1980], Jensen [1989]) suggests that such samples are adequate for characterizing individual trees.

A precision caliper (accurate to 0.001") was used to record six measurements from each fruit: (1) maximum nut length, (2) maximum nut diameter, (3) nut scar diameter measured parallel to maximum nut diameter, (4) maximum outer cup diameter, (5) inner cup diameter measured parallel to its maximum outer diameter, and (6) cup depth. Prior to data analysis these measurements were converted to mm. Two measures of cup scale size were calculated as follows: three scales were selected, midway between the cup rim and base and approximately equidistant from one another around the cup; using a 10X hand lens fitted with a micrometer, the greatest visible length and width of each of these scales was determined to the nearest 0.1 mm. These data were used to calculate a mean scale length and scale width for each cup.

These measurements provided a data matrix with eight columns; the number of rows corresponded to the number of fruits. One-way analysis of variance was used to determine the degree of among-tree variability for each character in each community. The data for each tree were then converted to a vector of character means. This yielded three data matrices with 16, 21, and 28 rows (= trees), respectively (data are available on request).

The three matrices of character x tree means were used as input for four different numerical taxonomic analyses. First, the original matrix was standardized by characters, and OTU-OTU taxonomic distances were derived from the standardized matrix. Second, values in the original matrix were transformed to common logarithms, and OTU-OTU taxonomic distances were derived from the log-transformed matrix. Third, the log-transformed matrix was used to create a variance-covariance matrix among characters, and the first principal component was derived from the variance-covariance matrix; Burnaby's sweep (Rohlf and Bookstein 1987) was used to "remove" the first component (viewed as a general size factor) from the log-transformed matrix, producing a "size-adjusted" matrix, which was then used for calculating OTU-OTU taxonomic distances. Fourth, a matrix of OTU-OTU distances was calculated from the original matrix using the F-weighting procedure described by Adams (1975).

Each of the four distance matrices was used as input for UPGMA cluster analysis, thus yielding four phenograms for each community.

Finally, a majority-rule consensus tree was prepared for each community.

Data input and analysis of variance were performed using SYSTAT, version 4.0. All other analyses were performed using NTSYS-pc, version 1.6 (Rohlf, 1990).

Besides the quantitative characters discussed above, three qualitative characters were recorded for each tree: cup scale tips free or appressed, the degree of pubescence of the inner surface of the cup, and the presence of rings of pits at the apex of the nut. The first two of these were recorded as two-state characters: (1) free scale tips (typical of *Q. velutina*) or appressed tips (typical of the other taxa); (2) inner surface of the acorn cup glabrous or with only a ring of pubescence around the nut scar (typical of *Q. coccinea* and *Q. imbricaria*), or uniformly pubescent (typical of the other taxa). Nut apex pitting was coded as a three-state character: conspicuous rings (typical of *Q. coccinea*), faint rings (typical of *Q. imbricaria*), or no rings (typical of the other taxa). Each tree was assigned a code based on observations made in the field as well as on the characteristics of the individual acorn samples. Although these qualitative characters were not used in the analyses, symbols have been added to the phenograms to indicate patterns of variation in them.

RESULTS AND DISCUSSION

The primary question being addressed in this study is whether or not patterns of morphometric variation in fruit morphology suggest hybridization. This is not the same as asking if the trees in each community can be grouped into distinct clusters corresponding to named taxa. While such clusters would be expected if there were no hybridization, they could only be evaluated in the context of an *a priori* assignment of each tree to a particular taxon. Such assignments are not a part of the approach used here.

It is important to note that in community 1, each tree was tentatively identified to species based on mid-summer observations of leaf and bark characters. Though this was not done for trees in communities 2 and 3, which were visited only in the fall, my observations while collecting, as well as the characteristics of the fruits, indicate that there were four species of *Q.* subg. *Erythrobalanus* in both these communities: *Q. coccinea*, *Q. falcata*, *Q. imbricaria*, and *Q. velutina*.

Community 1 may be viewed as a standard for evaluating the patterns of variation found in the other two communities. Specifically, analyses of leaf, bud, and fruit characters do not suggest hybridization in this community (Jensen 1988b). But if only fruit characters are considered (see Fig. 1), the evidence is more equivocal; in none of these analyses are four species clusters apparent. The analysis with the lowest degree of species-clustering is the size-adjusted analysis (Fig. 1C), which also has a higher cophenetic correlation than any other for community 1 (see Table 1).

The consensus tree for the four analyses from community 1 (Fig. 2) reveals that three trees identified as *Q. coccinea* cluster together in a majority of the analyses, as do two of the *Q. falcata* trees (F2, F4), and two of the *Q. velutina* trees (V2, V4). All trees identified as *Q. marilandica* occur in a single cluster in three of the analyses, but one *Q. velutina* tree is in this cluster as well. The consensus tree (Fig. 2) also indicates that individuals of three of the species (C3, F1, F3, and V3) fail to cluster consistently with any other individual or cluster.

The distributions of the three qualitative characters (Fig. 1) suggest that several trees in community 1 may be hybrids. For example, one of the trees (V1) tentatively assigned to *Q. velutina* does not have free scale tips typical of that species and it does not cluster with other *Q. velutina* in any analysis; instead, it always clusters with one or more trees assigned to *Q. marilandica*. Two trees (M1 and M3) assigned to *Q. marilandica* and one (V4) assigned to *Q. velutina* have faint pitting at the nut apex; this may indicate hybridization with *Q. coccinea*, but the evidence is meager.

The phenograms for community 2 are presented in Fig. 3. In each of these phenograms there are two primary clusters (ignoring the separation of tree U from all others in Fig. 3C) which correspond fairly well with the distributions of the three qualitative characters. In three analyses, all but two trees (B and P) having free scale tips are found in a single cluster, although there are several trees with appressed scale tips in that cluster. Trees C, D, E, G, H, K, N, and O all have characteristics suggesting they are *Q. velutina* (cups are pubescent on the inner surface and the scale tips are free) and, as a group, they tend to occur in one cluster along with three other trees (M, Q, and T) which have fruits more or less typical of *Q. coccinea*. The other cluster (in Figs. 3A, B, and D) contains four trees of uncertain affinity (B, I, L, and P),

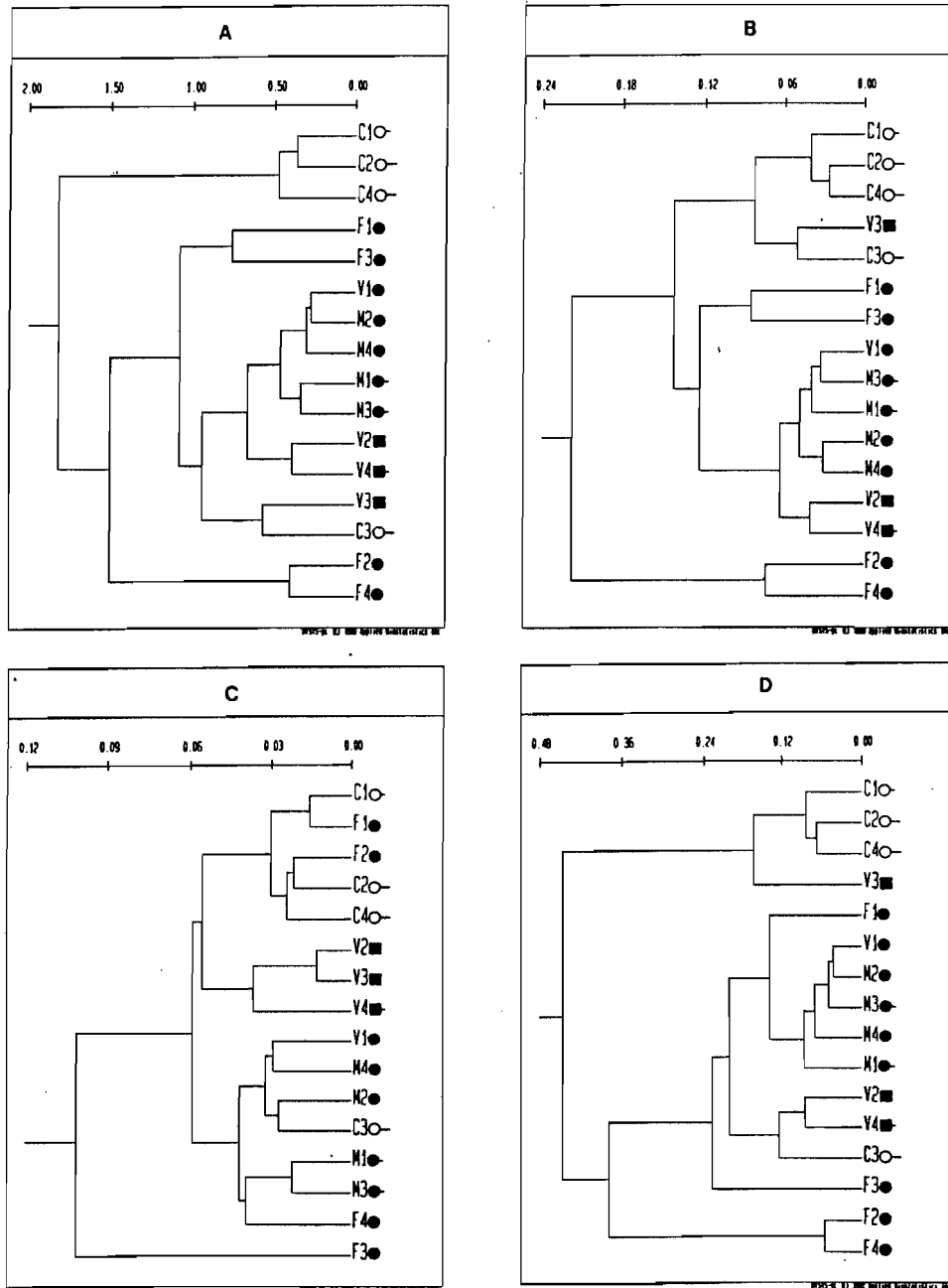


Figure 1. UPGMA phenograms derived from four distance matrices for community 1. A is based on standardized raw data, B on log-transformed data, C on size-adjusted log-transformed data, and D on F-weighted raw data. Letters in phenograms designate tree identifications based on leaf and bark characters: C = *Q. coccinea*, F = *Q. falcata*, M = *Q. marilandica*, and V = *Q. velutina*. Symbols denote qualitative characters of the fruits: circles = cup scale tips appressed, squares = cup scale tips free; filled symbol = inner surface of cup uniformly pubescent, open symbol = inner surface of cup glabrous or with only a ring of pubescence around the nut scar; long whisker = conspicuous rings at the apex of the nut, short whisker = faint rings at the apex of the nut, and no whisker = no rings at apex of nut.

Table 1. Cophenetic correlations from phenograms for communities 1 (Fig. 1), 2 (Fig. 3), and 3 (Fig. 5).

| Phenogram* | Community | | |
|------------|-----------|-------|-------|
| | 1 | 2 | 3 |
| A | 0.779 | 0.871 | 0.834 |
| B | 0.788 | 0.875 | 0.799 |
| C | 0.845 | 0.809 | 0.668 |
| D | 0.765 | 0.889 | 0.883 |

*See Figure captions for explanation.

one tree which is probably *Q. imbricaria* (A), and five trees (F, J, R, S, and U) tentatively identified as *Q. falcata*.

Figure 3C provides a distinctly different view of among-tree relationships from that suggested by Figs. 3A, B, and D. Though there are two primary clusters in Fig. 3C, the tree tentatively identified as *Q. imbricaria* clusters with most of the trees tentatively identified as *Q. velutina*. Furthermore, one of the trees tentatively identified as *Q. velutina* clusters with the *Q. falcata* trees, as do the three trees tentatively identified as *Q. coccinea*. Though this phenogram (Fig. 3C), based on the size-adjusted data set, has the lowest cophenetic correlation (Table 1) for this community, it does suggest that the phenetic relationships among these trees are greatly influenced by a general size factor.

The consensus indices for community 2 (Table 2) are much higher than for community 1, suggesting (as confirmed by the consensus tree, Fig. 4) a more common structure in the phenograms from community 2, particularly with respect to trees C, Q, T, D, E, K, N, O, G, H, and M.

The clustering patterns seen in Fig. 3 suggest that, based on the eight morphometric characters analyzed, there are two fairly well-defined groups. But the composition of these groups, and the pattern of clustering within each, is a function of the measure of taxonomic distance used. Trees B and P may be hybrids; whereas their quantitative characters appear most like those of trees believed to be *Q. falcata* (Figs. 3A, B, and D), their possession of cup scales with free tips, and the pattern of clustering seen in the size-adjusted analysis (Fig. 3C) suggest *Q. velutina*.

Interpretation of the results for community 3 is more difficult. Though the species composition is the same as in community 2, the sample is 1/3 larger (28 vs. 21). And the clustering patterns revealed by the phenograms (Fig. 5), the consensus indices (Table 2), and the consensus tree (Fig. 6) are less stable than in either community 1 or community 2.

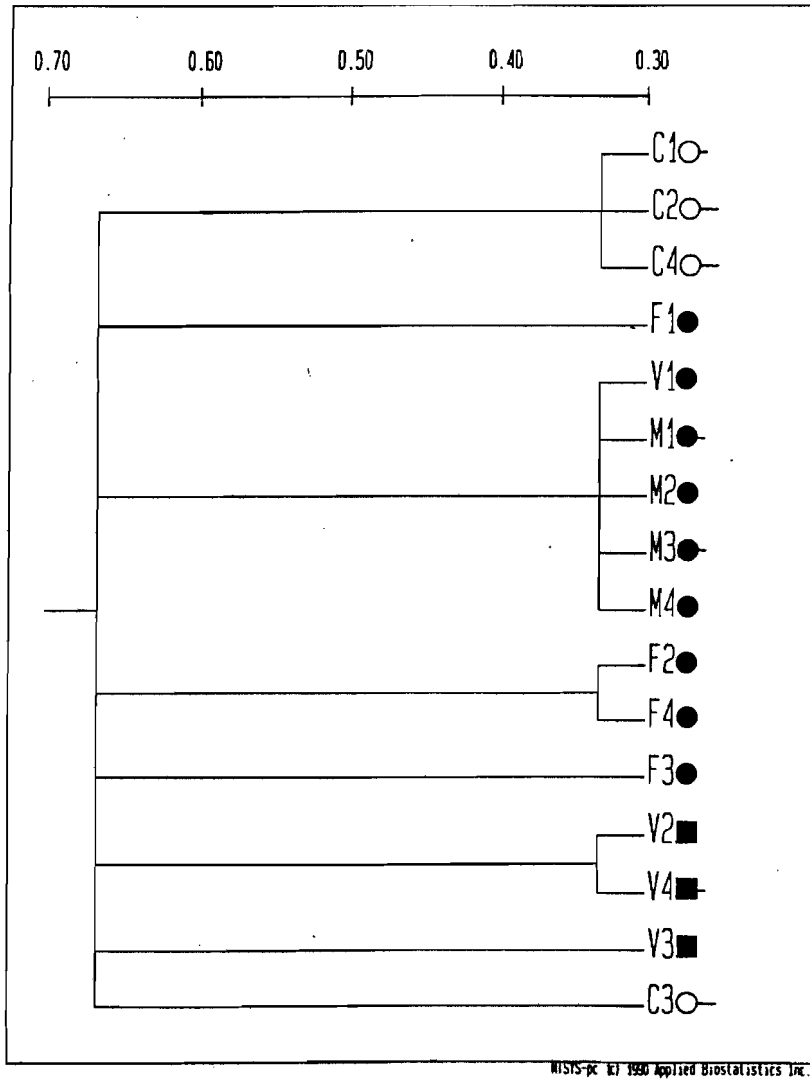


Figure 2. Majority rule consensus tree for the phenograms illustrated in Fig. 1. Letters and symbols as in Fig. 1.

Considering only fruit morphology, several trees in community 3 seem rather typical for each of four species. Only one tree (A) is tentatively identified as *Q. falcata*, and only one (X) as *Q. coccinea*. Eight trees (B, C, D, F, H, J, U, and V) are tentatively identified as *Q. imbricaria*, and three (O, 1, and 2) as *Q. velutina*. But the trees identified as *Q. imbricaria* or *Q. velutina* do not form distinct clusters in any of these analyses.

Figure 5 shows that trees with the same set of qualitative character states do not cluster together; neither appressed/free scale tips nor degree of pubescence of the inner cup surface correspond to any of the morphometric clusters. Several individuals of *Q. imbricaria* (F, H, and J) and *Q. velutina* (O and W) tend to cluster in two or three analyses, but the other

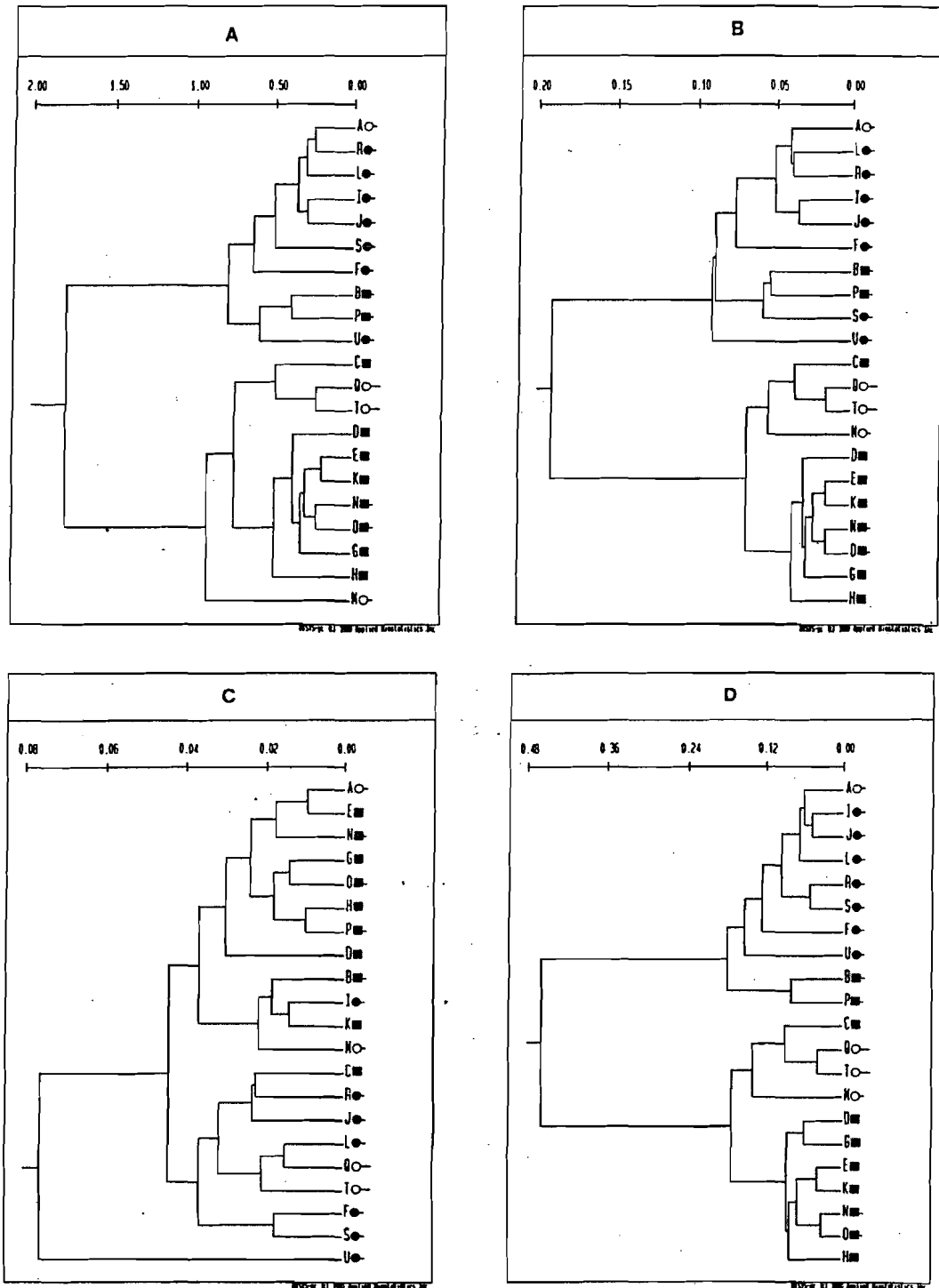


Figure 3. UPGMA phenograms derived from four distance matrices for community 2. A is based on standardized raw data, B on log-transformed data, C on size-adjusted log-transformed data, and D on F-weighted raw data. Letters in phenograms designate individual trees; symbols as in Fig. 1.

Table 2. Consensus indices corresponding to the majority-rule consensus trees for each community.

| Community | Consensus Indices* | | |
|-----------|--------------------|-------|--------|
| | CI(c) | CI(m) | CI(sf) |
| 1 | 0.286 | 0.143 | 15 |
| 2 | 0.526 | 0.350 | 135 |
| 3 | 0.192 | 0.038 | 10 |

*CI(c) = consensus fork index, CI(m) = Mickevich's index, and CI(sf) = levels sum index (see Rohlf [1982] for a discussion of these indices).

individuals of these two species show no particular pattern. Every tree in this community has nuts with rings of apical pits, suggesting extensive hybridization.

The consensus tree for community 3 (Fig. 6) reveals fewer consensus clusters than in communities 1 and 2. The lack of agreement among the four cluster analyses for community 3 is also evident in its consensus index (Table 2); both communities 1 and 2 have higher consensus indices.

The lack of consensus of the four cluster analyses for community 3 is also reflected in the cophenetic correlations (Table 1). Whereas Fig. 5D has the second highest cophenetic correlation (0.883) detected in this study, Fig. 5C has the lowest (0.668), and the range of values for this statistic from community 3 (0.215) is considerably higher than for either community 1 or 2 (both are 0.08).

The most nonconcordant clustering patterns in each of these three communities occur when size-adjusted taxonomic distances are employed. In communities 1 and 2 there is strong concordance among the phenograms based on raw distances, log-transformed distances, and F-weighted distances (Figs. 1A, B, and D; Figs. 3A, B, and D). The pattern is similar in community 3 (Figs. 5A, B, and D), though these clusters are more diffuse. Figures 1C, 3C, and 5C, based on size-adjusted data, suggest a decidedly different pattern of among-tree relationships. Comparison of these last three phenograms with the other three for each community reveals the impact of overall size differences on among-tree relationships. In particular, the two primary clusters seen in Figs. 1A, B, and D and Figs. 2A, B, and D represent a contrast between large-fruited and small-fruited trees. The distinction between large- and small-fruited trees is not as clear in community 3, but the general trend in Figs. 5A, B, and D is from small- to large-fruited trees as one moves down the phenogram.

Figures 1C, 3C, and 5C indicate similarity in overall shape. That is, if general size differences are removed the differences remaining should reflect similarities which are relatively size-independent (Somers 1986, Rohlf and Bookstein 1987). Though it is not certain that residual differences in size-adjusted data are valid indicators of shape differences (Bookstein

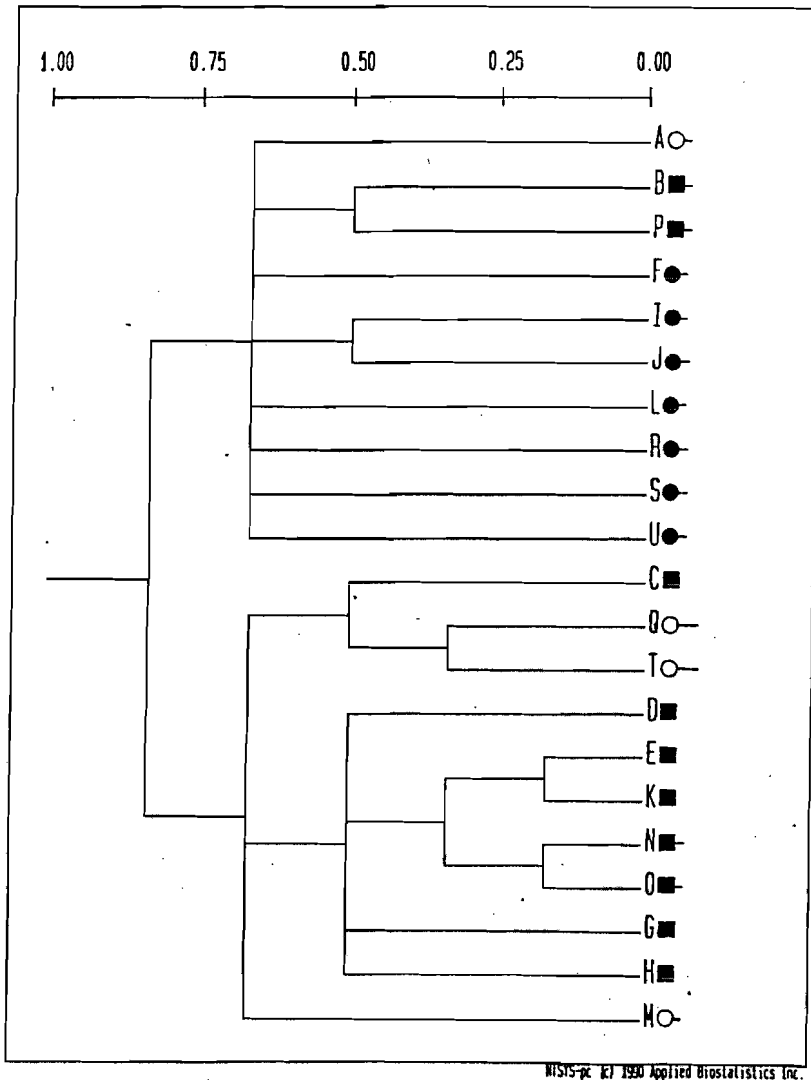


Figure 4. Majority rule consensus tree for the phenograms illustrated in Fig. 3. Letters designate individual trees; symbols as in Fig. 1.

1989), surely subjective evaluation of the patterns of data clustering based on nut and cup morphology suggests a common aspect of shape which differs from cluster to cluster.

What do these analyses suggest regarding hybridization in these three communities? In assessing this question I will assume that community 1 exhibits little or no hybridization. Recall that this view is based on earlier analyses of leaf and bud data (Jensen 1988b). Whereas those earlier analyses suggested little hybridization in community 1, the present analyses are more equivocal, though evidence of hybridization is still limited and subtle.

I assume that hybridization would have two effects, both the result of combinations of characters not seen in the parental taxa. First, different measures of phenetic similarity should

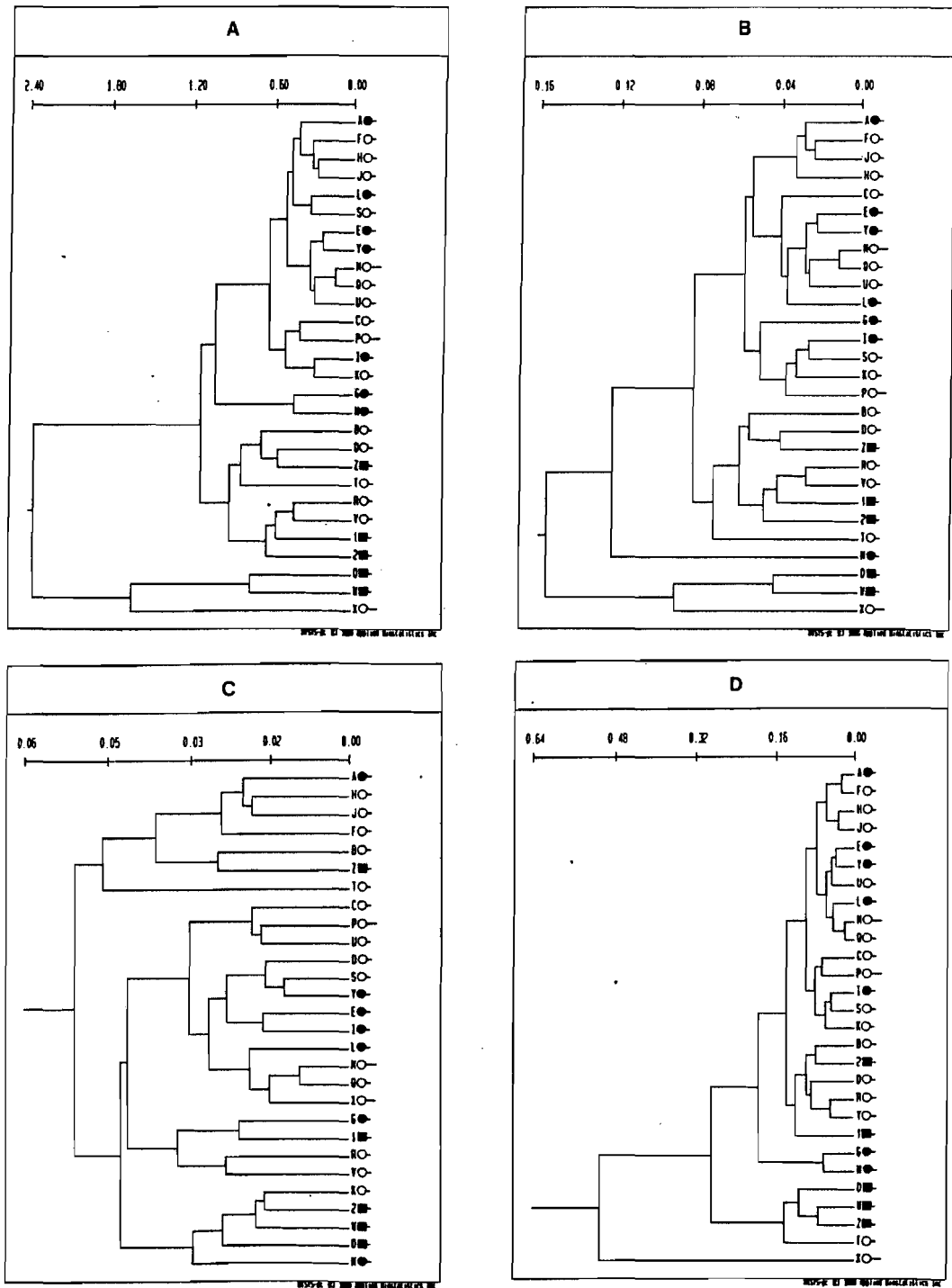
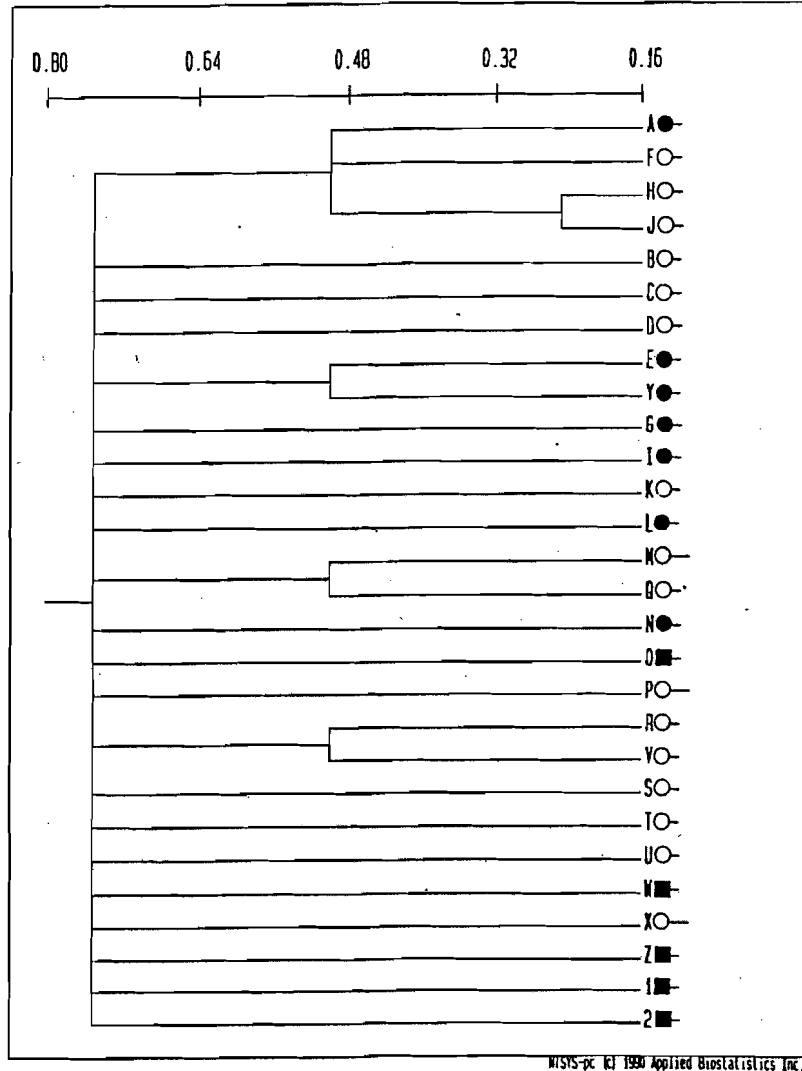


Figure 5. UPGMA phenograms derived from four distance matrices for community 3. A is based on standardized raw data, B on log-transformed data, C on size-adjusted log-transformed data, and D on F-weighted raw data. Letters and numbers in phenograms designate individual trees; symbols as in Fig. 1.



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Figure 6. Majority rule consensus tree for the phenograms illustrated in Fig. 5. Letters designate individual trees; symbols as in Fig. 1.

yield different views of among-tree relationships. The reason for this is that the different measures emphasize different components of character variation. This situation is especially evident in the four analyses of community 3 (Fig. 5), where the standardized and log-transformed analyses yield similar phenograms (Figs. 5A and B), but the size-adjusted and F-weighted analyses (Figs. 5C and D) are noticeably different from the former two and from each other.

Second, communities with few hybrid trees should show greater concordance of patterns of among-tree relationships than will communities with more hybrid trees. The greater concordance will be reflected in higher consensus indices and in the appearance of more common clusters in the consensus tree. Community 2 exemplifies this situation, with the highest

consensus indices of any of the three communities (Table 2), and the greatest agreement among its four analyses (Fig. 4).

One-way analysis of variance for each character in each community supports the above conclusions. As shown in Table 3, community 3 has the lowest F-values for seven of the eight characters, and community 1 has lower values than community 2 for five of the eight characters. If one assumes that hybrids exhibit greater within-tree variability than do their parental taxa, then the F-value results (an F-value is the ratio of within-tree variation to among-tree variation) suggest that community 3 has greater within-tree variation than do either communities 1 or 2.

Table 3. F-values for eight characters in each of three communities of oaks.

| Character | Community | | |
|--------------------------|-----------|------|------|
| | 1 | 2 | 3 |
| 1. Nut length | 82.6 | 93.5 | 45.7 |
| 2. Nut diameter | 85.6 | 40.0 | 32.8 |
| 3. Nut scar diameter | 36.5 | 36.3 | 21.8 |
| 4. Outer diameter of cup | 56.8 | 57.9 | 46.3 |
| 5. Inner diameter of cup | 47.7 | 39.8 | 37.8 |
| 6. Cup depth | 19.7 | 91.1 | 50.2 |
| 7. Cup scale width | 22.6 | 25.3 | 12.5 |
| 8. Cup scale length | 18.9 | 55.2 | 17.8 |

These analyses reveal that fruit morphology is quite varied in each of these communities and that trees apparently belonging to the same species do not form discrete clusters. Though the analyses are based exclusively on eight morphometric variables, the distributions of states of three qualitative characters are nonconcordant with morphometrically based clusters. Hybridization is apparently most common in community 3, but all three communities have trees exhibiting a mix of morphometric and qualitative characters such as might occur in hybrid trees.

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MULTIVARIATE ANALYSIS OF OVERSTORY VEGETATION OF LAND BETWEEN THE LAKES, KENTUCKY AND TENNESSEE

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ABSTRACT. One hundred thirty-seven stands from the uplands of Land Between The Lakes were sampled using two 0.06 ha plots per stand. Stand data were summarized and ordinated with DECORANA to identify patterns of woody vegetation. A coenocline was developed from the first axis ordination to depict species relationships along the gradient. The coenocline accounted for 51 percent of the variance in the vegetation data indicating a strong gradient. Plot data were also classified using COMPAH to determine the nature and extent of vegetation types in the study area. The following Dominance Types were found to occur at LBL: *Quercus prinus*, *Q. prinus-Q. alba*, *Q. stellata-Q. alba*, *Pinus echinata-Q. falcata*, *Q. alba*, *Q. velutina-Q. alba*, *Q. alba-Q. rubra*, *Q. alba-Fagus grandifolia*, and *F. grandifolia-Acer saccharum*. Environmental variables were then related to both the ordination sequence and classification using multiple regression and discriminant analysis, respectively. Topographic variables, followed by soil chemical and soil textural variables, were significantly related to the first ordination axis and to the group structure derived from COMPAH.

From the classification analysis, it was clear that both successional and compositionally stable stands occurred in the area. In order to refine the environment-vegetation relationships, stands were divided into compositionally stable (64) or successional (73) groups. The above analyses were performed on both sets of stands. DECORANA first axis ordination accounted for 68.3 and 42.4 percent of the coenocline variance for stable and successional stands, respectively. Further analyses on stable stands included a direct gradient approach with factorial analysis, deriving environmental adaptation values (EAV), and then using these values in a weighted averages ordination which accounted for 70.0 percent of the variance in the coenocline. The direct and indirect gradient analyses of stable stands were similar in rank order, but with the direct gradient analysis, mesophytic species are oriented more strongly toward the xeric end of the gradient. It is proposed that the direct gradient analysis is an indication of future forest composition, while the indirect analysis portrays the present composition found at LBL.

CONTRIBUTED PAPERS
SESSION II: ZOOLOGY AND ECOLOGY

Moderated by:

David Pitts
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THE LIVING LANDFILL: A WILDLIFE ENHANCEMENT PROGRAM

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ABSTRACT. A 959-acre landfill to serve west Tennessee was established in 1988 along the southern edge of Millington, Tennessee. While the primary purpose of the landfill is to provide an economical and environmentally sound method for the disposal of solid wastes, the objectives of the enhancement program are to support and protect the environmental integrity of the site and the adjacent riparian wetlands by stabilizing the soils and to provide the greatest diversity of food, cover and habitat for endemic and migratory wildlife. The enhancement program includes 900 acres of the 959-acre site, and consists of terrestrial and aquatic wildlife programs.

BIRDS UTILIZING THE MINOR E. CLARK FISH HATCHERY, ROWAN COUNTY, KENTUCKY

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ABSTRACT. An ongoing survey of avian species using the Minor E. Clark Fish Hatcher, Rowan County, Kentucky was started in 1980. A total of 219 species have been recorded. The habitat created by the construction of Clark Hatchery and the impoundment of nearby Cave Run Lake has influenced the utilization of this area by species not usually observed in this region of Kentucky.

THE KENTUCKY SPARROW-FREE BLUEBIRD BOX

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ABSTRACT. There are subtle differences in the nest site requirements of House Sparrows (*Passer domesticus*) and Eastern Bluebirds (*Sialia sialis*). By exploiting a combination of these factors I have developed a box that Eastern Bluebirds prefer to a standard bird house and that House Sparrows do not like.

The entrance to the house is a slot, made by having the front not reach to the roof. At some point it must be at least 28 mm high and at no point more than 30 mm. The front is hinged at the bottom so that it will swing open for inspection and cleaning. The box is only 75 mm (3 inches) deep. It must be mounted low (1-1.5 m) on a fence or post in the open in a rural area.

House Sparrows like a deep dark crevice, either provided by the structure or their nesting material. A shallow box with a wide entrance, an internal floor dimension no greater than 10 x 10 cm, and mounted low is not a suitable nest site for House Sparrows. Of course, behavioral evolution may change this picture.

**BANDING RECOVERIES, SITE FIDELITY AND SPRING ARRIVAL
PATTERNS OF MALE WHITE-EYED VIREOS (*Vireo griseus*)
IN SOUTHWESTERN VIRGINIA**

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ABSTRACT. Data on population stability of nearctic migratory passerines are becoming of increasing importance in light of changes in the habitat structure on both the breeding and wintering grounds. Data are presented here for five years of recovery for male White-eyed Vireos. Of all opportunities for return, 56.6% were recovered, corresponding well to estimates for other small migratory species. No individuals were observed to relocate, i.e. all remained faithful to previous territories, although some shifted such that the new territory overlapped the old. Most birds arrived between 17 and 30 April, with a median date of 24 April. Older birds arrived earlier than younger, as has been reported for other species. The arrival dates for individuals reliably predicted their arrival in the next year. Thus there is both age- and individual-specific timing of arrival. The results are discussed in the context of the ecology of both this species and other small migratory passerines.

A SOUTHERN APPALACHIAN BALD AS A PEREGRINE FALCON HACK SITE

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ABSTRACT. An evaluation was made of the reintroduction of Peregrine Falcons (*Falco peregrinus*) on Big Bald Mountain in northeastern Tennessee. One wild-caught and 20 captive-bred young Peregrine Falcons were hacked during the period 1987-1989. The treeless terrain of the hacking sites facilitated observation of the fledgling birds. The use of construction scaffolding proved cost-effective and less labor-intensive in providing an artificial temporary hacking tower. Use of the same hack site in consecutive years could result in fledgling mortality due to attacks by returning adults and subadults.

INTRODUCTION

The Peregrine Falcon (*Falco peregrinus*) was widely distributed in the United States during the first half of this century (Hickey 1942). But by the early 1960s breeding Peregrine Falcons had vanished from the eastern United States, and severe reductions of populations in the western United States were documented by Berger et al. (1969). Concern about this declining population prompted the U.S. Fish and Wildlife Service (USFWS) to place the Peregrine Falcon on the endangered species list in 1973, and to develop a recovery plan (USFWS 1979).

The major cause of extirpation of the Peregrine Falcon from many areas of the United States was reproductive failure caused by dichlorodiphenyltrichloroethane (DDT--a chlorinated hydrocarbon pesticide), and its metabolites (Hickey and Anderson 1969). Accumulation of this contaminant, obtained by the Peregrine through the food chain from small bird prey species, inhibits calcium incorporation into the eggshell, resulting in thin eggshells and nesting failures (Peakall 1976). This biological magnification of environmental organochlorine contamination to high concentrations in the tissues of top predators in the food pyramid causes embryonic mortality, adult mortality, and behavioral abnormalities in such species (Cade et al. 1971, Newton and Bogan 1974, Ratcliffe 1970).

The use of DDT was widespread in the United States after World War II. It was not until 1972 that the application of this pesticide in the U.S. was restricted (Burnham et al. 1978).

A survey of Peregrine Falcon eyries was conducted in the eastern U.S. in 1975 to determine the status of wild breeding Peregrines and to assess the suitability of potential release sites for captive-bred falcons. No breeding pairs or occupied eyries were found, but suitable habitat was present (Fyfe et al. 1976).

The possibility of reintroducing Peregrine Falcons into the wild was realized in 1973 when offspring from three North American subspecies of Peregrines--*Falco peregrinus anatum*, *F. p. peali*, and *F. p. tundrus*--were produced in captivity (Cade and Temple 1977). The

Peregrine Fund and Cornell University performed the first reintroductions of captive-bred Peregrine Falcons in the eastern United States; they released 16 young Peregrines using a technique known as hacking. (Cade and Temple 1977).

Hacking falcons is an ancient tradition practiced by falconers. It involves capturing wild nestlings and allowing them to learn to fly in a condition of semi-captivity, while they learn to hunt. The modern version of hacking, which uses mainly captive-bred birds, is defined by Barclay (1987) as "the controlled release of young raptors during the period of development from fledging to independence." This technique has become the most frequently used method in Peregrine Falcon restoration programs, and has resulted in reestablishing nesting pairs in the wild. In time, these hacked birds should establish a population that will be self-maintaining (Cade and Temple 1977, Sherrod and Cade 1978, Barclay and Cade 1983, Cade and Barclay 1984).

Harassment of released young by returning Peregrines and predation by Great Horned Owls (*Bubo virginianus*) are the two main causes of mortality during hacking (Cade and Barclay 1984).

Tennessee began Peregrine Falcon restoration efforts in 1984, using a site in Great Smoky Mountains National Park at Greenbriar Pinnacle. This site had physical features of a Peregrine eyrie, and during the three-year period from 1984 to 1986, 13 young captive-bred falcons were released there (Henry 1987). The sighting of returning subadult or adult Peregrines to this site in the spring of 1987 prompted a search for another suitable hack site within the state.

The purpose of this report is to evaluate an Appalachian bald as a reintroduction site for the recovery and management of an endangered species, the Peregrine Falcon.

METHODS

Hack Site

Big Bald Mountain (elevation 1681 m) is in the Unaka Mountains of Unicoi County, in northeastern Tennessee. Although the hack site is mostly in the Cherokee National Forest in Tennessee, access was gained by permission through private property located at Wolf Laurel Resort near Mars Hill, North Carolina.

The hack site at Big Bald Mountain was an open bald vegetative community with many species of grasses and other flowering plants. It was being invaded by woody shrubs, including: hawthorn (*Craetagus* spp.), serviceberry (*Amelanchier* spp.), mountain laurel (*Kalmia latifolia*), rhododendron (*Rhododendron* spp.), and viccinium (*Vaccinium* spp.). The grassy meadow consisted of approximately 50 ha of mountaintop and another 20-30 ha of open terrain across Big Stamp Gap, on and around Big Stamp Mountain (known locally as Little Bald).

The area supported a diverse avifauna, which provided an important prey base essential to the development of hunting behavior of fledged falcons (Sherrod et al. 1981, Sherrod 1983).

Towers and Hack Boxes

In 1987 a hacking tower was built from construction scaffolding. This tower provided a stable base for a wide platform on which to set the large wooden hack box. The tower was

erected in about one half-hour; within two hours, the platform and hack box were completely in place. I believe this represents the first use ever of this type of tower for hacking Peregrine Falcons. The scaffolding was easily transported in a standard sized pickup truck. Two people can easily erect and stabilize a 4.72 m tower using only a hammer and adjustable wrench.

In 1988 and 1989, two towers were erected approximately 50 m apart. Two towers were erected to achieve "clustering," a technique intended to saturate an area with birds before returning birds establish territories (the presence of territorial birds eliminates an area from further use as a release site [Henry 1988]).

The hack boxes (described in detail by Sherrod et al. 1981) were large, prefabricated, rectangular plywood boxes, approximately 152 cm x 122 cm. The front of the box was provided with a temporary slide-in predator guard, with metal bars facing inward, and 2.5 cm x 5.04 cm welded wire facing outward. The bars prevented the young falcons from breaking feathers prior to release; the wire prevented predators from capturing the fledglings from the outside. The boxes provided protection from weather and predators, and also confined the young birds until their release time. Gravel was placed in the bottom of the box for sanitation, and several large rocks served as perches. Attendants were on the site 24 hours a day to provide food for the young falcons, document behavior of the birds, and reduce human disturbance.

RESULTS AND DISCUSSION

Twenty-one Peregrine Falcons were released at Big Bald Mountain hack site from 1987 to 1989. All but one of the birds were captive-bred, and obtained from the Peregrine Fund, Incorporated. One wild-caught bird was obtained from USFWS enforcement personnel and transported to the site by M. Gilroy of the Peregrine Fund; this bird had been taken by poachers from a wild nest near the James River in Virginia.

In 1987, six birds, each about a month old, were placed in the single hack box. They were kept in the hack box for 12 days, except for the wild-caught individual, which was only in the box for five days prior to release. Two of the released birds remained at the site for only several days (one for six days, and the other for nine days) after release. The other four birds all remained at the site for at least 30 days after release. Observations of the hunting behavior of the released birds suggested it was normal. The released birds engaged in mock battles, stole food, and chased other species (primarily Turkey Vultures [*Cathartes aura*] and Ravens [*Corvus corax*]). A Red-tailed Hawk (*Buteo jamaicensis*) which landed on the hack tower was mobbed and driven off by all four falcons present on the site at the time.

One bird hacked at this site in 1987 was live-trapped and released in late fall of the same year at Hammonasset Beach State Park near New Haven, Connecticut (Hatcher 1988).

In 1988, seven falcons were hacked on Big Bald Mountain using two towers and two boxes (three birds in one box, four in the other). All these birds were approximately one month old when placed in the boxes. Three birds were kept in their box for 10 days, and four birds were kept in their box for only five days. All seven birds dispersed normally and their post-release hunting and chase behavior appeared normal.

Two weeks after release of these falcons, the head of a young chicken was found on a hack box. Five weeks after release, a subadult falcon was observed on the site and was driven off by one of the younger and more aggressive males.

Eight falcons were released on the site in 1989 from two towers with boxes (six birds in one box, two in the other). The six birds in one box were each 40 days old, and the two in the other box were each 35 days old. The six older birds were released after four days, and the two younger birds were released after 10 days. Seven of the birds dispersed normally and exhibited apparently normal hunting and chasing behavior.

Protection from the elements was planned and provided as well as possible. Higher elevations at lower latitudes experience climatic conditions similar to those of southern Canada. The hack site was characterized by cool summer temperatures and high winds over the treeless terrain.

Weather conditions at the hacking site were of special concern in 1989. Rainfall of more than seven inches above normal for the period was recorded, and the accompanying electrical storms jeopardized the safety of the attending personnel. On several occasions during electrical storms the attendants left the treeless terrain of the hack site and sought safety below the summit. Observations were hindered by heavy fog, which sometimes persisted for more than two days.

Adult or subadult Peregrine Falcons were observed on this site on 12 different days in 1989. Once a larger, older bird attacked one of the released birds. The larger bird hit the smaller bird from a stoop and drove the young bird to the ground, where it remained for some time. The young bird was later observed flying and behaving normally. Harassment by these aggressive intruders may have caused the early departure of one of the hacked birds--only four days after it was released from the box (J. R. Smith, pers. comm.). Cade and Barclay (1984) believed that 40 percent of all mortality of young captive-bred Peregrine Falcons at hack sites from 1975 to 1983 was attributable to owl predation or harassment by returning subadult or adult Peregrines.

Sherrod et al. (1981) list the following critical considerations when selecting a hack site or nesting site for returning Peregrine Falcons: (1) isolation from human disturbance, (2) security from predators, (3) protection from the elements, and (4) an adequate food supply. All of the above criteria were considered before selecting Big Bald Mountain as a hack site. Isolation from human disturbance was of primary concern. Although Big Bald Mountain is part of Cherokee National Forest and Pisgah National Forest, its eastern slope, approximately 0.8 km from the summit, has been maintained by the Wolf Laurel Resort. The Appalachian Trail transects the ridge and crosses the summit within 50 m of the hack tower site. Through negotiations with the management of Wolf Laurel Resort and representatives of the Appalachian Trail Association, arrangements were made to temporarily close the road and reroute the Appalachian Trail for 14 days. This gave the young birds time to strengthen their flight muscles so that if they were startled or flushed from their perches they would not be lost on the ground.

In 1987 precautions were taken to keep the site a secret, because we were unsure what publicity would do if the site's location were advertised. One local newspaper sharply criticized TWRA for their "hush-hush" attitude. In 1988 TWRA was less restrictive concerning media exposure, and allowed media visits to the site. In 1989 publicity was emphasized and educational pamphlets were printed and distributed to site visitors. Signs (PEREGRINE FALCON OBSERVATION AREA) were placed at points of entry to the mountain. Visitors were directed to the camp below the towers where spotting scopes and binoculars were made

available for people to watch the aerial acrobatics of this endangered species. One hiker stayed for four days, in awe of the magnificent birds.

Predation on the released falcons was not a problem at this site. Great Horned Owls were neither heard nor seen in the area, and mammalian predators posed no threat. Tracks of black bear (*Ursus americanus*) were seen along the road banks in all three years, but they were never observed near the hack towers. In 1989, one hacked bird was probably lost to harassment by returning older Peregrines. Competition with older conspecifics at some hack sites is as important an agent of mortality as predation. Saturation hacking of Peregrines in the Southern Appalachians will probably result in an increase in such mortality.

The proximity of the grassy balds, low interspersed shrubs, and the northern hardwood/cove hardwood forest at the base of the summit provided a diversity of prey bird habitats. The high diversity and density of avian prey species at the site were both important factors in assuring an adequate prey base for the released Peregrines.

CONCLUSION

Since 1984, 34 Peregrine Falcons have been hacked at two Tennessee sites. But nesting by this species in Tennessee since that time had not been documented through 1990. North Carolina also began hacking Peregrine Falcons in 1984, and seven confirmed pairs were identified in 1989 (A. Boynton, pers. comm.). A site near Alum Cave Trail in Great Smoky Mountains National Park shows much promise for becoming the site of Tennessee's first Peregrine Falcon nest since 1947. One pair was observed there exhibiting nesting behavior (including making a "scrape" for nesting) during the spring and summer of 1990 (K. Delozier, pers. comm.), on a ridge named Peregrine Ridge on a quad sheet! The downtown urban canyons in three of Tennessee's largest cities--Knoxville, Nashville, and Memphis--have also yielded reports of this endangered speedster in pursuit of pigeons and perched on window ledges as high as 30 stories. Robert M. Hatcher, Tennessee Wildlife Resources Agency Nongame and Endangered Species Coordinator, has placed a specially designed nesting platform atop the James K. Polk state office building and on a ledge of the 30th floor of the Life and Casualty Tower in Nashville, in an attempt to attract a nesting pair. Nest platforms are ready for placement on buildings in Memphis and Knoxville. There is thus reason for optimism for future Peregrine nesting in Tennessee.

Though the number of historical pairs of Peregrine Falcons in the Southern Appalachians is unknown, goals of at least 20 pairs for downlisting and 25 pairs for delisting the Peregrine Falcon from the endangered species list in the region have been established (USFWS 1987). Because of some mortality of newly hacked birds at this site, apparently caused by returning falcons hacked at this and nearby sites, Big Bald Mountain has not been used as a hack site since 1989. The exposed conditions on the bald mountaintop probably increased the vulnerability of newly released falcons to returning falcons. Peregrine Falcons tend to return to areas where they learned to fly when they begin breeding. This makes it important that intraspecific competition and interference, and the interplay of those activities with the ecological characteristics of a site be considered during the hack site selection process.

The contribution made at Big Bald Mountain to reestablish the Peregrine Falcon as a breeding species in Tennessee has been positive, and efforts to locate and document nesting along the fringe of the Appalachians will continue.

Pushed to the brink of extinction by anthropogenic environmental contamination, the Peregrine Falcon now appears to be on the road to recovery. Ironically, the rescue of the species may also be credited to man and his management of this fragile resource. Aldo Leopold's (1966) words seem to epitomize this species' dilemma: "There are some who can live without wild things, and some who cannot. Now we face the question whether a still higher 'standard of living' is worth its cost in things natural, wild, and free."

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ESTIMATED IRON INDUSTRY WOOD USAGE IN THE LBL REGION, 1843-1912

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ABSTRACT. In order to generate more precise maximum estimates of wood usage by the charcoal iron industry in the area now known as Land Between The Lakes (LBL) during the effective lifetime of the industry (1843-1912), I consulted primary and secondary historical sources for data on the longevity of the furnaces and estimates of their wood requirements. Estimates were usually expressed as acres per year (or per blast cycle) per furnace. My basic method was to multiply each furnace's years of operation by the estimated acres per year.

Two sorts of problems, however, required further investigation. The first concerned uncertainties about actual time in blast of individual furnaces. For some furnaces the sources were contradictory or vague about the years of operation, and occasionally a furnace was in blast for only a portion of a year. I used the maximum possible times in such instances, while noting in the text or notes where difficulties emerged. The second problem was the broad range of acre per year estimates (200, 300, and 500 acres per year per furnace). Since the lower estimates are from the pre-Civil War period (when the forest was essentially in a presettlement condition) and the higher estimates are post-Civil War (when the furnaces were largely exploiting second growth timber), I used the 500 acre per year estimate for furnace operations after 1865, and the 200-300 acre per year estimates for those in blast earlier. Various types of analysis and evidence were used to validate these assumptions.

I conclude that from 1843 to 1865, between 21 000 and 31 500 acres (13 to 18 percent of the area) were cut for charcoal. The maximum cut after 1865 I estimate at 11 000 acres (seven percent of the area). The cuts were unevenly distributed, the Kentucky portion being more heavily exploited than the Tennessee section. For Trigg County I estimate that 9000 to 10 500 acres were cut by 1865, and 8500 acres in the postwar period. In Lyon County between 7800 and 11 700 acres were cut before the Civil War, and some 2500 acres thereafter. In contrast, Stewart County accounted for 4200 to 6300 acres of timber cut before 1865, and none thereafter. To provide a clearer picture of the geographic scope and socio-environmental impact of the cutting for charcoal, accounts of each furnace in LBL are presented.

INTRODUCTION

Obviously the charcoal iron industry of the Western Highland Rim had a significant impact on the forests of the Land Between The Lakes region of Tennessee and Kentucky during the nineteenth and early twentieth centuries.¹ The goal of this essay is to develop more precise estimates of the volume, timing, and geographic extent of the industry's effects on the area's woodlands. Clarification of these issues will provide perspective for further assessments of the regional impact of other types of human activity, such as crosstie production. A more specific

historical understanding of these practices might aid our grasp of longterm ecological patterns and human influence upon them.

LITERATURE REVIEW

Available written sources, published and unpublished, stretching back over a century paint a picture of forest devastation. Yet the portrait has ambiguities. In 1874, Joseph B. Killebrew, soon to become Tennessee's Assistant Commissioner of Agriculture, Statistics, and Mines, described the consequences of iron production for timber resources.²

In the neighborhood of old furnaces, [the forest] has been cut down for a distance of three or four miles, and used in the making of charcoal. Sprouts put up every year, but the annual fires which sweep over the old "coalings" with devastating fury, destroy them. No new timber is taking the place of the old. Barren, sightless old fields, covered with Broomsedge, meet the eye on every hand.

Killebrew estimated that Stewart County's "timber supply, while abundant at present, is being consumed at the rate of 6,000 acres annually."

Writing more precisely about the LBL region in 1923, the manager of the Hillman Land Company, John Esselyton, described the 41,520-acre Hillman-DeGraffenried Tract of the Lyon and Trigg counties' portion of LBL. He noted that these lands had been "included within the area of the charcoal iron industry. Vast areas...were denuded of all timber, burned over, and since have grown up with worthless brush." Because he was answering a federal Forest Industry Questionnaire to determine his company's tax liability, he may have exaggerated the devastation. His purpose was to convince readers that the "amount and quality of the timber...is so small and inferior that the railroad ties produced from these lands cannot be called a timber operation within the meaning of the General Forest Industries Questionnaire." Nonetheless, he also reported that in 1913 the tract contained enough "merchantable timber" to produce an estimated 775 thousand railroad crossties or 24.8 million board feet. Clearly "vast areas" may have been "denuded," but even at this low harvest rate of approximately 600 board feet per acre, there were significant timber resources remaining.³

More recent observers have continued the theme. G. B. Shivery, writing in the 1940s, described conditions in the Stewart County forests from 1820 to 1885. After noting that one furnace south of the LBL region used 35 000 cords of wood in 1885, he concluded that because "the furnaces used such tremendous quantities of wood--much more than the annual growth of the forest--there was an increasing shortage of timber for charcoal. Abandonment of the furnaces was partly caused by this shortage of fuel." By his time, of course, recovery, particularly in the uplands, seemed well begun. He estimated that 64 percent of the county's area was forested, and he classified the timber as 42 percent "sawtimber," 22 percent "cordwood," and 36 percent as "below cordwood" in quality. Taking a broader view of the sources of human impact on forests in the Kentucky portion of LBL, James S. Fralish and Fred B. Crooks generalized in 1988 that: "Disturbance from fire, farming, timber cutting, and the

iron industry has substantially influenced forest community patterns so that they may be less recognizable today than they were 200 or 300 years ago."⁴

METHODS AND MATERIALS

As implied above, this study is historical--a reading of current and past observations on the impact of the iron industry on timber resources. There are general histories of the LBL region, county histories, local histories of the iron industry of Tennessee and Kentucky, geological and botanical reports, and archeological surveys available at the Woodward Library of Austin Peay State University, the Department of History and Philosophy of that institution, and the LBL research library at Golden Pond. Also, there is an extensive collection of published and unpublished materials on the history of LBL in the J. Milton Henry Collection at the Woodward Library, including a remarkable set of papers from the Hillman Land and Iron Company, which owned approximately 40 percent of the land in the Kentucky portion of LBL during the late nineteenth and early twentieth centuries. These sources are cited at appropriate points in endnotes.

Both impressionistic and quantitative statements were compared. As the evidence is often contradictory or ambiguous, I attempted to clarify data by such devices as map examination and to reconcile conflicts by noting differences in time or place of the reference. The details of these processes, along with the results, are reported in subsequent sections of this paper.

DISCUSSION

Estimates of Usage by the Various Furnaces

This first section gives data on operations and locales of the furnaces, divided by counties.

Stewart County, Tennessee

In 1854, Stewart County was the largest producer of pig iron in Tennessee, at 32 000 gross tons. Montgomery County was a distant second at 18 500. However, the most important of Stewart County's furnaces, both in terms of output and longevity, were south and southeast of the current LBL boundaries because ore deposits there were larger, of higher quality, and generally more accessible. In 1873, a decade after the Peytona Furnace ceased operation, five other county furnaces were still producing between 300 and 510 tons of pig iron a month.⁵

Peytona Furnace. The Peytona Furnace, located on the headwaters of Bear Creek about 6.5 miles west of Dover, was built by Thomas Kirkman in 1846 and 1847. According to local lore, the furnace was named after a notable Sumner County racehorse, but it seems more likely that both the horse and the furnace were named in honor of Balie Peyton and his brother, Joseph H. Peyton, both of whom served as Whig congressmen. Joseph Peyton died suddenly in 1845 while in office. Kirkman was a strong supporter of the Whig party, as were most of the Tennessee and Kentucky iron manufacturers of the era.⁶

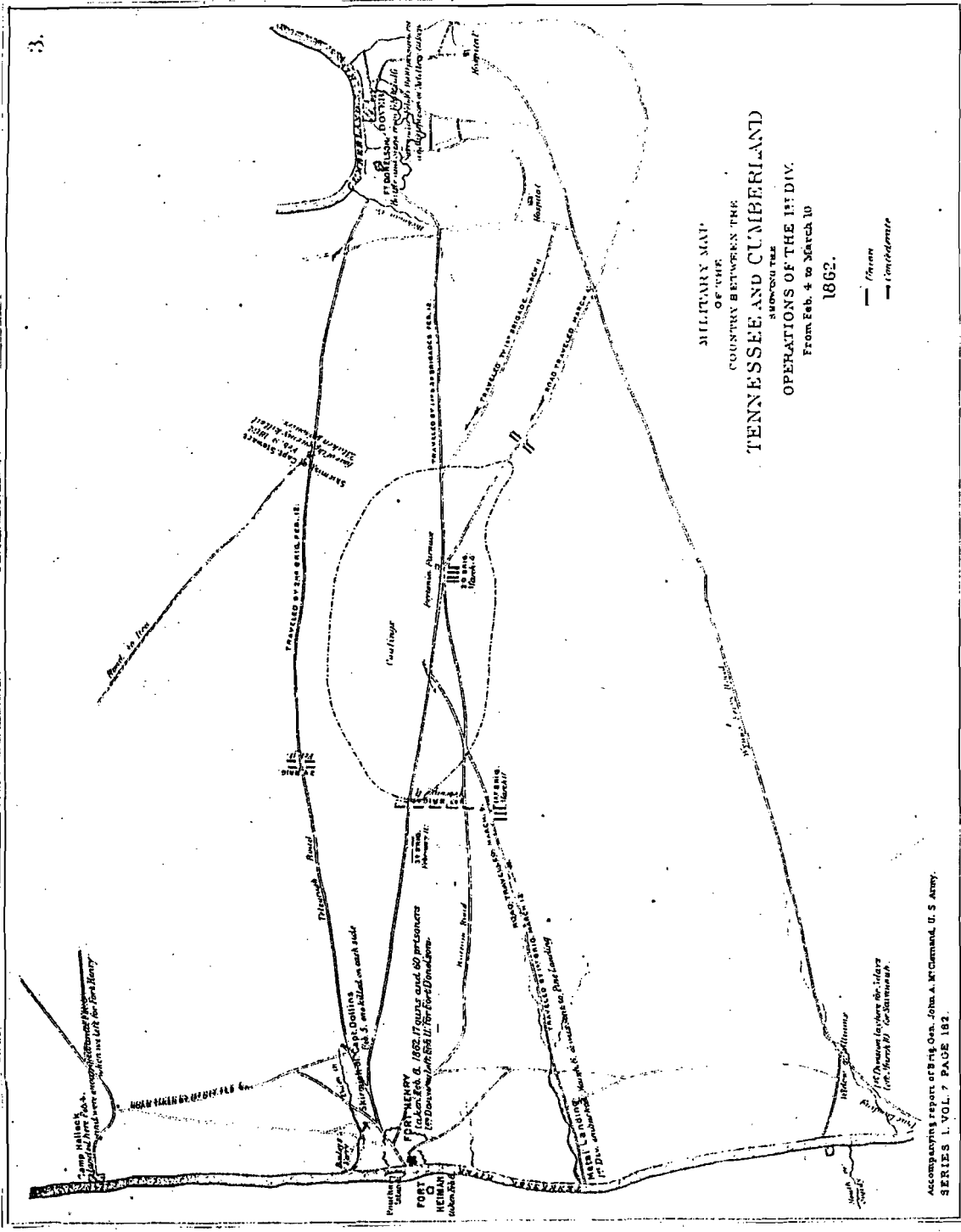
By the early 1850s the Peytona works employed approximately 60 whites and 75 slaves, producing around 1700 to 1800 tons of pig iron annually. The value of the plant was put between \$39,600 and \$40,000 in 1852. Its furnace was rebuilt in 1856. Peytona was still a thriving concern in 1860, making it one of the fortunate few to flourish in the region after the financial Panic of 1857.⁷

Beginning with an initial purchase of some 3799 acres on upper Bear Creek in 1845, Thomas Kirkman and his son accumulated as much as 17 000 acres, or some 27 square miles, of lands in and around LBL. The actual "coalins" for the furnace, however, constituted some five to six square miles, shaped in a rough oval, stretching along the old Ridge or Dover Road connecting Fort Henry to Dover. Located west of Pumpkin Ridge and mainly south and east of the current Blue Spring Road, these "coalins" did not penetrate down the creek toward the current Bear Creek Natural Area (see Map 1). In February 1862, Lt. Colonel James B. McPherson, Chief Engineer with the federal army enveloping Fort Donelson, mapped the old Ridge Road and others in the vicinity (see Map 2). On a landscape prominently spotted with "heavy timber," McPherson marked only one "clearing" of approximately three to four square miles located some 2.5 miles west of the Peytona Furnace site. This would have been the most recent cutting for charcoal at the western end of the "coalins." The territory between the "clearing" and the furnace was probably second growth timber recovering from earlier charcoal-making. McPherson described the "country between the two forts" generally as "very rolling, thickly covered with timber, and sparsely populated." After rendezvousing at the furnace and advancing over Pumpkin Ridge, federal troops "moved forward in line of battle" toward Ft. Donelson, "cautiously examining the ground in advance and on the flanks, which was very hilly and densely wooded." Obviously Peytona's decade and a half of operation had a significant impact along a portion of the old Ridge Road, but had left impressive, even forbidding forests both east and west of the "coalins" marked on Map 1.⁸

Since the Civil War the area around Peytona has remained "sparsely populated." In 1871 the property near the furnace itself was divided into town lots in a futile attempt to create a permanent town amid the ruins of the old "iron plantation" village. In 1874 Killebrew noted that, "At the old Peytona Furnace between the rivers, a colony of Germans have settled, and are giving their attention to grapes and nurseries. They are well pleased, and are prospering." However, that effort too apparently floundered amidst poor soil and the depression that gripped the nation in the mid-1870s. Apparently only scattered farming and timbering persisted. According to a 1940s "Forest Cover Map" of Stewart County, there remained only small blocks of "cleared land" around the headwaters of Bear Creek amidst a "hardwood forest." (See Map 3)⁹

Iron Mountain Furnace. Iron Mountain Furnace, located about four miles up Barrett Creek at what became Tharpe, was constructed in 1854 during a speculative boom in the local iron industry which soon ran its course. In that year there were twelve furnaces in Stewart County, up from five in 1850. By 1860, the county's working furnaces had constricted to four. Iron Mountain, along with its neighbor to the north, the Great Western, were among the products of this optimistic expansion.¹⁰

Initially, Iron Mountain and Great Western, under the same ownership, were to be supported by nearly 23 000 acres, purchased at a dollar an acre in 1855. In 1856 an additional



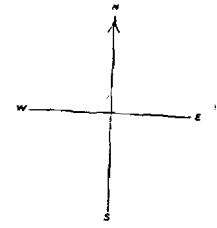
Accompanying report of Brig. Gen. John A. McClelland, U. S. Army.
SERIES I. VOL. 7. PAGE 182.

Map 1.

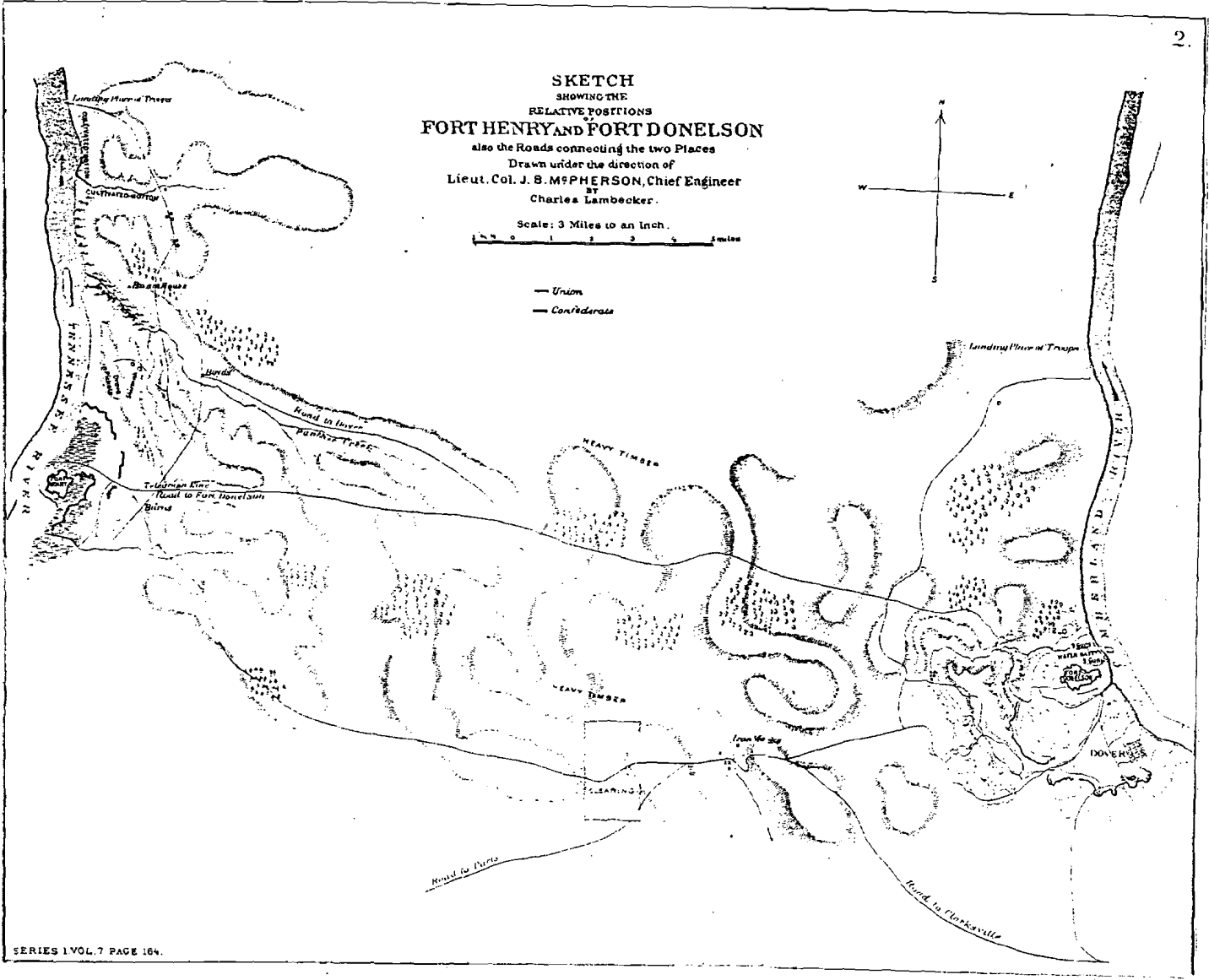
SKETCH
 SHOWING THE
 RELATIVE POSITIONS
 FORT HENRY AND FORT DONELSON

also the Roads connecting the two Places
 Drawn under the direction of
 Lieut. Col. J. B. M'PHERSON, Chief Engineer
 BY
 Charles Lambecker.

Scale: 3 Miles to an Inch.



— Union
 — Confederate



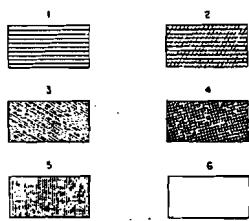
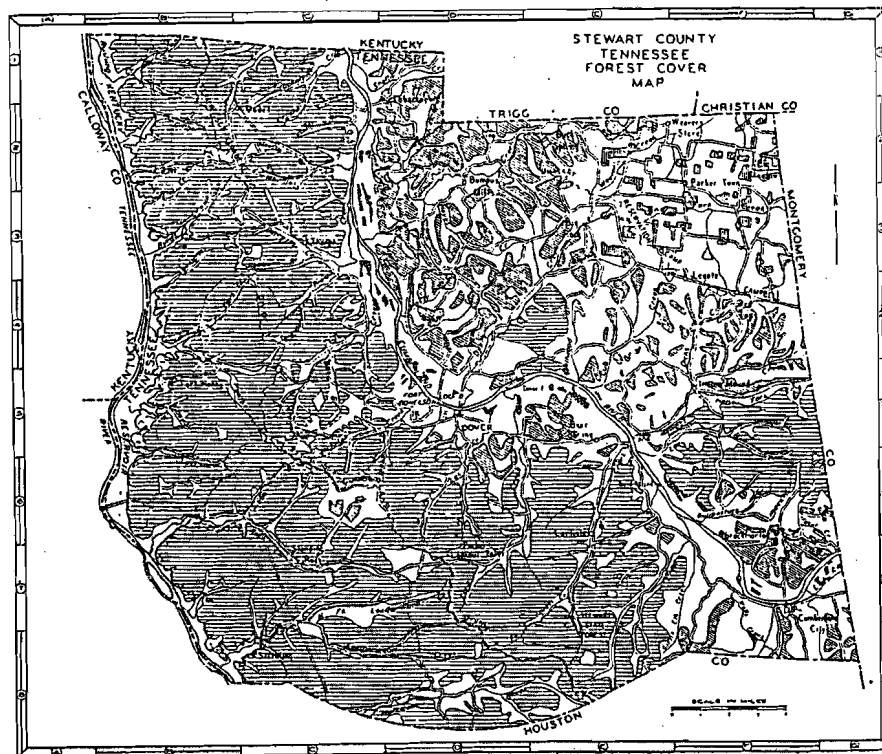


FIGURE 5.—Forest cover of Stewart County, Tenn.: (1) Hard wood forest, (2) pine-hardwood forest, (3) hardwood woodland, (4) river-bottom forest, (5) wet upland forest, (6) cleared land.



Map 3.⁹

2000 acres were acquired for a Tennessee River landing on Byrd Creek, and Cumberland access down Barrett Creek. Very little of these extensive lands were ever used to make charcoal (see Table 1). Indeed, the 2215 tons noted in the sources probably represent the lifetime production of the furnace, which may have been in blast no more than 46 weeks. In 1934, the Tennessee State Geologist, Ernest Burchard, judged from the quantity of slag in the vicinity of the ruins "that it does not appear to have a very large production of iron," possibly because "there was not a very abundant supply of iron ore in the immediate vicinity, as the only evidence of mining now visible consists of a few small pits on the neighboring hills." He mentioned reports of hauling ore from more distant points such as the Iron Valley portion of Byrd Creek and just west of Tip Top near the lower reaches of Bear Creek.¹¹

Besides poor sources of ore, Iron Mountain was also plagued by inadequate finances as indicated by changes among the partners owning both that furnace and Great Western. Given these difficulties, Iron Mountain went out of blast permanently even before the inflation of labor costs, the slave insurrection panic of 1856, and the economic depression which began in 1857. In its short, troubled history Iron Mountain Furnace made little impact on the surrounding forest. In 1859 the owners sold off much of the land, retaining one acre on the Cumberland as a landing in case of future development. There was an attempt after the Civil War to revive the furnace, but there is no evidence that it was ever again in blast.¹²

Table 1. Estimates of LBL iron furnace wood usage in acres per year, 1843-1912.

| County | Furnace | Maximum years of operation | No. of years | At 200 acres | At 300 acres | At 500 acres | |
|---------|---------------|----------------------------|--------------|--------------|--------------|--------------|------|
| Stewart | Peytona | 1847-62 | 16 | 3200 | 4800 | | |
| | Iron Mountain | 1854-55 | 2 | 400 | 600 | | |
| | Great Western | 1854-56 | 3 | 600 | 900 | | |
| Trigg | Empire | 1843-62 | 20 | 4000 | 6000 | | |
| | | Center | 1852-65 | 14 | 2800 | 4200 | |
| | | | 1879-83 | 5 | | | 2500 |
| | 1903-12 | | 10 | | | 5000 | |
| | Laura | 1855-65 | 11 | 2200 | 3300 | | |
| | | 1871-72 | 2 | | | 1000 | |
| Lyon | Fulton | 1845-62 | 18 | 3600 | 5400 | | |
| | | Mammoth | 1845-65 | 21 | 4200 | 6300 | |
| | | | 1874-78 | 5 | | | 2500 |

Hannible Allen Tharpe of Henry County, Tennessee, who bought 600 acres around the abandoned Iron Mountain furnace, may have been involved in this futile attempt to reopen the furnace. In any case, he started a store around which a small town grew after the war. By 1883, when a post office was opened in the community then officially called "Tharpe," there were saw and grist mills, a cotton gin, two churches, and a secondary school. Besides agricultural expansion, Tharpe's economy rested on the fact that the Cincinnati Cooperage Company purchased most of the old furnace lands after 1875 and "employed many people" in making barrels and tubs. J. B. Killebrew, writing of Stewart County in the early 1870s, observed that "Working in timber is the occupation of a large proportion of the people. The wood-choppers, stave-makers, sawyers, and shingle-makers are especially numerous between the rivers." Around the turn of the century railroad crossties replaced coopering, as the Ayer and Lord Tie Company and the Bartie Tie Company acquired the cooperage firm's holdings. By 1915 Tharpe still sported a grist mill, flour mill, planing mill, blacksmith's shop, tobacco prizing plant, and four retail stores, together with its school and churches. However, the farming and timbering expansion did not last through the 1920s. By 1952 there was but one store remaining.¹³

The forests around Tharpe and the Barrett Creek region were most affected by cutting for farming and in various timber industries from 1870 to 1925. The Stewart County "Forest Cover Map" of the 1940s shows "cleared land" all along the creek and some other points near roads and Cumberland River bottoms (see Map 3). Yet most of the region remained "hardwood forest," probably a young one growing up on abandoned farms and old timbering sites.

Great Western Furnace. The history of the Great Western Furnace closely parallels that of Iron Mountain. Experiencing one more blast cycle than its companion, this furnace required a maximum of 600 to 900 acres of timber for its charcoal production during its lifetime. It too then became the site of a farming and timbering community, Model, whose subsequent impact on the surrounding forests was much greater than the furnace's. Because of its excellent construction of local limestone and its brief career, the ruins of the Great Western Furnace are among the best preserved of any in the region. Long used as a landmark, even appearing on Union military maps, the site is currently listed on the National Register of Historic Places.¹⁴

After 1875 the furnace site on Prior Creek was purchased, as were the Iron Mountain lands, by the Cincinnati Cooperage Company which sought to create a "model town" as a real estate operation, thus giving the community its name. The utopian project failed but the village persisted. In 1887, when a post office was opened, the village contained two stores, a doctor, and a flour mill. There were plans to begin a sawmill. At least one lumber company was operating in Model during the 1910s. By 1920 there were some 500 people living in the town and another 500 in the district around it. From that date, as in other places in Stewart County, the population began to decline, according to one local historian, "as the supply of timber diminished and good land was made less productive by bad usage." By 1952 there were but 250 inhabitants in Model.¹⁵

Trigg County, Kentucky

The iron industry's impact on the forests of the Trigg County portion of LBL was more extensive than in the Stewart County region. Trigg County is the site of both the first furnace constructed in LBL (Empire), and the last one to cease production (Center).

During the 1830s and 1840s in southwestern Kentucky, as in the Western Highland Rim of Tennessee, there was a spate of iron furnace construction. Indeed, as early as 1815 there were several small operations around Eddyville, which are usually associated with Matthew Lyon, a prominent politician and entrepreneur. In the 1840s this manufacturing spread west across the Cumberland River into the LBL region. The Empire Furnace of Trigg and the Fulton and Mammoth Furnaces of what became Lyon County were founded before 1846, one year prior to the opening of Peytona in Stewart County.¹⁶

Empire Furnace. In 1843 Empire Furnace was the first of the LBL furnaces to begin production. It was located on the west bank of the Cumberland River opposite Rockcastle. For its "coalings," Thomas Tennessee Watson purchased in 1841 a large block of land centering on Ferguson Spring. The block reached west to the Tennessee River, south toward Golden Pond, and north beyond the Lyon County line. David Hillman bought a half interest in 1842 and became sole owner upon Watson's death in 1844. Hillman was the main developer not only of

Empire, but also of Center and Fulton Furnaces. Gradually his holdings evolved into the Hillman Land and Iron Company which dominated the Kentucky portions of what is now LBL into the 1930s.¹⁷

During the 1850s, Empire Furnace seems to have been one of the most productive in the area in terms of total tonnage, but among the least efficient in terms of tons per day in blast (see Tables 2 and 3). In 1852, 60 whites and 75 blacks labored to produce 1700 tons of pig iron. The total capital investment was estimated in that year as \$60,000. By the end of the decade however, Hillman appears to have been shifting Empire's labor force and other assets to the Center Furnace, which first went into blast in 1852. The Empire Furnace was finally abandoned in 1861-62.¹⁸

Table 2. Documented iron tonnage production, time in blast, with acres per ton estimate.

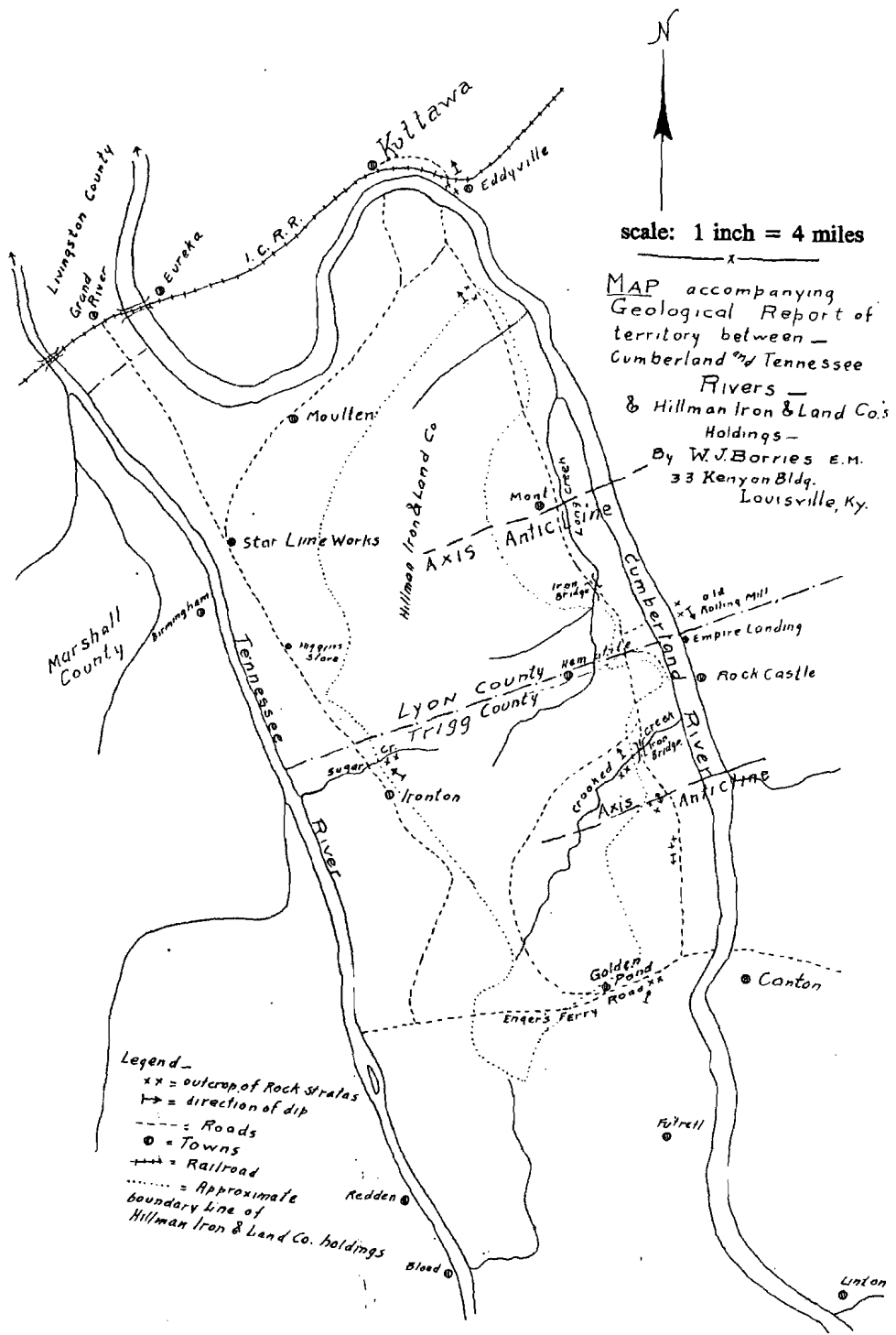
| County | Furnace | Year | Tons | Known time in blast | Acres used by 5-10 tons to acre estimate |
|---------|---------------|------|------|---------------------|--|
| Stewart | Peytona | 1850 | 1700 | | 170-340 |
| | | 1852 | 1800 | 7 months | 180-360 |
| | | 1854 | 1220 | | 122-244 |
| | | 1857 | 1812 | | 181-362 |
| | Iron Mountain | 1854 | 1015 | 4 months | 102-204 |
| | | 1855 | 1200 | 30 weeks | 120-240 |
| | Great Western | 1855 | 1350 | 34 weeks | 135-270 |
| Trigg | Empire | 1852 | 1700 | | 170-340 |
| | | 1856 | 1836 | 45 weeks | 184-368 |
| | Center | 1856 | 2140 | 46 weeks | 214-428 |
| | Laura | 1857 | 1638 | 44 weeks | 164-328 |
| Lyon | Fulton | 1852 | 1600 | | 160-320 |
| | | 1857 | 1044 | 22 weeks | 104-208 |
| | Mammoth | 1852 | 1800 | | 180-360 |
| | | 1857 | 1514 | 48 weeks | 151-302 |

Table 3. Acreage and tonnage per day estimates for documented years, 1850s.

| Furnace | Year | Tons | Tons per acre estimate | Acre a day estimate | Tonnage per day |
|---------------|------|------|------------------------|---------------------|-----------------|
| Peytona | 1852 | 1800 | 180-360 | 180 | 10.1 |
| Iron Mountain | 1854 | 1015 | 102-204 | 116 | 10.4 |
| | 1855 | 1200 | 120-240 | 180 | 6.6 |
| Great Western | 1855 | 1350 | 135-270 | 204 | 6.1 |
| Empire | 1856 | 1836 | 184-368 | 270 | 6.8 |
| Center | 1856 | 2140 | 214-428 | 276 | 7.7 |
| Laura | 1857 | 1638 | 164-328 | 264 | 6.2 |
| Fulton | 1857 | 1044 | 104-208 | 132 | 7.2 |
| Mammoth | 1857 | 1514 | 151-302 | 288 | 5.2 |

During its 20-year career, the Empire Furnace would have required a maximum of 4000 to 6000 acres of woodlands (probably less considering its gradually diminishing production late in the 1850s). These cuttings would have been along the river bottoms and immediate slopes now beneath Lake Barkley. One reason for the transfer away from Empire may have been that the timbering created land more valuable for agriculture than for "coalings." Hillman may have held the Empire lands for speculation and then sold them off. Detailed investigation of Trigg County land records might confirm this hypothesis. In any case, a 1935 map of the Hillman Land and Iron Company's landholdings (see Map 4)¹⁹ indicates that the company by that time had sold off most of its bottomlands.

Center Furnace. Center Furnace, 2.5 miles west of the Empire site, was near the current Woodlands Nature Center above Honker Lake. It was the jewel of the Hillman iron holdings, experiencing three periods of operation: 1852-1865, 1879-1883, and 1903-1912. Judging from admittedly sporadic evidence, Center was apparently the most productive furnace in the LBL region during the 1850s and among the most efficient (see Tables 2 and 3). In 1879 the ore associated with Center was assayed at 49.8 percent pure iron, unusually high for the area. To service the furnace Daniel Hillman even acquired a railroad right of way running by Crooked Creek to what is now Boardinghouse Hollow. He agreed to fence the route on both



Map 4.

sides, presumably to keep out roving cattle and wild animals. The railroad may have been operational before the Civil War.²⁰

After closing down near or at the end of the war, Center was re-opened by Arthur Hillman from 1879 to 1883. The depression of the mid-1880s, and competition, then forced another closure. Some 20 years later the firm of White and Dixon of Pittsburgh leased the furnace and its lands from the Hillman Land and Iron Company and resumed production in either 1903 or 1905, depending on the source. This last period of Center's career is the best documented. The whole operation at its peak--mining, "coaling," and manufacturing iron--required some 250 to 300 men. But occasionally the labor force was down to just over 100. Recruiting, housing, and paying an adequate labor supply was a perennial problem. About half the workers were black, as was the case before 1865, only now of course they were at least nominally free. Reportedly, even Chinese laborers were brought to the furnace. In any case, the company, as was common at the time, paid minimal wages, usually in silver. Occasionally during hard times payment was in script. Strong efforts were also made to restrict the workers' purchasing to a company store which gave liberal credit. Consequently, as one of the managers remembered, "by the end of the year, many of the men literally owed all of their salary to the company store."²¹

As with other furnaces, a small community grew up near the Center Furnace. This one was called Hematite. Besides "one large company store," there were "several boarding houses and flimsy, boxy homes for the Negro and white families who lived on money paid out by the operations" of Center. The buildings were strung along the road leading from the old Empire Furnace site "and up a sharp hill past Center Furnace." At the base of the hill were the houses of clerical workers and managers while the store was on the crest behind the furnaces. The pig iron was transported down the road to the landing and there loaded onto a large barge which for some of these years was regularly pushed to Kuttawa, Kentucky, by the steamboat "Anna Moriah." When Center Furnace closed permanently, the town of Hematite disappeared, leaving its name on a church on Taylor Creek located south of the original town.²²

Center Furnace was in blast for parts of 29 years over a 60-year period. To support its entire operation, it would have required a maximum of 10 300 to 11 700 acres of timber. However, given the fact that there were 14 years between the first and second periods of production and at least 20 between the second and third, much of the same acreage could have been cut over twice, making the impact more intensive perhaps, but less extensive than these raw numbers imply. Nonetheless, John Esslyton's description quoted earlier of "vast areas...denuded of all timber, burned over, and...since grown up with worthless bush" probably applied to the lands around Center Furnace in the early 1920s.

Laura Furnace. Laura Furnace, some two miles west of the Cumberland River up Laura Furnace Creek, was built in 1855, making it the last furnace to be constructed in the LBL region. The owners were the firm of Gentry, Gunn, and Company of Tennessee whose investment in the operation in that year was some \$40,000, a third less than the Hillman investment in the Empire operation to the north. This furnace required some 120 to 130 men who worked profitably until the financial panic of 1857. A new owner, George P. Wilcox, ran the faltering furnace until 1860-61 when he sold to a set of proprietors who attempted to keep the business going during the war. They in turn were bankrupted. In 1871 Pringle and

Company of Pittsburgh returned Laura to blast briefly, but ultimately failed. Subsequent sets of owners also proved unable to make the furnace economically viable.²³

Laura Furnace in its sporadic 13-year career used a maximum of 3200 to 4300 acres for charcoal. Given its inadequate finances, and uncertainty in the evidence as to whether it was actually in blast during all the years Wilcox and his immediate successors owned the furnace to 1865, these estimates of timber usage are generous.

Lyon County, Kentucky

Fulton Furnace. Fulton Furnace, some three miles north of Empire near what is now Fulton Bay, was begun in 1845 by Watson and Hillman and became part of the Hillman holdings. In 1852 Fulton employed 50 whites and 70 blacks in producing 1600 tons of iron, making it a slightly smaller operation than Empire, at least in that year. Its capital investment was put at \$40,000. Hillman's treatment of Fulton appears to have paralleled that of Empire Furnace. In 1857 Fulton was in blast for only 22 weeks and by 1862 it was abandoned. By the most generous estimate, Fulton Furnace would have run through 18 blast cycles and used 3600 to 5400 acres of woodland, most of it probably in bottomlands now underwater.²⁴

Mammoth Furnace. Mammoth Furnace, constructed in 1845 by Charles Stacker on what is now the north shore of Mammoth Furnace Bay opposite Hurricane Creek, deserved its name. In 1852 it represented an investment of \$75,000, by far the largest in the area to that date, and had a labor force of 60 whites and 85 blacks. That year it produced 1800 tons, a capacity matched only by Peytona Furnace in that and prior years. This productivity was surpassed later by Peytona, Empire, and Center Furnaces (see Table 2). Perhaps it was competition from Mammoth which helped encourage Hillman to found Center Furnace and then concentrate his assets on its development.²⁵

Unfortunately, little is known of this important operation. Even its years in blast after 1857 and before 1874 are conjectural. However, its possible 26 years in production make it the most credible competitor with Center Furnace for longevity and seriousness of impact on the forests of LBL. Also, if the 1865 end date of its first period of operation is correct, then there was only a nine year hiatus in its career from 1845-1878, suggesting that its effect on woodlands was about as extensive as the estimates of 6700 to 8800 acres imply. These cuttings probably were around Hurricane and Mammoth Furnace Creeks, concentrated on slopes generally west of the furnace site.

Estimates of Wood Usage

As noted, estimates of timber usage in the iron industry are usually expressed in terms of acres per year per furnace. These estimates for the Western Highland Rim furnaces range from 200 to 500 acres.²⁶ This broad range was refined by noting that the higher calculations derive from the period after the Civil War when much of the acreage being exploited had been cut over at least once. For instance, one 500-acre estimate comes from the experience of Center Furnace in the Trigg County portion of LBL during the era 1905-1912 when the policy was, according to its manager, to make charcoal of "scrub oak, black jack, and other small trees that

wouldn't be suitable for cross-ties.²⁷ Even if we restrict this high figure to the years 1865 to 1912, we may be exaggerating if other furnaces followed a different policy toward large trees or had better timber resources. That seems to have been the case, for instance, with the LaGrange Iron Works south of LBL which reported owning 40 000 acres of forest in the early 1870s. Each acre yielded, the company stated, 40-50 cords of wood, and the furnace used 10 000 cords per year. At that rate, the furnace's maximum cutting for charcoal must have been around 250 acres a year. Nonetheless, 500 acres per year per furnace seems a reasonable maximum estimate and is the one which Joseph B. Killebrew himself, who quoted the LaGrange figures, adopted as a maximum in his *Introduction to the Resources of Tennessee* in 1874.²⁸ For the earlier period, 1843-1865, the standard estimates, as cited in endnote 25, are 200 to 300 acres.

The next problem is establishing each furnace's years of operation. The furnaces operated sporadically, and information about them is incomplete. Thus I estimated the timing of production, just as I did the timber usage rates. Fortunately, virtually all available data on the furnaces of the Stewart County portion of LBL have been compiled by the Tennessee Division of Archeology and were published in 1988. For the Kentucky furnaces evidence is less reliable or complete, depending on the furnace.²⁹ For the purposes of this study, longer periods of operation are assumed whenever there is doubt, so as to derive maximum estimates of wood usage. The result of these calculations are reported in Table 1.

The validity of these estimates was tested by calculating how much wood was required to make a ton of iron and comparing this with the production of each furnace. Here too the evidence is sparse, but corroborative.³⁰ All of the readily available production figures for LBL furnaces come from the 1850s. On occasion these sources include not only annual production but also the "time in blast," meaning the number of weeks or months of the stated year in which the furnace was actually producing iron. These results are summarized in Table 2.

Also in Table 2 are estimates of tons of iron produced per acre of timber cut based on calculations of bushels of charcoal to cords of wood to cords per acre observations. Important variables are involved in such calculations. For instance, the number of bushels of charcoal produced per cord of wood varied according to the quality of the wood and the skill of the colliers. The number of cords per acre varied according to the quality of the forests and the degree of clear, as opposed to selective, cutting. Hence these estimates are stated as a range which turns out to be roughly five to ten tons of pig iron per acre.³¹ The calculations in Table 2 indicate that the overall estimates of wood usage in Table 1 are reasonable.

Additional evidence of the validity of my estimates is provided by assuming one acre per day during blast, (this figure is derived from sources independent of those used in Table 1). Because the blast cycle for a fully functional furnace lasted from 192 to 264 days (8-11 months of 6-day weeks), that assumption results in an estimate that agrees generally with the data in Tables 1 and 2.³² Moreover, this acre-a-day standard permits more precise estimates of the industry's impact during those years in which the actual time in blast is known. For instance, Iron Mountain's short career, with only 11 months in blast, probably involved less forest acreage (264 acres, calculated as above), than the 400 acre minimum suggested in Table 1, and closer to the 220 acre minimum indicated in Table 2. Similarly, this acre-a-day estimate indicates that the lower end of the scale on Table 2 is more apt to be correct in the case of Peytona in 1852.

Table 3 provides comparisons of these figures, plus a tonnage per day calculation which indicates each furnace's productivity during that documented blast cycle.

The medians for the low and high estimates of the annual tons per acre figures for the several furnaces are, respectively, 151 and 302 (Table 3). The average by this method is 150-301 tons per acre. By the acre-a-day annual measure, the median is 204 and the average 212 acres. These numbers suggest that for the period 1843 to 1865, wood usage per furnace per year in the LBL region was closer to 200 acres than to 300. However, considering the paucity and sporadicity of this data, and the fact that the furnaces used wood for construction and for fuel other than charcoal, it seems prudent to remain with the broad 200 to 300 acre estimate for that period and with the 500 acre a year estimate for the later era.

Summary of Overall Impact

If the estimates in Table 1 are reasonably accurate, some conclusions about the nature and timing of timber usage in the LBL iron industry are possible. First, the greatest impact on the region's forests occurred in the period before 1865. In those years between 21 000 and 31 500 acres were cut for charcoal, compared to some 11 000 acres after that date. Iron production and timber cutting peaked in the early 1850s, prior to the financial Panic of 1857. From that date to the outbreak of the Civil War the furnaces probably operated even more sporadically than before. After 1862 the iron industry in the Stewart County area of LBL ceased entirely, while the furnaces of the Kentucky portion were only occasionally in blast. Thus, extending the 200-300 acre per year per furnace estimate into the period 1857-1865 is probably generous, but advisable given the paucity of data for these years, and my goal of establishing a reasonable estimate of maximum plausible impact on the area's forests.

Another point is geographic. Using the 170 000 acre measurement for LBL as a whole--a conservative estimate for the region before the impoundment of the rivers--the 21 000 to 31 500 acres of forest cut before 1865 represent between 12 and 16 percent of the area's timber. The 11 000 acres cut after that year was about six percent of the land area. The impact was not uniform over the whole region, the industry's influence being much greater on the Kentucky forests of LBL than on Tennessee's Stewart County. In the Trigg County region I estimate that 9000 to 10 500 acres were cut for charcoal by 1865, and an additional 8500 acres were cut later. For Lyon, some 7800 to 11 700 acres of forest were used in the earlier period and about 2500 after 1865. In contrast, the Stewart County portion of LBL supplied around 4200 to 6300 acres of "coalings" to 1862, and none thereafter.

CONCLUSION

The maximum acreage of timber cut for the iron industry in the LBL region before 1865 is estimated at 21 000 to 31 500 acres, or 12 to 19 percent of the land area. Less than half that acreage is estimated to have been cut after 1865. Some cut over lands, particularly parts of those associated with Fulton and Empire furnaces, are now under Lake Barkley. The cutting was much greater in the Kentucky than in the Tennessee portions of LBL.

ENDNOTES

1. The author wishes to acknowledge gratefully the research assistance of Timothy Mohon, an APSU history major, as well as the advice of Professors Wayne Chester, David Snyder, and Thomas H. Winn. This work has been supported by the Center for Field Biology, APSU.
2. J. B. Killebrew, *Introduction to the Resources of Tennessee* (Nashville, 1874), p. 242; Stephen V. Ash, *Tennessee's Iron Industry Revisited: the Stewart County Story* (TVA, undated pamphlet), p. 38.
3. The standard crosstie measure was 8 ft. x 8 ins. x 6 ins. File 283, pp. 1-3, and file 286, pp. 10-11, Hillman Papers, J. Milton Henry Collection, Woodward Library, Austin Peay State University.
4. G. B. Shivery, "Forests," in M. E. Austin et al., *Soil Survey: Stewart County, Tennessee* (USDA, Series 1942, No. 3, 1953), pp. 197-98; James S. Fralish and Fred B. Cooke, "Forest Communities of the Kentucky Portion of Land Between the Lakes: A Preliminary Assessment," in David H. Snyder, ed., *Proceedings of the First Annual Symposium: The Natural History of the Lower Tennessee and Cumberland River Valleys* (Clarksville, Tn., 1988), p. 173, hereafter Snyder, *Proceedings*.
5. Burchard, *Brown Iron Ores*, pp. 31, 220; Killebrew, *Introduction to the Resources*, p. 238; Smith et al., *A Cultural Resource Survey*, pp. 47, 59.
6. Iris Hopkins McClain, "A History of Stewart County, Tennessee" (Typescript, Tennesseana Room, Woodward Library, APSU, 1965), p. 26; Burchard, *Brown Iron Ores*, pp. 41-42; Stewart County Historical Society, *Stewart County Heritage* (Dover, Tenn., 1980), p. 13; *Biographical Directory of the U.S. Congress: 1774-1989* (Washington, DC, 1989), pp. 1639-40.
7. Smith et al., *A Cultural Resource Survey*, pp. 104, 185; *Land Between the Rivers*, p. 44.
8. Ash, *Tennessee's Iron Industry*, p. 13; Henry, *Land Between the Rivers*, p. 44; *War of the Rebellion: A Compilation of the Official Records of the Union and Confederate Armies* (70 volumes in 128 parts, Washington, DC, 1880-1901), S1, VII, 161-62; Thomas Yoseloff, ed., *The Official Atlas of the Civil War* (New York, 1958), plate XI, maps 2, 3, 5. This evidence contradicts Jackie S. Carpenter and Edward W. Chester, "A Floristic and Vegetation Characterization of the Bear Creek Natural Area, Stewart County, Tennessee" in Snyder, ed., *Proceedings*, pp. 225-26.
9. Henry, *Land Between the Rivers*, p. 45; Killebrew, *Introduction to the Resources*, p. 934; Carpenter and Chester, "A Floristic and Vegetation Characterization," p. 225; Austin et al., *Soil Survey*, p. 199.
10. *Stewart County Heritage*, p. 13; Smith et al., *Cultural Resource Survey*, p. 37. Dickson County experienced an even more extreme boom, expanding from two furnaces in 1850 to six in 1854 and then down to only one in 1860.
11. Henry, *Land Between the Rivers*, p. 45; Burchard, *Brown Iron Ores*, pp. 39-40.
12. Smith et al., *Cultural Resource Survey*, pp. 44, 108-109.
13. *Stewart County Heritage*, p. 48; Newell A. Link, "An Inquiry into the Early County Court Records of Stewart County, Tennessee," (MA thesis, MTSU, 1952), p. 20; Killebrew, *Introduction to the Resources*, p. 933.

14. Henry, *Land Between the Rivers*, p. 45; Burchard, *Brown Iron Ores*, pp. 12, 39; Smith et al., *Cultural Resource Survey*, pp. 111, 184.
15. Link, "An Inquiry," pp. 15-16 (quote is p. 16): *Stewart County Heritage*, p. 48; Iris Hopkins McClain, "A History of Stewart County, Tennessee," (typescript, Tennesseeana Room, APSU library, 1965), p. 18.
16. J. Winston Coleman, "Old Kentucky Iron Furnaces," *Filson Club Quarterly* 31(1957), 238-39.
17. "Henry Research Correspondence I" file, J. Milton Henry Collection, APSU library.
18. Henry, *Land Between the Rivers*, pp. 40-41; Smith et al., *Cultural Resource Survey*, p. 185.
19. File 101, Hillman Papers, J. Milton Henry Collection, Woodward Library, Austin Peay State University.
20. Henry, *Land Between the Rivers*, p. 43; Stilgoe, *Common Language*, pp. 188-92 on fencing practices; TVA, *Iron Industry*, p. 2; N. S. Shaler, "The Limestone Area of Trigg, Lyon, and Caldwell Counties, known as 'Cumberland River Ores'," *Geological Society of Kentucky* 5(1880), 255-64.
21. Henry, *Land Between the Rivers*, pp. 55-57; TVA, *Iron Industry*, pp. 2-3; J. B. Gray, "Operation of Center Furnace (1905-1912)," p. 4 for quote; Interview with Marshall Major, 1966, in "Center Furnace" file, J. Milton Henry Collection, APSU library.
22. Paducah *Sun-Democrat*, 16 August 1959, B1; Louisville *Courier-Journal*, 9 January 1966, D5.
23. Henry, *Land Between the Rivers*, pp. 46-47; "Henry Research Correspondence I" file, J. Milton Henry Collection, APSU library.
24. Smith et al., *Cultural Resource Survey*, p. 185; Henry, *Land Between the Rivers*, p. 41; TVA, *Iron Industry*, p. 2.
25. Smith et al., *Cultural Resource Survey*, p. 185; Henry, *Land Between the Rivers*, p. 43.
26. Killebrew, *Introduction to the Resources*, p. 930; J. Milton Henry, *Land Between The Rivers* (Dallas, 1976), p. 75; Ash, *Tennessee's Iron Industry*, p. 22; establish the range.
27. J. B. Gray, "Operation of the Center Furnace (1905-1912)," p. 2, in Center Furnace file, J. Milton Henry Collection, APSU; Ash, *Tennessee's Iron Industry*, p. 22, too readily applies this high estimate to the whole history of the industry in the region.
28. Killebrew, *Introduction to the Resources*, pp. 242, 930.
29. For the longevity of Tennessee furnaces, see Smith et al., *A Cultural Resource Survey*, esp. pp. 49, 59. For Kentucky furnaces, see Tennessee Valley Authority, *The Iron Industry in the Land Between the Lakes* (1968), p. 2; Henry, *Land Between the Rivers*, pp. 40-41, 55-57; "Henry Research Correspondence I" file, J. Milton Henry Collection, APSU.
30. The figures here and in Table II are derived from Henry, *Land Between the Rivers*, pp. 40-45; Samuel D. Smith et al., *A Cultural Resource Survey of Tennessee's Western Highland Rim Iron Industry, 1790s-1930s* (Nashville, 1988), pp. 13, 104, 108-109, 185; Ernest F. Burchard, *The Brown Iron Ores of the Western Highland Rim, Tennessee* (Nashville, 1934), p. 223.

31. The formula used, 1 ton of iron = 160 to 200 bushels of charcoal = 4 to 8 cords wood = 1/10 to 1/5 an acre, was derived from Killebrew, *Introduction to the Resources*, pp. 237-42 and 930; Ash, *Tennessee's Iron Industry*, p. 22; Stilgoe, *Common Landscape*, p. 293; TVA, *Iron Industry*, p. 9; Smith et al., *Cultural Resource*, p. 13; John R. Stilgre, *Common Landscape of America, 1580-1845* (New Haven, 1982), p. 293.
32. Smith et al., *A Cultural Resource Survey*, p. 13.

A PRELIMINARY ECOLOGICAL LAND CLASSIFICATION SYSTEM FOR LAND BETWEEN THE LAKES

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ABSTRACT. Tree, shrub, and herb data from 135 stands at Land Between The Lakes were analyzed using clustering program COMPAH. Community groups were further divided using bedrock, soil, and topographic characteristics. *Quercus prinus* and *Q. stellata* were separated from other types by the presence of *Vaccinium arboreum* and other Ericaceous species. These two community types were separated on the basis of soil characteristics.

Cornus florida was the common mid-canopy tree in stands dominated by other tree species. Stands of compositionally stable *Quercus alba* were separated from successional stands of *Q. alba*, and compositionally stable stands of *Fagus grandifolia* and *Acer saccharum* by *Asimina triloba*, *Lindera benzoin*, or *Polystichum acrostichoides* which appeared in the latter. Specific site characteristics were associated with each ecological type.

Refinement of the system is continuing with field reconnaissance and incorporation of additional herbaceous and mid-canopy woody species as well as soil and topographic conditions. A vegetation map of Blockhouse Creek watershed and surrounding area has been generated using information on bedrock, soil, and topography in combination with research data on successional and compositionally stable forest communities. This research was supported by The Center for Field Biology, Austin Peay State University, Clarksville, Tennessee, and the Departments of Forestry and Geography, Southern Illinois University, Carbondale.

DECOMPOSITION OF PARTICULATE SUBSTRATES IN PERENNIAL STREAMS OF LAND BETWEEN THE LAKES

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ABSTRACT. Measurement of mass loss over time and qualitative examination (e.g., organic content, aquatic fungi composition, and C-N) of particles of known size range and derived from known sources form the basis for decomposition studies in perennial streams of Land Between The Lakes. Processing rates are being determined using coarse and fine particulates derived from tree species with simple leaves (i.e., sugar maple, sycamore, and white oak) typical of Land Between The Lakes riparian vegetation. Studies begun in fall 1989 address three major areas:

1. relative degree of impact on decomposition processes of replacement of sugar maple by white oak on disturbed riparian sites located within the boundaries of Land Between The Lakes (specifically Crockett Creek, Lost Creek, South Fork Panther Creek, and Prior Creek);
2. comparative decomposition of sugar maple, sycamore, and white oak in Lost Creek and Lost Creek Spring; and
3. relative influence of channel interstitial areas on decomposition processes in Lost Creek Spring and South Fork Panther Creek Spring.

Preliminary results of these studies will be presented along with recommendations for ongoing research efforts in highly variable lotic systems of Land Between The Lakes.

DESIGNING A BIOSPHERE RESERVE AREA AT LAND BETWEEN THE LAKES AS HABITAT FOR A MATURE FOREST SPECIES USING A SPATIAL DECISION SUPPORT SYSTEM

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ABSTRACT. We explored the design of a 44 km² Biosphere Reserve area at Land Between The Lakes as habitat for a mature forest species, the Pileated Woodpecker (*Dryocopus pileatus*). The purpose of the analysis was to develop a dynamic planning tool to determine the size and location of forest stands in the buffer zone that surrounds the core area of a Biosphere Reserve in order to meet specific ecologic criteria (e.g., population size, or total area of habitat) for successive 20-year planning periods. A habitat suitability index model for the Pileated Woodpecker developed by the U. S. Fish and Wildlife Service was modified to be consistent with the forest stand data generated by TWIGS, a forest stand simulator developed by the U. S. Forest Service, in order to evaluate how the habitat suitability of the forest stands in the core area and buffer zone change through time. These were combined with a Geographic Information System (pc-ARC/INFO) using Structured Query Language to create an interactive Spatial Decision Support System for designing the buffer zone under specific objective functions. The objective in this analysis was to maintain approximately 50 percent of the area in the Biosphere Reserve as optimal habitat for Pileated Woodpeckers. The stands in the core area and buffer zone were updated at 20-year intervals for a 60-year period (1990-2050). In 1990, only 2.5 percent of the combined core area and buffer zone was Class 1 habitat. This increased to nearly 80 percent of the area by 2050 if no timber harvesting took place. Thus, given the objective to develop and maintain 50 percent of the area in Class 1 habitat, timber harvesting would be allowed at the periphery of the buffer zone toward the end of the planning period. We conclude that buffer zone design: (1) requires explicit and specific management goals; (2) is an ongoing process since the roles played by the core area and buffer zone in meeting a specified management goal change through time.

INTRODUCTION

The area surrounding an existing or proposed nature preserve, e.g., Biosphere Reserve, may be the locale for intensive competition among alternative land uses. If the size and quality of the nature preserve are such that it is self-sufficient in meeting its specified objectives, this may be of little consequence, but most nature preserves must be supplemented by the surrounding landscape to maintain their biologic integrity. This interaction between a nature preserve and its surroundings is frequently viewed as a circular core area (the preserve devoted exclusively to meet an ecologic objective) surrounded by a donut-shaped buffer zone which may be put to multiple uses. Given the contentions that may arise over allocation of portions of a buffer zone to different land uses, there is a need to seek efficient allocation of resources to the several uses. Three issues arise, then: 1) What areas outside the core area are needed as a buffer zone to supplement the habitat within the preserve boundary? 2) How can land use

outside and adjacent to a preserve be adjusted to assure that it will be compatible with its objectives, while allowing for other land uses, including perhaps economic activity? 3) How does the area needed for a buffer zone change through time?

Models have been developed to deal with this "buffer zone" design problem. Newmark (1985) developed a boundary model based on the minimum viable population (MVP) for a species, and proposed that a "biotic boundary" that is outside the legal boundary of a natural area would demarcate the area needed to maintain existing ecological processes and a given assemblage of species. Practically, the biotic boundary was extended to include entire watersheds, and was not considered to change through time. By contrast, Schonewald-Cox and Bayless (1986) proposed to account for the interplay of biologic and economic needs in the landscape outside a preserve, and the ways they change through time. However, a practical means is needed to implement the concept of a dynamic buffer zone, to optimize land use within the buffer zone, and to assess how the need for a buffer zone changes through time.

The purpose of the research reported in this paper is to develop a Spatial Decision Support System (SDSS) that will facilitate buffer zone design, using a Geographic Information System (GIS) and supplemental programs to be described below. The data base for the SDSS is based on an area in Land Between The Lakes (LBL). Since the habitat requirements of particular species dictate the adequacy of core areas and the need for additional buffer zone area, we have developed the SDSS with one species in mind--the Pileated Woodpecker, *Dryocopus pileatus*, which favors mature forest. While this choice of species is arbitrary, and a number of other species might have been chosen, the Pileated Woodpecker is representative of species that require large blocks of mature timber, and provides a good test of the SDSS.

LOCATION OF STUDY

The SDSS was developed to analyze how land use within and external to a proposed Biosphere Reserve core area in LBL could be coordinated to meet multiple land use needs. Land Between The Lakes is administered by the Tennessee Valley Authority for a variety of goods and services. LBL is designated as a National Recreation Area, indicating the high priority given to recreation, including hunting. In addition, LBL is managed as wildlife habitat and for forest products. This mix of land use demands on LBL makes it necessary to coordinate land uses as much as possible, and to minimize conflicts inherent in the several uses, e.g., conflicts between timber production and development of wildlife habitat.

The study area is located on the Rushing Creek, Ky.-Tenn. 7.5 minute quadrangle map. The proposed Biosphere Reserve core area is designated by TVA as Working Area 39. It is bounded by Kentucky Lake on the southwest, and by four other Working Areas (38, 40, 41, and 44) that encircle it on the landward side. Working Areas 38, 40, 41, and 44 are considered in this analysis to be available as buffer zone to the extent needed. The total area of the core area and buffer zone is 44 km². Though mostly in the Tennessee River drainage, the study area does extend across the divide to the Cumberland River drainage.

Each Working Area is divided into a number of forest stands, each 10-50 ha in size. There are 385 stands in the study area.

METHODS

Designing the buffer zone involves selecting stands in Working Areas 38, 40, 41, and 44 (the buffer zone Working Areas) that meet site and locational criteria based on requirements (or preferences) of both Pileated Woodpeckers and management objectives. If more stands meet the site and locational criteria than are needed to satisfy the management objectives--which we have set as 50 percent of the area as Class 1 habitat for Pileated Woodpeckers--stands are selected by locational criteria (in this case by distance from the boundary of Working Area 39) until the management objective is achieved. This analysis is carried out at 20-year intervals (1990, 2010, 2030, and 2050) in order to take into account changes in the habitat quality of the stands in the study area, and the identity of stands in Working Areas 38, 40, 41, and 44 needed as buffer zone. The age and size class of all stands in the study area are updated, related to site and locational requirements of Pileated Woodpeckers, and specific stands in the buffer zone Working Areas are selected to comprise the updated buffer zone. This process thus calls for the following types of information:

1. The species composition and size class distribution for each stand in 1990. Field data provided by TVA were used.
2. A procedure to update the size class distribution of each stand at 20-year intervals. Stands were classified by community type and topographic position, and the stand simulator TWIGS was used to "grow" each class of stands.
3. A procedure to relate these stand characteristics to the habitat requirements of Pileated Woodpeckers. The habitat suitability index model was modified to accept data provided by TWIGS and to designate stands as Class 1 (the most suitable) through Class 4.
4. A procedure to identify locations of each stand relative to the core area and with respect to locational (as opposed to site) requirements of Pileated Woodpeckers. GIS was used for locational analysis.
5. A procedure to organize the information about stand characteristics and locations in order to select specific stands for the buffer zone at each date.

These components are organized as a Spatial Decision Support System (SDSS). The SDSS combines a Geographic Information System (pc-ARC/INFO), a timber stand simulator (TWIGS), a procedure to relate observed stand characteristics to simulated stand characteristics (Structured Query Language, SQL) and a Habitat Suitability Index (HSI) relevant to Pileated Woodpeckers. The role each of these plays in SDSS is discussed, beginning with the HSI for Pileated Woodpeckers.

Habitat Suitability Index for Pileated Woodpecker

The Pileated Woodpecker has a preferred combination of site- and landscape-level conditions for its habitat. Site requirements were organized as a Habitat Suitability Index by the U. S. Fish and Wildlife Service (Schroeder 1983). The habitat requirements as originally

specified relate to canopy closure, number of large (> 51 cm dbh) trees, number of tree stumps, total number of snags, and number of large (> 51 cm dbh) snags, and average dbh of snags and average dbh of large (> 51 cm dbh) snags. Each variable was translated into a Suitability Index with a range 0-1.0. Suitability Indexes for each variable were combined to derive an HSI, also with a range of 0-1.0. Likewise, Conner and Adkisson's (1976) discriminant function model of the stand characteristics relevant to Pileated Woodpecker nesting in West Virginia included stand basal area, stand density, and canopy height. We have translated these variables into variables that are output by TWIGS to create a modified HSI. The variables that we use are listed in Table 1. Four modified HSI classes were used, with Class 1 being optimum habitat for Pileated Woodpecker, and Class 4 being least favorable. The range of values for each modified HSI class is also specified.

Table 1. Habitat Suitability Index for Pileated Woodpecker, as originally designed by Schroeder (1983), and as modified for this study.

| <u>U.S. Fish & Wildlife Service HSI for Pileated Woodpecker (Schroeder 1983)</u> | | | | |
|--|--|-----------|-----------|---------|
| | <ol style="list-style-type: none"> 1. Percent tree canopy closure 2. Number of trees > 51 cm dbh per ha 3. Number of tree stumps > 0.32 m in height, or logs > 18 cm in diameter 4. Number of snags > 38 cm dbh per ha 5. Average dbh of snags > 38 cm dbh | | | |
| <u>Habitat Suitability Index Modified for TWIGS (present study)</u> | | | | |
| Factor | Class 1 | Class 2 | Class 3 | Class 4 |
| Basal Area m ² /ha | > 27.1 | 18.4-27.1 | 11.5-18.4 | < 11.5 |
| Tree Density > 51.8 cm, #/ha | > 5.1 | < 5.1 | < 5.1 | < 5.1 |
| Tree Density > 5.1 cm, #/ha | < 740 | < 740 | < 740 | < 740 |
| Avg. dbh all stems, cm | > 20.7 | < 20.7 | --- | --- |
| Avg. dbh > 51.8, cm | > 58.4 | < 58.4 | --- | --- |
| Snag Density #/ha | > 7.4 | < 7.4 | --- | --- |

Two spatial variables not included in prior HSI models for Pileated Woodpeckers were added using the GIS. One is distance to water. Schroeder (1983) points out that Pileated Woodpeckers generally drink before nesting for the night. Connor et al. (1975) found that Pileated Woodpeckers did not nest farther than 150 m from a water source, and most nests were within 50 m of water. Therefore stands were given a modified habitat site index on the basis of their intrinsic characteristics, as shown in Table 1, and distinguished on the basis of their distance from streams. The other variable added was distance from the boundary of Working Area 39, the proposed core area of the Biosphere Reserve. This is not relevant to HSI per se, but is a factor in determining the value of a stand for meeting the management objectives of the Biosphere Reserve.

Current Status of the Stands in the Study Area

The current vegetation of each stand in the study area was assessed using the most recent available forest inventory data from the Division of Forestry, TVA. Generally these data were based on field work conducted during 1985-1990, and thus represent current stand conditions. These data were provided on summary sheets for each stand, which show the number of stems by dbh class and species, number of dead trees (assumed to be snags), basal area of the stand, and pole timber and saw timber volumes. These data can be used to establish the current modified HSI for each stand. Also, they are the basic data needed to project stand characteristics into the future.

Modeling Stand Development

Although inventory data provide information about the current status of each stand, which can be translated into its HSI, it is necessary to predict how the HSI for each stand will change through time. TWIGS (Miner et al. 1988) was selected for this analysis. First, stands were classified into one of three community groups: successional white oak, compositionally stable white oak, and post oak-chestnut oak. This was done because it would have been prohibitive to model each of the 385 stands separately in TWIGS. These community types had been identified through cluster analysis of 135 mature stands at LBL (Franklin 1990). Further distinctions between community types were made on the basis of elevation and bedrock types (Fralish and Yang 1992). Using the location of each stand in the study area relative to the elevation and bedrock types characteristic of the three community types, each stand was assigned to one of the community types.

TWIGS (Miner et al. 1988), a growth-and-yield simulation program, was used to model stand development for each community type. The Central States variant of the model, which had been calibrated with forest inventory data from Indiana, Illinois, Missouri, and portions of Kentucky and Tennessee within LBL, was used. TWIGS can be used at two resolutions: for individual trees or for stand-level simulations; we used the latter. TWIGS operates using site index and TREEGEN, a tree list with stand level data and parameters that indicate the general shape of the diameter distribution of the stand. The TREEGEN files were created using the Weibull probability distribution function to describe diameter distributions at each stand age

using the method of Shifley and Lentz (1986). Site index was assigned to each community type based on field studies by James Fralish and his students (pers. comm.).

TWIGS was tested by comparing the measured and predicted stand structures of the mature stands in each community type at LBL. Data for 40-60 year old stands representative of each community type in the study area were obtained from TVA forest inventory records. These data were used to generate TREEGEN files, and the TREEGEN files were used with TWIGS to simulate stand structure of mature (≥ 100 year old) stands. The predicted structure of mature stands was compared with the structure of the measured mature stands. Based on the low percentage difference between predicted and measured stand structures, we conclude that TWIGS simulates stand development satisfactorily for each of the community types.

Once calibrated and tested, TWIGS was used to simulate the stand characteristics for a number of stand age classes, which we call "TWIGS-age," for each of the community types. Since the analysis was conducted for 20-year intervals, the TWIGS-age classes were 40-60, 60-80, 80-100, and 100-135 (i.e., mature stands). The stand characteristics of each age class were entered into a table, the TWIGS-age table. The entries in the TWIGS-age table were compared with the current characteristics of each stand in the study area and a TWIGS-age that corresponds to current stand structure was assigned to the stand. Future stand structure of each stand in the study area was forecast by referencing its future age, e.g., twenty years into the future, to the data in the next-higher TWIGS-age table.

Current and projected values of timber volumes were also included for each TWIGS-age for each community type. Current boardfoot volume of sawtimber, and pulpwood volume (cords/acre) for poletimber were included in order to clarify the trade-offs between designating stands for buffer zone as opposed to allowing timber harvesting.

In summary, each stand in the study area was classified into one of three community types; its TWIGS-age class was determined by matching its current stand structure with the structure for the community type at a particular TWIGS-age; future development of the stand was predicted as an update of its TWIGS-age, and future stand structure was assigned to the stand with reference to the TWIGS-age table for the community type (stand structure variables included stem density, basal area, and average dbh). Stand structure variables were then compared with the criteria in the modified HSI classification to assign a modified HSI class to the stand. Stand structure variables included stem density, basal area, and average dbh.

Geographic Information System

GIS was used to generate selected variables and to coordinate the analysis. The GIS used in this analysis is pc-ARC/INFO (ESRI 1989). The Working Area and stand boundaries were digitized to create a spatial data base for the study area based on maps provided by TVA. A map of elevation and of bedrock for the study area was also digitized. The stand locations were compared with elevation and bedrock data bases in order to assign each stand to a community type (Fralish and Yang 1992). In cases in which stands as designated by TVA occurred in two community types (e.g., they were bisected by the 500 foot [127 m] contour line), the TVA-designated stand was divided into two stands, each with its community type. Thus, the number of stands in the study areas which we are modeling is greater than the original number specified by TVA (661 vs. 385).

In addition, GIS was used to calculate the distance of each stand from water, which is a habitat requirement for nesting Pileated Woodpeckers (Conner et al. 1975). Stands were classified as less than, or greater than, 150 m from water. Each modified HSI was divided into two subclasses, ≤ 150 m, and > 150 m, from water.

Finally, the TWIGS-age tables and current stand structure of each stand were incorporated into the GIS. GIS was used for all subsequent analyses in order to assess the habitat quality of each stand at 20-year intervals for a planning period of 60 years.

Scenarios Used in the Simulations of Stand Development

Stand development and changes in the modified HSI of the stands were simulated for three 20-year periods (1990-2010, 2010-2030, 2030-2050). Two scenarios were run for this analysis. Management Strategy No. 1 does not allow timber harvesting in either the core area or the buffer zone Working Areas. This allows for stands to develop toward maturity throughout the study area. Management Strategy No. 2 does not allow timber harvesting in the core area (Working Area 39), and assures that 50 percent of the entire study area will become Class 1, while allowing for timber harvest of stands not needed as buffer zone. We stress that these two scenarios have been developed for illustrative purposes and do not represent management recommendations for this area.

RESULTS

The centerpiece of the SDSS used to analyze core-buffer zone interactions at LBL is the stand simulator, TWIGS. The characteristics of stands of the successional white oak community type at various TWIGS-age classes are shown in Table 2. The other two community types, stable white oak and post oak-chestnut oak, have comparable development trends.

Each TWIGS-age class has lower and upper bounds for stand density, basal area, average dbh of all stems and of stems > 51.8 cm, and timber volumes expressed in boardfeet (International 1/4 inch rule). Snag density and dbh are also considered. However, in this simulation, mortality for each TWIGS-age was not recorded. The simulation of standing timber shows decreasing stand density with age, but increasing basal area and average dbh, and the development of large (> 51.8 cm dbh) trees as the stand approaches a TWIGS-age of 100 years.

The economic value of the stands, represented as boardfeet of sawtimber, increases as TWIGS-age increases. Sawtimber volumes increase dramatically as stands mature, e.g., from 7400 boardfeet per ha at the beginning of the 80-100 year TWIGS-age to over 36 000 boardfeet at a TWIGS-age of 135 years in successional white oak stands. Consequently, the value of stands increases with age in two mutually exclusive dimensions--as an economic timber resource, and as habitat for species such as Pileated Woodpecker that favor mature forest stands.

Simulation of stand development for all stands in the study area in the absence of timber harvesting suggests how rapidly the stands will approach maturity and become Class 1 habitat for Pileated Woodpeckers. Table 3 summarizes the area of Class 1 habitat in the core area and buffer zone, and Figure 1 shows the location of these stands in 1990 and at the end of each of the next three management cycles. Currently, 1100 ha of the area (2.5 percent) is Class 1, all

Table 2. TWIGS-age table for the successional white oak community type.

| TWIGS age yrs. | Trees | | | | | Snags | |
|----------------------|-------------------------------|-------------------------------------|--------------------------------|----------------|-------------------------------------|--------------------------------|--------------------------|
| | Density > 5.1 cm st./ha | Basal area m ² /Ha | Density > 51.8 cm st./ha | Avg. dbh cm | Timb. vol. bdft/ha (Int. 1/4) | Density > 51.8 cm st./ha | Avg. dbh > 51.8 cm |
| 40 | 559 | 8.0 | 0 | 13.2 | 1270 | 0 | -- |
| 60 | 483 | 11.5 | 0 | 15.8 | 1720 | 0 | -- |
| 60 | 483 | 11.5 | 0 | 15.8 | 1720 | 0 | -- |
| 80 | 432 | 19.5 | 0 | 22.9 | 7400 | 0 | -- |
| 80 | 432 | 19.5 | 0 | 22.9 | 7400 | -- | -- |
| 100 | 381 | 24.6 | 15 | 26.4 | 18580 | -- | -- |
| 100 | 381 | 24.6 | 15 | 26.4 | 18580 | -- | -- |
| 135 | 279 | 34.4 | 48 | 37.1 | 36330 | -- | -- |

Table 3. Development of Class 1 Pileated Woodpecker habitat under Management Strategy No. 1--no timber harvest.

| Year | Core area | | Buffer zone | | Total study area | |
|------|-----------|-----|-------------|------|------------------|------|
| | % | ha | % | ha | % | ha |
| 1990 | 0 | 0 | 2.5 | 1100 | 2.5 | 1100 |
| 2010 | 1.5 | 680 | 16.5 | 7480 | 18.0 | 8160 |
| 2030 | 17.5 | 786 | 53.5 | 2354 | 71.0 | 3140 |
| 2050 | 20.6 | 910 | 58.0 | 2550 | 78.6 | 3460 |

in the buffer zone. By the year 2010, the area of Class 1 habitat will increase to 8160 ha, a minor proportion of which will be in the core area.

Many stands with the potential for becoming Class 1 habitat would do so in the succeeding management cycle. By 2030, 71 percent of the area would be in Class 1 habitat. As shown in Figure 1, the areas that have not attained Class 1 status are in valley bottoms, many of which are currently managed as open land, and some upland areas where stands develop Class 1 characteristics slowly. The trend continues for the third management cycle, after which 78.6 percent of the study area would be Class 1 habitat for Pileated Woodpeckers.

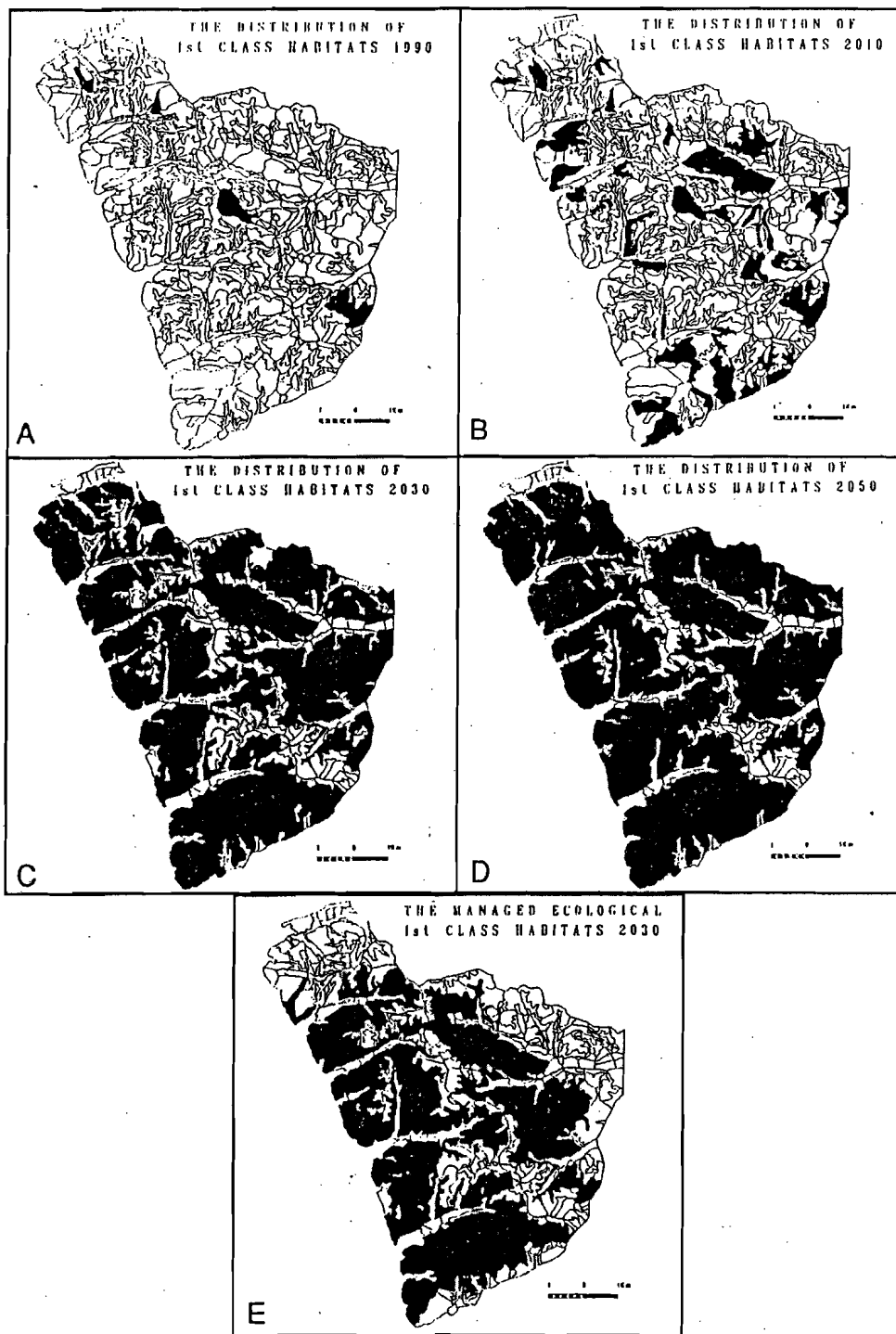


Figure 1. Development of Class 1 habitat for pileated woodpeckers in the LBL Study Area by two management options, No-Cut (Maps A-D), and with harvesting of selected stands (Map E).

This simulation suggests that significant areas of Class 1 habitat would develop over the next four decades, and that the economic value of the stands would also increase sharply. If in this simulation we limit the need for Class 1 habitat to 50 percent of the study area, it is clear that there is an opportunity to combine protection of the habitat qualities of the core area with timber harvesting in the buffer zone Working Areas. Simulation of Management Strategy No. 2 demonstrates one possible result of managing the area to limit Class 1 stands (and thus mature stands) to 50 percent of the study area.

Management Strategy No. 2 involves allowing Class 1 stands to develop until the desired area is achieved. Timber harvesting would not occur until 2010, when Class 2 stands would be harvested. Harvesting of Class 1 stands would begin in 2030 when the management goal of 50 percent of the study area in Class 1 stands would have been achieved. Timber harvesting would be restricted to outer portions of the buffer zone, greater than 1400 m from the core area boundary in this scenario. Table 4 shows the area of Class 1 habitat from 1990 to 2030. The impact of this management strategy is to reduce the area of Class 1 habitat in 2030 relative to the no-cut option. In 2030, there would be 2552 ha of Class 1 habitat, which is 58 percent of the study area. Thus, harvesting has reduced the area of Class 1 habitat by 20 percent, or nearly 600 ha. If the inner buffer zone (defined as buffer zone area within 1400 m of the core area) were allowed to be narrower, e.g., 1000 m, a greater area of Class 1 and Class 2 stands would have been eligible for harvesting, and the area in Class 1 habitat could have approached the 50 percent goal more closely. The impact of harvesting on the spatial distribution of Class 1 stands is shown by comparison of the two maps for 2030 in Figure 1; Figure 1C shows the location of Class 1 habitat in the no-cut option, and Figure 1E shows their location with harvesting. The core area undergoes the same trends in both options because timber harvesting is not allowed there. The inner buffer zone undergoes the same development because the stands are needed as buffer zone in both cases. The stands in the outer buffer zone, however, are harvested as they reach maturity, and do not remain as Class 1 stands.

The areas in Class 2-4 stands are also shown in Table 4. This suggests how the structure of the landscape changes as young stands mature. For example, many of the Class 3 stands in the core area and buffer zone in 1990 become Class 2 stands by 2010. Likewise, many of the Class 2 stands of 1990 will become Class 1 stands by 2010. The simulation for Management Strategy No. 2 was terminated in 2030 because of difficulty in modeling the recovery of harvested stands using TWIGS.

CONCLUSIONS

This exercise leads us to several conclusions. First, the analysis has shown how a buffer zone can be managed to meet management goals that relate to another part of the landscape, in this case a core area. In fact, attainment of management objectives for a core area that is not self-sufficient, as in our example, requires that a management plan for a buffer zone be developed so that the habitat in the buffer zone supplements that of the core area.

The importance of correctly identifying the stands to be set aside as buffer zone is suggested by the increasing commercial value of the stands as they mature. Timber volumes increase five-fold from the 80-100 TWIGS-age class to the ≥ 135 age class (see Table 2), concurrently with development of these stands into Class 1 habitat for Pileated Woodpeckers.

Table 4. Development of Class 1-4 habitats for Pileated Woodpecker under Management Strategy No. 2, involving selective harvesting of Class 2 stands in 2010 and Class 1 stands in 2030.

| <u>Class 1 Habitats</u> | | | | | | | |
|-------------------------|-------------|------------------|-----|--------------------|------|-------------------------|------|
| Year | <u>Goal</u> | <u>Core area</u> | | <u>Buffer zone</u> | | <u>Total study area</u> | |
| | % | % | ha | % | ha | % | ha |
| 1990 | 2.5 | 0 | 0 | 2.5 | 1100 | 2.5 | 1100 |
| 2010 | 18.0 | 1.5 | 680 | 16.5 | 7480 | 18.0 | 8160 |
| 2030 | 50.0 | 17.5 | 770 | 40.5 | 1782 | 58.0 | 2552 |

| <u>Class 2-4 Habitats--Percent of Study Area</u> | | | | | | |
|--|--|--------|----------------|--------|----------------|--------|
| Year | <u>Class 2</u> | | <u>Class 3</u> | | <u>Class 4</u> | |
| | Core | Buffer | Core | Buffer | Core | Buffer |
| 1990 | 11.1 | 31.9 | 13.5 | 35.5 | 1.0 | 4.5 |
| 2010 | 18.9 | 51.1 | 4.8 | 14.0 | 0.4 | 2.8 |
| 2030 | — (end of planning period for Management Strategy No. 2) | | | | | |

Being able to specify which stands are needed for the buffer zone, and which can be devoted to other purposes, increases options for land managers.

Second, integrating the management of a core area and its surrounding buffer zone is an ongoing and dynamic process since the habitat qualities of both change between planning cycles. Managers must be able to respond to changes in the spatial structure of habitat in both core area and buffer zone. These changes might result from predictable trends in stand species composition and size classes, as we have modeled them in this analysis, or from less predictable disturbances such as fire, windthrow, or changing timber values and demand.

Finally, the management decisions involved are too complicated to be resolved without a sophisticated database and analytic capability when any significant area is to be managed. In this analysis, 385 stands in five Working Areas were tracked over a 60-year period, and their changing roles in providing habitat for Pileated Woodpeckers were assessed. A GIS coupled with a stand simulator such as TWIGS, a way to evaluate habitat quality such as the modified HSI, and an SDSS to organize databases and provide a structure for exploring management options are all needed for efficient forest management over extended periods.

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