PROCEEDINGS OF THE SEVENTH SYMPOSIUM ON THE NATURAL HISTORY OF LOWER TENNESSEE AND CUMBERLAND RIVER VALLEYS

HELD AT BRANDON SPRING GROUP CAMP
LAND BETWEEN THE LAKES
FEBRUARY 28 AND MARCH 1, 1997

Sponsored by:

The Center for Field Biology
Austin Peay State University, Clarksville, Tennessee

and

Center for Reservoir Research
Murray State University, Murray, Kentucky

and

Tennessee Valley Authority - Land Between The Lakes
Golden Pond, Kentucky

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PREFACE

The Seventh Symposium on the Natural History of Lower Tennessee and Cumberland River Valleys was held at Brandon Spring Group Camp in TVA's Land Between The Lakes on February 28 and March 1, 1997. This biennial gathering of naturalists, field biologists, and others interested in related topics was sponsored by The Center for Field Biology at Austin Peay State University, the Center for Reservoir Research at Murray State University, and Land Between The Lakes.

The symposium began Friday afternoon with brief welcoming comments from representatives of the three sponsoring institutions. Representing Austin Peay State University and The Center for Field Biology was its Director, Dr. Benjamin P. Stone. Dr. Gary Boggess, dean of the College of Arts and Sciences, spoke on behalf of Murray State University and its Center for Reservoir Research. Mr. Richard Lowe, specialist and team leader, represented Land Between The Lakes. Three invited presentations, each related to the theme "Long-term Monitoring of Ecosystems," followed. The first speaker, Dr. David Lenat, North Carolina Division of Environmental Management, examined long-term trends in macroinvertebrate populations in North Carolina. Long-term and comparatively short-term monitoring of a central Appalachian forest ecosystem (the Fernow Experimental Forest) in West Virginia was the topic of the second report, presented by Dr. Ted Angradi of the USDA's Northeastern Experiment Station. The final presentation Friday afternoon, given by Dr. J. Whitfield Gibbons of the University of Georgia's Savannah River Ecology Laboratory, was a review of the lessons learned about herpetofaunal species diversity after three decades of research at the Savannah River Site in South Carolina. Included in these proceedings are abstracts of Drs. Lenat's and Angradi's presentations, and a fully developed report of Dr. Gibbons' address.

Friday evening Robert and Andrea English, co-owners of the consulting firm Learning Through Environmental Awareness (LEAPS), presented an intriguing multimedia program on the voices of Tennessee's frogs and toads. While projecting superior color slides (most produced in the field under natural conditions) of each of the state's 21 species of anurans, tape recordings (also recorded under natural conditions) of their vocalizations were played with high-quality sound equipment. Following the audio-visual part of the program, Andrea explained the Tennessee Amphibian Monitoring Program, the part LEAPS is playing in it, and the need for volunteers to serve as frog loggers across the state.

Contributed papers were read Saturday morning. The large number of contributions necessitated holding three sessions. Session I, entitled "Zoology and Aquatic Biology" had 16 presentations and was moderated by Dr. Steven Hamilton, Austin Peay State University. Session II, "Aquatic Biology and Water Quality," with 14 talks, was moderated by Dr. David S. White, Murray State University. Moderating the 17 reports in Session III, "Botany," was Dr. Edward W. Chester, Austin Peay State University. Contributors were invited to publish an abstract, short communication, or full paper in the proceedings. While most opted to publish only an abstract, 16 full-length papers (seven from Session I, three from Session II, and six from Session III) and one short communication (from Session I) were submitted and are presented in this document.

The style and format of these proceedings follow those established in previous proceedings of the symposium series. Dr. Scott edited the invited papers and abstracts and was responsible for putting together the finished document; Drs. Hamilton and White edited abstracts and papers from Contributed Papers, Sessions I and II; and Dr. Chester edited abstracts and papers from Contributed Papers, Session III.

ACKNOWLEDGMENTS

The editors thank Ms. Marilyn Griffy and Ms. Natasha Emmons for assistance in organizing and coordinating activities leading up to and throughout the symposium. We also recognize the participation of many APSU Center for Field Biology undergraduate and graduate research assistants for their help before and during this event. Many abstracts and manuscripts were typed and corrected by Ms. Griffy, who also saw to details of the proceedings front matter. Ms. Laurina Lyle provided assistance with the proceedings' cover and printed photographs. The help of these individuals and others not mentioned was critical to the success of the symposium and completion of these proceedings. As all complete manuscripts were reviewed by a minimum of two persons, we are indebted to those who participated in this task. Their comments and suggested changes greatly enhanced the quality of the final product. While we (the editors) strived for an error-free publication, chances are some errors went undetected. Consequently, we assume responsibility for any mistakes generated during the editorial process.

SYMPOSIUM REGISTRANTS

Following, in alphabetical order, is a list of those individuals who registered at the 1997 symposium. Institutional affiliation (when available), city (of the person's institution or home), and state are also given.

Jennifer Anderson, Austin Peay State University, Clarksville, Tennessee; **Paul Andreadis**, University of Tennessee, Knoxville, Tennessee; **Ted Angradi**, USDA, Northeastern Forest Experiment Station, Parsons, West Virginia; **James Armstrong**, Murray State University, Murray, Kentucky; **Bill Atkinson**, Hopkinsville Community College, Hopkinsville, Kentucky; **Leigh Barber**, Austin Peay State University, Clarksville, Tennessee; **Joseph Barnes**, Vanderbilt University, Nashville, Tennessee; **Carol Baskin**, University of Kentucky, Lexington, Kentucky; **Jerry Baskin**, University of Kentucky, Lexington, Kentucky; **Jeanne Beals**, Austin Peay State University, Clarksville, Tennessee; **Glynn Beck**, Kentucky Geological Survey, Henderson, Kentucky; **Rick Beckler**, Austin Peay State University, Clarksville, Tennessee; **Lisa Benjamin**, Kentucky Wesleyan College, Owensboro, Kentucky; **Jane Benson**, Murray State University, Murray, Kentucky; **George Benz**, Tennessee Aquarium, Chattanooga, Tennessee; **Alan Bottomlee**, Austin Peay State University, Clarksville, Tennessee; **Cindy Bowman**, Murray State University, Murray, Kentucky; **Karen Brinkley**, Murray State University, Murray, Kentucky; **Christopher Brooks**, Murray State University, Murray, Kentucky; **Michelle Brown**, Austin Peay State University, Clarksville, Tennessee; **Scott Brown**, Austin Peay State University, Clarksville, Tennessee; **John Byrd**, Clinton High School, Clinton, Tennessee; **Angelo Bufalino**, Austin Peay State University, Clarksville, Tennessee; **Pamela Bufalino**, Austin Peay State University, Clarksville, Tennessee; **Willodean Burton**, Austin Peay State University, Clarksville, Tennessee; **Nancy Buschhaus**, University of Tennessee, Martin, Tennessee; **Jeremy Butrick**, Murray State University, Murray, Kentucky; **Rebecca Carmack**, Austin Peay State University, Clarksville, Tennessee; **Emily Chambers**, Austin Peay State University, Clarksville, Tennessee; **Edward W. 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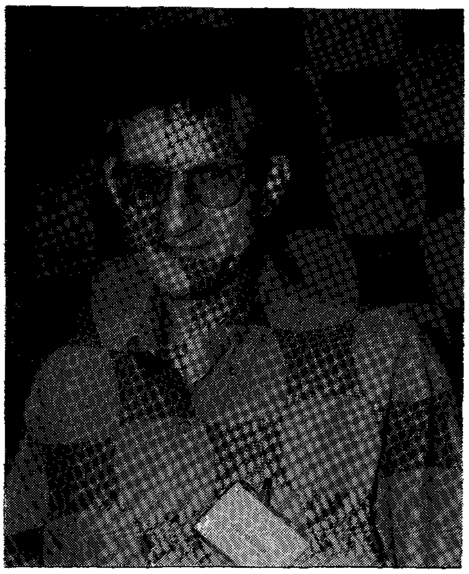
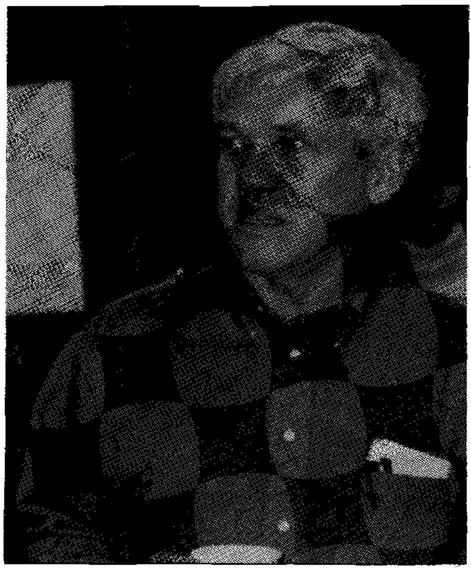
SYMPOSIUM PARTICIPANTS

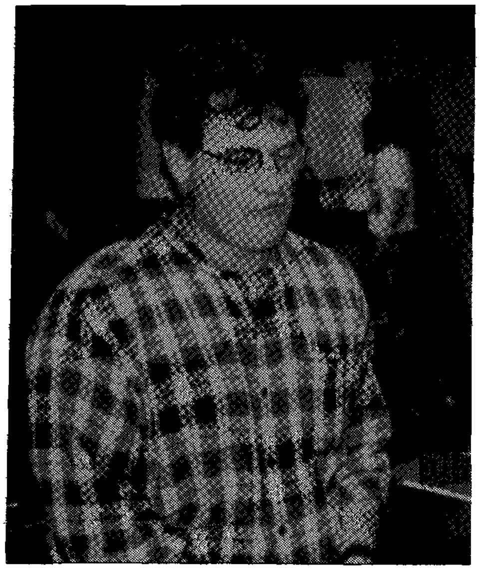
INVITED SPEAKERS



David R. Lenat

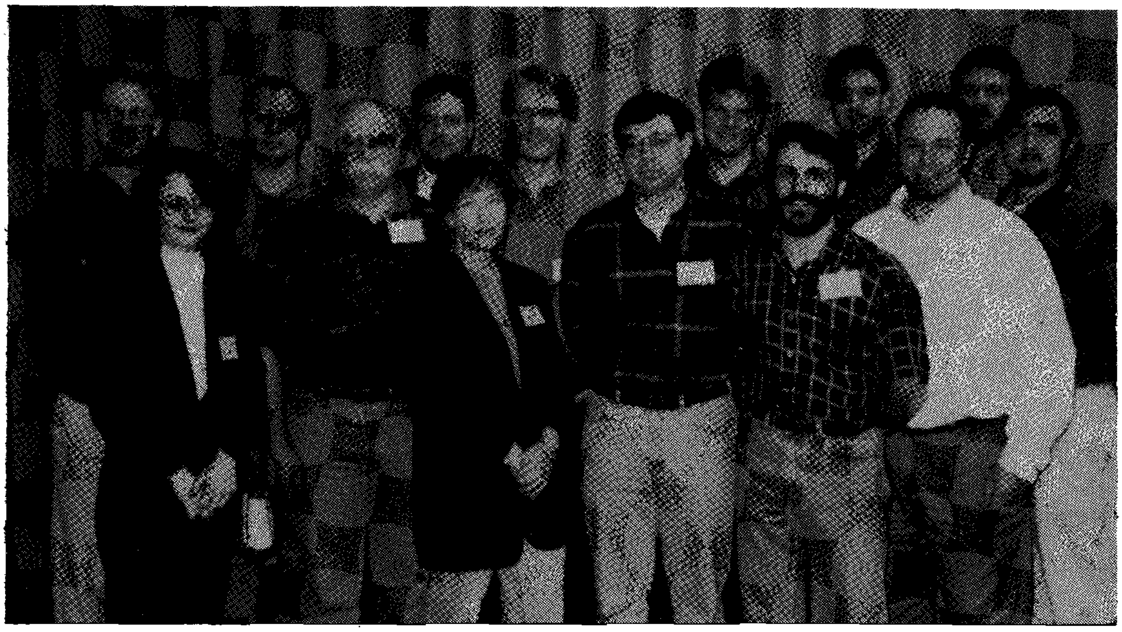


J. Whitfield Gibbons



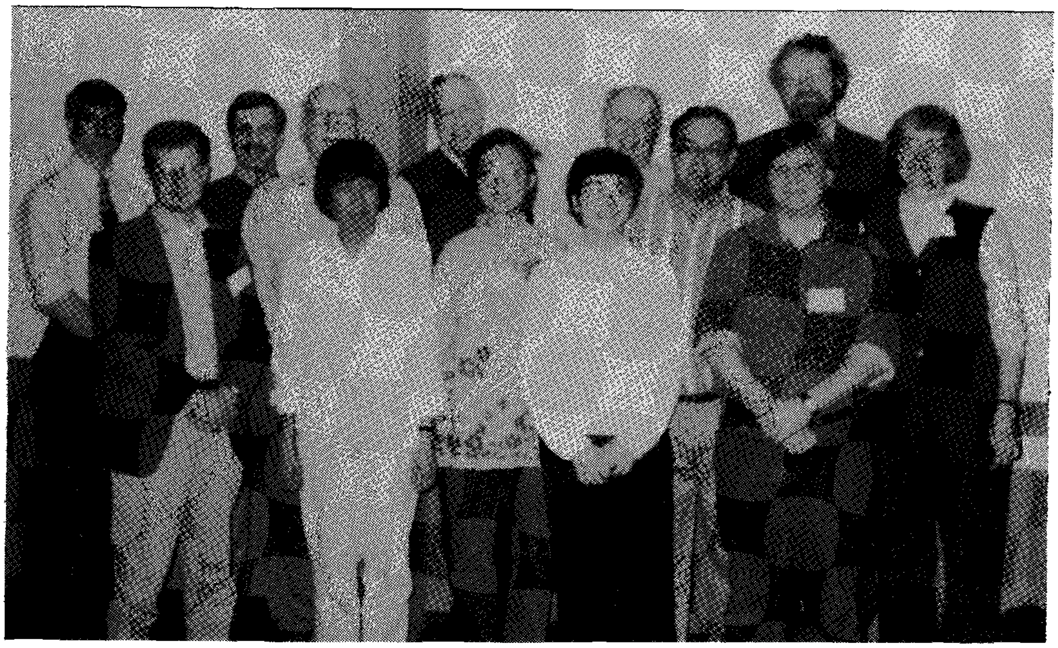
Ted R. Angradi

Robert and Andrea English
Evening Program



Session I: Zoology and Aquatic Biology - (from left) Angelo Bufalino, K. Brinkley, George W. Benz, A. Floyd Scott, Joseph C. Whitaker, Colleen M. White, Peter V. Lindeman, Alan K. Bottomlee, James S. Armstrong, Paul T. Andreadis, Darren P. Reed, Vincent Evan Stanford, Steve J. Fraley, and Jeffrey J. Herod. Not pictured: Leanne N. Jenkins and Howard H. Whiteman.

Session II: Aquatic Biology and Water Quality - (from left) Joseph R. Schiller, George Kipphut, Willodean D.S. Burton, Granger L. Ridout, Frank Satterfield, David White, John Rundle, Tom Kind, John VanStone, Lidija Halda-Alija (front), Steve Fraley, William E. Spencer. Not pictured: R.D. Hoyt.



Session III: Botany - (from left) Scott Franklin, Jeffery L. Walck, David D. Close, Hal R. DeSelm, Siti N. Hidayati, James S. Fralish, Zhizhi Qing, Xiaojie Li, Edward W. Chester, Jerry M. Baskin, Jefferson G. Lebkuecher (front), Joe Schibig, and Carol C. Baskin.

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CONTRIBUTED PAPERS

SESSION I: ZOOLOGY AND AQUATIC BIOLOGY

Saturday, March 1, 1997

Moderator:

Steven Hamilton
Austin Peay State University

Editors:

Steven Hamilton
Austin Peay State University

and

David White
Murray State University

A LUNAR RHYTHM IN THE FORAGING ACTIVITY OF NORTHERN WATER SNAKES (REPTILIA: COLUBRIDAE)

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ABSTRACT. I examined the relationship between the lunar cycle and nocturnal foraging activity of Northern water snakes, *Nerodia sipedon*, in the Little River, Blount Co., TN. Censuses were conducted during all four moon phases in each of four different lunar cycles, three cycles in 1995 and one in 1996. I walked a standardized transect through the shallows 1-3 h after sunset, searching with a handheld spotlight for snakes in the water. Census length averaged 44 min and the number of snakes seen ranged from 1-17 (mean = 6.6). There was a significant, positive correlation between water temperature and the number of snakes seen ($r = 0.66$). After accounting for thermal differences, a repeated measures ANOVA rejected the hypothesis that numbers of snakes seen were equal in each moon phase ($p = 0.026$). Significantly more snakes were seen during dark and waning moon phases than during bright and waxing phases ($p = 0.005$). Though the comparison was not significant ($p = 0.056$), there was a trend for the last quarter to have greater snake activity than the first quarter, despite the moon being half illuminated in each phase. Low light conditions may enhance snakes' foraging success by reducing the ability of prey fishes to visually detect them. Conversely, the snakes themselves may experience a lower risk of predation; potential, visual predators of snakes (bullfrog, snapping turtle, screech owl, night heron) have been observed during night fieldwork. In addition to lunar illumination, timing of moonrise/set may be relevant to understanding the effects of the lunar cycle. This study focuses attention on the fact that both endogenous and environmental cues may act to initiate feeding in reptiles. More generally, the results illustrate how the environment can mediate predator-prey interactions in aquatic systems.

INTRODUCTION

Many of an animal's activities recur with a characteristic frequency. The biological rhythms with daily and annual periodicities are the best studied examples (Aschoff 1981). However, other ultradian (shorter than 24 h) and infradian (longer than 24 h) rhythms have been found to have major importance in certain biological systems. Lunar cycles, for example, are particularly well studied in the nearshore marine environment, where the gravitational pull of the moon contributes to tidal fluctuations (Neumann 1981). Other lunar rhythms are a consequence of the variation in intensity of lunar illumination as the moon changes phase. Brightness varies from 0.0009 lux at the new moon (=just starlight) to 0.215 lux at the zenith of the full moon (Austin *et al.* 1976). Moonlight dependent effects on nocturnal animals are often reported in the context of visually mediated predator-prey interactions (Lima and Dill 1990). Such effects of lunar light level raise both ultimate and proximate questions. In terms of fitness, do predatory success or predator avoidance vary with lunar phase? Proximately, are moonlight fluctuations important in understanding the mechanistic control of food intake in nocturnal animals? In those animals that exhibit lunar rhythms, is there an endogenous circalunar clock, or are responses elicited by external stimuli?

Among studies of vertebrate behavioral rhythms, there is a paucity of work on reptiles and amphibians (Rusak 1981); the reptile studies that have been done have primarily addressed rhythms in locomotor activity and behavioral thermoregulation. Underwood (1992) reviewed the literature on endogenous rhythms in reptiles, but focused primarily on daily rhythms and circadian clocks. In order to begin to address the proximate and ultimate issues raised above, I examined the effect of the lunar cycle on a nocturnally foraging snake. The Northern water snake, *Nerodia sipedon* (L.), is a semiaquatic colubrid that eats mainly fishes (Brown 1958) and forages primarily from 1800-0000 h (Ernst and Barbour 1989). In addition to a desire to explore lunar effects on this nocturnal reptile, part of my motivation for the present study was born of personal frustration. Having searched for *N. sipedon* on many seemingly ideal summer nights, I have been puzzled as to why I have seen many snakes on some nights, but only very few on others.

METHODS

The study was conducted on the Little River in Blount Co., TN, at the eastern edge of the Ridge and Valley physiographic province. With headwaters in the Great Smoky Mountains, the Little River has not, like most rivers in eastern Tennessee, been impacted by large scale impoundment and still supports a diverse fish fauna (Etnier and Starnes 1993). The study site is near rivermile 22, elevation 275 m, immediately downstream from Peery's Mill Dam (Fig. 1). The principal woody, riparian vegetation is alder (*Alnus*), dogwood (*Cornus*), and willow (*Salix*); waterwillow (*Justicia*) dominates the emergent vegetation. The water is clear (Secchi readings near 3.0 m; Heacock 1995) and fast flowing over a gravel and cobble substrate. Northern water snakes are abundant at the site.

I established a transect that began at the base of the dam, paralleled the west shore 50 m in a downstream direction, crossed the main channel, circumnavigated two thirds of an elliptical (80 X 20 m) island, followed a gravel bank below the island for 30 m, then doubled back and completed the perimeter of the island (Fig. 1). The site was censused by walking the transect beginning 70-180 min (mean=107) after sunset. Censuses took an average of 44 min, with some seasonal variation due to changes in water level and height of emergent vegetation. I slowly walked along in ankle to knee deep water, visually scanning for snakes with a portable, 12 V spotlight. I have found *N. sipedon* to be quite conspicuous at night; when their head emerges from the water, the light colored chin is readily lit by spotlight. Any nonneonate snake (see below) observed in the water was counted as a foraging animal. Snakes that were on the shore or perched in vegetation and that were obviously wet were also counted as foragers. When a snake was noted, I continued on without disturbing it. On the parts of the transect that involved doubling back (Fig. 1), I only counted snakes that were of a different size class than those seen on the first pass. Censuses in September overlapped the parturition season. Newborn snakes (readily distinguished from nonneonates based on size) were not counted in order to avoid attributing their appearance to the lunar cycle when it might be due to a chance timing of birth. Upon completion of each census, air and water temperatures were measured to the nearest 0.2 °C with a rapid reading, mercury thermometer, and recorded along with census duration, number and location of snakes seen, and weather conditions.

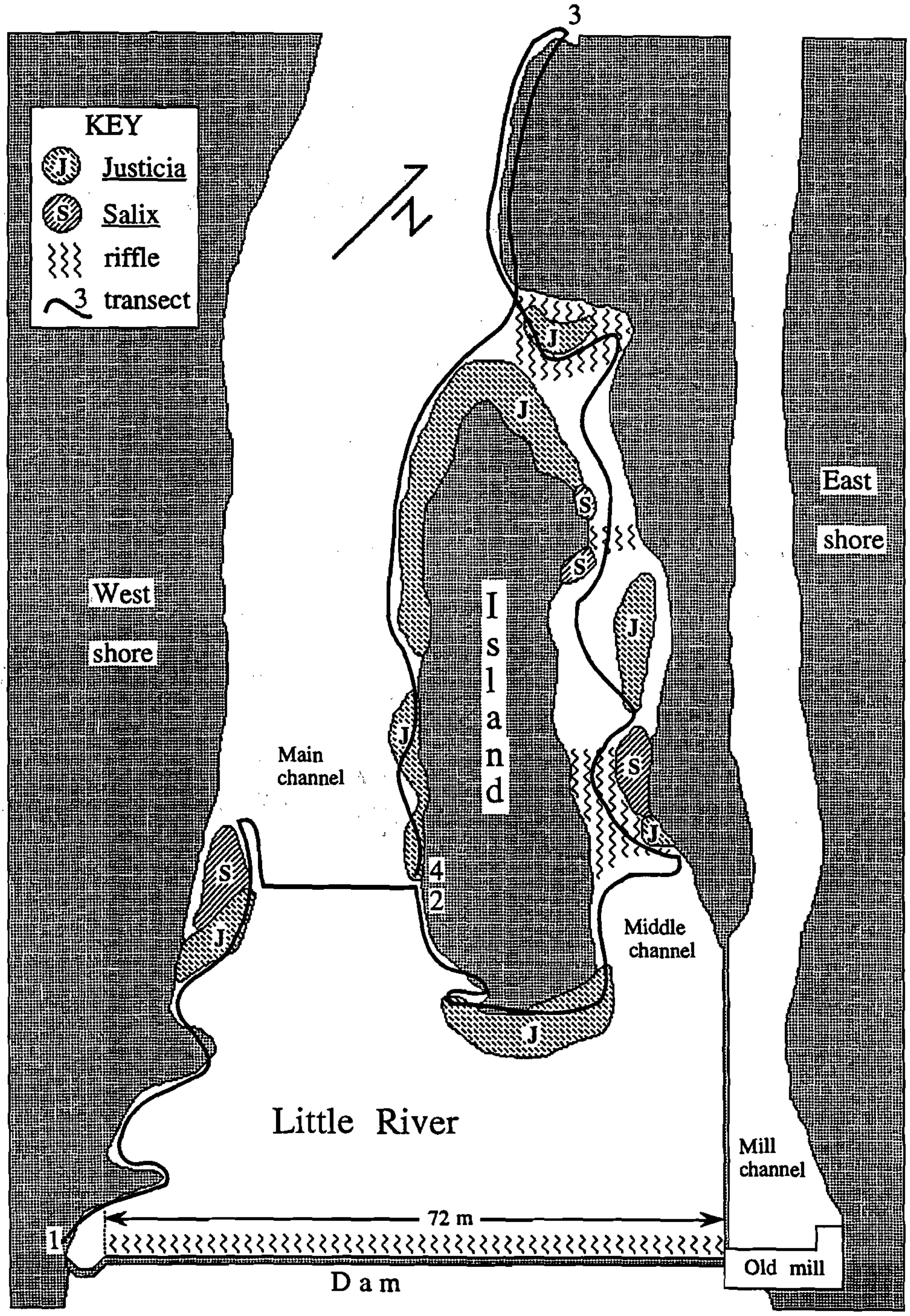

Figure 1. The study site at Peery's Mill on the Little River, Blount Co., TN. The census transect began near the west end of the dam at the point labeled "1", and followed the path depicted by the dark line. It took approximately 15 min to walk from point 1-2, 20 min from point 2-3, and 10 min from point 3-4.

I conducted censuses during each of the four phases of a lunar month, i.e. new moon, first quarter (=waxing half moon), full moon, and last quarter (=waning half moon). Four different lunar cycles were censused, three in 1995 and one in 1996. These four time blocks are referred to below as Early 95 (26 May-20 June), Mid 95 (14 July-4 August), Late 95 (25 August-15 September) and Late 96 (14 August-5 September). The time of a given census was set to be ± 60 h of the exact time of the intended moon phase. This time window allowed me to census near a particular phase while avoiding any inclement weather on a given day. The time between consecutive censuses within one lunar cycle ranged from 5-12 d (mean=7.4). The sky was mostly clear during 10 censuses, equal parts clear and cloudy for three, and completely overcast for three. Data on timing of lunar phases were obtained online from the U. S. Naval Observatory, Astronomical Applications Laboratory (URL: http://aa.usno.navy.mil/AA/data/).

Since temperature strongly affects all aspects of snake biology and performance (Lillywhite 1987), I controlled for temperature differences between censuses by using residuals from a pooled regression of number of snakes seen per census as a function of water temperature. A repeated measures ANOVA of the relative number of snakes seen (i.e. the number above/below that predicted by temperature) tested the null hypothesis of equality between the different moon phases. A repeated test was used because of the possibility of seasonal effects (other than temperature) that would make censuses within a given lunar cycle more similar to each other than to those in other cycles. The alpha level for the ANOVA was set at p=0.05.

RESULTS

The numbers of snakes seen per census ranged from 1-17 (mean=6.6). There was a strong, positive relationship (r^2=0.434) between numbers of snakes seen and water temperature (Fig. 2). Relative number of snakes seen (the residuals from the regression) ranged from +5.1 to -4.2, and varied in a "U" shaped pattern over the lunar cycle (Fig. 3). A repeated measures ANOVA rejected the null hypothesis of equal means between moon phases (F=4.97, p=0.026). The data suggested two post hoc comparisons: Relative numbers of snakes seen were analyzed to compare "Dark moons" (= new moon and last quarter) and "Bright moons" (= full moon and first quarter). An unplanned contrast of Dark and Bright moons was highly significant (F=13.76, p=0.005). Another post hoc test compared the relative numbers of snakes seen during the two half moon phases (i.e. first and last quarters) . This comparison was not significant (p=0.056), though a trend for the last quarter to have higher snake activity was apparent (Fig. 3).

DISCUSSION

Both temperature and moon phase were significantly correlated with water snake foraging activity. Mechanistically, a temperature correlation would undoubtedly be attributable to the thermal dependencies of snake physiology (Lillywhite 1987). Warmer snakes have higher rates of metabolism, need more food, and were closest to their preferred body temperature (approximately 28 °C; Lillywhite 1987) at the warmest water temperatures seen in this study. A strong association between moon phase and snake foraging activity has previously been underappreciated. Before discussing this relationship, I should address the nature of the change in snake activity. It is unlikely that most of the water snake population goes without eating for two week periods during bright moons. Based on my personal observations, water snakes appear to feed much more frequently than this. The measure of snake activity I used reflects the proportion of the population that is actively hunting. Thus, I interpret the moon phase as affecting the probability that a snake will be hunting on a given night. One way such an effect might be manifested is by a change in the frequency of foraging. Hypothetically, for example, a one third reduction in number of snakes seen would occur if snakes foraged every night during a dark moon period, but every third night during bright nights.

Earlier comments on the possible effects of moonlight on snake collecting (Klauber 1939, Kauffeld 1957,1969) did not immediately lead to increased scrutiny of the issue. In the last 15 years, however, the importance of lunar phenomena has been described in both freshwater and desert snakes (Table 1). Lunar cyclicity has now been reported for three genera of nocturnal, piscivorous snakes from two families on three different continents. These results suggest that lunar cycles are a ubiquitous mediator of predator-prey interactions of aquatic snakes. However, it is not clear whether the ultimate determinant of the rhythm is the role of these snakes as predators or as prey.

Table 1. Correlations between moon phase/illumination and snake activity in the field and enclosures.

Species (Family)	Habitat	Correlate of dark moon	Source
Trimeresurus flavoviridis (Viperidae)	Enclosure	Delay emergence till low illumination	1
Lycodonomorphus bicolor (Colubridae)	Freshwater lentic	Higher % of snakes with food	2
Acrochordus arafurae (Acrochordidae)	Freshwater lentic	More snakes active	3
Nerodia sipedon (Colubridae)	Freshwater lotic	More snakes active	4
Crotalus cerastes (Viperidae)	Desert	More prey captures recorded	5
Crotalus viridis (Viperidae)	Enclosure	More extensive movements, and greater use of open areas	6

Sources: 1 - Yamagishi 1974, 2 - Madsen and Osterkamp 1982, 3 - Houston and Shine 1994, 4 - this study, 5-Bouskila 1995, 6-Clarke *et al.* 1996

In general, although vision can play a part, tactile sensation and chemoreception are the most important modalities guiding predatory behavior of water snakes (Brown 1958, Drummond 1983). Thus, any differences in snake foraging success would not be attributable to changes in the ability of snakes to see their prey (cf. Skutelsky 1996). Instead, light levels may act indirectly by affecting the ability of prey fishes to detect predators. Although examples of nontidal, lunar rhythms in fishes are few (Gibson 1978), the migratory activity of eels (*Anguilla*) in rivers is highest during dark moon phases (Tesch 1977, Gibson 1978). In reviewing the daily patterns of fish activity, Helfman (1986) characterized a number of fish families as being solely diurnal. The demands of night and day vision being somewhat incompatible in fish visual systems (Helfman 1986), strictly diurnal fishes have good day vision at the expense of night vision. Having generally poor night vision, diurnal fishes may be even more vulnerable to snakes on nights with less light (i.e. dark moons). Of the important groups of prey fishes reported for *N. sipedon* (Brown 1958, Ernst and Barbour 1989), many minnows (Cyprinidae) and darters (Percidae) are considered diurnal (Helfman 1986, Craig 1987) . Furthermore, neither strongly diurnal nor nocturnal fishes see well at twilight, and the activity and foraging success of predatory fishes increases greatly at this time (Helfman 1986). In the context of lunar cycles, the implication of these studies of daily cycles is that light levels that impair the vision of fishes would make them more vulnerable to piscivorous snakes. Relying mainly on nonvisual senses, more snakes may forage on dark nights because of predictably higher chances of success.

An effect of the lunar cycle on the vulnerability snakes to their own predators should also be considered. It may be the case that more snakes restrict their activity on bright nights because of greater predation risk from visual predators. During the course of night field work in streams and rivers of eastern Tennessee, I have observed a number of potential predators of water snakes (Table 2). Of this suite, bullfrogs, night herons, screech owls, and perhaps snapping turtles rely heavily on vision to detect prey. To the extent that most of a snake population consists of younger individuals, population level changes in activity will be particularly apparent when they involve small animals. During most nighttime visits to the study site I saw large bullfrogs hunting in the shallow water. Many of the smaller *N. sipedon* that I have observed were also in shallow water, so it may well be that large frogs are important predators of small snakes. In general, it should be noted that predatory success of and predator avoidance by snakes may not be mutually exclusive. Both selection pressures may have influenced the evolution of increased activity during dark moons.

Table 2. Potential water snake predators that were seen during night field work in rivers and streams of eastern Tennessee.

Common name	Scientific name
Longnose Gar	*Lepisosteus osseus*
Bullfrog	*Rana catesbeiana*
Snapping Turtle	*Chelydra serpentina*
Spiny Softshell Turtle	*Apalone spinifera*
Mink	*Mustela vison*
River Otter	*Lutra canadensis*
Raccoon	*Procyon lotor*
Black Crowned Night Heron	*Nycticorax nycticorax*
Screech Owl	*Otus asio*

In terms of the proximal causation of behavioral rhythms, it is a core tenet of ethology that internal and external stimuli interact to produce behavior. Biological rhythms, including those with daily, lunar, and annual cycles, are exemplary phenomena. For many biological rhythms, endogenous biological clocks with a variety of periods keep time quite precisely, even in environments where external cues are held constant (reviews in Brady 1979, Aschoff 1981). However, because of a slight mismatch between internal and external periods, such rhythms need to be entrained by recurrent, reinforcing cues from the environment. Endogenous circadian clocks are well known in reptiles (Jones 1974; Underwood 1992), but no studies have mechanistically investigated lunar clocks in reptiles. The results of the present study offer little to distinguish between a truly endogenous clock and a system that is driven solely by extrinsic, environmental cues. One census conducted during a first quarter featured a typically low number of snakes despite there being a continuous cloud cover. This single observation offers weak evidence for an endogenous clock.

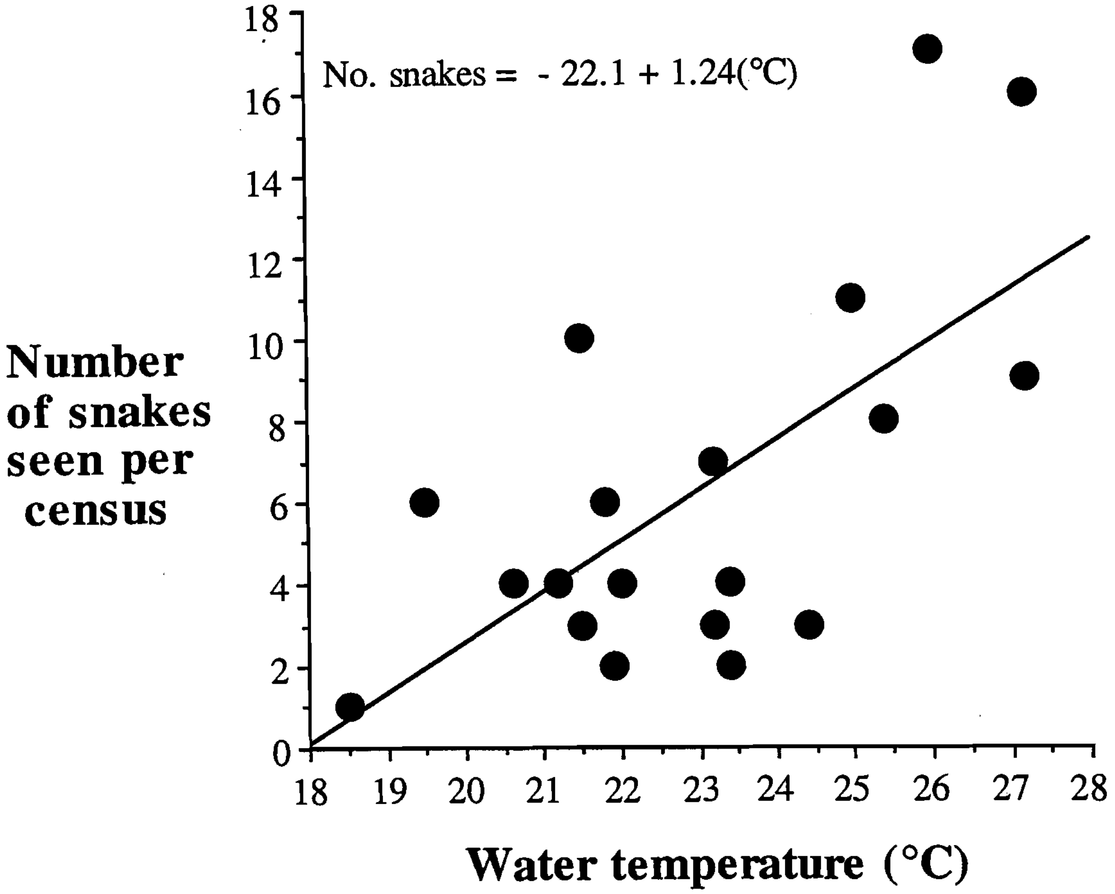

Figure 2. The number of snakes seen per census as a function of water temperature. Data are included from an additional three censuses that were not part of the lunar cycle study, but which were conducted in an identical manner.

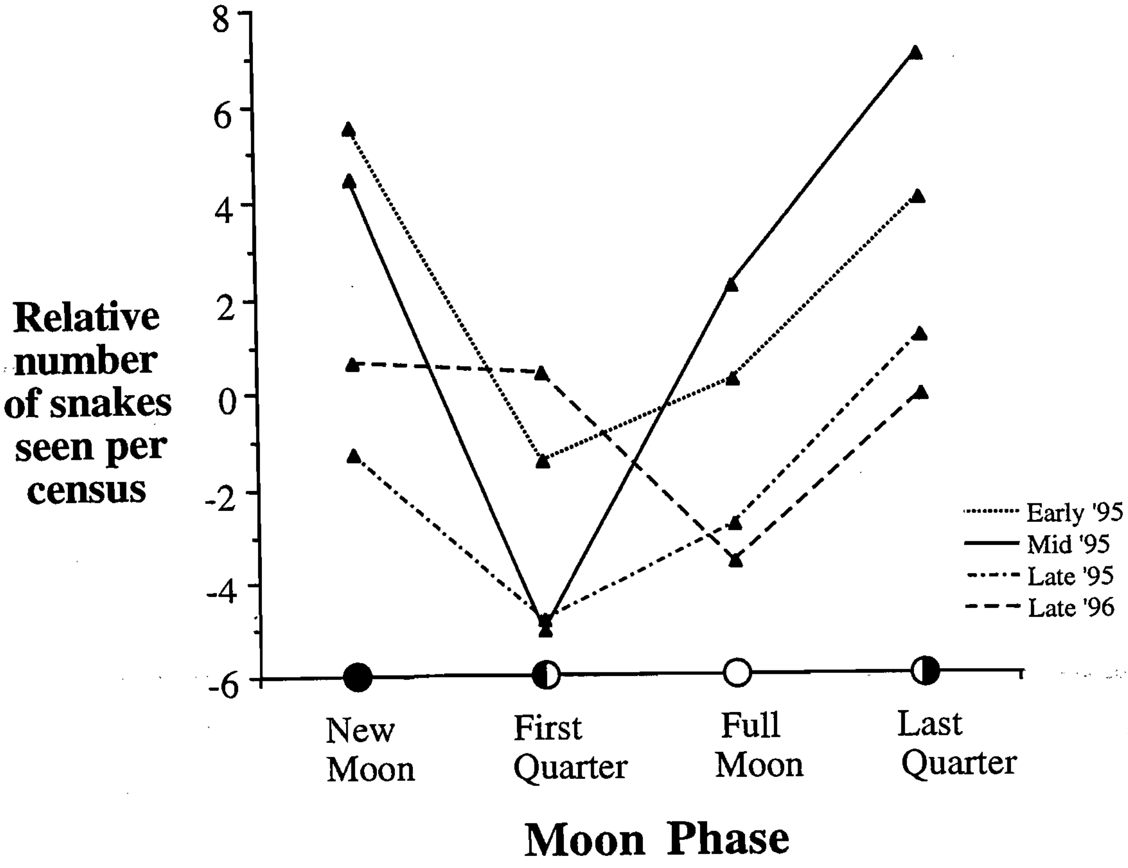

Figure 3. Relative number of snakes seen (= amount more or less than expected based on temperature) as a function of lunar phase. Each line symbol connects the points within a given lunar cycle.

The data suggest that all half moons may not be alike, as there were noticeably more snakes foraging during the last quarter than during the first quarter (Fig. 3). The first quarter had the lowest snake activity in three out of four lunar cycles, and also had the single, lowest value of snake activity in the entire study; the last quarter had the highest snake activity in two out of four censuses, and had the single, highest value for the study. The post hoc comparison of these two moon phases was not significant ($p=0.056$). However, given the small sample size of this comparison, I conclude that the effect size is large enough to be considered biologically meaningful. The specific moon phase in which freshwater eels (*Anguilla*) show a pronounced peak in migratory activity is the last quarter (Tesch 1977, Gibson 1978). Regarding snakes, Madsen and Osterkamp (1982) suggested that snake foraging activity decreased from new moon to full moon. However, inspection of the data (their Fig. 2) indicates that, in fact, the last quarter was the peak in proportion of snakes containing food, and that the first quarter was the trough. Collectively, these observations suggest that the illumination level *per se* of moon phases is not the only relevant factor influencing lunar rhythms. This distinction is worthy of consideration, as previous studies in enclosures have examined mainly the effect of light level (Yamagishi 1974, Clark *et al.* 1996). Another, overlooked factor is the daily timing of lunar ascent and descent.

A regular relationship exists between the phase of the moon and the time of day when the moon is above the horizon. This relationship is illustrated with data from the four lunar phases of April 1997 (Fig. 4). During the new moon, the entire night is dark. During the last quarter, though, there is a period of darkness in the first half of the night, before the half moon rises. Since all of the censuses in the present study fell during the early night (1-3 h after sunset), it may be that high snake activity during the last quarter reflects the concentrating of the whole night's activity into a shorter period of time. During their active season, water snakes show a pronounced tendency for crepuscular/early evening feeding, even when held in the laboratory under *ad libitum* food conditions (my unpublished data). As discussed above, there is a period of vulnerability of fishes to predators that occurs during early evening (Helfman 1986). In such a case, the full moon phase can potentially be more productive for a predatory water snake than the dimmer first quarter. Since the full moon rises approximately at sunset (Fig. 4), it may not ascend to the relevant (i.e. activity suppressing) height before the evening feeding peak. However, the first quarter moon is at its zenith approximately at sundown, remaining high in the sky in the early evening. In this context, it is noteworthy that the moon is dimmer at the horizon than at zenith due to atmospheric attenuation (Austin *et al.* 1976), and that the moon's light is often blocked by topography or vegetation when near the horizon. Such a phenomenon could explain why snake activity during the full moon phase is often higher than during the first quarter (this study; Madsen and Osterkamp 1982). Thus, in addition to endogenous lunar cyclicity, another mechanism can potentially produce a lunar rhythm: a circadian rhythm interacting with moonrise/set times that vary around the lunar cycle (see Neumann 1981).

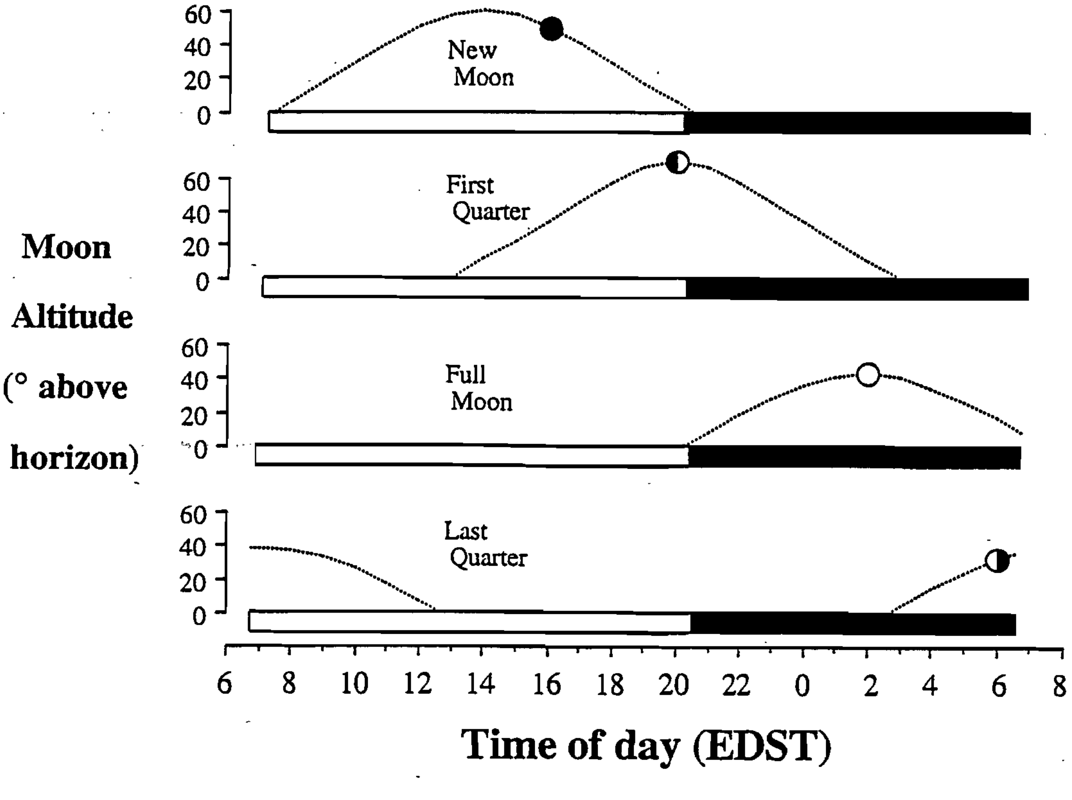

Figure 4. The height of the moon above the horizon on the days of the four lunar phases in April 1997. The data for Maryville, Blount Co., TN that are plotted here were obtained online from the U. S. Naval Observatory (see Methods).

Although lunar rhythms have historically been studied mainly in reference to the tidal responses of marine organisms (Gibson 1978, Neumann 1981), increasing scrutiny in nonmarine habitats has revealed lunar effects in a variety of animals. It seems likely that the phenomenon exists for many nocturnal taxa in habitats where vision mediates predator-prey interaction (Lima and Dill 1990). In the context of acting as visual predators, and on the practical side, I would encourage snake researchers to investigate lunar cyclicity in the course of their field collecting of nocturnal taxa.

SUMMARY AND CONCLUSIONS

1) There is greater water snake foraging activity at higher water temperatures.

2) There is greater water snake foraging activity during dark and waning moons. Predation both by and upon the snakes may be relevant to understanding the origin and maintenance of this phenomenon.

3) Changes between moon phases in the timing of lunar ascent/descent may be an important part of lunar rhythms in addition to changes in illumination.

4) Lunar rhythms probably await discovery in many taxa of predators and prey in aquatic systems. If nothing else, it may help guide the researcher in choosing the times for field collecting.

ACKNOWLEDGMENTS

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NEST-SITE SELECTION OF GRAY SQUIRRELS, *SCIURUS CAROLINENSIS* (RODENTIA: SCIURIDAE): IMPLICATIONS FOR MANAGEMENT IN WESTERN KENTUCKY

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ABSTRACT. Management methods for gray squirrels can be more effective with knowledge of the nesting sites preferred by gray squirrels (*Sciurus carolinensis*). The location of leaf-nests of gray squirrels were compared among three different forest habitats: Larger-tree, old (116-125 years) continuous-forest habitat (3 sites, 2 ha each), smaller-tree, young (85-92 years) continuous-forest habitat (3 sites, 2 ha each), and isolated woodlot (106 years) habitat (1 site, 3 ha). The isolated woodlot contained a significantly fewer number of small (dbh<20 cm) and total number of trees than either continuous-forest habitat. The isolated woodlot had a significantly higher density of nests (12.5 nests/ha) than the larger-tree or smaller-tree continuous-forest habitats (3.2 ± 0.9 nests/ha and 3.3 ± 0.3 nests/ha, respectively). The density of gray squirrels in the isolated woodlot (13.2 squirrels/ha) was also significantly greater than in the larger-tree and smaller-tree continuous-forest habitats (1.9 ± 0.6 and 1.8 ± 1.0 squirrels/ha, respectively). Gray squirrels chose significantly fewer small size trees (dbh<20 cm) and significantly more medium size trees (dbh 20-50 cm) for leaf-nest placement than expected based on tree availability. Gray squirrels chose large size trees (dbh>50 cm) for leaf-nest placement in accordance with tree availability. Sizes and species of nest-trees preferred by gray squirrels need be taken into account when managing for this game species. Timber harvesters should be made aware of the possible destruction of preferred nest-sites when cutting medium to large size trees, especially oaks and other food-producing species of trees.

INTRODUCTION

Nest-site selection is an important component of animal behavior that has important ramifications for an individual's future reproductive effort and success (Stone *et al.* 1996). Nest-sites must be equipped to avoid predators and provide a suitable environment to rear young (Tittensor 1970). One group of mammals that has been used frequently in studies of nest-sites is the tree squirrels (Sciuridae).

The main focus of studies on nest-sites of tree squirrels has been the physical characteristics of nest-sites. Characteristics of a nest-site include the species, height, and dbh (diameter at breast height) of a nest-tree, number of trees in contact with a nest-tree, height of nest from the ground, and food availability at the nest-site. These characteristics will, presumably, affect the reproductive success of tree squirrels and, therefore, population densities of tree squirrels in a given area.

Preferences for specific nest-site locations have been documented for several species of tree squirrels. Leaf-nests of tassel-eared squirrels in the Coconino National Forest were located in trees with a dbh of 30.48 - 104.14 cm and were found 4.88 - 27.43 m above the ground in trees 6.10 - 33.53 m high (Keith 1965). In Grand Canyon National Park, an average leaf-nest height of 15 m, in trees averaging 50 cm dbh (dbh ranges were from 30 to 76 cm), was recorded (Hall 1981). The average dbh of trees used for leaf-nest placement by fox squirrels in Ohio woodlots was 40.64 cm (Baumgartner 1943). Red-bellied squirrels on Tomogashina Island, Japan placed their leaf-nests at a height that was 70% of nest-tree height (Setoguchi 1991). In areas of pine and mixed pine-hardwood forests in central Georgia, gray squirrels placed leaf-nests in trees with a dbh of 20 - 60 cm more often than expected, in trees <20 cm less often than expected, and in trees >60 cm in proportion to their availability (Edwards and Guynn 1995). Studies in deciduous and mixed forest areas in Vancouver, British Columbia, indicated that preferred locations for placement of gray squirrel leaf-nests averaged 11.94 m in height (Robinson and Cowan 1954). Canopy cover, ground and brush cover, and the presence of food resources also influence densities and nest-sites of gray squirrels (Flyger and Gates 1982, Nixon and Hansen 1987).

The study of nest-site selection by gray squirrels, and methods to maintain or manipulate densities, is of significance to game, forest, and urban managers. Gray squirrels are the most heavily hunted species of tree squirrel in the United States. Roughly 40,000,000 are harvested annually with the heaviest portion of the harvest in southern states (Flyger and Gates 1982). A mixture of nut-producing species of trees, such as oaks and hickories, provide an important part of the diet of gray squirrels. Gray squirrels also feed on seeds, fungi, fruit, buds, and the cambium layer beneath the bark of trees.

Gray squirrels prefer to nest in naturally-occurring dens (*i.e.*, tree cavities); however, they also frequently build leaf-nests (Fitzwater and Frank 1944). Most management plans have focused on providing suitable nest-sites for gray squirrels (Flygar and Gates 1982). Game managers have often recommended that old, hollow, heart-rotted, or diseased trees be saved as den trees for gray squirrels (Sanderson 1975). Sanderson (1975) recommended that vigorous pole- and saw-timber trees might also provide dens and should be recognized in forestry management practices. An alternative to management practices that focus on den availability is management that maintains or manipulates the availability of preferred sites for placement of leaf-nests by gray squirrels. Management for leaf-nests would be of particular value in habitats with few den trees available.

Within western Kentucky, nest-site selection and management of gray squirrels is of particular interest because gray squirrels are found commonly in many different habitat types and are an important game species. The wildlife management division of Tennessee Valley Authority's Land Between The Lakes (LBL), Kentucky, uses prevalence of gray squirrels as an indicator of mature hardwood forests (Tennessee Valley Authority 1994). The goal of game management has been to allow the removal of that portion of the gray squirrel population which is annual surplus and would be lost to natural causes if not hunted (Mosby *et al.* 1977). Better knowledge of nest-site selection by gray squirrels would assist in developing management plans that aim to maintain a desired density of gray squirrels. Once the characteristics of suitable nesting locations are better understood, such locations can either be created or destroyed to maintain a desired squirrel density. A better understanding of factors that influence or determine placement of leaf-nests by gray squirrels is needed for more effective and efficient management.

The objective of our research was to investigate the density and location of leaf-nests in forest habitats. Deciduous forest habitats with larger-sized and older trees were expected to contain a greater number of naturally-occurring tree cavities, which could be used as den sites, than younger-aged deciduous forests with smaller-sized trees. The higher prevalence of cavities would allow for higher densities of gray squirrels (Uhlig 1956). Larger-tree forests would also contain a greater supply of food provided by mature trees, such as oaks and hickories. Greater food availability has a direct effect on litter sizes (Barkalow *et al.* 1970), hence, a greater density of gray squirrels. Younger-aged/smaller-tree forests were expected to have fewer squirrels and a higher frequency of leaf-nests per squirrel than larger-tree forests because of lower availability of tree cavities and food.

We also investigated the placement of leaf-nests by gray squirrels in different forest habitats. Habitat structure can affect the number and placement of leaf-nests (*e.g.* Fitzgibbon 1993). Differing habitat structures provide more or fewer preferred locations for leaf-nests.

MATERIALS AND METHODS

Study locations were chosen based on three requirements: 1) study locations must be in no-hunting zones, 2) study locations found in continuous-forest habitats must be in different-aged stands of woods, and 3) one habitat must contain a forest structure different from a continuous-wooded environment. Potential study locations of the continuous-forest habitat were identified at LBL in Trigg County, Kentucky. The 12 potential study locations were located in the Environmental Education Area (EEA) in the northwest portion of LBL between Mulberry Flat and Silver Trail roads (Fig. 1).

We used harvest maps and tree cores to determine which locations to use for continuous-forest study plots. Harvest records of 1976, 1983, 1987, and 1990, provided by the Forestry Department of LBL, were used to determine which areas we would sample. Tree cores were taken from the four largest white oaks (*Quercus alba*) in each of the 12 potential two-hectare study locations. Cores were then examined with a dissecting microscope to count the growth rings present. The mean age of cores from the four white oaks provided a good estimate of forest-age for each potential study location (E. Schmeckpeper, pers. comm. Forestry Department, Tennessee Valley Authorities, Land Between The Lakes, Golden Pond, KY). We chose the three locations that were estimated to be the oldest forest to represent a "larger-tree continuous-forest" habitat. Likewise, the three locations that contained the youngest forest comprised a "smaller-tree continuous-forest" habitat. In addition to continuous-forest habitats, a more disturbed isolated woodlot habitat that had not been hunted within the last 10 years was used to represent an alternate forest structure. The "isolated woodlot" habitat was located in Calloway County, Kentucky (Fig. 1). These selections resulted in seven study locations representing three different habitats.

We subdivided the smaller-tree continuous-forest habitat into three sites, two hectares in size each. The estimated age of trees in the smaller-tree forest habitat ranged from 85 to 92 years. The mean dbh of white oaks sampled to determine the age of the forest was 39.0 cm ± 0.3 SE. All sites within the smaller-tree continuous-forest habitat contained, and were bordered by, woods that had received some form of cutting within the last 20 years. The smaller-tree continuous-forest sites were located in the NW portion of the EEA at LBL (Fig. 1).

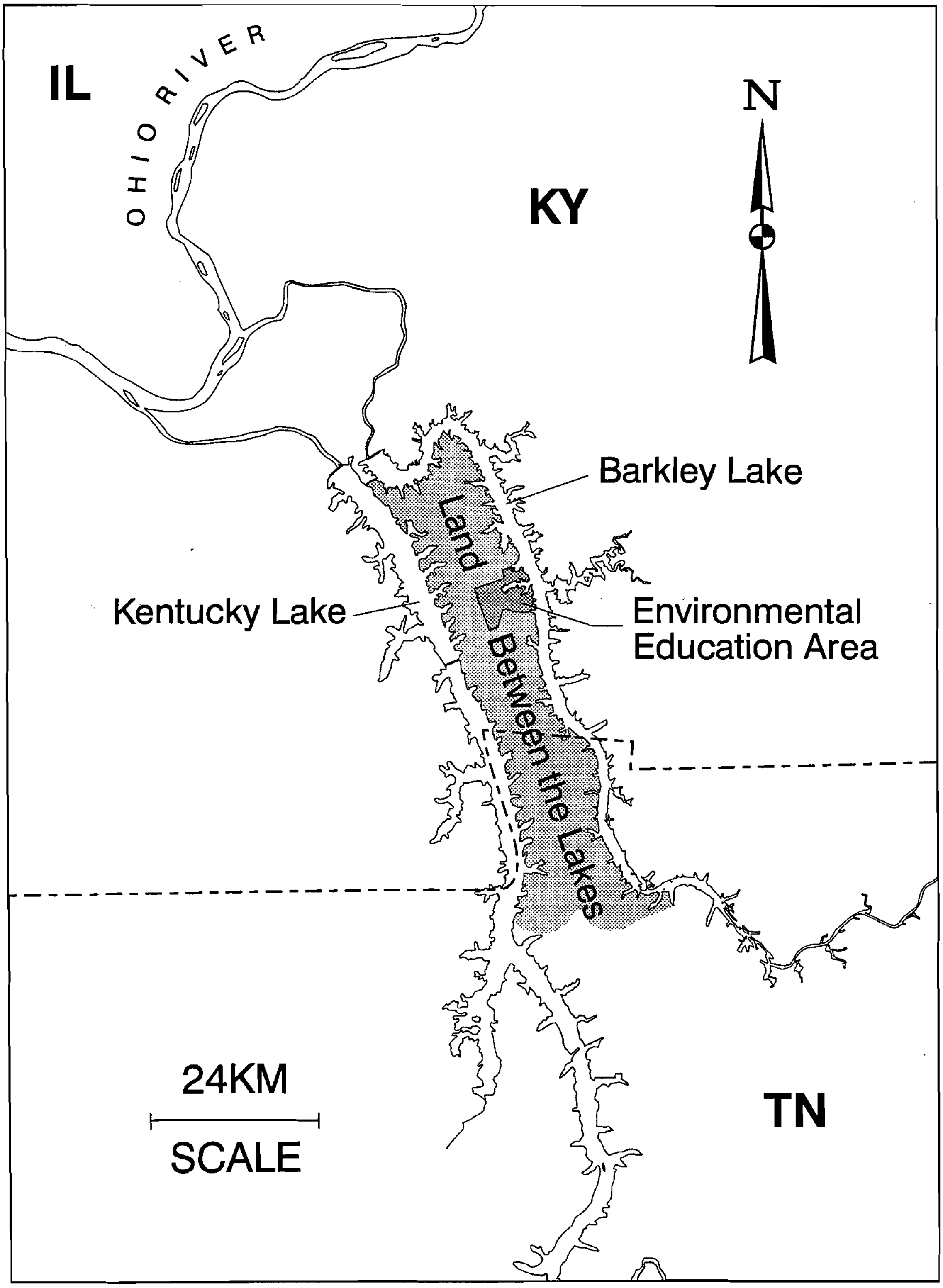

Figure 1. Map of the study area. All continuous forest habitats were located in the Environmental Education Area of Land-Between-the-Lakes. The isolated woodlot was located west of LBL in Calloway County, Kentucky.

The larger-tree continuous-forest habitat was also subdivided into three sites, two hectares in size each. The estimated age of the trees in the larger-tree continuous-forest habitat ranged from 116 to 125 years. The mean dbh of white oaks sampled to determine the ages was 47.3 cm ± 1.6 SE. Larger-tree continuous-forest sites all contained, and were bordered by, woods that had not been cut within the last 20 years. These sites were located in the southwest portion of the EEA at LBL (Fig. 1).

The isolated woodlot was studied as one intact site, three hectares in size. The woodlot was bordered on one side by highway, one side by a cattle field, and on two sides by agricultural fields. The isolated woodlot contained some developed area (*e.g.*, buildings) that comprised slightly less than one hectare of the total woodlot. The mean age of the trees cored in the isolated woodlot was 106 years. The mean dbh of white oaks sampled to determine the age was similar to that of the old-continuous forest, at 46.2 cm ± 0.8 SE.

We made measurements of vegetation in each of the study sites to estimate the habitat characteristics of each habitat. Within each of the seven study sites, measurements were made in five areas, 30 m in diameter each, to determine the amount and type of vegetation present. Four of these five areas were in the corners of the sites (35 m from the corner, at a 45° angle). The fifth sample area was in the center of the site. A total of 35 sample areas (seven study sites with five sample areas each) were sampled for habitat characteristics.

Because gray squirrels are mainly arboreal, we focused our measurements on the vegetation to characterize each habitat. Within each of the 35 sample areas, all species of trees, number of trees, proportion of total trees for each tree species, and dbh of trees were recorded. Snags (dead trees) were categorized as a separate species of tree. The dbh of trees was measured using a forester's caliper (Haglof, Sweden; ±1 cm) and were categorized into small trees (<20 cm), medium trees (20 - 50 cm), and large trees (>50 cm). Trees were defined as any woody vegetation ≥3 cm in dbh. The measurements of trees in the five sample areas within a study site were combined to determine mean values for each study site within a particular habitat. The total basal area of trees (Cox 1990) was also determined for each habitat and converted to m^2/acre. Vegetative cover was measured from 0-3 m in height in each sample area using a profile board (Nudds 1977).

The density of gray squirrels in each of the seven study sites was estimated to determine whether a correlation existed between leaf-nest densities and squirrel densities. Because live-trapping was largely unsuccessful, we used line transects to estimate the densities of gray squirrels. We walked two transects (223.6 m) diagonally across each of the seven study sites on three different occasions. Transects were walked during morning or late afternoon hours in May, 1995. The Hayne's method (Hayne 1949) was then used to estimate squirrel density.

All measurements taken of trees in which leaf-nests were found, and measurements of the location of leaf-nests within nest-trees, were used to characterize nest-sites. Leaf-nests of gray squirrels that were present within the seven study sites were found during late fall and early winter 1995, when leaves were absent from the trees. Each of the seven study sites was carefully examined twice, with the aid of 7 X 35 Nikon binoculars, so that all leaf-nests were found. Absolute densities of leaf-nests were determined for each habitat and compared with the densities in the other habitats studied. For each tree that contained a leaf-nest, the tree species was recorded. The height of nest-trees was determined using a Suunto clinometer (±1.0 %) and the dbh was measured with a forester's caliper.

We then counted the number of trees in contact with each nest-tree. Trees with branches touching any portion of the tree that contained a leaf-nest were counted. The mean number of trees in contact with nest-trees was then calculated for each habitat.

We also made measurements that characterized the placement of leaf-nests by gray squirrels. We measured the height of each nest (± 1.0 cm), using a clinometer. The distance that leaf-nests were located from the edge or dripline of a tree and the distance of each nest from the trunk or center of the nest-tree was measured (± 0.1 m). If leaf-nests were not located in line with the main trunk of the tree, compass bearings, measured to the nearest 45° (*i.e.*, N, NE, E, SE, S, SW, W, NW), were taken from the center of the tree to the location of nest placement.

We used one-way analyses of variance (ANOVA) and Tukey's HSD (Honest Significant Difference) pairwise comparisons to determine significant differences in the dependent variables among the habitats. The dependent variables were number of trees, number of tree species, and number of trees in each dbh range (small trees, medium trees, and large trees). Chi-square (X^2) tests of independence were used to compare the proportion of trees within each size range to the proportion of trees not contained within that size range among the three habitats. Chi-square tests of independence were also used to compare the proportion of trees within each species of tree to the proportion of trees not within that tree species among habitats.

We used one-way ANOVAs and Tukey's HSD tests to determine whether the habitat types contained significantly different densities of squirrels and leaf-nests. Characteristics of nest-sites of gray squirrels were analyzed to determine any differences in the location of nests among habitat types. One-way ANOVAs and Tukey's HSD tests were used to compare the species of the nest-tree, height of nest-tree, dbh of nest-tree, height of nests, density of leaf-nests, distance of the nest from the trunk and edge of the nest-tree, and compass direction to the nest.

Chi-square analyses were used to test for significant differences between the number of nests expected and the number of nests observed in each habitat, based on the availability of trees in each dbh size range and the availability of each species of tree. One-way ANOVAs and Tukey's HSD tests were used to determine differences among habitats in the number of trees, number of tree species, and the number of trees in contact with the nest tree. SAS (1990) Version 6.08 was used for all statistical analyses. Data were tested for homoscedasticity and normality prior to use of ANOVAs. A P value of 0.05 was used to indicate statistical significance. All data in text are present as means ± 1 S.E.

RESULTS

Oaks (*Quercus* spp.), hickories (*Carya* spp.), dogwoods (*Cornus* spp.), and snags were the most common species of trees found. Oaks and hickories comprised 10 of the 26 species of trees found within the three habitats (Table 1). The proportions of individual species of trees differed significantly among habitat types for 14 different species of trees ($P < 0.05$, X^2 test, Table 1). The number of species of trees did not differ significantly among habitats ($P > 0.05$, ANOVA, Table 2). The percent vegetative cover from 0-3 m in height also did not differ significantly among habitats.

Table 1. The percentage of each tree species and mean number of species (± 1SE) found in the smaller-tree continuous forest, larger-tree continuous forest, and isolated woodlot habitats. Snags (dead or decaying trees) were categorized as a separate species. Different superscripts within the same row represent significant differences in percent of the total number of trees among habitat types (X^2 test, $P < 0.05$).

Species	Smaller-tree continuous forest	Larger-tree continuous forest	Isolated woodlot
Cornus florida	24.6^{A}	31.7^{B}	12.9^{C}
Quercus alba	19.8^{A}	25.0^{B}	4.0^{C}
snags	14.9	15.5	9.9
Ostrya virginiana	8.0^{A}	2.4^{B}	4.0^{AB}
Quercus stellata	6.8^{A}	4.1^{B}	5.9^{AB}
Quercus coccniea	6.6^{A}	3.9^{B}	6.9^{AB}
Carya glabra	6.2	8.6	5.0
Sassafras albidum	4.8^{A}	2.1^{B}	0.0^{B}
Viburnum nudum	3.5^{A}	0.4^{B}	0.0^{AB}
Quercus marilandica	1.2^{A}	0.7^{A}	7.9^{B}
Quercus velutina	1.1	0.7	0.0
Carya tomentosa	0.6	1.0	2.0
Acer rubrum	0.6^{A}	0.6^{A}	8.9^{B}
Carya ovalis	0.6^{A}	2.4^{B}	0.0^{AB}
Prunus americana	0.3	0.0	0.0
Carya ovata	0.2^{A}	0.5^{A}	8.9^{B}
Liriodendron tulipifera	0.2	0.0	0.0
Nyssa sylvatica	0.2	0.0	2.0
Ligustrum vulgare	0.0	0.0	1.0
Fagus grandifolia	0.0^{A}	0.4^{AB}	2.0^{B}
Prunus serotina	0.0^{A}	0.0^{A}	12.9^{B}
Sambucus canadensis	0.0^{A}	0.0^{A}	2.0^{B}
Celtis spp.	0.0	0.0	1.0
Juniperus virginiana	0.0	0.0	1.0
Ilex opaca	0.0	0.0	1.0
Ligustrum vulgare	0.0	0.0	1.0
Mean # of species	8.3 ± 0.3	8.3 ± 0.3	7.8 ± 1.8

Table 2. Mean density estimates (±1 SE) of gray squirrels and of leaf-nests built by gray squirrels in the smaller-tree continuous-forest, larger-tree continuous-forest, and isolated woodlot habitats. Different superscripts within the same column represent significant differences ($P < 0.05$, ANOVA).

	Leaf-nest density (number/ha)	Gray squirrel density (number/ha)
Smaller-tree continuous forest	3.3 ± 0.3^B	1.8 ± 1.0^B
Larger-tree continuous forest	3.2 ± 0.9^B	1.9 ± 0.6^B
Isolated woodlot	12.5^A	13.2^A

The number and proportion of trees within each dbh size range differed among the habitats (Fig. 2). The larger-tree continuous forest contained a significantly lower proportion of trees within the medium-sized dbh range than did the smaller-tree continuous forest or isolated woodlot habitats. The isolated woodlot habitat contained a significantly greater proportion of trees within the large-sized dbh range than did either continuous-forest habitat ($P < 0.05$, X^2 test, Fig. 2). The basal area of trees in the isolated woodlot (737 m^2/acre) was far less (64%), however, then that in the continuous forests.

The mean density of gray squirrels was significantly greater in the isolated woodlot than in either continuous-forest habitat ($P < 0.05$, ANOVA, Table 2). In the isolated woodlot, squirrel densities were approximately six times greater than the densities in the continuous forests.

The mean densities of leaf-nests built by gray squirrels were similar to the densities of gray squirrels. There were significantly more leaf-nests in the isolated woodlot than in either continuous- forest habitat ($P < 0.05$, ANOVA, Table 2). Continuous habitats contained a ratio of approximately 1.5 - 2 leaf-nests per gray squirrel, while the isolated woodlot contained approximately a 1:1 ratio of leaf-nests to gray squirrels.

Gray squirrels showed a preference for specific species of trees, especially oaks, for placement of leaf-nests in each habitat (Table 3). In the smaller-tree continuous forest, more leaf-nests were placed in scarlet oaks than expected based on the availability of tree species ($P < 0.05$, X^2 test). In the larger-tree continuous forest, gray squirrels chose significantly fewer flowering dogwoods and significantly more post oaks for leaf-nest placement than expected. In the isolated woodlot habitat, significantly more leaf-nests were found in white oaks than expected based on the availability of tree species. Oak trees accounted for 69 percent of the tree species with leaf-nests. Oaks and hickories combined accounted for 89 percent of the tree species with leaf-nests.

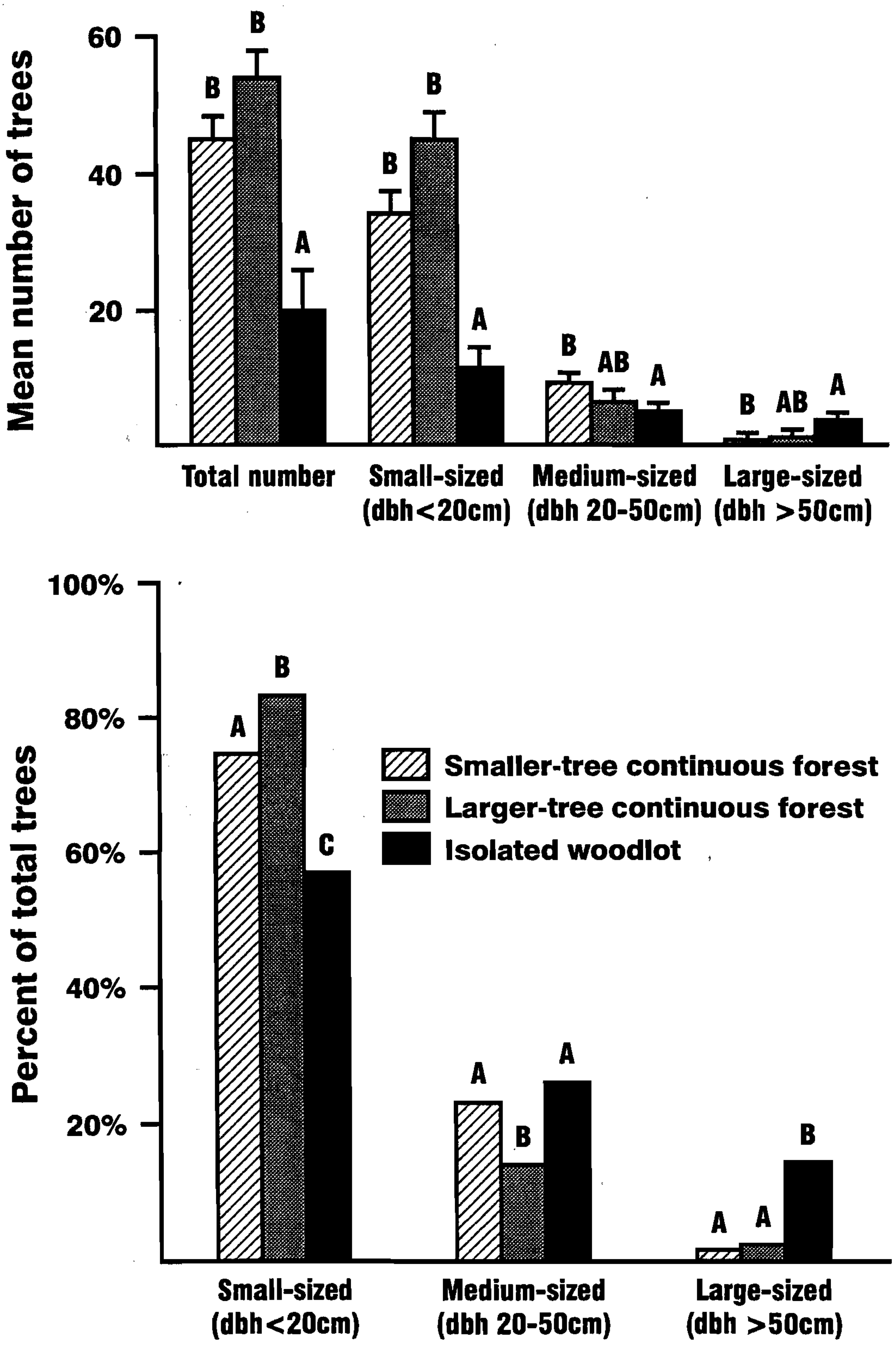

Figure 2. Top: Mean number of trees (± 1 SE) for each forest habitat. Different letters within each size range represent significant differences among mean values ($P < 0.05$, ANOVA). Bottom: The percent of the total number of trees for each forest habitat. Different letters within each size range represent significant differences among proportional values ($P < 0.05$, X^2 test).

Table 3. Number of gray squirrel leaf-nests found in the most prevalent species of trees in the smaller-tree continuous-forest, larger-tree continuous-forest, and isolated woodlot habitats. Superscripts (+ and --) indicate significant selection for or against a species of tree for leaf-nest placement.

	Quercus alba (white oak)	*Cornus florida* (fl. dogwood)	*Carya glabra* (pignut hickory)	*Q. coccinea* (scarlet oak)	*Q. stellata* (post oak)
Smaller-tree continuous forest	7	0	1	5^+	3
Larger-tree continuous forest	9	0^{--}	3	2	4^+
Isolated woodlot	7^+	1	2	4	3

There were no significant differences in the mean height of leaf-nests, height of nest-trees, or dbh of nest-trees among the habitats ($P > 0.05$, ANOVA, Table 4). Gray squirrels chose significantly fewer small-sized and significantly more medium-sized trees for placement of leaf-nests in each habitat than would be expected based on the availability of trees of these sizes ($P < 0.05$, X^2 test, Fig. 3). Gray squirrels chose larger-sized trees in accordance with their availability in each habitat.

The number of trees in contact with nest-trees did not differ significantly among the three habitats ($P > 0.05$, ANOVA). The smaller-tree and larger-tree continuous forests contained a mean number of 2.9 ± 0.3 and 2.8 ± 0.2 trees in contact with a nest-tree, respectively. The isolated woodlot contained a slightly greater average of 3.6 ± 0.4 trees in contact with a nest-tree.

There were no significant differences among the three habitats in the distance that leaf-nests were placed from the center or edge of the nest-tree ($P > 0.05$, ANOVA, Table 4). When data from all habitats were combined, more than three-fourths (78.1%) of all nests studied were located against the main trunk of the nest-tree.

Table 4. Mean measurements (±1SE) of trees that contained a leaf-nest and of leaf-nest placement. Nest distance was the distance from the center of a nest-tree to the center of the leaf-nest in that tree.

	Height of leaf-nest (m)	Height of nest-tree (m)	dbh of nest-tree (m)	Distance of nest from center of tree (m)	Distance of nest from edge of tree (m)
Smaller-tree continuous forest	15.0±1.6	23.0±1.5	40.6±2.8	0.8±0.3	4.1±0.5
Larger-tree continuous forest	13.2±0.9	20.9±1.2	35.0±3.8	0.4±0.3	4.0±0.4
Isolated woodlot	13.1±1.0	20.1±1.2	34.9±3.0	0.5±0.4	3.4±0.4

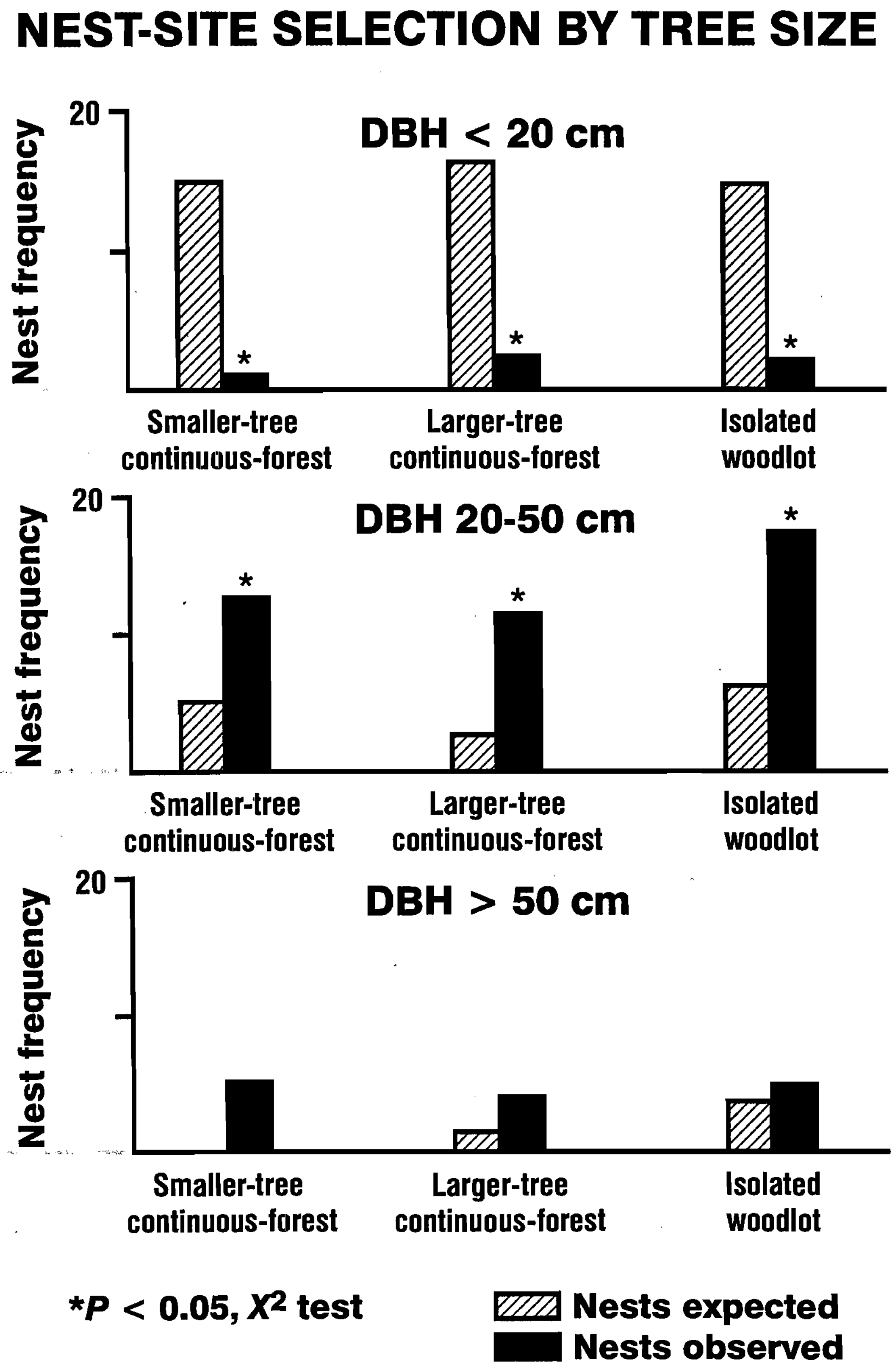

Figure 3. Number of gray squirrel leaf-nests expected and observed within each dbh size range in the smaller-tree continuous forest, larger-tree continuous forest, and isolated woodlot habitats. Expected values were based on the availability of trees in each dbh size range.

DISCUSSION

Gray squirrels chose similar locations for placement of leaf-nests in each of the habitats that we studied. The consistency of placement of leaf-nests indicated that specific characteristics of trees were important for nest-site selection, regardless of habitat type. Knowledge of these important nest-site characteristics are of practical value in management practices.

Many similarities in habitat characteristics were found between the larger-tree and smaller-tree continuous-forest habitats. Surprisingly, the total number of trees, number of trees within each size range, and basal area of trees did not differ significantly between the continuous-forest habitats (Fig. 2). If the ages and sizes of trees in the continuous-forest habitats studied had been more different, differences in the densities of squirrels in these habitats might have occurred (*e.g.*, Buchanan *et al.* 1990).

The species composition of trees in forest habitats can affect the densities of gray squirrels. For example, gray squirrel densities in northern Wisconsin were highest in mature maple/oak habitats as compared to habitats containing many birch (*Betula*), pine (*Pinus*), fir (*Abies*), or cedar (*Thuja*) species of tree (Riege 1991). Because oaks and hickories were abundant and were suitable as nest-tree species in our study, each of the habitats studied could be expected to support a relatively high density of gray squirrels. Only the isolated woodlot had a high density of gray squirrels, however.

The isolated woodlot was found to be a different type of habitat, as compared to the continuous forests, in regards to proportions of individual species of trees, total number of trees, number of small-sized dbh trees, proportions of small-sized and large-sized dbh of trees, and total basal area of trees (Table 1, Fig. 2). The high densities of gray squirrels found in the isolated woodlot could be attributed to a combination of factors. One factor was the greater number and proportion of large-sized trees (dbh > 50 cm) found in the isolated woodlot (Fig. 2). Densities of leaf-nests of gray squirrels in areas of isolated woodlots in England and, therefore, densities of gray squirrels, were higher in isolated woods that had a high density of large trees (Fitzgibbon 1993). Results from a Wisconsin study showed that acorn production from red oaks increased linearly with the basal area of the tree (Riege 1991). In each of our habitats, large-sized trees were used for leaf-nest placement in accordance with their availability (Fig. 3) and, more large-sized trees were found in the isolated woodlot than in the continuous-forest habitats. The isolated woodlot would, therefore, be expected to contain a high density of squirrels.

A second factor that may have contributed to higher densities of gray squirrels in the isolated woodlot was the presence of a larger woods located nearby. Isolated woodlots found in close proximity of another woods at least 0.5 ha in size were more likely to contain a greater density of gray squirrel leaf-nests than woodlots without nearby woods (Fitzgibbon 1993). A third factor contributing to the higher densities of gray squirrels in the isolated woodlot may have been a greater food supply. Agricultural fields bordering two sides of the isolated woodlot provided an additional food source (*e.g.*, corn) not present in continuous forest habitats. An increased food supply would support higher densities of squirrels (Uhlig 1956, Burger 1969, Manski *et al.* 1981).

The densities of gray squirrels that we estimated in continuous forests in western Kentucky averaged slightly greater than 3 squirrels/ha. Densities of gray squirrels were usually less than 3 squirrels/ha in continuous forests in North Carolina, and were usually less than 3.6 squirrels/ha on the edge of continuous-forest woods in state forests in West Virginia (Barkalow *et al.* 1970, Uhlig 1956). The density of squirrels that we estimated in the isolated woodlot was 12.5/ha, agreeing with the high densities reported in other small woods (Don 1985, Gurnell 1987). Studies have shown that the densities of gray squirrels in small (< 10 ha) woodlots can be as high as 16 squirrels/ha (Doebel and McGinnes 1974). In urban parks, densities can be even greater, with 21 squirrels occurring per hectare (Manski *et al.* 1981).

As expected, we found greater densities of leaf-nests in habitats that contained greater densities of gray squirrels (Table 2). Previous studies have used the densities of leaf-nests/ha as a predictor of the density of gray squirrels/ha (Fitzgibbon 1993). These predictions were based on a ratio of 1.6:1 leaf-nests per gray squirrel (Don 1985). The prediction method was considered accurate for the densities of squirrels found in continuous-forest habitats but, underestimated gray squirrel densities in isolated woodlots. Our results for the continuous-forest habitats were similar to the predicted ratio, at 1.5 - 2 leaf-nests per gray squirrel. In the isolated woodlot, however, the predicted density underestimated the gray squirrel density, with our ratio being one leaf-nest per gray squirrel.

The species of trees that gray squirrels chose for placement of leaf-nests in our study was consistent with results from a previous study in areas of pine and mixed pine-hardwood forests in central Georgia (Edwards and Guynn 1995). In central Georgia, more leaf-nests were found in oaks and fewer were found in dogwoods than expected based on availability of tree species. Our results indicated significant selection for a species of oak for placement of leaf-nests in each habitat type that we studied. Each species of oak that was chosen more frequently for placement of leaf-nests than expected (Table 2), comprised less than 6.5 percent of the total trees found within that habitat type. Despite their relatively low abundance, species of oak were preferred for placement of leaf-nests, perhaps because they often contained many characteristics of nest-trees that were preferred by gray squirrels. These favorable characteristics included a medium-sized dbh and preferred tree height. Also, the food provided by oaks would influence nesting locations. Nixon and Hansen (1987) reported that leaf-nests are usually built in or near favored food trees in late summer.

The flowering dogwood was the only species of tree actively selected against for nest placement, based on the availability of tree species. Flowering dogwood was selected against in the larger-tree continuous forest, where it comprised greater than 30 percent of the total trees. Flowering dogwood trees usually had a smaller dbh (< 20 cm) and, therefore, may have been less suitable for placement of leaf-nests. Height of flowering dogwoods was often far below the height of trees used for nest placement. Food supply was probably not a factor in selection against dogwoods because its fruit is readily eaten by gray squirrels (Edwards and Guynn 1995).

Gray squirrels chose trees of similar height and dbh for placement of leaf-nests in each habitat. The nest height chosen for placement of leaf-nests was also consistent among habitats. Gray squirrels most often placed their leaf-nests at approximately 65 percent of the total tree height, using trees that averaged 21.4 ± 1.3 m in height, and that had a mean dbh of 37 ± 3.2 cm. Gray squirrels in central Georgia also chose trees with a medium-sized dbh (20 - 60 cm) for placement of leaf-nests (Edwards and Guynn 1995).

Leaf-nests were most often placed against the main trunk of nest trees in all habitats studied. Similar results have been reported in other studies of nesting sites of gray squirrels. In a Connecticut study, only 3.4 percent of leaf-nests were built on lateral branches away from the trunk (Fitzwater and Frank 1944). Gray squirrels in an introduced population in British Columbia also preferred nest locations that were against the main trunk of nest trees (Robinson and Cowan 1954). Placement of leaf-nests against the main trunk increases the stability of a nest.

To increase potential nesting sites for gray squirrels, we suggest managing for the size and species of trees most often selected by gray squirrels for nest placement. The consistency of nest-sites chosen by gray squirrels, regardless of habitat characteristics, indicated that management of size and species of trees would be useful in management plans in diverse habitat types or structures. Management procedures that would be expected to increase potential nesting sites of gray squirrels include maintaining the presence of species of oak with a dbh of a medium size (20 - 50 cm). These oaks should be approximately 15-30 m in height and have other trees nearby, allowing the branches of the surrounding trees to act as multiple pathways by which a squirrel can pass through the canopy. Encouraging the growth of mature trees with large crowns will also increase mast production and, therefore, food supply. Species of trees with trunk and size characteristics that are similar to those of oaks (*e.g.*, mockernut, shagbark, and red hickories) and that provide a food source, might also prove to be favorable species of trees for gray squirrel leaf-nests. Further research needs to be conducted in geographic areas other than those studied here to confirm whether or not the sizes and species of trees, trees in contact with a nest-tree, and location of nest placement within nest-trees are of importance to nest-site selection by gray squirrels in other habitat types and forest structures.

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RESULTS OF AN ONGOING SURVEY OF METAZOAN SYMBIONTS OF FRESHWATER MUSSELS (UNIONIDAE) FROM KENTUCKY LAKE, TENNESSEE

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ABSTRACT. A total of 500 unionid mussels (Unionidae) comprising eight species (*Amblema plicata*, *Elliptio cressidens*, *Fusconaia ebena*, *Fusconaia flava*, *Megalonaias nervosa*, *Quadrula metanevra*, *Quadrula pustulosa*, *Quadrula quadrula*) have been examined in an ongoing study of the metazoan symbionts of mussels in Kentucky Lake, Tennessee. Sampled mussels have all been gathered between Tennessee River miles 87 and 198. To date, 13 taxa of symbionts have been found, together representing six phyla (Platyhelminthes, Nematoda, Annelida, Mollusca, Tardigrada, and Arthropoda), 12 families, and at least 13 genera and species. Approximately 90% of the collected symbionts were parasites representing four species (*Aspidogaster conchicola*, *Cotylogaster occidentalis*, *Cercaria filicauda*, and *Unionicola* sp.). Over 99% of all parasites belonged to the Aspidogasteridae (two species) and Unionicolidae (one species). A flatworm, *Aspidogaster conchicola* (Aspidogasteridae) and a mite, *Unionicola* sp. (Unionicolidae) were the only parasites which exhibited overall prevalences greater than 10% in some mussel species. *Aspidogaster conchicola* infected all eight of the studied mussel species and within species exhibited overall prevalence values ranging from 14-73% and corresponding overall mean intensity values from 1.0-7.8 worms per mussel. *Unionicola* sp. infected six of eight studied mussels species and exhibited overall prevalence values ranging from 0-94.6% and corresponding overall mean intensity values from 0-8.4 mites per mussel. All parasite taxa collected to date in this study are known to exhibit one or two host life cycles, and those with two host life cycles utilize fishes as definitive hosts. None of the collected parasites have been reported to infect humans.

INTRODUCTION

The southeastern United States is the center of diversity for the freshwater mussel family Unionidae. This regional unionid fauna has historically consisted of at least 269 species, together representing 91% of North America's freshwater mussels (Neves *et al.* in press). Within the Southeast, the states of Alabama and Tennessee historically have possessed the richest unionid faunas (175 and 132 species, respectively) (see Neves *et al.* in press). Tennessee's unionids have resided in all of its five major drainages where ideal aquatic habitats for this diverse fauna have existed.

Throughout North America, Unionidae is experiencing an unprecedented decline in both numbers of species and numbers of individuals due to various environmental factors which all seem associated with human activity (Marking and Bills 1979, Schmidt *et al.* 1989, Stolzenburg

1992, Williams *et al.* 1992). Within Tennessee, 20 species of freshwater mussels are federally listed as endangered species (Hatcher 1995). Because of the commercial importance of some unionids (McGregor and Gordon 1992) and due to the potential use of unionids as valuable indicator organisms capable of detecting minute levels of aquatic toxicants (Jacobson *et al.* 1993), recent state, federal, and private conservation efforts have focused on the management, propagation, and culturing of native freshwater mussels. To ensure the applied success of these efforts, basic natural history information about unionids is needed to allow resource managers and biologists to properly care for captive individuals and to facilitate the monitoring of wild populations and the identification of species in need of management.

A thorough understanding of the overall impact of parasitism on wild unionid populations does not exist. This is unfortunate because parasites can play important roles in wild and captive populations, and the dearth of information on this subject makes it impossible to evaluate the potential significance of parasitism regarding unionid aquaculture. Much of the literature dealing with parasites of freshwater mussels is dominated by geographically scattered parasite records associated with taxonomic accounts that generally lack temporal scope. Many of these reports have documented the presence of parasites without supplying data concerning prevalence and intensity of infection, or quantitative estimates of total parasite burdens. Some studies, however, have focused more closely on the natural parasite burdens of unionids (e.g., Kelly 1899, Najarian 1955, Hendrix and Short 1965, Flook and Ubelaker 1972, Danford and Joy 1984), and most recently Duobinis-Gray *et al.* (1991) and Vidrine and Wilson (1991) have reported prevalence and mean intensity data respectively for a species of parasitic flatworm in Kentucky and for some parasitic mites in Tennessee that infect some unionid species.

This report presents results to date of an ongoing study designed to gather additional information about the parasites naturally occurring in wild unionid populations via a survey of the metazoan associates of several species of freshwater mussels within the Tennessee River system. In addition to documenting parasite presence, the study was designed to provide information regarding parasite prevalence and intensity, as well as preliminary information regarding histopathology associated with parasitic infection. This report does not present all of the results gathered to date regarding this ongoing project, and readers interested in results obtained during the first two years of this study should consult Curran and Benz (1994, 1995).

MATERIALS AND METHODS

A total field sample of 500 unionid mussels comprising eight species was collected for this study between May 1994 and July 1996 by Tennessee Wildlife Resources Agency (TWRA) biologists in Kentucky Lake (an impoundment of the Tennessee River). Field samples were gathered as a series of ten collections from three localities within the reservoir (TN river mile *circa* 88, TN river mile 168, and TN river mile *circa* 197) (Fig. 1). Mussels were placed in individual plastic bags along with species identification labels. Biologists included a data sheet providing information concerning locality of the collection, collection date, collectors' names, and the approximate water depth of the collection with these field samples. Bagged mussels were placed on ice in an insulated container and were shipped to the laboratory within two days of capture. At the laboratory, mussels were stored in a refrigerator (6.5°C) and were examined within 14 days of their arrival.

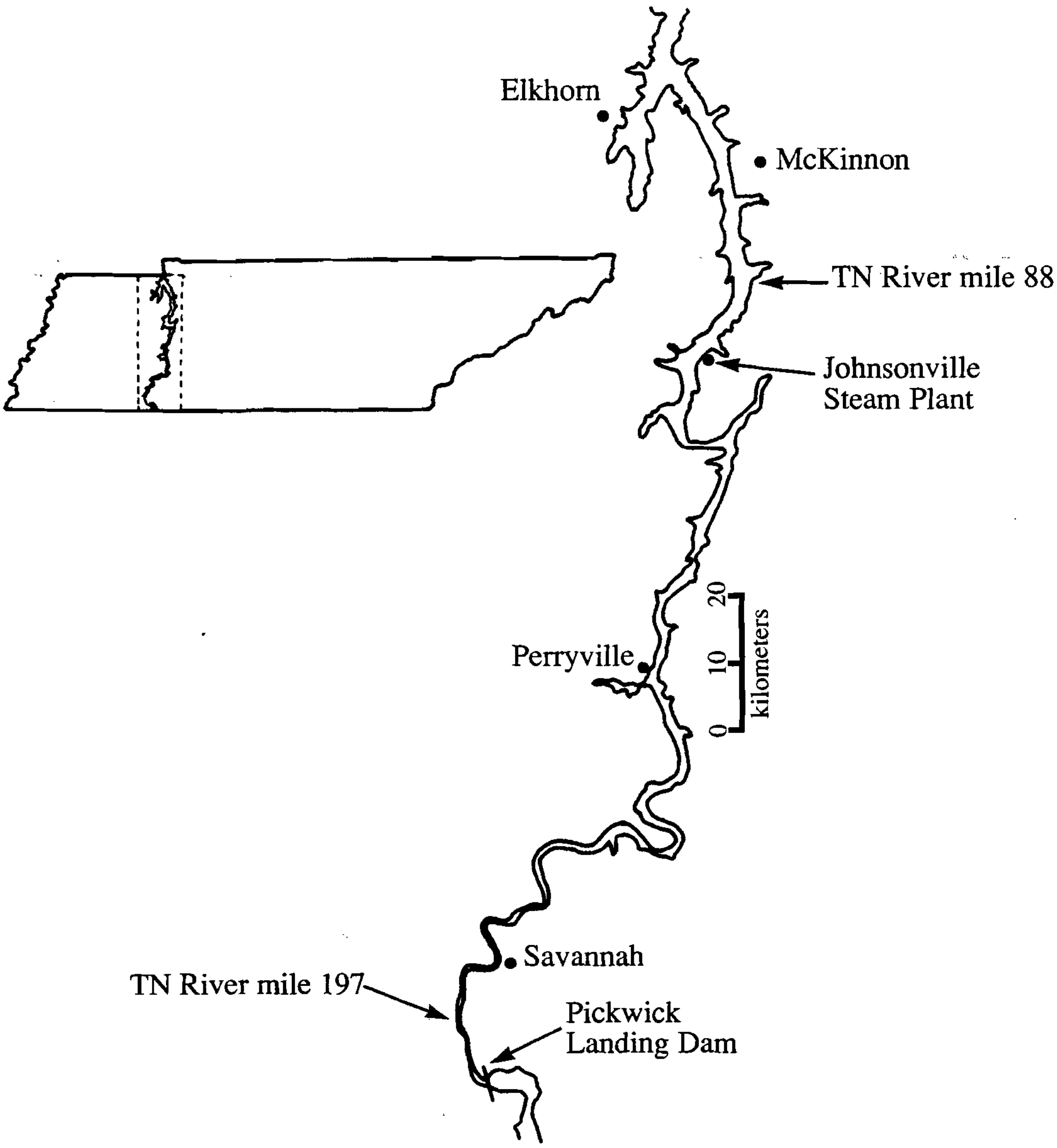

Figure 1. Map showing the 177 km reach of Kentucky Lake (between Tennessee River miles 88 and 197) where mussels were sampled (TN river mile *circa* 88, river mile 168, and river mile *circa* 197).

Four-hundred and eighty-six mussels (Table 1) were examined using the following procedure: water from the collection bag and the outside of the shell was examined for organisms using a dissection microscope. The shell was then opened using a blunt scalpel and the mantle liquid was drained into a petri dish and examined for organisms. Lastly, the soft tissues were examined under low magnification, dissected, and re-examined under low magnification for symbionts. Soft tissues examined included those of the mantle, foot, gills, digestive gland, stomach, intestine, kidney, gonad, and pericardium. Mussels sampled during the last five field collections were shipped to the laboratory bagged in batches rather than individually. Because of the possibility of cross contamination of external symbionts between batched individuals which would bias survey results, the external shells of batched mussels were not examined quantitatively. In addition to the aforementioned examinations, mussels were sexed using wet mount preparations of squashed gonad tissues that were examined for the presence of sperm or glochidia/eggs using a compound microscope. Mussels whose sex could not be determined were excluded from subsequent analysis requiring an identified sex.

Table 1. Numbers of unionids (Unionidae) collected and examined for metazoan symbionts from three regions in Kentucky Lake (Tennessee).[1]

	Tennessee River Mile Localities										
	circa 88						168	*circa* 197			
	Date										
Unionid Species	05/04/94	05/23/94	02/17/95	06/05/95	12/14/95	07/09/96	04/19/95	07/26/94	12/06/94	12/14/95	TOTALS
Amblema plicata	-	13	4	18	-	-	-	-	-	1	36
Elliptio cressidens	-	-	-	-	-	-	16	-	-	-	16
Fusconaia ebena	10	14	20	20	49	24	24	14	19	21	215
Fusconaia flava	-	14	4	-	-	-	-	-	-	-	18
Megalonaias nervosa	-	-	-	15	-	-	20	-	-	-	35
Quadrula metanevra	-	-	-	-	-	-	-	14	18	7	39
Quadrula pustulosa	-	-	12	-	22	-	17	-	-	20	71
Quadrula quadrula	7	13	20	8	6	-	-	-	-	2	56
TOTALS	17	54	60	61	77	24	77	28	37	51	486

[1] Numbers in table do not include 14 mussels which were used in histopathology studies (see text for details).

Mussels from the first five collections were individually weighed using an electronic balance. The following weights (g) were recorded: total weight (i.e., shell and soft tissues), soft weight (i.e., total weight of all soft tissues including the retractor and adductor muscles), and shell weight (i.e., weight of shell without retractor and adductor muscles). Because of a problem which rendered the balance useless, morphometrics (maximum length and maximum width of right valve [cm]) rather than weight were recorded for mussels gathered during the last five field collections.

Metazoan symbionts collected from the examined mussels were fixed, preserved, identified, and stored using standard laboratory techniques (see Pritchard and Kruse 1982), and data regarding the locations of symbionts were recorded. While some symbionts were identified to the level of species, higher level taxa (e.g., genus, family) were used where appropriate to identify others.

A total of 14 mussels comprising four species were selected for histological examination (2 *Amblema plicata*; 2 *Fusconaia ebena*; 9 *Quadrula pustulosa*; 1 *Quadrula quadrula*). Examinations of these mussels differed from those discussed above in that the aforementioned organs were excised using a scalpel and examined under low magnification prior to relaxation and fixation in Bouin's fixative or 10% buffered formalin. Fixed organs were later transferred to 70% ethyl alcohol. Portions of each organ to be examined were isolated and dehydrated through a graded series of alcohols, cleared with xylene, and embedded in paraffin wax using standard histological techniques. Thin tissue sections were cut (12μm serial intervals) using a rotary microtome, and were subsequently stained with Gill's hematoxylin and eosin, and permanently mounted on slides using standard histological techniques. Mounted tissue sections were examined using brightfield microscopy.

Symbiont prevalence and density indices were calculated for each of the two most commonly collected parasites. Symbiont prevalence was defined as the percent of individuals associated with the symbiont in a given host population (or sample), and was calculated as follows:

$$P_{yx_t} = \frac{C_{yx_t}}{N_{yx_t}} \times 100$$

where:

P_{yx_t} = the prevalence of symbiont species x in host species y at time t,

C_{yx_t} = the number of hosts of species y found associated with symbiont species x at time t,

and

N_{yx_t} = the total number of host species y examined for symbiont species x at time t.

Symbiont density (sometimes referred to as intensity) was defined as the mean number of symbionts found with associate hosts in a given host population (or sample), and was calculated as follows:

$$D_{yx_t} = \frac{\sum_{1}^{N_y} A_{yx_t}}{N_{yx_t}}$$

where:

D_{yx_t} = the mean density of symbiont species x associated with host species y at time t,

$\sum_{1}^{N_y} A_{yx_t}$ = the sum of the total number of symbiont individuals of species x collected from each individual species y host examined at time t,

and

N_{yx_t} = the total number of host individuals of species y associated with symbiont species x at time t.

To determine whether parasite burdens differed among the unionid species inhabiting the three collection localities in this study, nested analysis of variance models (ANOVA) were constructed from the parasite prevalence and mean intensity data collected for each of the eight species of unionids. Locality was nested in the host species variable of the models. Separate models were constructed for *Unionicola* sp. and *Aspidogaster conchicola* data. An analysis of variance model was used to examine whether *Aspidogaster conchicola* was found more often in the kidney versus the pericardium of infected unionids. Analysis of variance models were used to separately examine whether parasite prevalence and parasite mean intensity differed among individual unionids of different shell lengths. For these analyses, data from the eight examined host species were lumped and separate analyses were carried out for *Unionicola* sp. and *Aspidogaster conchicola*. Analysis of variance models were used to separately examine whether parasite prevalence and parasite mean intensity differed among unionids of various total weights. For these analyses, data from the eight examined host species were lumped and separate analyses were carried out for *Unionicola* sp. and *Aspidogaster conchicola*. Analysis of covariance models (ANCOVA) were conducted to separately determine whether prevalence and mean intensity values for parasites infecting unionids were different in male versus female unionids. In these models, maximum shell length was used as the covariant parameter. For these analyses, data from the eight examined host species were lumped and separate analyses were carried out for *Unionicola* sp. and *Aspidogaster conchicola*. Analysis of covariance models were conducted to separately determine whether prevalence and mean intensity values for parasites infecting unionids was different between male and female unionids. In these models, total mussel weight was used as the covariant parameter. For these analyses, data from the eight examined host species were lumped and separate analyses were carried out for *Unionicola* sp. and *Aspidogaster conchicola*. For all ANOVA and ANCOVA analyses significance was assessed at $\alpha = 0.05$.

Chi-square tests were performed to determine whether the two most common parasite taxa (*i.e.*, *Aspidogaster conchicola* and *Unionicola* sp.) were independently distributed among individual mussels of each respective host species. The number of observed occurrences of each of the four possible results (i.e., no parasites; aspidogastrid only; unionicolid only; aspidogastrid and unionicolid together) was compared to the number of expected occurrences. The probability of either parasite taxon (aspidogastrid or unionicolid) occurring in a mussel was assumed to be equal to its observed overall prevalence in that species of mussel. The probability of either parasite taxon not occurring in a particular mussel species was calculated as 1 minus the observed overall prevalence in that species of mussel. Expected chi-square values were calculated by multiplying the sample size by the probability that one of the four possible combinations would occur (i.e., no parasites; aspidogastrid only; unionicolid only; aspidogastrid and unionicolid together). The calculated chi-square values for each possible combination were totaled for each of the eight mussel species examined and compared to tabled critical values for the chi-square statistic ($\alpha = 0.05$, df = N-1). In instances when calculated chi-square values were less than or equal to tabled critical values, the presence of the two parasite taxa in mussels was considered to be independent. When calculated chi-square values were greater than tabled critical values, the presence of the two parasite taxa in mussels was considered to be related.

Statistical Analysis Systems© (SAS) software was used throughout this study to perform the ANOVA, ANCOVA, and chi-square analyses outlined above. In instances when the results of any of the aforementioned statistical tests are not mentioned in this report, the reader is hereby advised that test results identified nothing of significance.

RESULTS

Thirteen taxa were found associated with the 500 unionids examined. Together, these symbionts represented six phyla (Platyhelminthes, Nematoda, Annelida, Mollusca, Tardigrada, and Arthropoda), 12 families, and at least 13 genera and species (Table 2). Arthropoda was the most taxon rich of the six phyla and was represented by five genera. Platyhelminthes was represented by three species, all of which were internal parasites of mussels. Nematoda was represented by one genus and Tardigrada was represented by a single species. Five individual oligochaetes represented the only annelids found, and two individual molluscs (a snail and a fingernail clam) were found within the incurrent siphons of separate mussels. Nematodes, annelids, and the tardigrade were all found on the external surface of their unionid associates. Four of the five arthropod taxa were insects found externally on unionids. The fifth arthropod taxon was a parasitic mite (*Unionicola* sp.) which was found internally. By far, the two most common symbiotic taxa were *Aspidogaster conchicola* and *Unionicola* sp., both of which were internal parasites.

Table 2. Metazoan symbionts collected in association with eight species of mussels (Unionidae) sampled from three areas in Kentucky Lake (Tennessee River miles *circa* 88, 168, and *circa* 197) between May 1994 and July 1996. Asterisks denote trematode infections consisting of many daughter sporocysts and cercariae.

Unionid Species	Sample Site [1] (date)	Metazoan Symbiont	Location on/in Host	Number of Associates Collected
Amblema plicata	87.4 (06/05/95)	*Aspidogaster conchicola*	pericardial cavity and lumen of kidney	25
		Unionicola sp.	gill filaments	10
	88.1 (02/17/95)	*Aspidogaster conchicola*	pericardial cavity and lumen of kidney	11
		Unionicola sp.	gill filaments	8
		Dorylaimus sp.	external shell	2
		larval chironomid	external shell	1
		larval gorgoderid	viscera	1*
	89.0 (05/23/94)	*Unionicola* sp.	gill filaments	56
		Aspidogaster conchicola	pericardial cavity and lumen of kidney	24
		Dorylaimus sp.	external shell	13
		larval chironomid	external shell	3
		larval trichopteran	external shell	1
	197.6 (12/14/95)	*Unionicola* sp.	gill filaments	3
Elliptio cressidens	168.0 (04/19/95)	*Aspidogaster conchicola*	pericardial cavity and lumen of kidney	10
		Cotylogaster occidentalis	intestine	1
Fusconaia ebena	87.1 (12/14/95)	*Aspidogaster conchicola*	pericardial cavity and lumen of kidney	103
	87.4 (06/05/95)	*Aspidogaster conchicola*	pericardial cavity and lumen of kidney	25
	88.1 (05/04/94)	*Aspidogaster conchicola*	pericardial cavity and lumen of kidney	12
		Dorylaimus sp.	external shell	7
		Unionicola sp.	gill filament	1
	88.1 (02/17/95)	*Aspidogaster conchicola*	pericardial cavity and lumen of kidney	54
		larval chironomids	external shell	9
		Dorylaimus sp.	external shell	5
	88.1 (07/09/96)	*Aspidogaster conchicola*	pericardial cavity and lumen of kidney	34
	89.0 (05/23/94)	*Aspidogaster conchicola*	pericardial cavity and lumen of kidney	43
		Dorylaimus sp.	external shell	10
		larval ceratopogonid	external shell	1
		tardigrade	external shell	1
	168.0 (04/19/95)	*Aspidogaster conchicola*	pericardial cavity and lumen of kidney	51

Table 2. continued.

Unionid Species	Sample Site [1] (date)	Metazoan Symbiont	Location on/in Host	Number of Associates Collected
Fusconaia ebena (cont.)	197.6 (07/26/94)	*Aspidogaster conchicola*	pericardial cavity and lumen of kidney	36
		Dorylaimus sp.	external shell	4
	197.6 (12/06/94)	*Aspidogaster conchicola*	pericardial cavity and lumen of kidney	28
		oligochaetes	external shell	2
		Dorylaimus sp.	external shell	1
	197.6 (12/14/96)	*Aspidogaster conchicola*	pericardial cavity and lumen of kidney	20
Fusconaia flava	88.1 (02/17/95)	*Dorylaimus* sp.	external shell	9
		Aspidogaster conchicola	pericardial cavity and lumen of kidney	3
		larval chironomid	external shell	1
	89.0 (05/23/94)	*Dorylaimus* sp.	collection bag wash and external shell	11
		larval chironomids	external shell	1
Megalonaias nervosa	87.4 (06/05/95)	*Unionicola* sp.	gill filaments	93
		Aspidogaster conchicola	pericardial cavity and lumen of kidney	5
	168.0 (04/19/95)	*Unionicola* sp.	gill filaments	169
Quadrula metanevra	197.6 (07/26/95)	*Aspidogaster conchicola*	pericardial cavity and lumen of kidney	17
		Dorylaimus sp.	collection bag wash and external shell	5
		Unionicola sp.	gill filaments	4
	197.6 (12/06/94)	*Aspidogaster conchicola*	pericardial cavity and lumen of kidney	13
		Unionicola sp.	gill filament	5
		Dorylaimus sp.	external shell	2
		larval chironomids	external shell	2
		larval gorgoderids	viscera	1*
		larval trichopteran	external shell	1
		larval epheneropteran	external shell	1
		snail	incurrent siphon	1
		fingernail clam	incurrent siphon	1
	197.6 (12/14/96)	*Aspidogaster conchicola*	pericardial cavity and lumen of kidney	5
		Unionicola sp.	gill filaments	3
Quadrula pustulosa	87.1 (12/14/96)	*Unionicola* sp.	gill filaments	89
		Aspidogaster conchicola	pericardial cavity and lumen of kidney	24
		Cotylogaster occidentalis	intestine	1
	88.1 (02/17/95)	*Unionicola* sp.	gill filaments	52
		Aspidogaster conchicola	pericardial cavity and lumen of kidney	28
		larval gorgoderids	viscera	1*
	168.0 (04/19/95)	*Unionicola* sp.	gill filaments	265
		Aspidogaster conchicola	pericardial cavity and lumen of kidney	11
		Cotylogaster occidentalis	intestine	1
		larval gorgoderids	viscera	1*
	197.6 (12/14/96)	*Unionicola* sp.	gill filaments	37
		Aspidogaster conchicola	pericardial cavity and lumen of kidney	18
		larval gorgoderids	viscera	3*
		Cotylogaster occidentalis	intestine	1
Quadrula quadrula	87.1 (12/14/95)	*Aspidogaster conchicola*	pericardial cavity and lumen of kidney	15
		Unionicola sp.	gill filaments	14
	87.4 (06/05/95)	*Aspidogaster conchicola*	pericardial cavity and lumen of kidney	27
		Unionicola sp.	gill filaments	24

Table 2. continued.

Unionid Species	Sample Site [1] (date)	Metazoan Symbiont	Location on/in Host	Number of Associates Collected
Quadrula quadrula (cont.)	88.1	*Unionicola* sp.	gill filaments	21
	(05/04/95)	*Aspidogaster conchicola*	pericardial cavity and lumen of kidney	15
		Dorylaimus sp.	collection bag wash and external shell	10
		larval chironomids	external shell	1
		larval trichopterans	external shell	1
	88.1	*Aspidogaster conchicola*	pericardial cavity and lumen of kidney	135
	(05/23/94)	*Unionicola* sp.	gill filaments	24
		Dorylaimus sp.	collection bag wash and external shell	28
		larval chironomids	external shell	2
		oligochaetes	external shell	3
	88.1	*Aspidogaster conchicola*	pericardial cavity and lumen of kidney	97
	(02/17/95)	*Unionicola* sp.	gill filaments	24
		Dorylaimus sp.	collection bag wash and external shell	6
	89.0	*Aspidogaster conchicola*	pericardial cavity and lumen of kidney	158
	(05/04/94)	*Dorylaimus* sp.	collection bag wash and external shell	38
		Unionicola sp.	gill filaments	37
		unionicolid larvae	external shell and internal wash	4
		larval chironomids	external shell	3
	197.6	*Unionicola* sp.	gill filaments	4
	(12/14/95)	*Aspidogaster conchicola*	pericardial cavity and lumen of kidney	2

[1] Tennessee River mile locality.

Aspidogaster conchicola (Aspidogasteridae) (Fig. 2) was collected from all of the eight unionid species examined in the study. A total of 923 *Aspidogaster conchicola* was collected from the 486 unionids sampled (Table 2). Four-hundred and twelve (44.6%) were collected from the kidneys of their hosts, while 511 (55.4%) were collected from the pericardial cavities of their hosts. Of the 923 *Aspidogaster conchicola* collected, 21 were juveniles. In *Fusconaia ebena, Aspidogaster conchicola* was found to infect the kidney significantly more often than the pericardial chamber ($p = 0.0001$), while in *Quadrula metanevra* this worm was found significantly more often in the pericardial chamber than in the kidney ($p = 0.0106$). No statistical difference was noted for the remaining six mussel species regarding kidney versus pericardium as sites of this parasite.

Overall prevalence of infection values for *Aspidogaster conchicola* ranged from 14.3% in *Megalonaias nervosa* (N = 35) to 73.2% in *Quadrula quadrula* (N = 56) (Table 3). For seven of the eight species of mussels examined, no significant difference in the prevalence of infection with *Aspidogaster conchicola* was found among the three study areas. A significant difference in the prevalence of *Aspidogaster conchicola* between the *circa* 88 river mile area and 168 river mile locality was found in *Megalonaias nervosa* ($p = 0.0330$). Regarding this result, 33% of the *Megalonaias nervosa* (N = 15) collected from the *circa* 88 river mile area were infected with *Aspidogaster conchicola,* but this parasite was not found in any of the *Megalonaias nervosa* (N = 20) collected from the 168 river mile locality.

Figure 2. Kidney cross sections (12 μm thick) of *Quadrula pustulosa* stained with Gills hematoxylin and eosin. Top: uninfected kidney showing typical renal epithelium. Bottom: kidney infected with *Aspidogaster conchicola*. Note parasite (arrow) in center of renal lumen and normal appearing renal epithelium.

Table 3. Prevalence of infection (P) for *Aspidogaster conchicola* from eight species of unionids collected from three areas in Kentucky Lake, Tennessee. N = number of unionids examined.

	Tennessee River Mile Localities																					
	circa 88												168		*circa* 197							
	Date																					
	05/04/94		05/23/94		02/17/95		06/05/95		12/14/95		07/09/96		04/19/95		07/26/94		12/06/94		12/14/95		OVERALL	
Unionid Species	N	P	N	P	N	P	N	P	N	P	N	P	N	P	N	P	N	P	N	P	N	P
Amblema plicata	-	-	13	77%	4	25%	18	61%	-	-	-	-	-	-	-	-	-	-	1	0%	36	61%
Elliptio cressidens	-	-	-	-	-	-	-	-	-	-	-	-	16	35%	-	-	-	-	-	-	16	35%
Fusconaia ebena	10	70%	14	79%	20	85%	20	75%	49	63%	24	79%	24	60%	14	64%	19	53%	21	67%	215	68.8%
Fusconaia flava	-	-	14	0%	4	80%	-	-	-	-	-	-	-	-	-	-	-	-	-	-	18	16.7%
Megalonaias nervosa	-	-	-	-	-	-	15	33%	-	-	-	-	20	0%	-	-	-	-	-	-	35	14.3%
Quadrula metanevra	-	-	-	-	-	-	-	-	-	-	-	-	-	-	14	64%	18	53%	7	71%	39	64.1%
Quadrula pustulosa	-	-	-	-	12	83%	-	-	22	59%	-	-	17	47%	-	-	-	-	20	50%	71	59.2%
Quadrula quadrula	7	57%	13	100%	20	65%	8	75%	6	50%	-	-	-	-	-	-	-	-	2	50%	56	73.2%

Overall mean intensity values for *Aspidogaster conchicola* infections were low, ranging from 1.0±0.0 to 2.7±2.5 in seven of the eight species of unionids examined (Table 4). The overall mean intensity of *Aspidogaster conchicola* infections was highest in *Quadrula quadrula*, with infections averaging 7.8±8.1 worms (Table 4). No significant differences in mean intensity were found for *Aspidogaster conchicola* infections in any of the eight species of unionids examined among the three study areas (p = 0.1919). Seasonal variation in *Aspidogaster conchicola* prevalence and mean intensity values was not casually apparent, however, lack of a temporally robust sample prevented statistical testing for possible seasonal effects.

Histological sections revealed no pathologies associated with *Aspidogaster conchicola* infections (Fig. 2). This parasite was always found in either the pericardial or renal cavities. No encapsulated *Aspidogaster conchicola* individuals were observed.

A total of 953 *Unionicola* sp. (Unionicolidae) was collected from five of the unionid species examined (Table 5). *Unionicola* sp. adult and larval stages (nymphs) were all found on the demibranchs of unionids. *Elliptio cressidens* (N = 16) and *Fusconaia flava* (N = 18) did not harbor mite infections. Only one of 215 *Fusconaia ebena* examined was infected with unionicolids, and this individual harbored only a single mite. Prevalence of *Unionicola* sp. was highest (94.6%) in *Quadrula quadrula* (N = 56), and nearly as high (92.9%) in *Quadrula pustulosa* (N = 71). Only 28.2% of the *Quadrula metanevra* (N = 39) examined were infected by mites. A significant difference in the prevalence of *Unionicola* sp. infecting *Megalonaias nervosa* was found between the *circa* 88 river mile area and 168 river mile locality (p = 0.0103). Seventy-three percent of the *Megalonaias nervosa* (N = 15) collected from the *circa* 88 river mile area were infected with *Unionicola* sp., while 95% of *Megalonaias nervosa* (N = 20) collected from the 168 river mile locality harbored these parasites. A significant difference in the prevalence of *Unionicola* sp. infection between sampling localities was also found regarding *Quadrula pustulosa*. Unionicolids were found at a significantly (p = 0.003) lower prevalence in *Quadrula pustulosa* at the *circa* 197 river mile area (prevalence = 70%) than at the other two river areas (prevalences both = 100%). A difference in the mean intensity of *Unionicola* sp. infections between study localities was found for *Quadrula pustulosa*, with this parasite being found in significantly (p = 0.001) higher numbers at the 168 river mile locality (Table 6). Seasonal trends in *Unionicola* sp. prevalence and mean intensity were not casually apparent, however, lack of a robust temporal sample prevented statistical testing for possible seasonal effects.

Individuals of six of the eight mussel species examined (i.e., *Amblema plicata*, *Fusconaia ebena*, *Megalonaias nervosa*, *Quadrula metanevra*, *Quadrula pustulosa*, and *Quadrula quadrula*) were often simultaneously infected with *Aspidogaster conchicola* and *Unionicola* sp. (Table 7). The chi-square analysis used to assess the dependence of multiple infections only denoted infections of *Aspidogaster conchicola* and *Unionicola* sp. in *Fusconaia ebena* to be dependent upon one another.

Table 4. Mean intensity, standard error, and range of infection for *Aspidogaster conchicola* from eight species of unionids collected from three areas in Kentucky Lake (Tennessee River) Tennessee. N = number of unionids examined.

	Tennessee River Mile Localities																					
	circa 88												168		*circa* 197							
	Date																					
	05/04/94		05/23/94		02/17/95		06/05/95		12/14/95		07/09/96		04/19/95		07/26/94		12/06/94		12/14/95		OVERALL	
Unionid Species	N	I[1]	N	I	N	I	N	I	N	I	N	I	N	I	N	I	N	I	N	I	N	I
Amblema plicata	-	-	13	2.4±8.4 (1-4)	4	4.0±0.0 (4)	18	2.3±1.6 (1-5)	-	-	-	-	-	-	-	-	-	-	1	0	36	2.7±1.8 (1-7)
Elliptio cressidens	-	-	-	-	-	-	-	-	-	-	-	-	16	1.7±0.8 (1-3)	-	-	-	-	-	-	16	1.7±0.8 (1-3)
Fusconaia ebena	10	1.7±0.9 (1-3)	14	3.9±2.5 (2-8)	20	3.2±2.0 (1-8)	20	1.8±1.1 (1-5)	49	3.4±3.7 (1-15)	24	1.8±1.1 (1-5)	24	3.4±3.1 (1-14)	14	3.7±2.7 (1-10)	19	2.8±2.4 (1-7)	21	1.4±0.6 (1-3)	215	2.7±2.5 (1-15)
Fusconaia flava	-	-	14	0	4	2.3±2.5 (1-8)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	18	1.0±0.0 (1)
Megalonaias nervosa	-	-	-	-	-	-	15	1.0±0.0 (1)	-	-	-	-	20	0	-	-	-	-	-	-	35	1.0±0.0 (1)
Quadrula metanevra	-	-	-	-	-	-	-	-	-	-	-	-	-	-	14	1.9±1.5 (1-5)	18	1.2±0.4 (1-2)	7	1.0±0.0 (1)	39	1.4±1.0 (1-5)
Quadrula pustulosa	-	-	-	-	12	2.8±2.2 (1-8)	-	-	22	1.9±1.3 (1-5)	-	-	17	1.4±1.1 (1-4)	-	-	-	-	20	1.6±0.9 (1-4)	71	2.0±1.5 (1-8)
Quadrula quadrula	7	13±10.5 (1-40)	13	12±10.5 (1-40)	20	7.5±8.1 (1-32)	8	4.5±1.9 (2-7)	6	5.0±5.3 (1-11)	-	-	-	-	-	-	-	-	2	2.0±0.0 (2)	56	7.8±8.1 (1-40)

[1] I = mean intensity of infection ± SD, range of intensity of infection in parentheses.

Table 5. Prevalence of infection (P) for *Unionicola* sp. from eight species of unionids collected from three areas in Kentucky Lake, Tennessee. Adult and nymph mites are grouped together. N = number of unionids examined.

	Tennessee River Mile Localities																					
	circa 88												168		*circa* 197							
	Date																					
	05/04/94		05/23/94		02/17/95		06/05/95		12/14/95		07/09/96		04/19/95		07/26/94		12/06/94		12/14/95		OVERALL	
Unionid Species	N	P	N	P	N	P	N	P	N	P	N	P	N	P	N	P	N	P	N	P	N	P
Amblema plicata	-	-	13	92%	4	100%	18	28%	-	-	-	-	-	-	-	-	-	-	1	100%	36	61.0%
Elliptio cressidens	-	-	-	-	-	-	-	-	-	-	-	-	16	0%	-	-	-	-	-	-	16	0.0%
Fusconaia ebena	10	1%	14	0%	20	0%	20	0%	49	0%	24	0%	24	0%	14	0%	19	0%	21	0%	215	0.47%
Fusconaia flava	-	-	14	0%	4	0%	-	-	-	-	-	-	-	-	-	-	-	-	-	-	18	0.0%
Megalonaias nervosa	-	-	-	-	-	-	15	73%	-	-	-	-	20	95%	-	-	-	-	-	-	35	88.6%
Quadrula metanevra	-	-	-	-	-	-	-	-	-	-	-	-	-	-	14	29%	18	21%	7	43%	39	28.2%
Quadrula pustulosa	-	-	-	-	12	100%	-	-	22	100%	-	-	17	100%	-	-	-	-	20	70%	71	92.9%
Quadrula quadrula	7	71%	13	100%	20	95%	8	88%	6	100%	-	-	-	-	-	-	-	-	2	100%	56	94.6%

Table 6. Mean intensity, standard error, and range of infection for *Unionicola* sp. from eight species of unionids collected from three areas in Kentucky Lake, Tennessee. Adult and nymph mites are grouped together. N = number of unionids examined.

	Tennessee River Mile Localities																					
	circa 88												168		*circa* 197							
	Date																					
	05/04/94		05/23/94		02/17/95		06/05/95		12/14/95		07/09/96		04/19/95		07/26/94		12/06/94		12/14/95		OVERALL	
Unionid Species	N	I[1]	N	I	N	I	N	I	N	I	N	I	N	I	N	I	N	I	N	I	N	I
Amblema plicata	-	-	13	4.7±2.1 (2-8)	4	2.0±0.8 (1-3)	18	2.0±1.2 (1-4)	-	-	-	-	-	-	-	-	-	-	1	0	36	3.5±2.1 (1-8)
Elliptio cressidens	-	-	-	-	-	-	-	-	-	-	-	-	16	0	-	-	-	-	-	-	16	0
Fusconaia ebena	10	1.0±0.0 (1)	14	0	20	0	20	0	49	0	24	0	24	0	14	0	19	0	21	0	215	0.0±0.0 (1)
Fusconaia flava	-	-	14	0	4	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	18	0
Megalonaias nervosa	-	-	-	-	-	-	15	8.4±4.2 (4-18)	-	-	-	-	20	8.7±9.5 (2-46)	-	-	-	-	-	-	35	8.4±7.8 (2-46)
Quadrula metanevra	-	-	-	-	-	-	-	-	-	-	-	-	-	-	14	1.0±0.0 (1)	18	1.3±0.5 (1-2)	7	1.0±0.0 (1)	39	1.1±0.3 (1-2)
Quadrula pustulosa	-	-	-	-	12	4.0±1.7 (3-7)	-	-	22	3.7±3.9 (1-20)	-	-	17	16.6±13.8 (2-40)	-	-	-	-	20	2.6±1.6 (1-5)	71	6.6±9.1 (1-40)
Quadrula quadrula	7	4.2±4.4 (2-12)	13	2.8±1.4 (1-5)	20	4.0±1.7 (2-7)	8	3.4±0.5 (3-4)	6	2.3±1.0 (1-4)	-	-	-	-	-	-	-	-	2	2.0±0.0 (2)	56	3.3±1.8 (1-12)

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[1] I = mean intensity of infection ± 1SD, range of intensity of infection in parentheses.

Table 7. Chi-square comparisons of observed frequency distributions (occurrence) and expected frequency distributions of two symbiont taxa (*Aspidogaster conchicola* and *Unionicola* sp.) in eight species of unionids.

Mussel Species: Symbiont Species Assemblage	Observed Frequency (number of mussels inhabited)	Expected Frequency (number of mussels inhabited)	χ^2
Amblema plicata[1]			
(N=36)			
None	6	5.4756	0.05022196
Worm Only	8	8.5644	0.03719436
Mite Only	9	8.5644	0.02215536
Worm and Mite	15	13.3956	0.19216006
Elliptio cressidens[2]			
(N=16)			
None	12	10	0.4
Worm Only	6	6	0.0
Mite Only	0	0	n/a
Worm and Mite	0	0	n/a
Fusconaia ebena[3]			
(N=215)			
None	68	63.92724	0.25947271
Worm Only	148	140.96776	0.35080645
Mite Only	0	3.15276	3.15276
Worm and Mite	1	6.95224	5.09607853
Fusconaia flava[4]			
(N=18)			
None	15	14.994	n/a
Worm Only	3	n/a	n/a
Mite Only	0	n/a	n/a
Worm and Mite	0	n/a	n/a
Megalonaias nervosa[5]			
(N=35)			
None	2	3.41943	0.58921561
Worm Only	2	0.57057	3.58110333
Mite Only	28	26.57557	0.07634835
Worm and Mite	3	4.43443	0.46400314
Quadrula metanevra[6]			
(N=39)			
None	10	10.0303164	9.1631E-05
Worm Only	19	17.9716836	0.05883893
Mite Only	4	3.9394836	0.00092962
Worm and Mite	7	7.0585164	0.00048511
Quadrula pustulosa[7]			
(N=71)			
None	1	2.056728	0.54293716
Worm Only	5	2.984272	1.36152448
Mite Only	29	26.911272	0.16211737
Worm and Mite	37	39.047728	0.10738627

Table 7. continued.

Mussel Species: Symbiont Species Assemblage	Observed Frequency (number of mussels inhabited)	Expected Frequency (number of mussels inhabited)	χ^2
Quadrula quadrula[8] (N=56)			
None	1	0.795424	0.05261513
Worm Only	1	2.172576	0.63285909
Mite Only	15	14.212576	0.04362591
Worm and Mite	38	38.819424	0.01729690

[1] $\chi^2_{\text{Total}} = 0.30173174$; $\chi^2_{\text{critical}} = 7.815$ (df = 3, $\alpha = 0.05$).
[2] χ^2_{Total} = n/a; χ^2_{critical} = n/a (df = 3, $\alpha = 0.05$).
[3] $\chi^2_{\text{Total}} = 8.85911769$; $\chi^2_{\text{critical}} = 7.815$ (df = 3, $\alpha = 0.05$).
[4] χ^2_{Total} = n/a; χ^2_{critical} = n/a (df = 3, $\alpha = 0.05$).
[5] $\chi^2_{\text{Total}} = 4.71067042$; $\chi^2_{\text{critical}} = 7.815$ (df = 3, $\alpha = 0.05$).
[6] $\chi^2_{\text{Total}} = 0.06034529$; $\chi^2_{\text{critical}} = 7.815$ (df = 3, $\alpha = 0.05$).
[7] $\chi^2_{\text{Total}} = 2.17396528$; $\chi^2_{\text{critical}} = 7.815$ (df = 3, $\alpha = 0.05$).
[8] $\chi^2_{\text{Total}} = 0.74639704$; $\chi^2_{\text{critical}} = 7.815$ (df = 3, $\alpha = 0.05$).

In addition to *Aspidogaster conchicola* and *Unionicola* sp., two other internal parasites were collected from unionids. A second member of Aspidogasteridae, *Cotylogaster occidentalis*, internally infected several unionids (Table 2). One *Cotylogaster occidentalis* was found in an *Elliptio cressidens* and one other in a *Quadrula pustulosa* collected at the 168 river mile locality. *Cotylogaster occidentalis* was also found in *Quadrula pustulosa* collected at the *circa* 88 and *circa* 197 river mile areas (a single worm found in each of two *Quadrula pustulosa* collected at the *circa* 88 river mile area, and a single worm found in a *Quadrula pustulosa* collected at the *circa* 197 river mile area) (Table 2).

The digenean family Gorgoderidae was represented by one taxon, which was found in three unionid species examined (one *Amblema plicata* collected at the *circa* 88 river mile area; one *Quadrula metanevra* collected at the *circa* 197 river mile area; and five *Quadrula pustulosa*, one collected at the *circa* 88 river mile area, one collected at the 168 river mile locality, and three collected at the *circa* 197 river mile area) (Table 2).

Gorgoderid infections consisted of large numbers of larval stages (sporocysts). Sporocysts (Fig. 3) were densely packed within the digestive gland, gonad, and viscera surrounding the foot of infected mussels. Identification of these parasites was based on the morphological characters exhibited by the rhopalocercous cercariae developing within each sporocyst (Fig. 3). These cercariae resembled those of *Cercaria filicauda*, a species described by Fischthal (1951) from study material collected from unionids in Illinois.

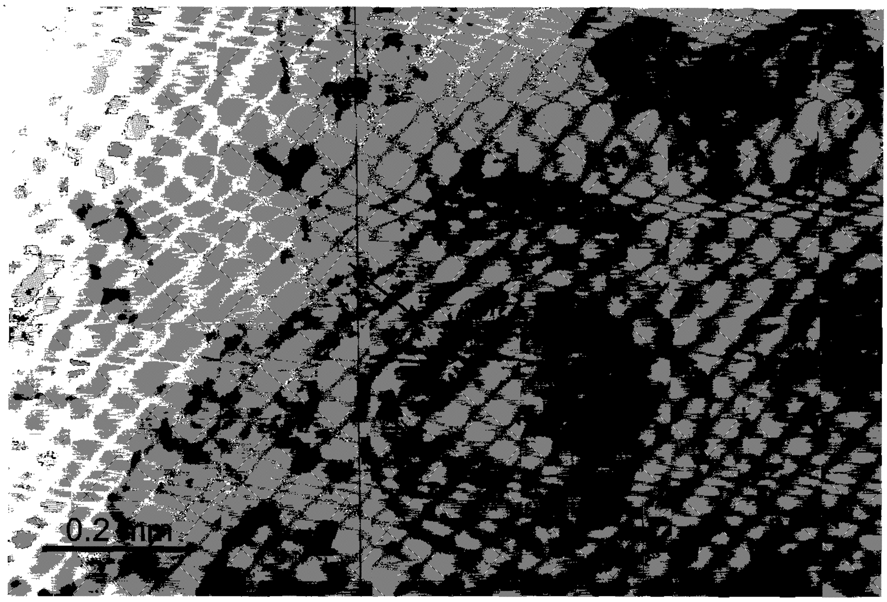

Figure 3. *Cercaria filacauda* (Gorgoderidae) from *Quadrula pustulosa*. Cross section of daughter sporocyst (containing one visible cercaria) embedded in viscera of mussel. Note corrugated tail section of cercaria (arrow).

DISCUSSION

Nine of thirteen taxa collected from the 500 unionids examined in this study (four insect taxa, one oligochaete, one fingernail clam, one snail, one nematode, and one tardigrade) are common free-living members of aquatic benthic communities. We consider these taxa to have been coincidentally associated with the sampled unionids and regard them as commensals or accidental associates that have no detrimental impact on unionid populations. Four taxa collected during this study (*Aspidogaster conchicola*, *Cotylogaster occidentalis*, *Unionicola* sp., and *Cercaria filicauda*) were found inside unionids, seemingly indicating more intimate relationships with these mussels. Each of these taxa are generally considered parasitic.

Aspidogaster conchicola was the only internal parasite collected from all eight of the unionid species we examined from Kentucky Lake. Recently, Duobinis-Gray *et al.* (1991) examined 219 mussels (ten species) from 17 localities in Kentucky Lake (12 localities in Kentucky and 5 localities in Tennessee). Nine of ten unionid species they examined were infected with *Aspidogaster conchicola*, and overall they reported a prevalence of 28.8% and an overall mean intensity of 2.5 *Aspidogaster conchicola* per mussel (Duobinis-Gray *et al.* 1991). Regarding the four unionid species shared by the present study and that of Duobinis-Gray *et al.* (1991), the latter authors reported a prevalence of 29.1% and a mean intensity of 1.9 for *Aspidogaster conchicola* in *Amblema plicata*, a prevalence of 100% and a mean intensity of 1.0 in *Fusconaia ebena*, a 7.4% prevalence and a 5.2 mean intensity in *Megalonaias gigantea* (= *Megalonaias nervosa*), and a 45% prevalence and a 2.4 mean intensity in *Quadrula quadrula*. These prevalence and mean intensity values are all respectively equal to or lower than those reported herein for the same host taxa (see Tables 3 and 4).

In a similar examination of unionids conducted in West Virginia, Danford and Joy (1984) surveyed 500 unionids (22 species collected from a total of 32 localities) for aspidogastrid parasites and found seven species harboring *Aspidogaster conchicola*. Overall, Danford and Joy (1984) reported a prevalence of 9.4% for this infection and they provided prevalence and intensity values for two of the unionid species we also report on herein. Regarding these two species, Danford and Joy (1984) reported a prevalence of 7% and a mean intensity of 4.0 for *Aspidogaster conchicola* in *Amblema plicata*, and a prevalence of 2% and a mean intensity of 2.0 in *Quadrula pustulosa*. These values are lower than those we report herein for these two unionid species collected from Kentucky Lake (see Tables 3 and 4).

Aspidogaster conchicola is a common and widespread parasite of molluscs in North America that sometimes occurs at relatively high prevalence levels in wild populations (e.g., see Hendrix *et al.* 1985). Unlike many parasites, *Aspidogaster conchicola* shows little phylogenetic mediated host specificity within Mollusca (i.e., it does not seem to be restricted to particular natural taxonomic groups of freshwater mussels or snails). Historically, *Aspidogaster conchicola* has been collected from at least 85 unionid species, as well as from four species of gastropods (Hendrix *et al.* 1985). These parasites live in the pericardial and renal cavities of their mollusc hosts where they are thought to consume blood cells and large particulate matter suspended in the hemolymph (Halton 1972).

Pauley and Becker (1968) were the first to describe pathology induced by *Aspidogaster conchicola* in unionids. While examining heavy *Aspidogaster conchicola* infections in the pericardial and renal cavities of *Anodonta californiensis* and *Anodonta oregonensis* they observed distention and distortion of the renal cavities with associated renal metaplasia (i.e., reduction of the columnar epithelium and loss of cilia). Fibrosis of the connective tissue underlying the damaged epithelial tissue was noted, but no evidence of hemocytic infiltration was observed in the damaged epithelium of these two unionid species. In *Gonidea angulata*, they reported no damage to the pericardial or renal tissues, but the parasite was found to be encapsulated by host tissues in areas outside the pericardial and renal cavities, including the muscle and connective tissues of the foot, hemolymph vessels, digestive tubules, and the intestinal lumen. Using various staining techniques Pauley and Becker (1968) determined that the capsules lacked collagen and consisted of elongate fibroblasts, and that they were similar to capsules known from marine bivalve/parasite interactions (see Cheng and Burton 1965). Each capsule contained a living parasite, and often also contained host hemocytes. Pauley and Becker (1968) concluded that metaplasia in pericardial and renal tissues of the two *Anodonta* spp. was a chronic condition caused by heavy infections of *Aspidogaster conchicola*, while encapsulation was an acute response to this parasite when located in unusual sites within *Gonidea angulata*. Bakker and Davids (1973) reported similar damage associated with *Aspidogaster conchicola* infection of the pericardial and renal epithelia of *Anodonta anatina*. They attributed the observed damage to the influence of the parasite's ventral sucker on the host epithelium rather than to the feeding activity of the parasite. Huehner and Etges (1981) described the encapsulation of *Aspidogaster conchicola* in the pericardial and renal tissues of several unionid species from Ohio (*Anodonta marginata*, *Anodonta grandis*, *Lampsilis siliquoidea*, *Lampsilis ventricosa*, *Lasmigona complanata*, and *Quadrula quadrula*). They found encapsulated parasites in regions of their unionid hosts outside the pericardial and renal cavities, especially in regions dorsal to the digestive gland and anterior to the pericardial chamber. The capsules contained host cells and either a single living worm, a moribund worm, or a mass of embryonated eggs. In two instances they observed three recently hatched juvenile worms and empty egg shells within capsules. Huehner and Etges (1981) suggested that encapsulation by the host occurred most often when *Aspidogaster conchicola* strays into areas outside of the pericardial or renal cavities, and that encapsulation is probably a contributing factor to the mortality of this parasite.

Based on limited histological evidence, Gentner (1971) speculated that *Aspidogaster conchicola* feeds on host blood cells. Huehner *et al.* (1989) suggested that the ventral disc of *Aspidogaster conchicola* secretes digestive enzymes that allow it to feed on pericardial and renal epithelia of unionid hosts. The secretion of digestive enzymes from the ventral disc combined with mechanical feeding using a muscular buccal sucker might provide a mechanism to create the damage described by Pauley and Becker (1968) and Bakker and Davids (1973). Interestingly, Rohde (1975) and Rohde and Sandland (1973) provided evidence that another species of aspidogastrid feeds on host epithelial tissues.

In this study, histological examinations provided no evidence supporting the notion that the ventral disc of *Aspidogaster conchicola* is secretory and destructive to epithelial tissue as proposed by Huehner *et al.* (1989). We also did not find any evidence of renal metaplasia or damage to the pericardial epithelium in any of the unionids that we histologically examined, nor did we find any encapsulated *Aspidogaster conchicola* in these mussels (although one of us [SC] has observed this phenomenon in *Anodonta implicata* collected from northeastern North America).

The life cycle of *Aspidogaster conchicola* is not yet entirely understood. It is thought to be a one host life cycle which takes place within a molluscan host (Fig. 4). Adults worms live in the pericardial and renal cavities of their unionid hosts where they release embryonated operculate eggs which probably leave the pericardial/renal complex through the nephridiopore and get shunted to the external aquatic environment via the excurrent siphon. Bakker and Davids (1973) showed that these eggs do not hatch while in the aquatic environment, but instead they hatch only after entering a unionid. How the eggs infect the new unionid host and how the infection is manifested in the pericardial chamber of the host is as yet unclear. Bakker and Davids (1973) suggested that the eggs hatch on the demibranchs and the cotylocidia (larvae) then migrate through the nephridiopore to the kidney. These larvae then develop in the kidney and move to the pericardial chamber when they mature (Bakker and Davids 1973). A second hatching possibility might be that the eggs require digestive enzymes for hatching to occur, and thus must be swallowed and pass through the gut of the unionid host (Huehner and Etges 1972, 1977, Rohde 1975). The cotylocidium would then migrate through the intestine, out the anus to the nephridiopore, into the suprabranchial chamber, then to the renal cavity, and finally into the pericardial chamber where it would develop to adulthood.

A plausible but never demonstrated alternative sequence of events in which the eggs never leave the original host mussel has also been proposed (Williams 1942). In this scenario, eggs released in the pericardial or renal cavities of a unionid would hatch in place rather than exit the host. There they would develop directly within the host along side their parent worms. This particular scheme provides an efficient mechanism for autoinfection that might ultimately result in large numbers of parasites within hosts.

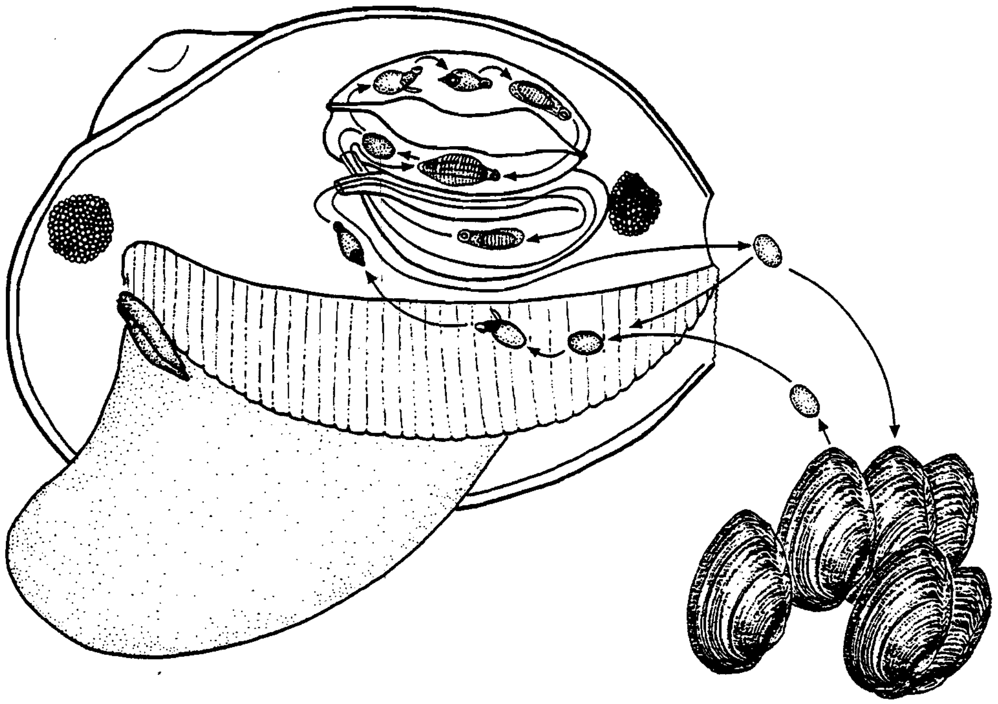

Figure 4. Possible life cycle pathways of *Aspidogaster conchicola* (Aspidogasteridae). Adult worms live in the pericardial chamber or kidney of the unionid host. Operculate eggs containing embryos are shed by adult worms, and might follow one of three general developmental pathways. Via the first, eggs hatch and larvae develop into adults within the kidney or pericardial chamber. In this manner individual mussels might become infected with ever greater numbers of worms by a process known as autoinfection. Through the second possible pathway, eggs pass out of the kidney and into the suprabranchial chamber via the excretory pore. Subsequently, they are ejected into the external environment via the excurrent siphon. Liberated eggs become infective when they are inhaled by a mussel through the incurrent siphon. Inhaled eggs become trapped on the gills where they hatch, liberating larvae which move through the excretory pore into the kidney. Worms develop into mature adults in the kidney or pericardial chamber. Via the third possible life cycle pathway (not depicted in this illustration) an embryonated egg which has entered the branchial chamber is swallowed and passes through the gut of the unionid host. This stimulates the egg to hatch and the cotylocidium then migrates through the intestine, out the anus and into the excretory pore to ultimately mature in the kidney or pericardial chamber. It should be noted that none of these three pathways have been conclusively documented. (mussel schematic modified from Olsen 1962)

Our data did not support the observation that juvenile worms mature in the kidney of the host and then move to the pericardial chamber as reported by Bakker and Davids (1973). We encountered only 21 juvenile worms, and these young worms were found in both the kidneys and pericardial chambers of unionids. We also found many adult *Aspidogaster conchicola* in the kidneys of all eight examined species of unionids, and furthermore, in *Fusconaia ebena* adult *Aspidogaster conchicola* were found to infect the kidney significantly more often than the pericardial chamber.

Given our incomplete understanding of the life cycle of *Aspidogaster conchicola*, this species' documented ability to cause disease (see Pauley and Becker 1968, Bakker and Davids 1973), and its typical high prevalence and sometimes high intensity in wild unionid populations as documented herein and in previous studies (e.g., Kelly 1899, Duobinis-Gray *et al.* 1991), we believe that *Aspidogaster conchicola* has some potential to detrimentally impact the survival of wild and captive mussels. Our view regarding this matter is founded on the premise that in wild populations or closed or semi-closed aquaculture conditions with high densities of potential hosts, transmission rates could become abnormally elevated and result in unnaturally high parasite burdens that might be associated with debilitating diseases. It should also be noted that the wide host range of this parasite should facilitate interspecific transmission in some wild mussel communities or under polyculture conditions.

Throughout this study the aspidogastrid *Cotylogaster occidentalis* was found more infrequently than its relative *Aspidogaster conchicola*. *Cotylogaster occidentalis* is thought to complete its life cycle directly within a unionid host in a fashion similar to *Aspidogaster conchicola*. Unlike *Aspidogaster conchicola*, however, *Cotylogaster occidentalis* is known to develop and live in the intestine of the freshwater drum, *Aplodinotus grunnions* (Fig. 5; Dickerman 1948). Fish become infected when they feed on infected molluscs (Dickerman 1948). Despite this ability to exploit a vertebrate host which is relatively more vagile than a unionid and which might facilitate its horizontal transmission, *Cotylogaster occidentalis* typically occurs in much lower prevalence in unionid communities than does *Aspidogaster conchicola* (see Table 2). *Cotylogaster occidentalis* is also found in low prevalence in freshwater drum populations (Simer 1929, Dickerman 1948). It is interesting to note that *Cotylogaster occidentalis* and *Aspidogaster conchicola* each seem to rely on a different mode of transmission (i.e., the colonization of new hosts) to fulfill their life cycles. *Aspidogaster conchicola* relies on transmission via the liberation of an embryonated egg while *Cotylogaster occidentalis* uses a ciliated, free-swimming larva. These two transmission modes seem clearly different. However, studies are needed to determine how different transmission modes might affect the realized prevalence levels of these two closely related species.

Larval gorgoderid infections (Gorgoderidae) identified during this study consisted of one species, *Cercaria filicauda*; one of nine gorgoderid rhopalocercous cercarial types known from freshwater bivalves in North America (see Fischthal 1951, Flook and Ubelaker 1971). Generic and specific designation for digeneans is based on adult characters. However, it is possible to assign cercaria to family based on larval characteristics. When only larval stages of digeneans are found, researchers categorize unknown cercaria in the genus *Cercaria* and assign a specific epithet based on either physical characteristics of the larvae or on host affiliations. *Cercaria filicauda* is a member of the subfamily Gorgoderinae and is characterized by having a long filament attached posteriorly to a corrugated transformable tail (Fig. 3). Without exception, members of the Gorgoderinae have two host life cycles (Fig. 6) that utilize a unionid as the intermediate host and a fish or toad (depending on the particular gorgoderid species) as the definitive vertebrate host (Fischthal 1951). Within the intermediate host, a single gorgoderid miracidium develops into a mother sporocyst, which in turn produces the second generation of daughter sporocysts asexually. It is within these second generation sporocysts that the rhopalocercous cercariae develop. These cercariae have no free-living existence, and they transform into metacercariae by encysting within the sporocysts. Sporocysts containing metacercariae exit the unionid host through the excurrent siphon and are eaten by the definitive vertebrate host. Metacercariae break free in the stomach of the vertebrate and migrate to the urinary bladder where they take up residence as adults.

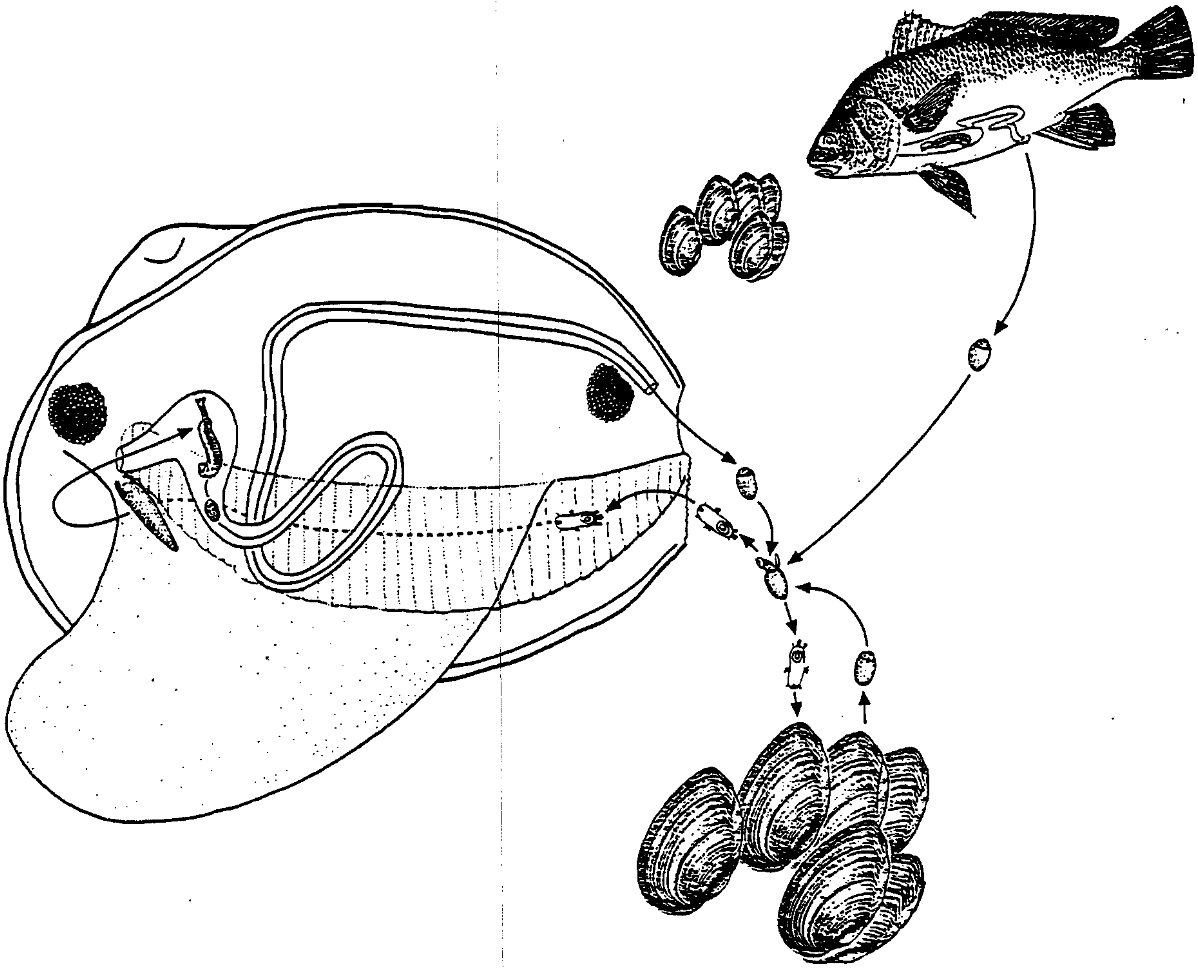

Figure 5. Life cycle of *Cotylogaster occidentalis* (Aspidogasteridae). Adult worms live in stomach or intestine of unionid host. Operculate eggs containing embryos are shed by adult worms and pass out of the mussel with feces via the anus. Free in the environment, the egg hatches and liberates a ciliated larva (cotylocidium) which actively seeks and infects a unionid host by entering the incurrent siphon. Larvae pass from the gills to the mouth, where they enter the digestive tract and mature. Freshwater drum presumably become infected with worms by eating infected molluscs. In the fish host, *Cotylogaster occidentalis* matures in the intestine. Gravid worms have been collected from fish hosts (see Dickerman 1948), and we assume that eggs passed from fish hosts will hatch to liberate larvae that can infect molluscs. Because eggs must develop in the external environment for several days before hatching, it is likely that autoinfection is not a highly developed component of this species' life cycle. (mussel schematic modified from Olsen 1962; fish modified from Scott and Crossman 1973)

Due to the low levels of prevalence reported here for gorgoderid infections, and because a definitive vertebrate host is required for these digenes to produce future parasite generations, we feel that these parasites could not significantly impact a cultured mussel population existing in a closed or semi-closed system without the presence of definitive hosts. However, it might be possible for very heavily infected mussels captured in the wild and transferred into captive systems to become compromised by these infections.

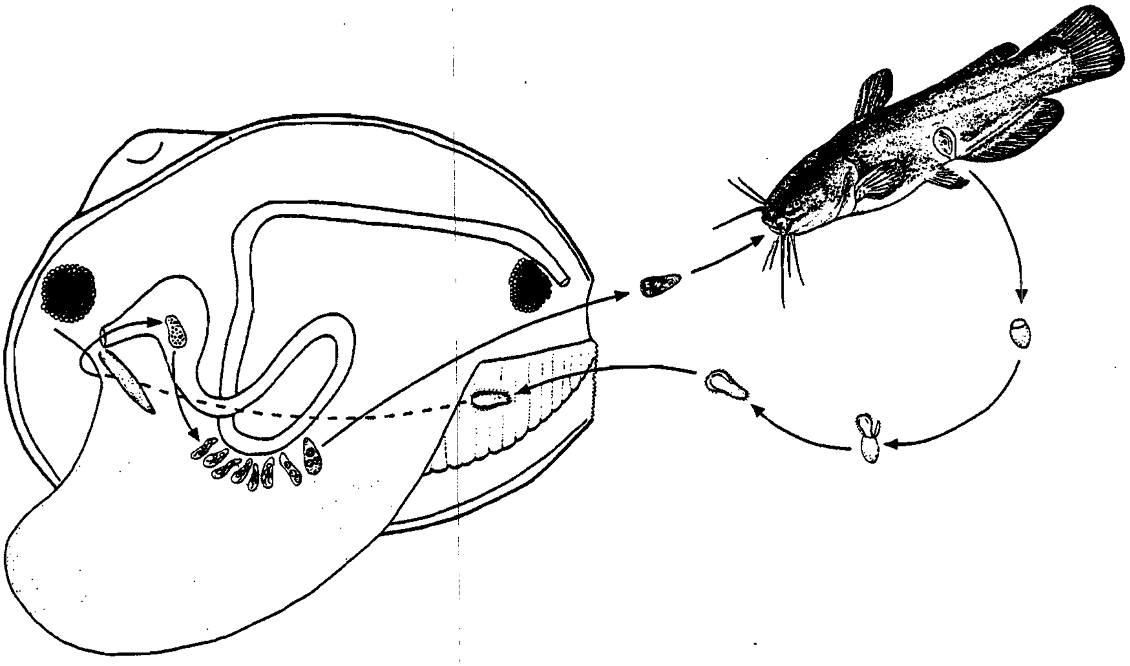

Figure 6. Generalized life cycle of species within Gorgoderinae (Digenea). Adult worms live in fish urinary bladder. Embryonated, operculate eggs are released into environment via urogenital opening. Free swimming miracidium hatches from egg and enters unionid via incurrent siphon. Miracidium travels into digestive system and develops into mother sporocyst. Mother sporocyst migrates to gonads/viscera and develops into many daughter sporocysts. Rhopalocercariae (typically 3-6) develop within daughter sporocyst. Cercariae transform into metacercariae within daughter sporocysts. Daughter sporocysts containing metacercariae migrate out of mussel and are eaten by fish host. Ingested parasites migrate to urinary bladder and develop into mature worms. (mussel schematic modified from Olsen 1962; fish modified from Scott and Crossman 1973)

A unionicolid mite (*Unionicola* sp.) was another important parasite found infecting unionids from Kentucky Lake in this study. The prevalence and mean intensity values reported here from six of the eight unionid species that were infected with *Unionicola* sp. are similar to those reported by Vidrine and Wilson (1991) for unionids collected from the Stone and Duck rivers in central Tennessee in 1956 and 1962. From the Stone River, they reported that 20 of the 29 species of unionids examined harbored *Unionicola* infections, with an overall prevalence of 58.2%. From the Duck River, they reported that 13 of 20 species of examined unionids were infected with *Unionicola*, with an overall prevalence of 59%. Fourteen *Unionicola* species were collected from mussels gathered in the Stone River and 11 species were associated with mussels taken from the Duck River. While we are not sure how to interpret these relatively high levels of unionicolid species richness as compared to our results in Kentucky Lake, it could be suggested that greater relative levels of habitat diversity within sampled sections of the Stone and Duck rivers might be responsible for the greater species richness reported by Vidrine and Wilson (1991).

Members of the genus *Unionicola* parasitize freshwater mussels worldwide (Cook 1974). In revising the genus *Unionicola*, Vidrine (1986) presented descriptions of species found in North America. A typical unionicolid life cycle (Fig. 7) as described by Mitchell (1955), begins when the adult female oviposits between the gill filaments or on the mantle of a mussel using her highly modified genital spines. In one to three weeks, larvae hatch from the deposited eggs. These larvae either leave the mussel through the excurrent siphon or they enter a dormant period and remain encysted for up to a year without further development. During spring, larvae free in the surrounding environment re-enter unionids and encyst in epithelial tissue of the mantle around the incurrent siphon or in the gills. Once encysted, this larva is known as a nymphochrysalis. An active, predaceous, sexually immature deutonymph emerges from the nymphochrysalis after several weeks and leaves the mussel for a temporary free-living existence. After feeding extensively in the water column on plankton, the deutonymph returns to a unionid host to complete its development into an adult. The deutonymph enters the mussel and encysts in the gill lamellae forming an imagochrysalis. The imagochrysalis persists for a period of a few days before the adult mite emerges from it. Soon after emergence, mites reach sexual maturity and mating occurs in the unionid host. Most unionicolid species spend the majority of their adult lives in the water column, and occupy unionids for shorter periods to mate and deposit eggs.

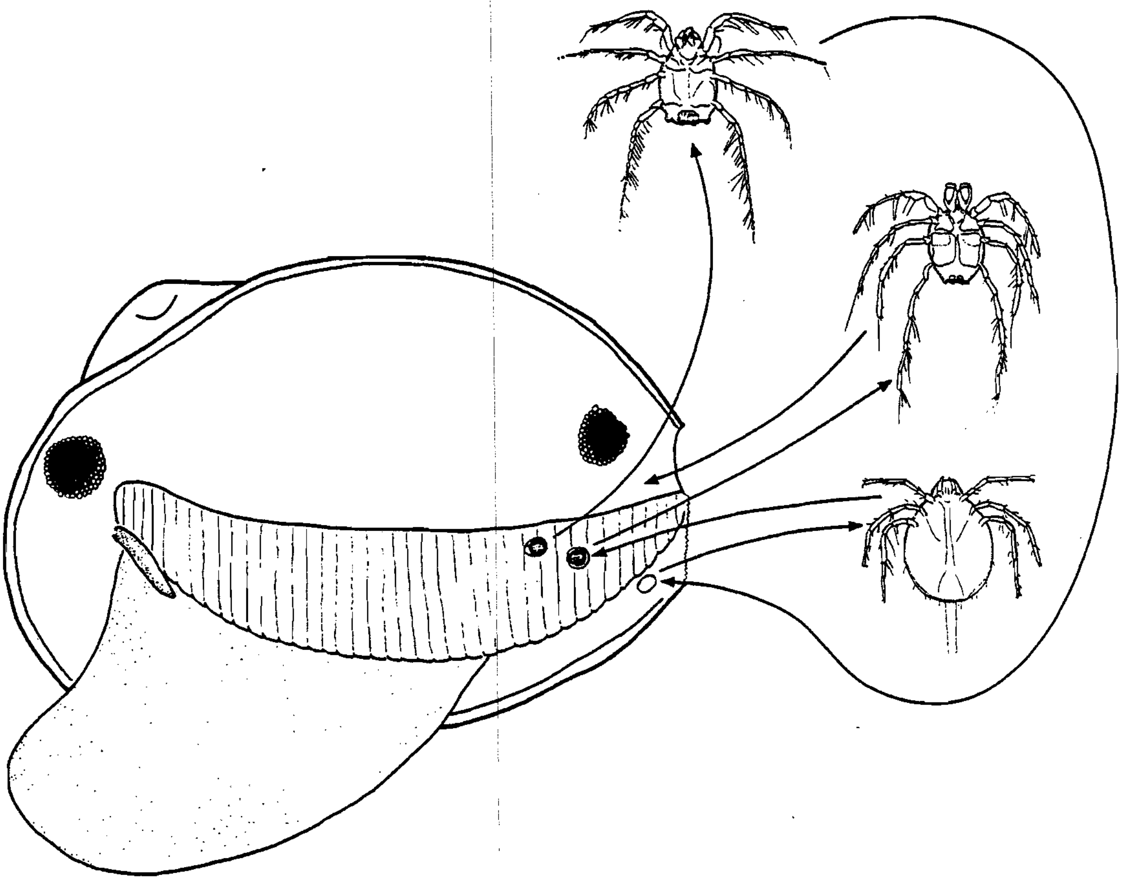

Figure 7. Generalized unionicolid (Unionicolidae) life cycle. Adult female (top) enters unionid and deposits eggs in mantle near incurrent siphon or in the gill filaments. In several weeks eggs hatch and larvae (bottom right) leave mussel to live free in environment. During spring, larvae enter mussels and encyst in epithelial tissues of the gills or mantle. Encysted larvae are known as nymphochrysales. In several weeks a larva (deutonymph; middle right) hatches from the nymphochrysalis and leaves the mussel. After feeding in the water column on plankton, the deutonymph returns to a mussel and encysts in the gill tissues forming an imagochrysalis. In several days an adult emerges from the imagochrysalis. Soon after emerging as adults, mating occurs on the gills. Most unionicolid species spend the majority of their adult lives in the water column. (mussel schematic modified from Olsen 1962; mites modified from Mitchell 1955)

Different unionicolid species have been reported to cause different types of damage to their hosts, and in turn they elicit different pathological responses. Some unionicolids are reported to ingest host cells and thus cause feeding associated disease in unionids (e.g., see Baker 1976, 1977). Baker (1976) showed that *Unionicola intermedia* can attach to the gills of mussels using its pedipalps, and its tarsi can become deeply imbedded in the gill tissue of its host. This produces tissue damage resulting in leukocytic infiltration (i.e., edema and inflammation of the area below the damaged epithelium by host blood cells). As mentioned above, additional damage to mussel hosts can be caused by female mites during oviposition (Mitchell 1965). Macroscopic observations of dissected unionids during this study did not reveal any apparent damage caused by unionicolid mites on the gills. Histological examination of the gills of three species of unionids (*Quadrula quadrula*, *Quadrula metanevra*, and *Quadrula pustulosa*) revealed no leukocytic infiltration within gill tissue inhabited by adult mites. Our observations suggest that individual unionicolids may not always significantly harm their unionid hosts, and that when they do cause harm, the tissue damage is hard to ascribe to them because of their vagile nature. Finally, we are unable to predict whether these mites could ever establish high enough densities within cultured mussel populations to cause reduced mussel survivorship.

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HISTOLOGICAL ANALYSIS OF GONAD DEVELOPMENT IN ZEBRA MUSSELS (BIVALVIA: DREISSENIDAE) FROM THE TENNESSEE AND OHIO RIVERS

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ABSTRACT. Zebra mussels were collected from Kentucky Lake and the Ohio River with the aid of SCUBA monthly between March 1996 and February 1997. During the reproductive season, mussels were collected weekly. Mussels from each river were fixed in 10% buffered formalin, dehydrated, embedded in paraffin, sectioned and stained with hematoxylin and eosin. Sections from each specimen were histologically examined, sexed and assigned to gametogenic stages based on gamete morphology and gonad maturity. Gonad maturity was determined by types and arrangement of tissue in the gonad. Seven gametogenic stages were observed during the reproductive season. The stages were identified as resting, early development, later development, ripe, spawning, redevelopment, and spent. Kentucky Lake zebra mussels matured and spawned slightly later than those in the Ohio River. By June, zebra mussels in both rivers were at approximately the same stage in reproductive development. Redevelopment of eggs in the gonad suggested that eggs were continually shed until the spent stage was reached in mid-October. Gonad development of males and females appeared to be synchronous. The reproductive season lasted approximately one month longer in Kentucky Lake than in the Ohio River. Eosinophilic cells were more numerous in late-stage zebra mussels from the Ohio River.

INTRODUCTION

The zebra mussel (*Dreissena polymorpha*) is an exotic pest species first discovered in North America in 1988 (Hebert *et al.*, 1989). Since their introduction, zebra mussels have spread throughout the Mississippi River system to Louisiana. Populations of zebra mussels have increased dramatically in almost every river system in which the species is found. Zebra mussels have proved to be a threat to the native Unionidae in the Ohio River because they can attach to unionid mussels in such large numbers that they interfere with feeding and respiration (Baker and Hornbach, 1997). Although zebra mussels are found in great abundance in the Ohio River, they have not become abundant in the Tennessee River, where they occur mainly at barge mooring facilities.

The purpose of this study was to determine if zebra mussels were undergoing normal reproductive development in the Tennessee River. Zebra mussels are known to reproduce successfully in the Ohio River. Therefore, zebra mussels collected from the Ohio River were assumed to develop normally and were used as a control. The histological development of the gonads in zebra mussels from both the Tennessee and Ohio Rivers was observed and compared over an 8-month period to determine any differences in reproductive development.

MATERIALS AND METHODS

Zebra mussels were collected by SCUBA monthly, between March 1996 and October 1996. Mussels were collected from Dam 52 on the Ohio River and from two sites in Kentuky Lake on the Tennessee River: one at Anderson Bay, and the other at the barge mooring cells near Kentucky Dam (Fig. 1). During the peak reproductive season (May through September) mussels were collected weekly. A minimum of 10 mussels from each site were shelled, fixed in 10% buffered formalin, dehydrated, embedded in paraffin, sectioned and stained with hematoxylin and eosin (Gray, 1964). Each specimen was labeled with an identification code.

Each specimen was examined at 100x magnification, sexed and assigned to a gametogenic stage based on the work of Shafee and Daoudi (1991). Gonad maturity was determined by types and organization of tissues in the gonad. Seven gametogenic stages were observed during the reproductive season (Table 1). Gametes were measured and counted to aid in stage assignments. Males were examined at 600x magnification for sperm counts. Females were examined at 200x for egg and follicle measurements and egg counts. Eosinophilic cells were counted at 600x in both males and females.

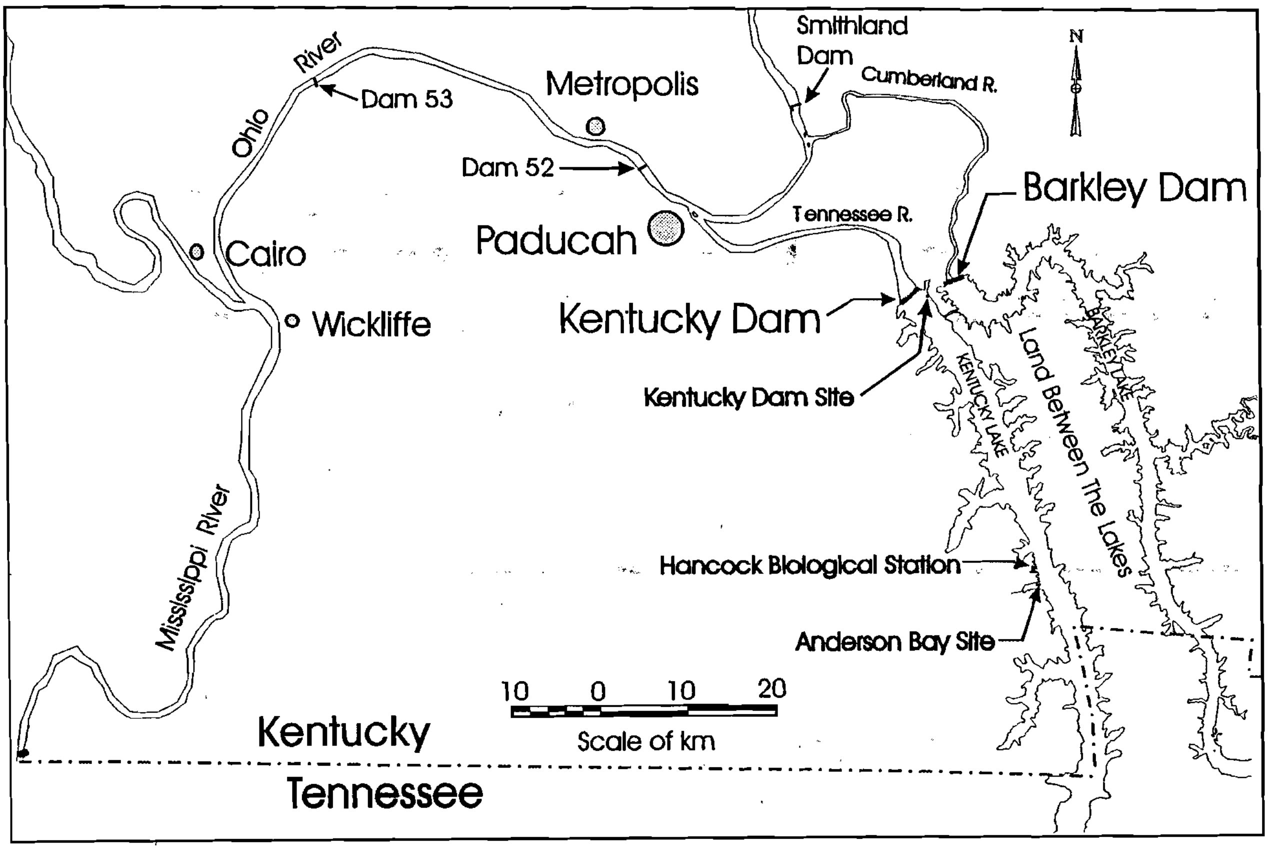

Figure 1. Map of zebra mussel collection sites on the Ohio and Tennessee Rivers. Mussels were collected from Dam 52 on the Ohio River and from two sites (Kentucky Dam, Anderson Bay) on the Tennessee River.

Table 1. Stages of gonadal development of zebra mussels (modified from Shafee and Daoudi, 1991)

Stage	Gonadal development
Stage 0: Resting	Sex indeterminate; connective tissue present in gonad; few or no identifiable gametes present.
Stage 1: Early development	Germinal cells present; ovarian follicles clearly defined; no mature gametes present.
Stage 2: Late development	Some mature gametes present; follicle and egg size small; tubules remain tightly packed, well organized.
Stage 3: Ripe	Large numbers of mature gametes present; follicles packed, small; tubules packed.
Stage 4: Spawning	Follicles larger, fewer gametes present; still large numbers of mature gametes; partially empty lumen in male tubules.
Stage 5: Redevelopment	Eggs present in all stages of development; follicles partially empty, large; in males, large numbers of spermatocytes present on outer edge of tubules; tubules less organized. Eosinophilic cells begin to invade gonad.
Stage 6: Spent	Follicle and tubule walls thicken; connective tissue invades gonad; eosinophilic cells present in large numbers; degenerating gametes present.

RESULTS AND DISCUSSION

The results of this study are presented in Tables 2 and 3. Early in the reproductive season, female zebra mussels from the Ohio River appeared to be maturing faster than males from the same site (Table 2). However, in May male zebra mussels from the Ohio River seemed to have surpassed the females in reproductive development. From June to October, female zebra mussels were consistently observed one developmental stage ahead of the males. Variance in sample size may account for the apparent change in rate of reproductive development.

Zebra mussels collected from the Tennessee River went through most stages of gonadal development at approximately the same time as those in the Ohio River. In March, the small sample size (4 mussels) from the Tennessee River probably accounts for the smaller number of reproductive stages observed. A smaller percentage of females was observed spawning in the Tennessee River than in the Ohio River in June. However, a larger proportion of Tennessee River females collected in June were in the ripe stage.

Continued development of gametes was noted after the first spawning stage in both Ohio and Tennessee River zebra mussels. The late observation of ripe and spawning stages (September, October) in Tennessee River zebra mussels suggests that Tennessee River zebra mussels may have a second major spawning event (Table 2). The absence in Ohio River zebra mussels of a second "ripe" stage, in which follicles and tubules are packed with mature gametes suggests one major spawning event, after which zebra mussels continually release small numbers of gametes until the gonads are spent (Haag and Garton, 1992).

Preliminary findings suggest that zebra mussels in the Ohio River have more eosinophilic cells present in the later stages of gametogenic development than are present in Tennessee River mussels in the same developmental stages (Table 3). Tennessee River mussels appear to have eosinophilic cells present in small numbers throughout the reproductive season. In Ohio River mussels, eosinophilic cells are usually absent until the spent stage when they invade the gonad in large numbers.

Table 2. Percent of male and female zebra mussels from the Ohio and Tennessee Rivers in different reproductive stages by month (March-October 1996).*

	Ohio River		Tennessee River	
Month	Males	Females	Males	Females
March	Stage 1: 70% Stage 2: 20% Stage 3: 10% (n=30)	Stage 1: 20% Stage 2: 52% Stage 3: 24% Stage 6: 4% (n=25)	Stage 1: 50% Stage 3: 50% (n=2)	Stage 2: 100% (n=2)
April	Stage 1: 21% Stage 2: 50% Stage 3: 18% Stage 4: 11% (n=28)	Stage 1: 3% Stage 2: 56% Stage 3: 41% (n=34)	Stage 0: 12.5% Stage 2: 62.5% Stage 3: 12.5% Stage 4: 12.5% (n=8)	Stage 1: 8% Stage 2: 42% Stage 3: 33% Stage 6: 17% (n=12)
May	Stage 2: 11% Stage 3: 11% Stage 4: 78% (n=9)	Stage 2: 17% Stage 3: 33% Stage 4: 50% (n=6)	Stage 1: 50% Stage 2: 25% Stage 3: 12.5% Stage 4: 12.5% (n=8)	Stage 3: 100% (n=1)
June	Stage 3: 11% Stage 4: 67% Stage 5: 11% Stage 6: 11% (n=9)	Stage 2: 10% Stage 3: 30% Stage 4: 50% Stage 6: 10% (n=10)	Stage 3: 13% Stage 4: 75% Stage 5: 6% Stage 6: 6% (n=16)	Stage 2: 4% Stage 3: 52% Stage 4: 29% Stage 5: 15% (n=27)
July	Stage 5: 100% (n=4)	Stage 5: 100% (n=3)	Stage 5: 100% (n=5)	Stage 4: 12.5% Stage 5: 87.5% (n=8)
August	Stage 5: 100% (n=1)	Stage 0: 33% Stage 6: 67% (n=3)	Stage 5: 100% (n=2)	Stage 6: 100% (n=2)

Table 2. Continued

September	Stage 5: 100% (n=1)	Stage 5: 17% Stage 6: 83% (n=6)	Stage 4: 27% Stage 5: 55% Stage 6: 18% (n=11)	Stage 3: 33% Stage 4: 7% Stage 5: 27% Stage 6: 33% (n=15)
October	Stage 0: 50% Stage 6: 50% (n=4)	Stage 0: 17% Stage 6: 83% (n=6)	Stage 5: 20% Stage 6: 80% (n=5)	Stage 0: 11% Stage 3: 5% Stage 5: 16% Stage 6: 68% (n=19)

*Stage 0 (resting stage) mussels were listed as male or female if degenerating sperm or eggs were observed. There was no method of determining sex other than histological examination.

Table 3. Mean number of eosinophilic cells (± S. E.) observed at 600x per 16.9 x 10^3 μm^2 gonadal area in different reproductive stages of Tennessee and Ohio River mussels collected between March-October 1996.

	Ohio River		Tennessee River	
Stage	Males	Females	Males	Females
Resting (0)	2.5 ± 0.5	2.5 ± 2.5	*	14.5 ± 13.5
Early development (1)	2.4 ± 0.71	2.2 ± 1.3	1.0 ± 1.0	*
Late development (2)	1.0 ± 0.33	3.9 ± 0.91	1.1 ± 0.51	4.0 ± 2.4
Ripe (3)	0.6 ± 0.31	1.8 ± 0.42	0.4 ± 0.4	2.9 ± 0.84
Spawning (4)	.81 ± 0.56	1.9 ± 0.75	.65 ± 0.27	3.6 ± 1.3
Redevelopment (5)	1.9 ± 1.7	3.3 ± 1.9	2.3 ± 0.78	7.7 ± 1.8
Spent (6)	7.7 ± 3.8	20.4 ± 5.23	4.1 ± 1.8	8.8 ± 1.8
All Stages	1.7 ± 0.34	5.5 ± 1.1	1.6 ± 0.35	5.9 ± 0.78

*Data not available.

Egg quality appears better in Ohio River mussels than in Tennessee River mussels. In other species of bivalve, such as *Ruditapes decussatus*, ameobocytic cells function to destroy unspawned gametes (Shafee and Daoudi, 1991; Ituarte, 1997; Bielefeld, 1991). The eosinophilic cells observed in zebra mussels appear to digest unspawned gametes (Fig. 2). It is possible that these cells may serve some regulatory function in the gonad by destroying gametes which are of poor quality, thereby conserving energy and nutrients (Bielefeld, 1991).

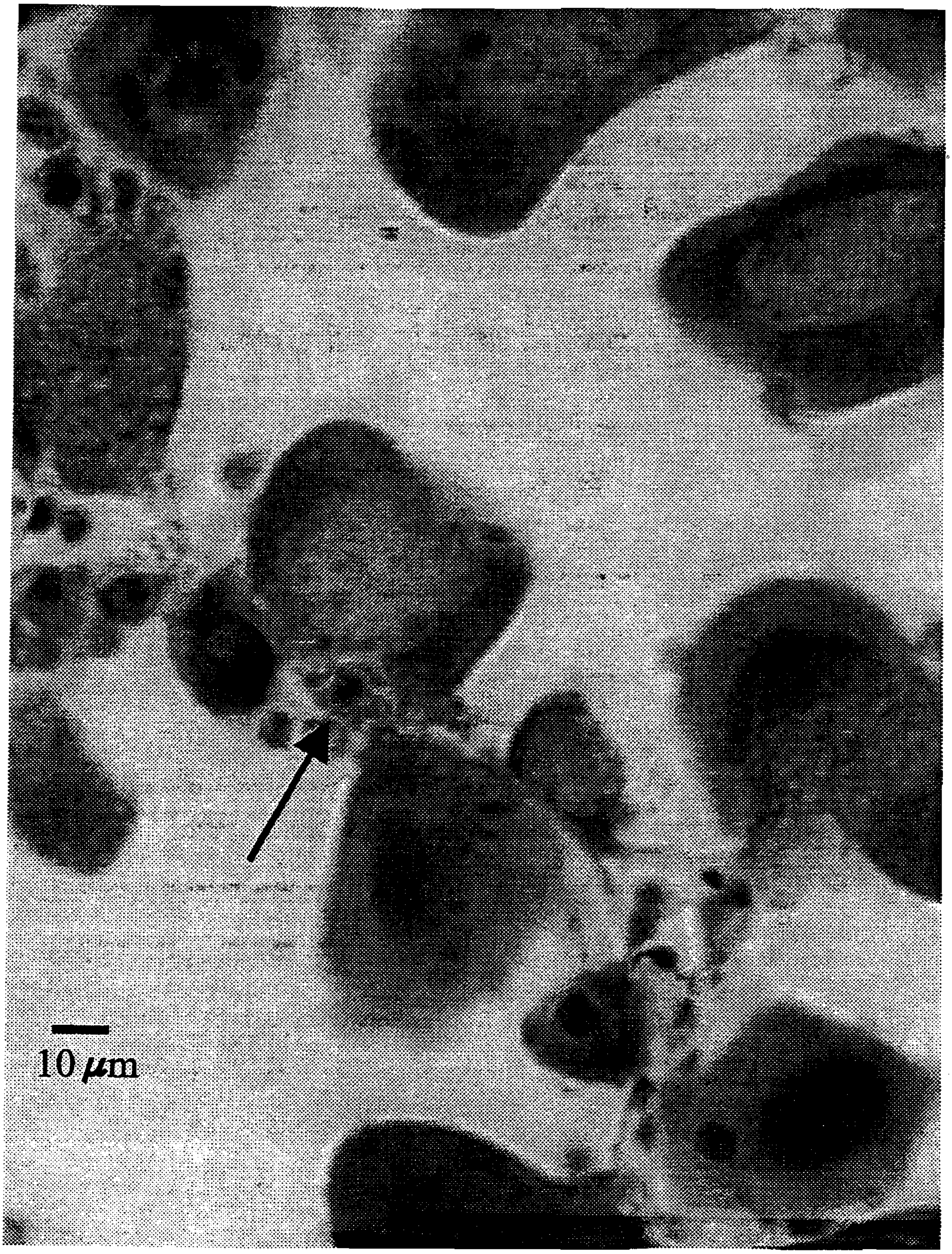

Figure 2. Female zebra mussel collected June 6, 1996 in the redevelopment stage. An eosinophilic cell appears to be attacking an unspawned mature egg. (600x)

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DISTRIBUTION AND POPULATION CHARACTERISTICS OF ZEBRA MUSSELS, *DREISSENA POLYMORPHA*, (BIVALVIA: DREISSENIDAE) IN KENTUCKY LAKE, KENTUCKY

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ABSTRACT. Zebra mussel (*Dreissena polymorpha*) occurrence, distribution, and population characteristics within the Kentucky portion of Kentucky Lake were investigated between June 1995 and October 1996. Eighty-eight sites, each with a search area of 20 m^2 (1760 m^2 total), were surveyed by SCUBA divers equipped with 1m^2 quadrat frames. Two of the sites had zebra mussels, one near Kentucky Dam (TRM 23.4) and the other at Anderson Bay (TRM 45.4). The two sites have been chosen as long-term monitoring stations. Both sites were adjacent to barge mooring facilities. Samples of 10-30 zebra mussels were collected at least twice monthly from each site between April and October 1996, 335 at the Kentucky Dam site and 221 at Anderson Bay. Zebra mussel density was 26.8/m^2 at Kentucky Dam and 5.45/m^2 at Anderson Bay. Shell length ranged from 3.5-38.3 mm ($\bar{x}$ = 19.1) at Kentucky Dam and 1.1-27.7 mm ($\bar{x}$ = 12.4) at Anderson Bay. Other allometric characteristics for Kentucky Dam and Anderson Bay respectively were mean shell height 9.7 and 6.9 mm, mean shell width 9.8 and 6.2 mm, and mean wet weight 1.20 and 0.38 g. Assuming that adult mussels are greater than 10 mm in length, 88.7% (297) of Kentucky Dam and 68.3% (151) of Anderson Bay zebra mussels were of reproductive size. Based on the Kentucky Lake survey, zebra mussels occurred in low densities and only at sites associated with barge activity. The two populations being studied differ in allometric characteristics. There is no indication of veliger development and settling at these sites or at any of the other 86 sites. Apparently, zebra mussels are being transported into Kentucky Lake attached to barges, and although growth of adults occurs, successful reproduction does not appear to occur.

INTRODUCTION

Investigators in Europe and North America have documented zebra mussel (*Dreissena polymorpha*) invasion rate, population structure, reproduction, and many other characteristics (Mackie *et al.* 1990; Claudi and Mackie 1994; O'Neill and Dextrase 1994; Johnson and Carlton 1996). Differences between populations in Europe and the Great Lakes have been documented (McMahon 1996; Marsden *et al.* 1996). Comparisons of various parameters have been used to answer some questions about the ecological impact of zebra mussels (Hebert *et al.* 1991; MacIsaac 1996). Distribution, density, reproduction, and allometric characteristics of zebra mussel populations are being used to determine their success in Kentucky Lake, Kentucky. Zebra mussels were first discovered in the lower Tennessee River in 1991 (TVA 1991). There are no descriptive or quantitative data pertaining to characteristics of zebra mussels within the Kentucky portion of Kentucky Lake. Zebra mussel data would allow comparisons within Kentucky Lake and other areas. Characteristics of the zebra mussel populations will be useful to gauge how successful zebra mussels may become within Kentucky Lake.

Describing population characteristics of this invader is the first part in long-term research examining the effects of zebra mussels on the invertebrate community, especially the freshwater mussel community within Kentucky Lake and the Tennessee River. The Tennessee River has a rich assortment of native freshwater mussels. Assessments of commercial mussel resources in Kentucky Lake indicate two commercially important species, the washboard (*Megalonaias nervosa*) and mapleleaf (*Quadrula quadrula*), that are declining in numbers (Sickel *et al.* 1996). These two species could be more vulnerable to extirpation due to zebra mussels. Mussel resources are commercially valuable to the region. Research in the Great Lakes and other areas in the United States suggests that zebra mussels are a direct threat to native mussel assemblages (Ricciardi *et al.* 1995). If zebra mussels successfully invade Kentucky Lake, they could influence the survival and long-term management decisions involving the freshwater mussel community.

STUDY AREA AND METHODS

Kentucky Lake encompasses 296.6 km of the Tennessee River (Sickel *et al.* 1996). Drainage area of the Tennessee River to Kentucky Dam is 104,118 square km (Lowery *et al.* 1990). Kentucky Lake is impounded by Kentucky Dam located on the Tennessee River 36.0 km from the confluence with the Ohio River (at Tennessee River mile 22.4). The reservoir extends south 296.6 km to Pickwick Dam (at TRM 206.7). The Kentucky portion of Kentucky Lake extends south from Kentucky Dam to the Kentucky-Tennessee border, a distance of 64.4 km (at TRM 62.4) west of the channel and 43.1 km (at TRM 49.2) east of the channel.

A commercial mussel survey of 86 sites representing levee, overbank, shoreline, and embayment habitat types also included location and occurrence of zebra mussels (Sickel *et al.* 1996). Eighty-six sites each had a sample area of 20 m^2 which was searched by SCUBA divers. Because of limited visibility, each diver used a 1 m^2 quadrat frame to provide a quantitative aid for searching the sediment. The quadrat was a metal square divided into 4 sections to allow the diver to search 1 m^2 while using the smaller squares for orientation and greater search efficiency. At each site, two divers would descend a 30.5 m transect line that was knotted every 3.0 m to alert divers of search areas. Each diver searched along one side of the transect line. Searches were done at knots where divers would collect all the mussels within the quadrat and place them in mesh bags. Data on the unionids were collected, and the shells were examined for zebra mussels or byssal plaques. Two additional sites were surveyed using the same methods in the spring of 1996: one site is near Kentucky Dam (TRM 23.4); the other at the mouth of Anderson Bay (TRM 45.4) (Fig. 1).

Allometric data of shell length, shell height, shell width, and whole wet weight were collected on zebra mussels. Shell length was measured as the greatest distance from umbo to distal margin. Shell height was the greatest distance from ventral surface to the dorsal margin. Shell width was measured as the greatest distance perpendicular to the hinge along ventral surface. Measurements were obtained to the nearest 0.01 mm using an electronic digital caliper (Mitutoyo, Ltd.). Wet weight was measured as shell and visceral mass intact. Measurements were made to the nearest 0.001g using a Mettler 100 AC balance. ANOVA single factor test was performed on results.

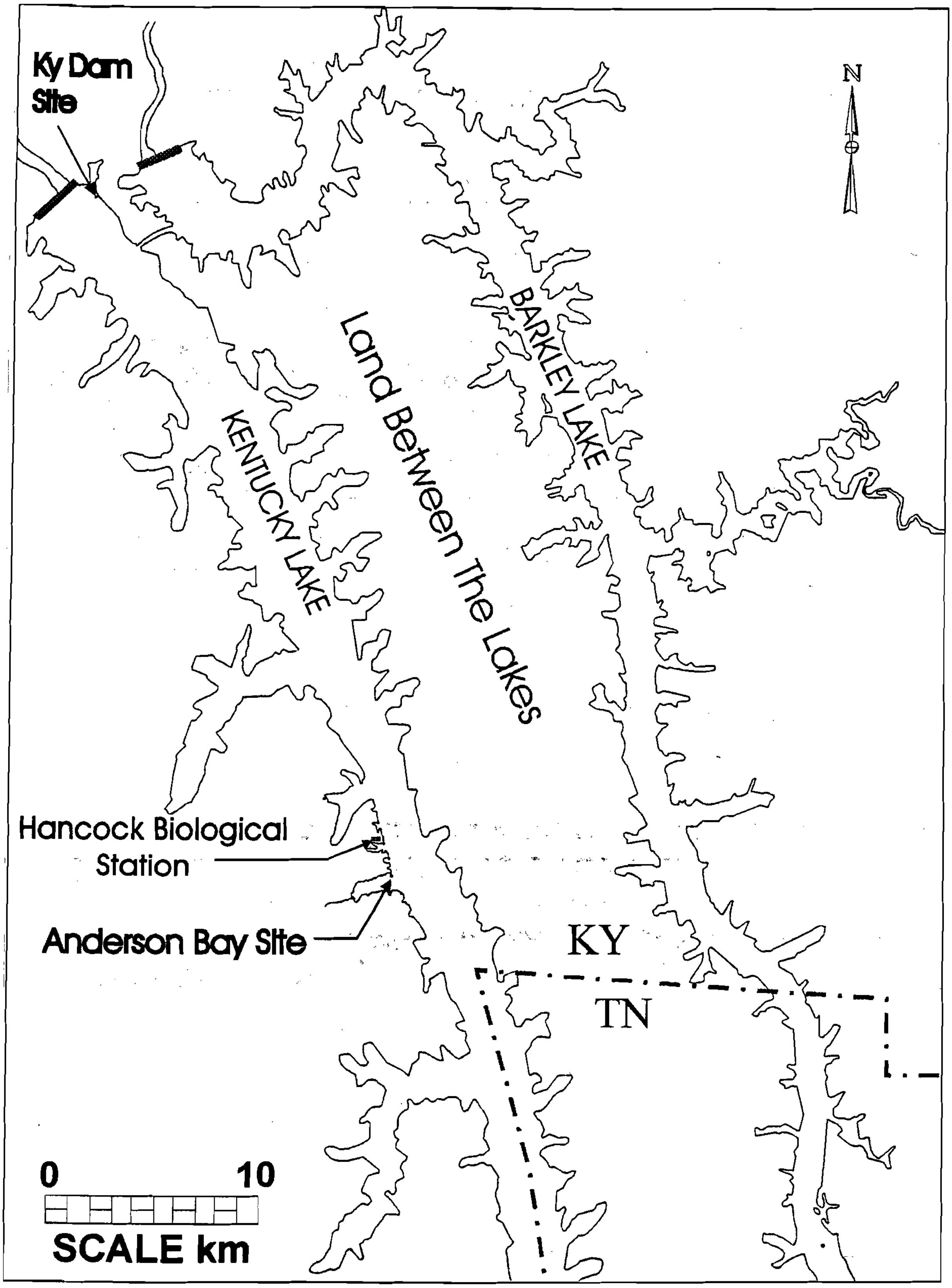


Figure 1. Map of Kentucky portion of Kentucky Lake indicating locations of long-term zebra mussel monitoring sites at Kentucky Dam and Anderson Bay.

RESULTS

The survey of 88 sites consisting of a total search area of 1760 m^2 found zebra mussels at only 2 sites; near Kentucky Dam (TRM 23.4) and at Anderson Bay (TRM 45.4) (Fig. 1). Both sites have barge mooring facilities. Zebra mussel densities were 26.8/m^2 and 5.4/m^2 respectively.

Allometric data were based on samples collected from April through October 1996 (Fig. 2 and 3). Sample size was 335 zebra mussels from TRM 23.4 and 221 from TRM 45.4. Shell length at TRM 23.4 ranged from 3.4-38.2 mm ($\bar{x}$ = 19.1) and 1.1-27.7 mm ($\bar{x}$ = 12.4) at TRM 45.4. Shell height ranged from 1.2-17.3 mm ($\bar{x}$ = 9.7) and 0.76-14.3 mm ($\bar{x}$ = 6.9). Shell width ranged from 1.8-20.5 mm ($\bar{x}$ = 9.8) and 0.60-15.2 mm ($\bar{x}$ = 6.2). Wet weight ranged from 0.002-6.85 g ($\bar{x}$ = 1.20) and 0-2.95 g ($\bar{x}$ = 0.38).

ANOVA single factor test was performed on a ratio of height to width to determine if zebra mussels had the same ratio at each site. Ratio of height to width was significantly different between sites (F = 1832.423; *df* = 1, 554; P = 8E-178). Zebra mussels at TRM 23.4 were wider than tall and TRM 45.4 zebra mussels were taller than wide (Table 1). Monthly length frequencies were plotted for May, June, July, and August to describe growth. ANOVA single factor test was performed on average length for the months to test for no change. The monthly length frequencies at TRM 23.4 had average lengths of 10.60, 18.80, 18.96, and 21.24 mm (Fig. 4). There was a change in length over the 4 months (F = 18.32; *df* = 3, 84; P = 3.11E-09) (Table 2). Length frequencies for TRM 45.4 were 7.1, 12.0, 11.5, and 13.3 mm (Fig. 5). There was a significant change in mean length over the 4 months (F = 14.68; *df* = 3, 170; P = 1.51E-08) indicating growth is occurring in Kentucky Lake.

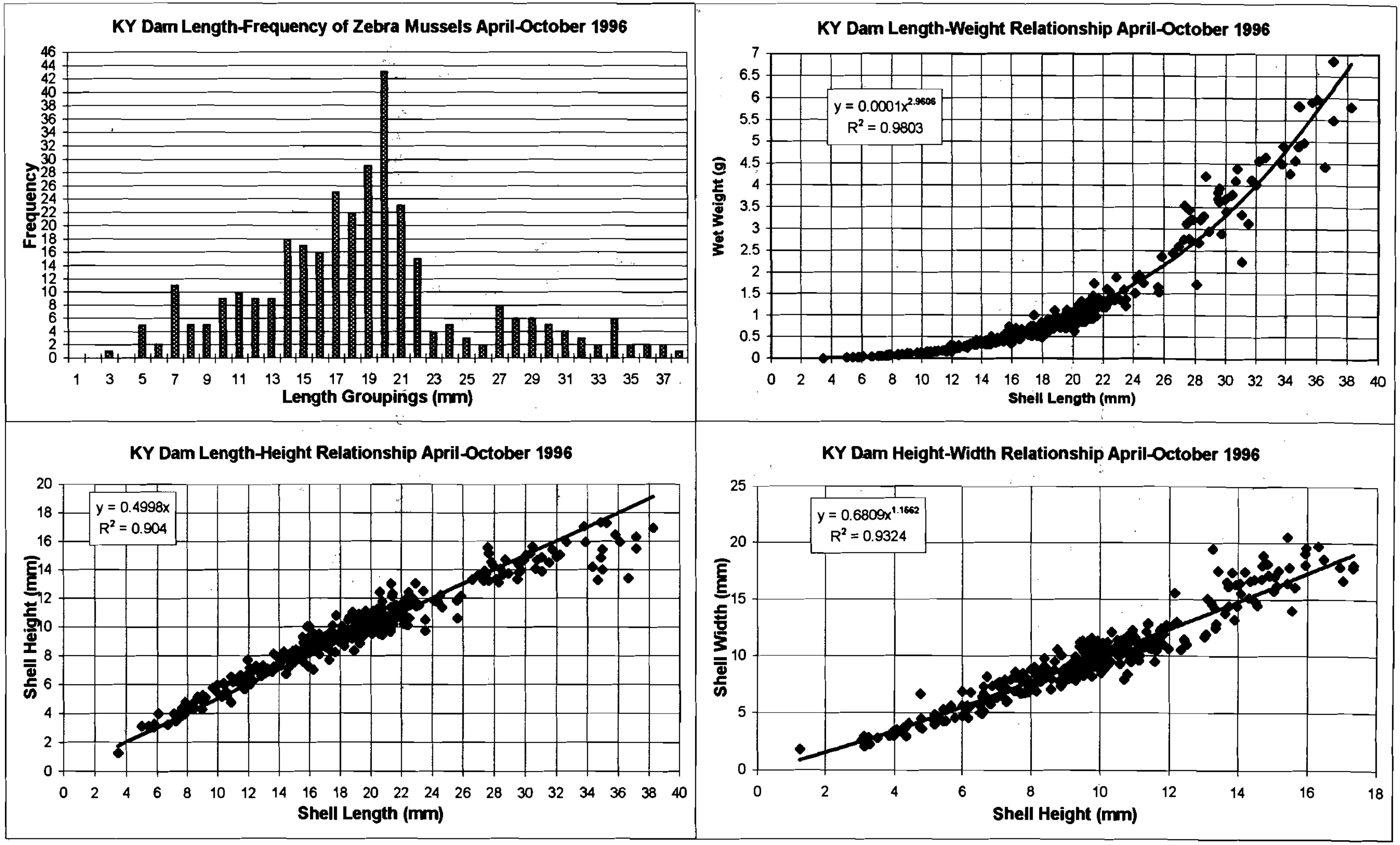
Table 1. ANOVA single factor test for significant difference between height/width ratio of zebra mussels from Kentucky Dam and Anderson Bay sites.

SUMMARY

Groups	*Count*	*Sum*	*Average*	*Variance*
KY Dam Ratio H:W	335	343.0354	1.023986	0.0173073
Anderson Ratio H:W	221	1742.645	7.88527	8.58831

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	6268.64	1	6268.636	1832.423	8E-178	3.8583
Within Groups	1895.21	554	3.420955			
Total	8163.84	555				



KY Dam Length-Frequency of Zebra Mussels April-October 1996

KY Dam Length-Weight Relationship April-October 1996

KY Dam Length-Height Relationship April-October 1996

KY Dam Height-Width Relationship April-October 1996

Figure 2. Summary of data for length-frequency, length-weight, length-height, and height-width collected from zebra mussels near Kentucky Dam, April-October 1996.

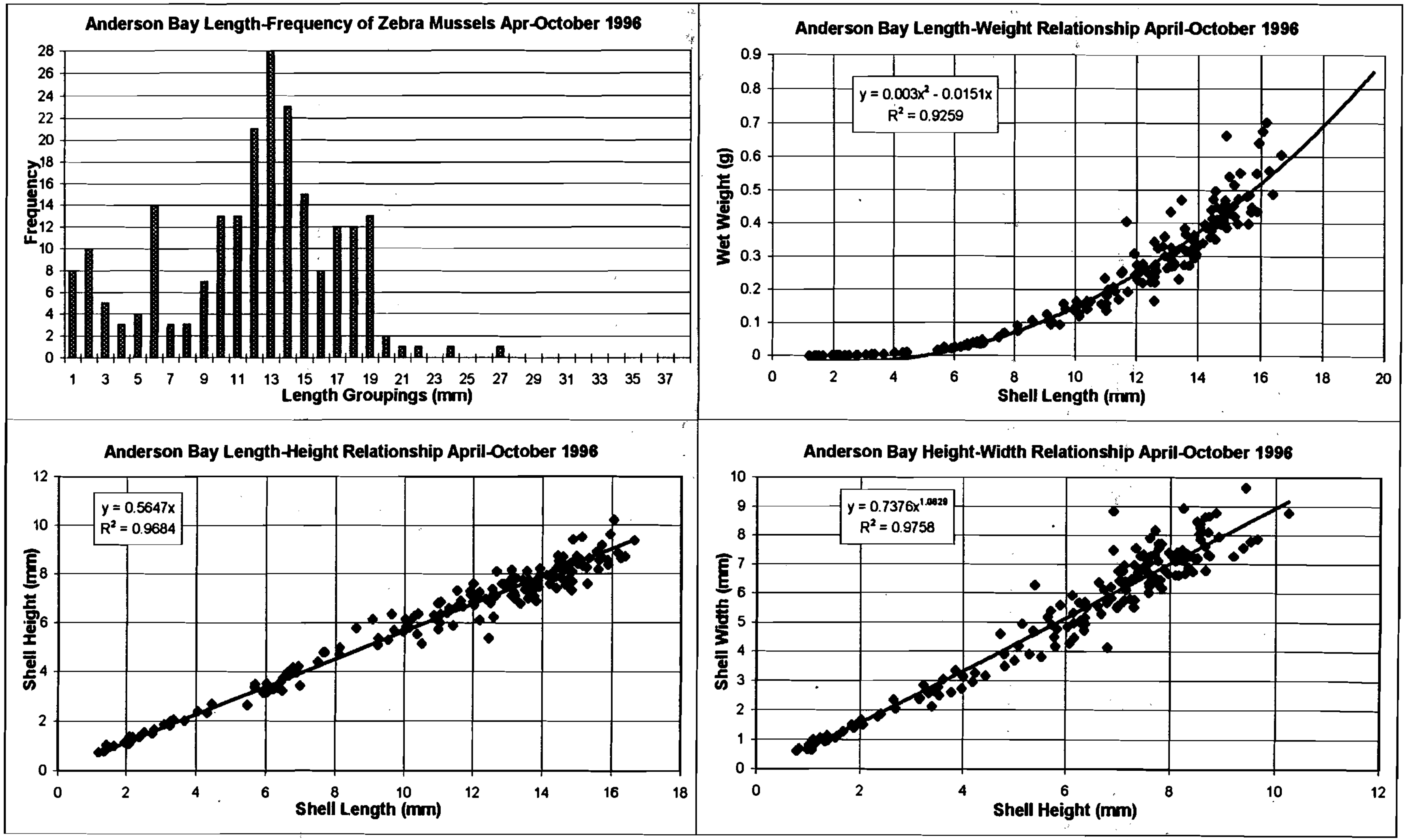


Figure 3. Summary of data for length-frequency, length-weight, length-height, and height-width collected from zebra mussels in Anderson Bay, April-October 1996.

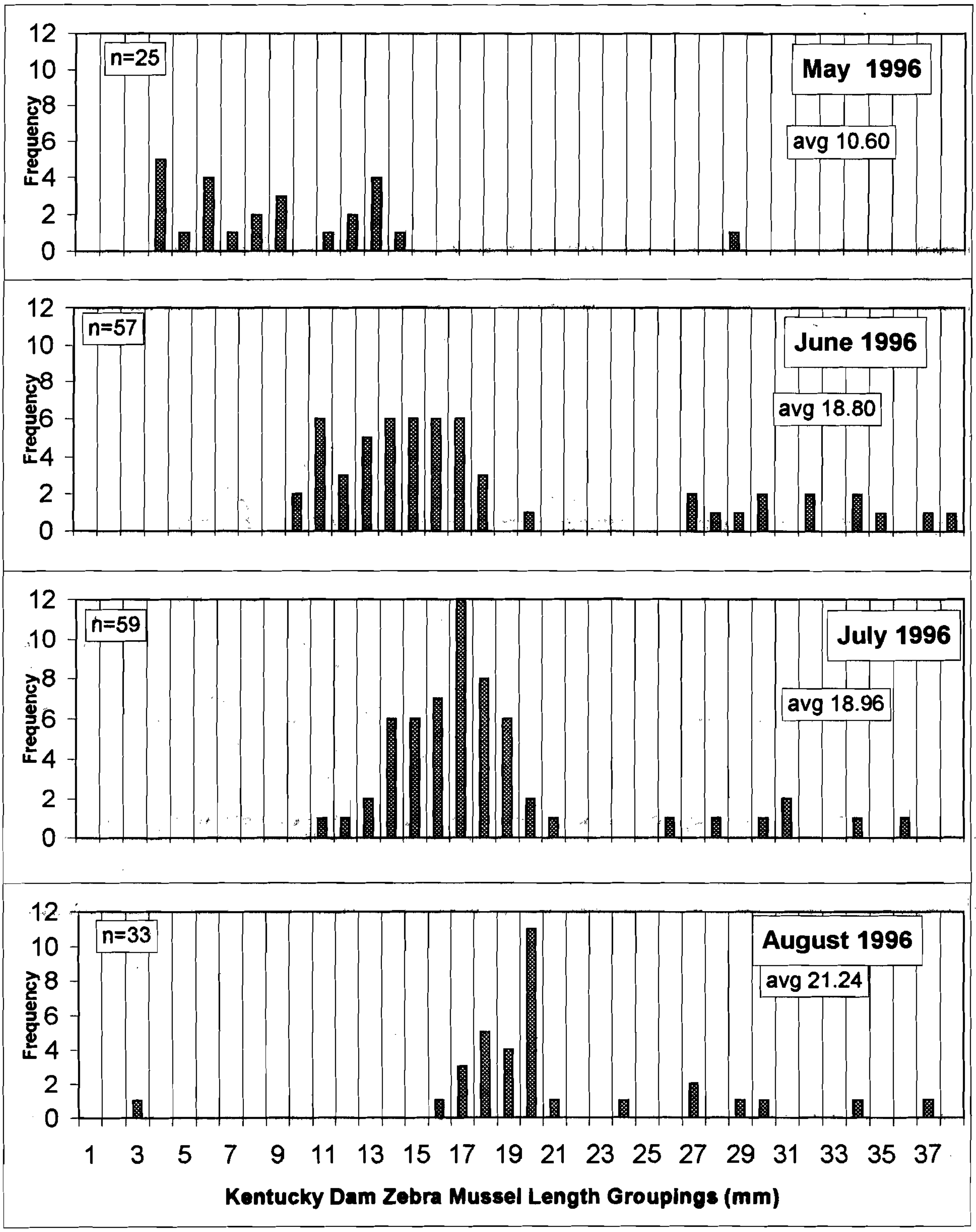


Figure 4. Monthly length-frequencies of zebra mussels from near Kentucky Dam for May, June, July, and August 1996.

Table 2. ANOVA single factor test for significant monthly growth of zebra mussels at Kentrucky Dam and Anderson Bay sites.

ANOVA: Single Factor
Anderson Monthly Growth
SUMMARY

Groups	*Count*	*Sum*	*Average*	*Variance*
Monthly Total May 1996 Length (mm)	15	106.07	7.07133	4.73671
Monthly Total Jun 1996 Length (mm)	10	120.06	12.006	32.3887
Monthly Total Jul 1996 Length (mm)	31	356.25	11.4919	7.46642
Monthly Total Aug 1996 Length (mm)	32	426.7	13.3344	1.17012

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	404.34	3	134.78	18.3173	3.1e-09	2.71323
Within Groups	618.078	84	7.35808			
Total	1022.42	87				

ANOVA: Single Factor
KY Dam Monthly Growth
SUMMARY

Groups	*Count*	*Sum*	*Average*	*Variance*
Monthly Total May 1996 Length (mm)	25	265.02	10.6008	27.6308
Monthly Total Jun 1996 Length (mm)	57	1071.64	18.8007	61.5834
Monthly Total Jul 1996 Length (mm)	60	1137.84	18.964	28.5377
Monthly Total Aug 1996 Length (mm)	32	679.69	21.2403	36.3476

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	1794.16	3	598.055	14.6872	1.5e-08	2.65776
Within Groups	6922.31	170	40.7195			
Total	8716.48	173				

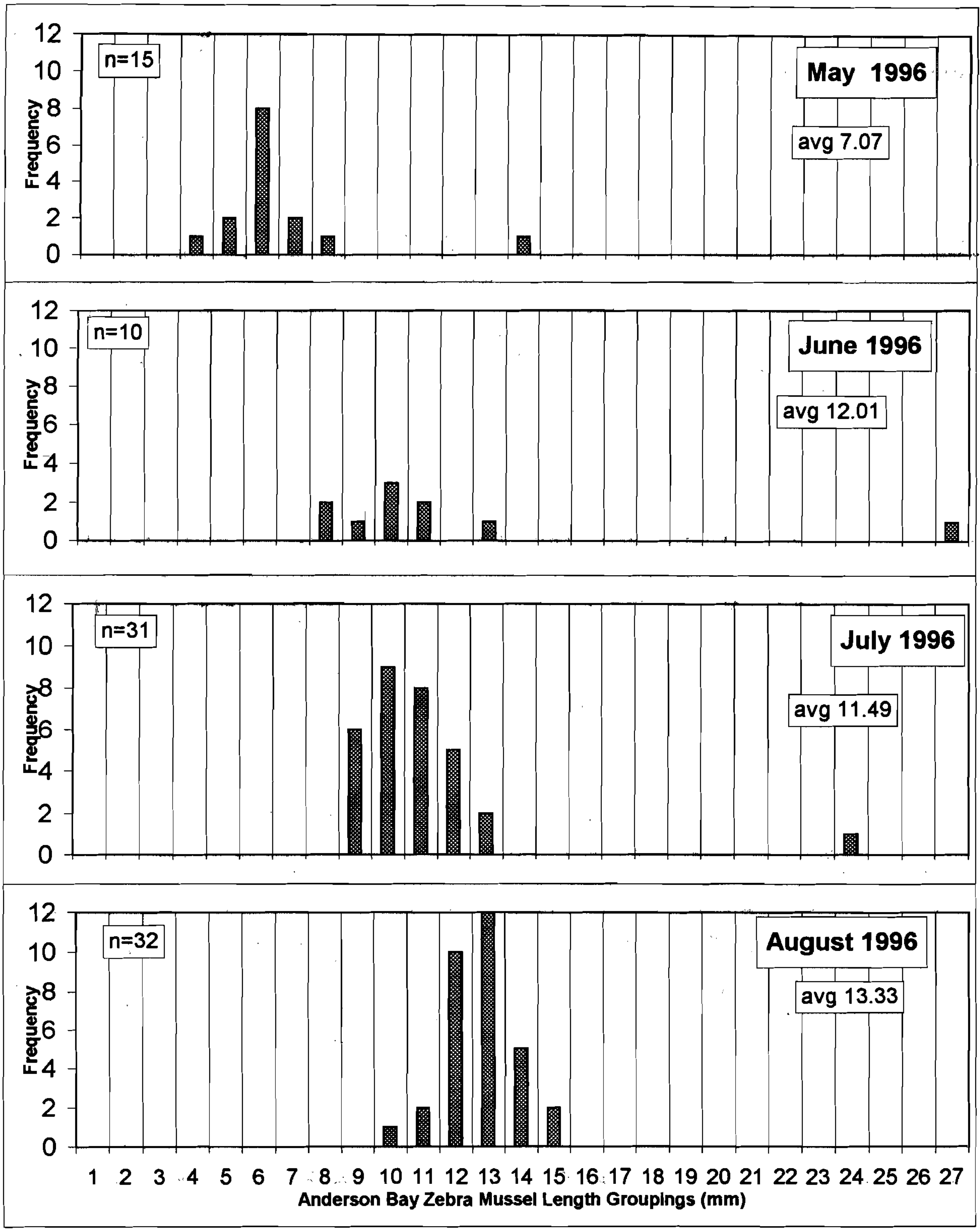


Figure 5. Monthly length-frequencies of zebra mussels from Anderson Bay for May, June, July, and August 1996.

DISCUSSION

Zebra mussels were found at two sites which were classified as a shoreline (TRM 23.4) and embayment (TRM 45.4) habitat type. Both sites are being used by us for long-term monitoring. The zebra mussel densities at these sites are extremely low compared with data from the Great Lakes (Roberts 1990). Physical and chemical factors within Kentucky Lake probably are limiting densities and distribution.

Comparison of allometric data from near Kentucky Dam and Anderson Bay show differences that may be influenced by local environmental and chemical factors. Shell length data from near Kentucky Dam and absence of juveniles suggest that no settlement by postveligers is occurring. We believe that individuals are being brought in by barges. The absence of postveligers, individuals with a 1-3 mm shell length range, indicates that reproduction is not occurring (Martel 1993). In contrast, Anderson Bay length frequency data indicate that 1-3 mm individuals are present. The absence of veligers in plankton samples suggests that these small juveniles entered the population by falling from barges. Comparing length ranges, Anderson Bay zebra mussels are smaller than Kentucky Dam zebra mussels. Age was not determined, therefore it is not known if the smaller size at Anderson Bay is a result of slower growth or smaller size at recruitment. The timing of barge activity and origin of barges at each site probably influences the size of the zebra mussels more than differences in growth rate. Sprung (1993) found zebra mussels that were sexually mature at shell lengths between 3-16 mm. If we use a conservative size of >10 mm for an adult zebra mussel, then 88.6% at Kentucky Dam and 68.3% of zebra mussels at Anderson Bay are of reproductive size. Samples for veligers are being collected, but no veligers have been found.

Length frequencies were used to determine growth. The average length increased 10.6 mm in 4 months for Kentucky Dam zebra mussels. The average length increased 6.2 mm for the same time period at Anderson Bay. There appears to be a difference in the rate of growth between the 2 sites. We are not certain if the difference in growth rate is a physiological difference at varying sizes or if the difference is related to the physical habitat. We believe that changes in length-frequency data is a good indicator of growth, but we are attempting to use better methods to quantify growth of individuals. Another difference is the ratio of height to width. Generally, Kentucky Dam zebra mussels are wider than they are tall. Anderson Bay mussels are taller than they are wide. Shell allometric components change with length and age which may explain the differences we found between Kentucky Dam and Anderson Bay zebra mussels (Bitterman *et al.* 1994).

Morphology has direct effects on the survival of an organism in relation to its environment. One factor for zebra mussel survival and possible success is morphology. Success can only happen if the morphology is advantageous. The second factor which is being investigated is the water chemistry in Kentucky Lake compared with other areas that have zebra mussels. Further research needs to be focused on describing differences in morphology in relation to the physical environment.

ACKNOWLEDGMENTS

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A COMPARISON OF LARVAL DEVELOPMENT IN THE ZEBRA MUSSEL, *DREISSENA POLYMORPHA*, (BIVALVIA: DREISSENIDAE) UP TO THE FREE-SWIMMING TROCHOPHORE STAGE IN TENNESSEE AND OHIO RIVER WATER

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ABSTRACT. In 1991 zebra mussels (*Dreissena polymorpha*) were first reported in the lower Ohio and Tennessee Rivers. Since that time, zebra mussel populations have increased dramatically within the lower Ohio River but not the Tennessee River. Speculation has been made that zebra mussel reproduction in Tennessee River water may be negatively affected by inadequate water quality, possibly due to low Ca^{++} ion concentration. To determine if zebra mussels from the Tennessee River are producing viable gametes capable of development, zebra mussels were collected from the Kentucky Lake portion of the Tennessee River and artificially spawned in the laboratory. Artificial spawning was induced by external applications of 10^{-4} M serotonin (5-Hydroxytryptamine, 5-HT) solution. Both male and female gametes were released in abundance and fertilization readily occurred in Tennessee River water. Once fertilized, eggs were divided and placed into separate petri dishes with some containing Ohio River water and others containing Tennessee River water. The dishes were continually stirred and observations on development were made for 7 hours. Eggs in both Ohio and Tennessee River water began dividing a little over 1 hour after fertilization and continued developing at a steady rate. The first signs of movement resulting from cilia development occurred approximately 5-6 hours after fertilization in Ohio River water and approximately 6-7 hours after fertilization in Tennessee River water. Development up to the free-swimming trochophore stage successfully occurred in both Ohio and Tennessee River water.

INTRODUCTION

The zebra mussel, *Dreissena polymorpha,* was first discovered in North America in Lake St Clair in 1988 (Herbert *et al.* 1989). It is thought that this exotic mussel was introduced into the Great Lakes region through discharge of ballast water from European shipping traffic, as have been many other invading species (Sprules *et al.* 1990). Since the introduction of this exotic mussel into North American waters, it has spread rapidly due in part to its unique life cycle. The zebra mussel is unusual among freshwater mollusks in having a free-swimming planktonic larval stage, similar to that of many marine bivalves. All other native freshwater mollusks have either a brief parasitic larval stage or direct development within the mantle cavity of the adult mussel (Garton and Haag 1993, Sprung 1993).

Zebra mussels are dioecious broadcast spawners, releasing their gametes in enormous quantities directly into the water column. Fertilization occurs externally, with development following in the open water. After fertilization larvae first pass through a free-swimming lecithotrophic period, called the trochophore, lasting approximately 1-2 days. It is at this stage that ciliary development occurs and movement begins. The trochophore period ends with the formation of a D-shaped shell and a velum, a larval organ of feeding and locomotion. Larvae then enter into its planktotrophic phase, called the veliger. The time in which larvae remain in the planktonic stage varies between 10-90 days and is largely dependant on the environmental conditions present at a particular site. As larvae develop, their limits for various environmental conditions tend to increase (Nichols 1993). When larval development is complete, veligers will metamorphose into shelled settling juveniles. At this time the byssal gland develops and the production of byssal threads for attachment begins (Ackerman 1994).

Zebra mussels become sexually mature when they reach approximately 5 mm in length (Nichols 1996). Spawning occurs when gonadal maturity is reached. The event of spawning is believed to be highly synchronous within individual populations, occurring over a period of 6-8 weeks (Haag and Garton 1992). Environmental influences such as chemicals, temperature, and photoperiod may regulate synchronous development of gametes and possibly provide specific trigger stimuli for spawning in both sexes (Ram *et al.* 1996). Experiments have shown that the presence of gonadal fragments or sperm introduced into water containing females with ripe gametes will induce spawning (Waltz 1978, Sprung 1987).

Zebra mussel oocytes are arrested at the germinal vesicle stage (prophase I) within the ovary until spawning is induced causing development up to metaphase I, at which time they are again arrested until fertilization (Fong *et al.* 1994a). Serotonin (5-Hydroxytryptamine, 5-HT) has been identified as the chemical stimulant present in mussels of both sexes which causes the induction of spawning (Ram *et al.* 1993). Serotonin or related compounds released with gametes may mediate the synchronization of spawning among individuals (Fong *et al.* 1994a). The presence of serotonin can cause the induction of germinal vesicle breakdown allowing fertilization to occur in both in vivo and in vitro ovaries (Fong *et al.*1994b).

In the fall of 1991 zebra mussels were first discovered in the lower Ohio and Tennessee Rivers (TVA, 1991). Since this time populations have proliferated in the Ohio River but not in the Tennessee River. Two small zebra mussel populations have been located within the Kentucky Lake portion of the Tennessee River in Kentucky. The largest population contains densities of only 27 mussels per square meter. Both populations are located adjacent to mooring cells where adult mussels are believed to have dropped off of moored barges, becoming permanent residents to Kentucky Lake.

Due to the extreme increase in population numbers of zebra mussels and the presence of veligers within the water column in the Ohio River, it is apparent that spawning and development is occurring there. Mussels are present in the Tennessee River, but a population explosion has not occurred as is the case in the Ohio River. The lack of population increase could be due to a lack of necessary environmental conditions. One such condition which could be controlling zebra mussel populations in the Tennessee River is low Ca^{++} concentrations. Shell growth in zebra mussels requires Ca^{++} from the environment. The Ca^{++} concentrations present in the Tennessee River throughout 1996 ranged between 17-25 mg/L. This range falls below the minimal limits determined to be necessary for zebra mussel eggs to develop. Adult zebra mussels normally found in water with moderate to high Ca^{++} concentrations will survive low environmental Ca^{++} concentrations, providing the bathing fluid contains Mg in minimal amounts (Dietz *et al.* 1994). The intention of this study was to determine if zebra mussels present in the lower Ohio and Tennessee Rivers were producing the gametes necessary for spawning to occur and, if so, will gametes develop up to the free-swimming trochophore stage.

MATERIALS AND METHODS

Zebra mussels were collected from one site on the lower Ohio River and two sites on the Kentucky Lake portion of the Tennessee River (Fig. 1). The mussels were collected in the Ohio River at the Army Corps of Engineers Dam 52, at river mile 938.9 near Brookport ,Il. In Kentucky Lake, mussels were collected at river mile 23.5 near Kentucky Dam and also in Anderson Bay at river mile 45.1. Some mussels collected 21 April 1996 from both bodies of water were sacrificed to enable observations of gonadal tissue under a microscope, to determine if ripe gametes were present.

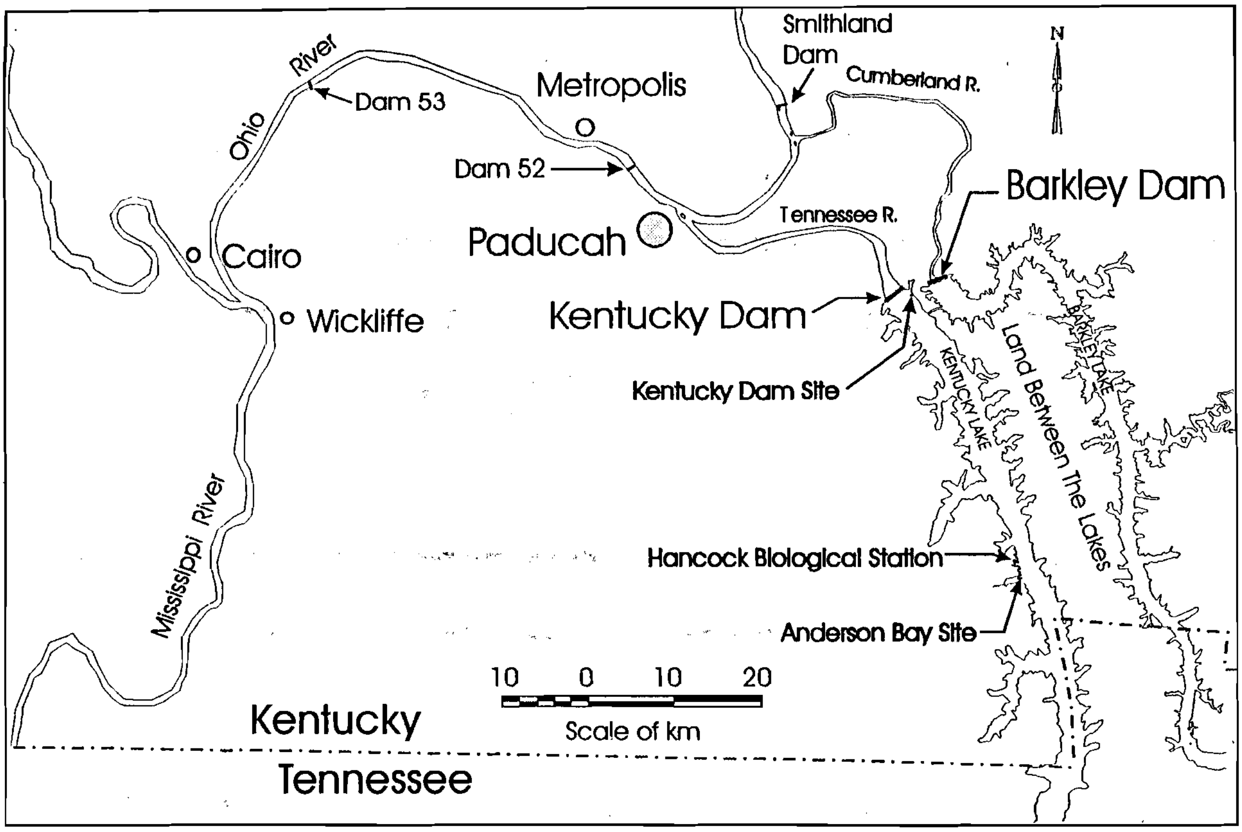

Figure 1. Location of zebra mussel collection sites for both the Ohio River and Tennessee River

Once it was verified that ripe gametes were present, spawning was artificially induced to determine if mussel from both bodies of water were indeed capable of spawning. Spawning of freshly collected mussels was artificially induced by an external application of serotonin. Ram *et al.* (1993) determined that external applications of either 10^{-3} or 10^{-4} M solution of serotonin would artificially induce spawning in both sexes of zebra mussels. Individual mussels were placed in 25 ml beakers containing 10 ml solution comprised of serotonin and filtered Tennessee River water. The water was filtered with 1.2 μm millipore filters. Mussels were left in the serotonin solution for 15-30 minutes, then removed and rinsed with deionized water and placed into another

25 ml beaker containing fresh filtered Tennessee River water. Originally a $10^{-3.5}$ M concentration serotonin solution was used and the mussels were left in solution for 30 minutes. Male mussels would begin to spawn after being in the serotonin solution for only 10-15 minutes. In order to allow for the release of the sperm into fresh water, the time the mussels were left in solution was reduced to 15 minutes. A reduction in time was instituted because it was unknown what affects the serotonin would have on the gametes if they were allowed to come into direct contact. After several trials the serotonin solution was lowered to a 10^{-4} M concentration and the mussels continued to spawn.

Once spawned the gametes were combined to determine if fertilization would occur in Tennessee River water. After egg release occurred, 2 drops of water containing sperm were added to the water containing newly released eggs. Approximately 30 minutes after the gametes were combined, a number of eggs were removed and placed into several petri dishes. Some dishes contained Ohio River water and the others Tennessee River water. Periodical observations on development were made for 7 hours after fertilization.

RESULTS

Zebra mussels from both the Ohio and Tennessee Rivers were found to contain developing gametes necessary for spawning to occur (Fig. 2). A total of 8 attempts were made to artificially induce spawning in mussels collected from both bodies of water from 6 June 1996 to 24 September 1996. Sperm was released by males between 10-15 minutes after the application of serotonin. Spawning in females did not occur as rapidly, with eggs being released between 1-1.5 hours after the application of serotonin (Fig 3). The first indication that fertilization had been successful occurred approximately 10 minutes after fertilization, with the release of the first polar body (Fig. 4). Eggs cleaved for the first time approximately 1 hour after fertilization (Fig. 5), with the second cleavage following approximately 1.5 hours after fertilization. The third cleavage occurred approximately 2 hours after fertilization (Fig. 6). Fertilized eggs continued to develop in water from both sources up to the free-swimming trochophore stage. Movement, after fertilization, first occurred in Ohio River water between 5-6 hours and between 6-7 hours in Tennessee River water (Fig. 7).

Throughout June, 4 attempts were made to induce spawning and observe development. All of these attempts were successful and development readily occurred up through 7 hours after fertilization. In July, 2 attempts were made and only one was successful. On 2 July 1996 freshly collected mussels were successfully spawned in the laboratory and development occurred, with some developing up to the trochophore stage in water from both sources. First signs of movement in Ohio River water occurred between 5-6 hours after fertilization. In Tennessee River water movement first occurred approximately 6 hours after fertilization.

The other attempt on 15 July 1996 was unsuccessful and gametes were not produced by freshly collected mussels when artificially stimulated to spawn. The same held true 1 August 1996 when another attempt was made to artificially stimulate spawning. Although a few eggs were found in 2 of the containers, none appeared to be fully developed and no sperm was produced to test for fertilization. Then 24 September 1996 another attempt was made to spawn mussels collected from Kentucky Lake. This time spawning was successful and gametes from both sexes were produced in abundance. In the latter attempt fertilization did not readily occur as it had in earlier attempts in June.

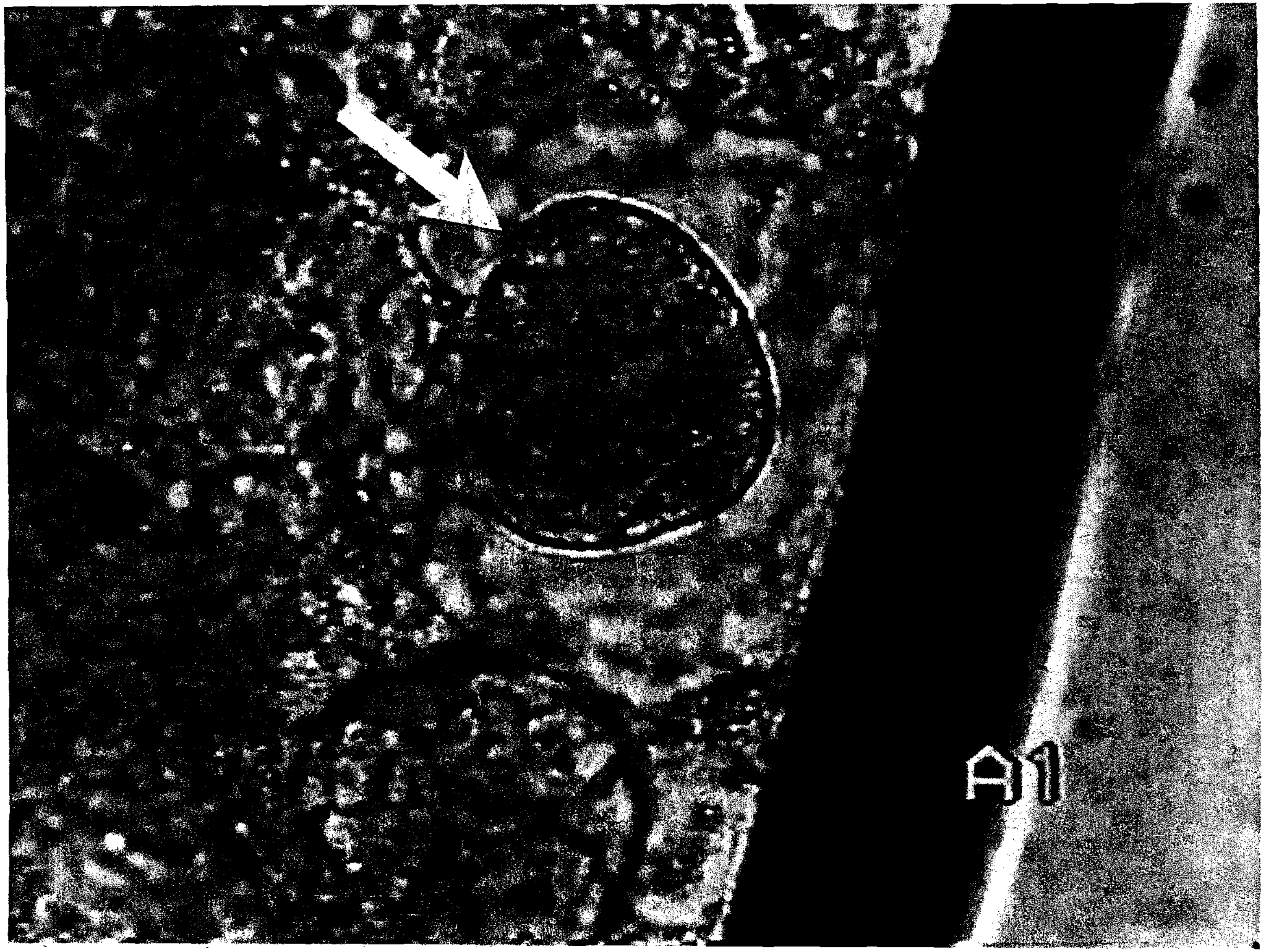

Figure 2. Living tissue of female zebra mussel showing developing egg attached to stalk. Mussel collected 21 April 1996 from the Ohio River at Dam 52 near Brookport, Il.

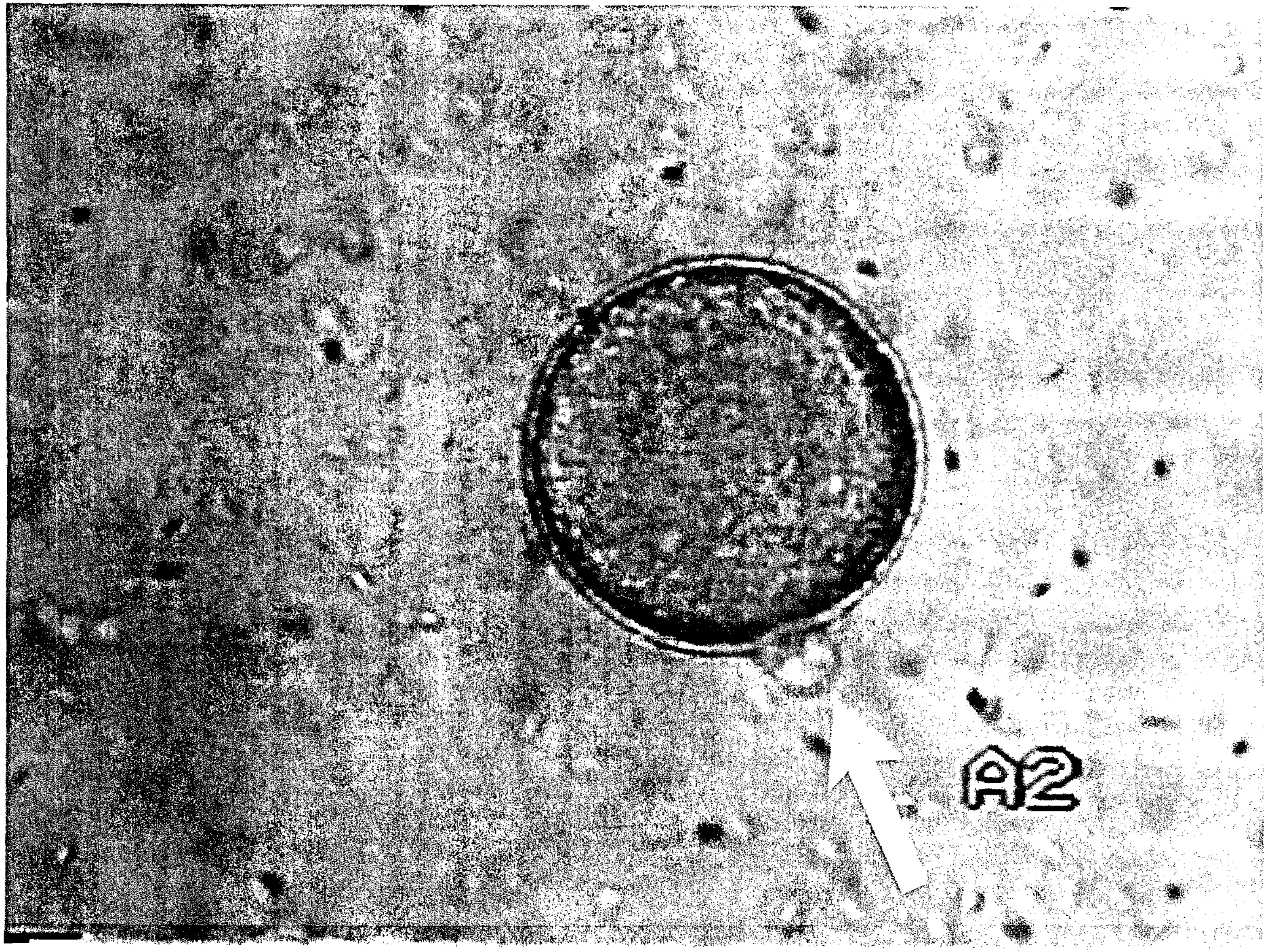

Figure 3. Zebra mussel egg showing release of first polar body after fertilization in Tennessee River water. Live sperm still present around egg. Mussels collected 6 June 1996 from Kentucky Lake. Spawning induced by external application of serotonin.

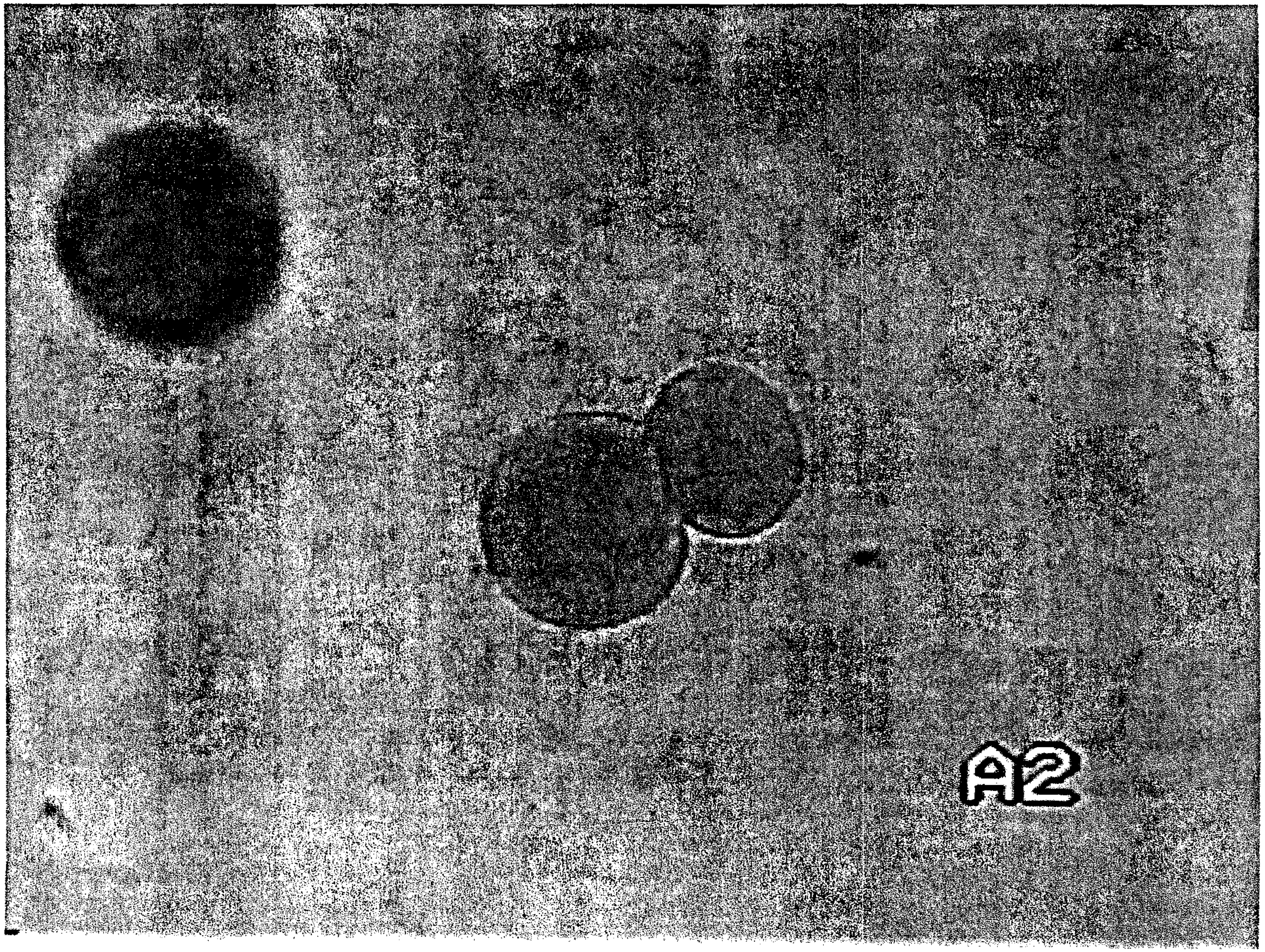

Figure 4. Zebra mussel egg just after first cleavage (top) approximately 1 hour after fertilization, next to egg which has not began development (bottom). Fertilization and cleavage occurred in Tennessee River water. Mussels collected 6 June 1996 from Kentucky Lake. Spawning induced by external application of serotonin.

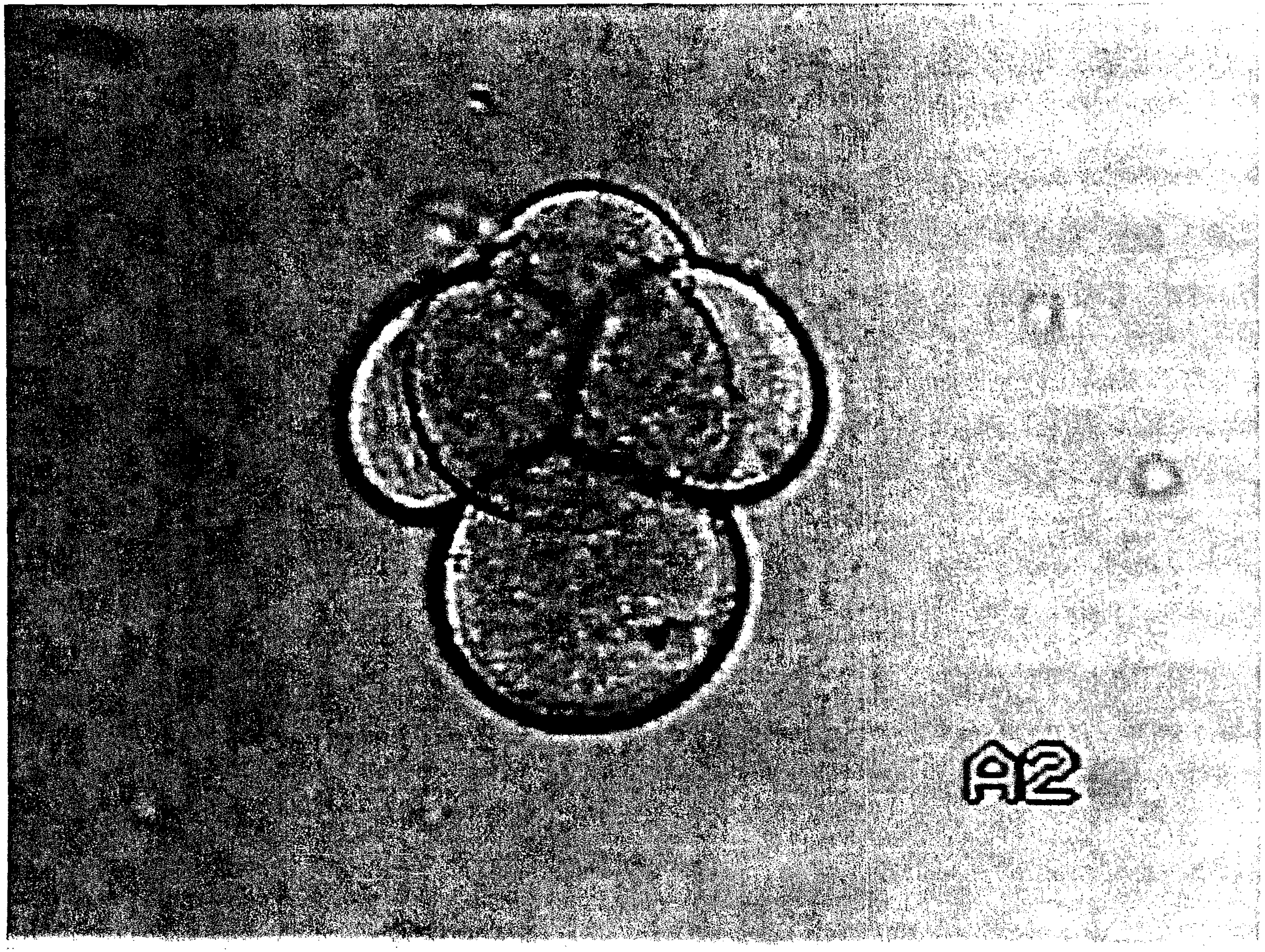

Figure 5. Zebra mussel egg approximately 2 hours after fertilization in Tennessee River water. Development through 3rd cleavage, up to the 5 cell stage has taken place. Mussels collected 6 June 1996 from Kentucky Lake. Spawning induced by external application of serotonin.

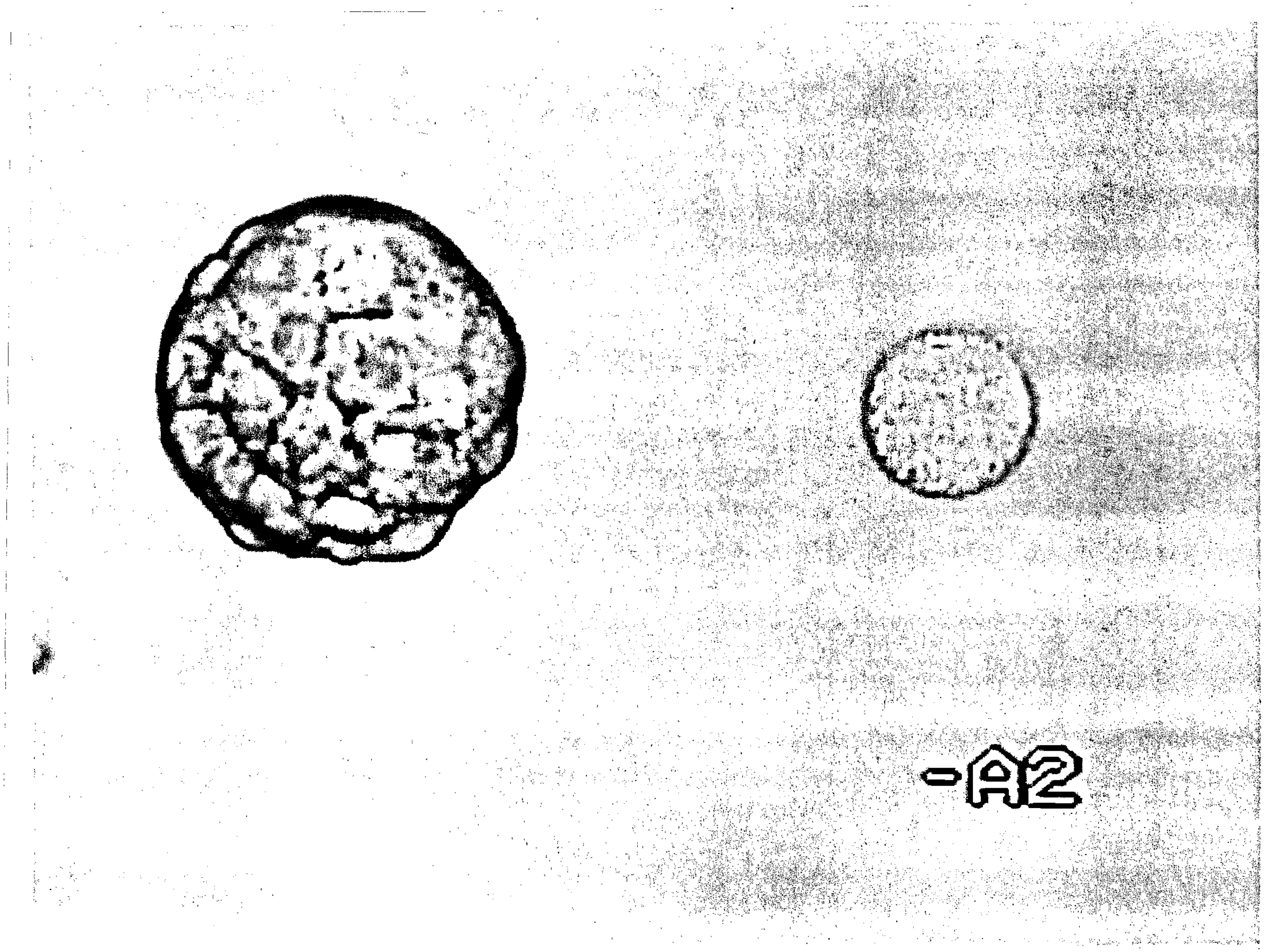

Figure 6. Comparison of zebra mussel egg approximately 5 hours after fertilization (bottom), to one that has not been fertilized (top). All development occurred in Tennessee River water. The reason for such a noticeable size difference between these two is due to the fact the unfertilized egg is showing rapid deterioration. Mussels collected 6 June 1996 from Kentucky Lake. Spawning induced by external application of serotonin.

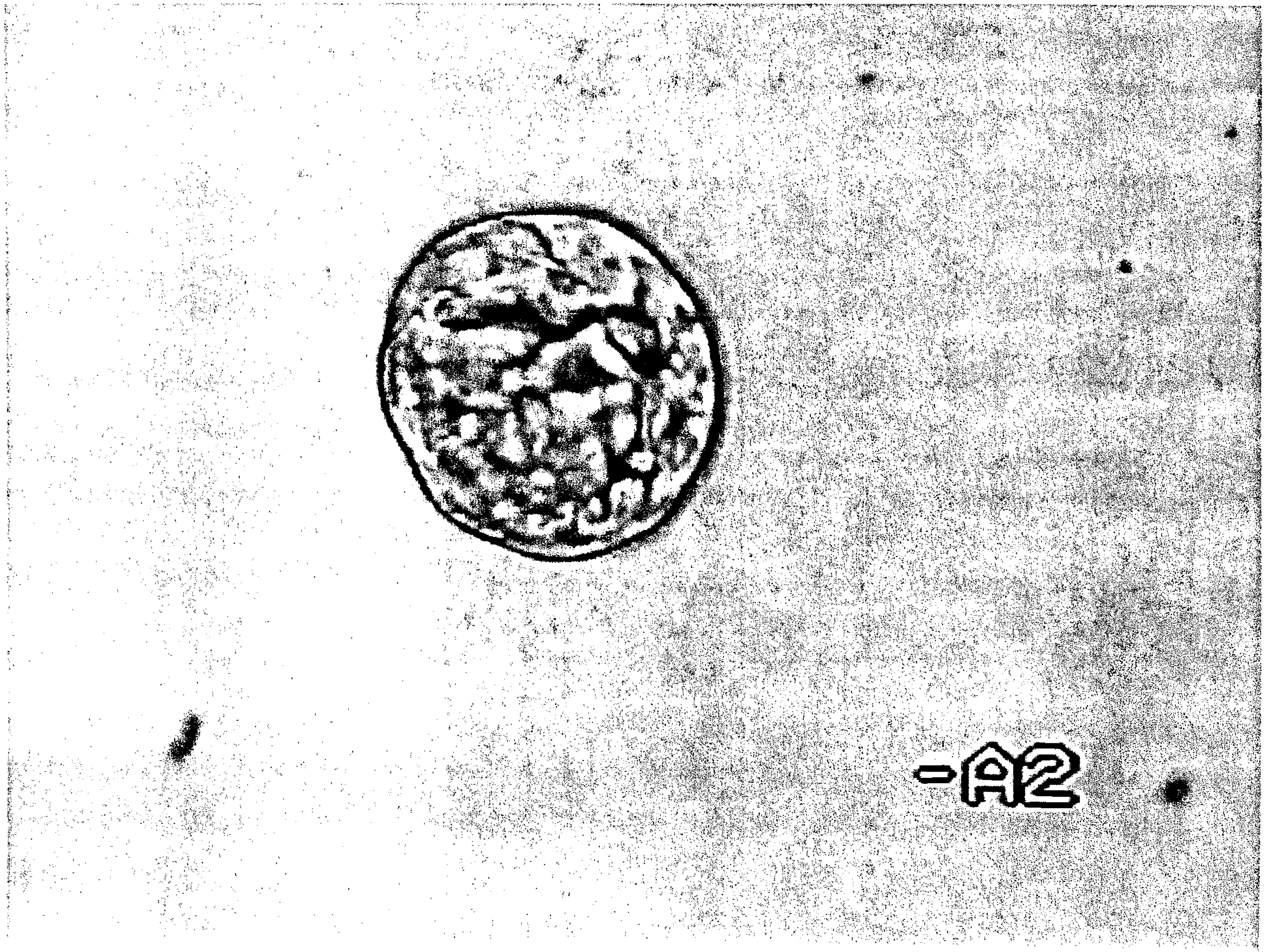

Figure 7. Free-swimming trochophore just after beginning movement due to ciliary development, approximately 7 hour after fertilization in Tennessee River water. Development up to this stage under laboratory conditions were successful in both Ohio and Tennessee River water. Mussels collected 2 July 1996 with spawning being induced by external application of serotonin.

On 15 July 1996 when no gametes were produced from freshly collected mussels, some mussels which had been collected from Kentucky Lake and held in the laboratory in aquaria for several weeks were artificially induced to spawn and gametes were obtained. As before fertilization was allowed to occur and eggs were separated into two separate dishes containing Tennessee River water. Out of 22 eggs placed into one dish 81.8% cleaved at least once, with 18.2% of all the eggs placed in this dish developing up to the free-swimming trochophore stage after 6.5 hours. In the other dish 43 eggs were placed, of which 90.7% cleaved at least once with 53.5% reaching the trochophore stage. Again 24 September 1996 mussels were spawned and only Tennessee River water was used to observe development of fertilized eggs. Throughout this attempt 91 eggs were separated and placed into water with sperm present. Only 13.2% of the eggs went through at least one cleavage of development, with 87.7% not showing any development at all. Out of all eggs introduced to sperm only 8.8% developed up to the trochophore stage.

DISCUSSION

Development of eggs continued and was observed periodically for the first 7 hours of development in both Ohio and Tennessee River water. Throughout this time, uniform development in both water sources continued readily. The only noticeable difference was that development to the free-swimming ciliated trochophore stage occurred approximately one half hour earlier in Ohio River water than in Tennessee River water. The time required for the development of zebra mussel larvae after fertilization has been found to be temperature dependant, with development occurring more rapidly in warmer water (Waltz 1978, Sprung 1987, Nichols 1993). Water temperature was not recorded throughout the experiments and could be the reason for varied developmental times up to the free-swimming trochophore stage between the different sources of water.

Environmental factors other than temperature also play an important role in the development of zebra mussel eggs. Sprung (1987) determined that temperature, pH, and calcium concentration are the most important factors concerning zebra mussel egg development. When comparing required environmental conditions with conditions present in both Ohio and Tennessee River water throughout 1996 (Table 1), not all of the conditions were met for either body of water. In Ohio River water pH levels fell below the required ranges for short periods of time. pH apparently is not affecting spawning because an abundance of veligers was found in water samples throughout the warm summer months. pH could be limiting the number of larvae which develop up through the settling stage, but whether or not it is the case is not know at this time.

Tennessee River water varied from the requirements in having low Ca^{++} concentrations. As stated earlier in the introduction, Ca^{++} is required by zebra mussels for shell development. Zebra mussels are able to survive in water with extremely low Ca^{++} concentrations but no previous studies have looked at egg development in water with low Ca^{++} concentrations. In other studies mussels were removed from naturally reproducing populations, and only after spawning had been induced were the larvae introduced to water with low Ca^{++} concentrations. It is not known if the mussels present in Kentucky Lake are reproducing naturally.

Table 1. Environmental requirements for the development of zebra mussel eggs determined by Sprung (1987) compared with environmental conditions found in the Lower Ohio and Tennessee Rivers throughout 1996.

	Ca^{++} (mg/L)		pH		Temp. (°C)	
	min	max	min	max	min	max
Requirements	40	60	7.4	9.4	12	26
Ohio River	28.08	54.56	7.2	7.97	5	29
Tennessee River	17.65	25.67	7.59	8.74	4	29

Nichols (1996) stated that possibly Zebra mussels, as with other bivalves, can obtain Ca^{++} from their food supply thus not being dependant on dissolved Ca^{++} ions in water. A food route would explain the ability of adult zebra mussels to survive in water with low Ca^{++} concentrations; however, the extremely small size of food utilized by larvae may not be a source of Ca^{++} adequate to enable total development and formation of a shell. Sprung (1987) found that larvae reared in Ca^{++} levels below 40 mg/L could develop, with the number of crippled larvae increasing with decreasing levels of calcium. Claudie and Mackie (1994) indicated that Ca^{++} levels of 25 mg/L would be sufficient for massive infestations.

Mussels collected from the same population in the Kentucky Lake portion of the Tennessee River at Kentucky Dam released gametes at two separate times throughout this study, when serotonin was applied. Gametes were produced in abundance by mussels collected throughout June and in the first week of July. Mussels collected from the same population did not spawn, when introduced to serotonin until the end of September. Prior research indicates that in order for spawning in zebra mussels to be artificially induced by serotonin, the gonads must be fully mature (Ram *et al.* 1993, Ram and Nichols 1993). Because spawning was induced in June and September, the population of zebra mussels may have had two separate times throughout the year when ripe gonads were present with gametes ready to be spawned.

Mature gametes present at two separate times throughout the year could be explained by two possibilities. Either the population of mussels being studied retained some of their gametes after the initial maturation process or the original set of gametes were not released once they first became mature and were reabsorbed only to mature again later in the season. Ram *et al.* (1993) found that zebra mussels are able to spawn two and in some instances three times, with repeated applications of serotonin. They discovered that the second spawn could be induced only one day after the first, with the number of gametes being produced always declining with each additional spawn. It is possible that zebra mussels can retain some of their gametes to be spawned at a later date. Through histological analysis Haag and Garton (1992) found that few individuals retained gametes after the first spawning event and/or any residual volume of gametes remaining after the first spawning event was small and not readily detectable by standard histological techniques.

The spawn induced in September produced abundant numbers of gametes, but development did not occur as readily as had in earlier attempts in June, as over 80% of the eggs produced did not show any development once fertilized. Due to such high percentages of occurrence of fertilization in prior attempts, the eggs released in the latter attempt may not have been fully developed and therefore not capable of being fertilized at this time. As stated above, other researchers found that spawning could be induced in mussels only when the gonads were fully ripened. The spawning of eggs before becoming fully developed could be an indicator that the eggs were not spawned when they first became ripe and were retained until a later date. When mussels from this same population were induced to spawn later in the season, there gametes were released even though the eggs were not fully developed. The spawning of undeveloped eggs in September also could indicate gametes had been retained after an initial spawning event due to being poorly developed at that time. Poor environmental conditions or other factors could have inhibited continued eggs development until being released unconditionally once the gonads ripened for the second time.

Mussels found in both the Ohio River and the Kentucky Lake portion of the Tennessee River are producing viable gametes which are capable of developing at least up through the free-swimming trochophore stage. It is not known if mussels found in Kentucky Lake are naturally spawning. All samples of mussels from the Tennessee River were collected near barge mooring cells. It is not known if Kentucky Lake mussels were newly introduced from the moored barges above or were residents of the lake for a substantial period of time. Either way, Kentucky Lake mussels are producing gametes and these gametes, as shown above, can develop at least partially in Tennessee River water.

ACKNOWLEDGMENTS

This research was funded by the Mussel Mitigation Trust, the Shell Exporters of America, Inc. and the Center for Reservoir Research. Also, special thanks go out to the staff and students at Murray State University's Hancock Biological Station for always offering a helping hand or tidbits of information whenever needed.

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OHIO RIVER DAM CONSTRUCTION: SHORT-TERM IMPACTS ON BALD EAGLE (*HALIAEETUS LEUCOCEPHALUS*, [AVES: ACCIPITRIDAE]) POPULATIONS

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ABSTRACT. Shoreline densities and distributions of wintering bald eagles (*Haliaeetus leucocephalus*, [Aves: Accipitridae]) were compared to examine the impacts of an ongoing lock-and-dam construction project on the Ohio River between Kentucky and Illinois. Survey data were collected once weekly from mid-December through mid-March in the winter of 1994/95 (ongoing dam construction) and compared to survey data from 1987/88 (pre-dam construction). Proportional densities of bald eagles in a one-mile interval centered at the dam site, during the 1994/95 surveys, were significantly reduced from proportional densities that occurred during the 1987/88 surveys ($P=0.0024$). A marginally significant reduction in proportional densities of bald eagles occurred in a six-mile interval centered at the dam site during the 1994/95 surveys when compared with the 1987/88 surveys ($P=0.07$). A marginally significant shift in quarter-mile distributions along the entire river-study segment also occurred between the two survey periods ($P=0.06$). These results indicated that bald eagles were avoiding the area of dam construction and that the distribution of bald eagles may be shifting away from the area of dam construction. We recommend that further studies be conducted to determine long-term impacts of dam placement on bald eagles.

INTRODUCTION

To ensure the continued success of the bald eagle, a better understanding of the role that human-related activities play in determining distributions and densities of this species is necessary (Buehler *et al.* 1991). The response of bald eagles to human-related activities has varied with food availability/abundance, perching habitat, cover habitat, and type, level, and duration of the disturbance (Knight and Knight 1984, McGarigal *et al.* 1991, Grubb *et al.* 1992). Numerous studies have shown that bald eagles tend to avoid areas subjected to human developments and activities, even when all other habitat requirements appear to be met (Stalmaster and Newman 1978, Knight and Knight 1984, Fraser *et al.* 1985, McGarigal *et al.* 1991). The effects of human-related disturbance can result in higher energy demands, decreased foraging efficiency, increased foraging effort, and ultimately decreased winter survivorship (Stalmaster and Newman 1978, Dixon and Chapman 1980, Knight and Knight 1986, Craig *et al.* 1988).

Increasing our understanding of the effects of human-related activities will assist resource managers when evaluating or devising management activities, or when considering other actions that have the potential to affect bald eagles. A better understanding of interactions between humans and bald eagles will be increasingly important as the species expands its range and increases in numbers, and as human developments expand. The objective of our research was to determine the effects of construction of a new lock and dam on the density and distribution of bald eagles along the Ohio River.

STUDY AREA

The study area was located in far Western Kentucky and covered approximately 65 km (40 mile) of the Ohio River shoreline between the cities of Paducah, Kentucky and Cairo, Illinois (Fig. 1). The bridge on Interstate 24, that crosses the Ohio River near Paducah (river mile 941), bounded the upstream end of the river segment. The downstream end was defined by the confluence of the Ohio and Mississippi Rivers (Ohio River Mile 981.0) near Cairo. Unlike most river systems in the United States, the mile increments of the Ohio River increase as the river progresses downstream.

Construction for the Olmsted Lock and Dam Project began in 1993 and is scheduled for completion in 2007. Ongoing-construction of the replacement dam is occurring at river mile 964 (Fig. 1). Construction efforts at the time of our study were focused on the Illinois side of the Ohio River, with construction work extending approximately one-fifth of the way across the river. The width of the Ohio River at the site of dam construction is ca. 1220 m.

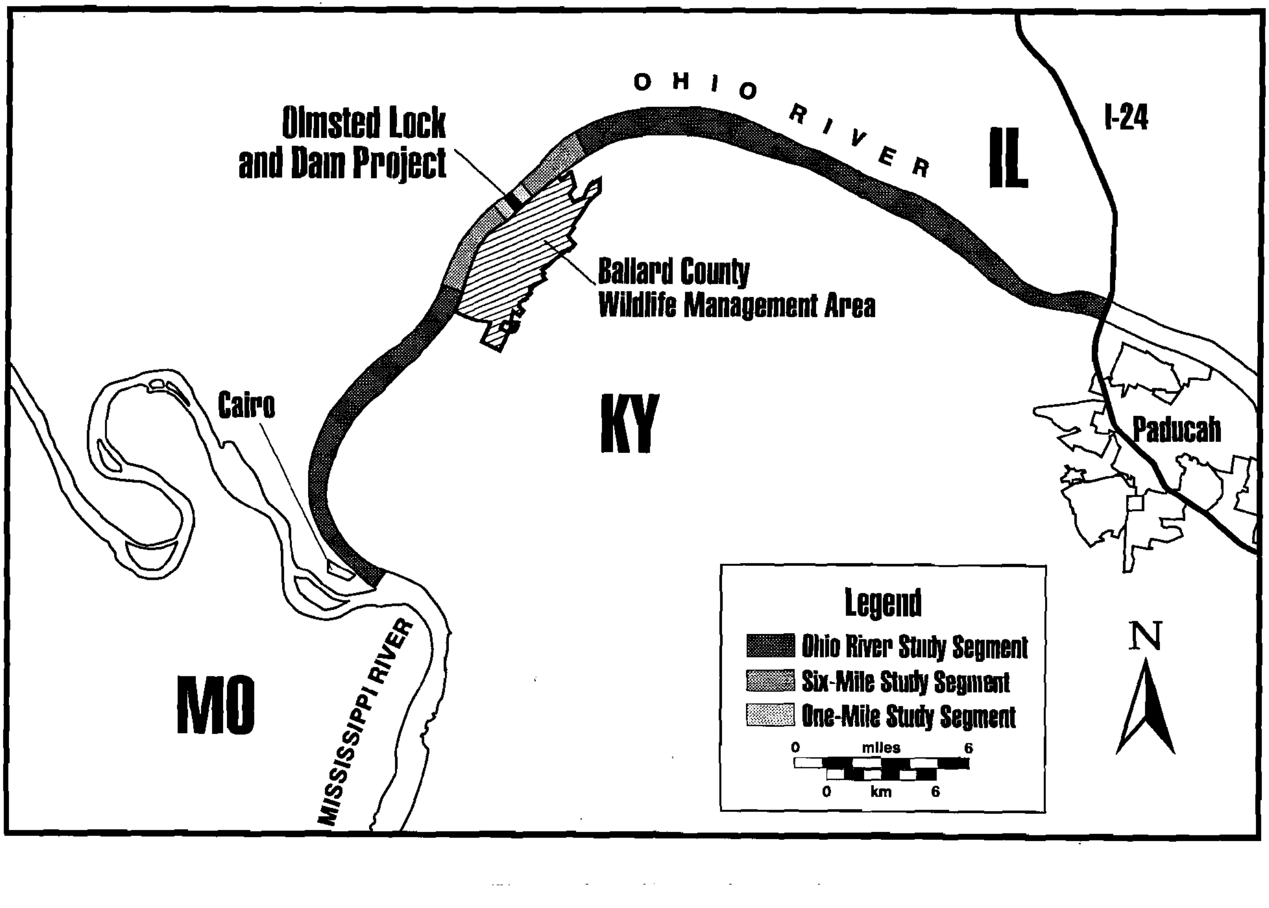

Figure 1. Entire 65 km (40 mile) study segment of the Ohio River containing smaller one- and six-mile study segments. The site of dam construction and BCWMA are shown as points of reference.

The Kentucky Department of Fish and Wildlife Resources owns Ballard County Wildlife Management Area (BCWMA), which lies adjacent to the Ohio River shoreline between river miles 962.75 and 968.75 (Fig. 1). The site where the Olmsted Lock and Dam is being constructed places the dam within the shoreline area of BCWMA. Managed primarily as a wintering area for waterfowl, BCWMA is closed yearly to public access from 01 October to 15 March. Because of the high quality of the resources and the low level of human disturbance, BCWMA has become an important wintering ground for bald eagles (Anderson *et al.* 1984, Wethington 1994, White 1996). The management area is also an important resource for nesting bald eagles, with two active nests occurring on the management area at the time of this study.

METHODS

Aerial surveys of bald eagles along the Ohio River were conducted during the winter of 1994/95. The survey methods that we used duplicated surveys conducted during the winter of 1987/88 (White unpubl.). The density and distribution of bald eagles along the Ohio River in 1987/88, prior to dam construction, was compared with the density and distribution when construction was ongoing in 1994/95.

Our 1994/95 survey flights began on 22 December 1994 and continued through 09 March 1995 with a total of 10 survey flights conducted. Surveys were conducted once per week, except for the weeks of 25 December and 26 February. Seven of the surveys were conducted in conjunction with aerial counts of waterfowl at two management areas in the region. The remaining three surveys were conducted exclusively for the collection of data on the density and distribution of bald eagles.

All aerial surveys were conducted at low altitude (approximately 30.5 - 45.75 m) parallel to the shoreline of the Ohio River. The aircraft was a Cessna, single engine, four-person aircraft. The survey crew consisted of one pilot along with one or two spotters. All surveys were initiated between 0745 hrs and 1340 hrs CST. The shoreline in Illinois was surveyed first, flying downstream from the Interstate 24 bridge near Paducah, Kentucky toward Cairo, Illinois. The shoreline in Kentucky was surveyed on the return trip to the bridge on Interstate 24. Flight time for a round trip was approximately 1 h 10 min for survey flights that included counts of waterfowl. Average flight times for surveys that involved only data collection on bald eagles were 50 min. Weather conditions and aircraft/pilot availability influenced the dates and times of survey flights.

The location (±300 m) of each bald eagle that was observed during a survey flight was plotted on U.S. Army Corps Engineers Ohio River Navigation Maps, Charts 1-9. The charts included numerous geographically recognizable reference points to ensure accurate recording of observed eagles. We classified each bald eagle that was observed as perched or flying, based on its activity at first sighting. The 1994/95 distribution of wintering bald eagles along the Ohio River, by river quarter-mile, was then assembled by compiling the individual surveys.

Statistical Analysis

To investigate the impact of dam construction on the densities of bald eagles in the area of dam construction, we selected two smaller study segments from the 65 km (40 mile) river study segment. A one-mile and a six-mile study segment were selected with the site of dam construction located in the center of each segment (Fig. 1). The one-mile segment included the shoreline area between river miles 963.5 and 964.5. The six-mile segment began at river mile 961 and ended at river mile 967. To compare our survey data with the 1987/88 survey data (White unpubl.), the proportion of bald eagles within the one- and six-mile study segments was calculated for each survey period. A standard normal test for the comparison of two proportions was used to compare the two survey periods (Sokal and Rohlf 1981).

To test for a shift in the distribution of bald eagles along the entire river study segment between the two survey periods, we used the density of bald eagles within each river quarter-mile. We constructed graphs which displayed the cumulative percent frequencies of bald eagles progressing along each river quarter-mile. The "D" statistic from the Kolmogorov/Smirnov test was used to locate significant shifts in the quarter-mile distributions (Conover 1980). The value of "D" for rejection (D-max) at $\alpha=0.05$ was calculated using the following formula:

$$D = \left(\sqrt{\frac{-\ln(\alpha/2)}{2}}\right)\left(\sqrt{\frac{n_1+n_2}{n_1 n_2}}\right)$$

A *P*-value was calculated for the observed D-max as follows:

$$P = 2e^{\left[-2D^2(n_1 n_2/n_1+n_2)\right]}$$

All data in text are presented as mean ± 1 S.E.

RESULTS

Total density of bald eagles along the entire river study segment was reduced by 66% during the 1994/95 surveys as compared to the 1987/88 surveys (Table 1). A total of 387 bald eagles were observed during the 10 survey flights conducted in 1987/88, averaging 38.7 bald eagles per survey (± 28.45). The number of bald eagles observed during the 1994/95 surveys totaled 129, averaging 12.9 per survey (± 8.58).

A 90% reduction in the number of bald eagles within the one-mile study segment was found when comparing the 1994/95 surveys with the 1987/88 surveys (Table 2). A total of five bald eagles was observed in the one-mile interval during the 1994/95 surveys, while the total observed during the 1987/88 surveys was 49. The proportional density within the one-mile interval was also reduced significantly, by 69%, during the 1994/95 surveys when compared with the 1987/88 surveys (P=0.0024).

Table 1. Total and mean number of bald eagles observed along the Ohio River between Paducah, Kentucky and Cairo, Illinois during aerial surveys conducted during the winters of 1987/88 (White unpubl.) and 1994/95.

	Survey Period	
	1987/88	1994/95
Number of surveys	10	10
Total number of eagles observed	387	129
Mean number/survey ± 1 S.E.	38.7 ± 28.45	12.9 ± 8.58

Table 2. Number and proportion of bald eagles observed within the one- and six-mile study intervals at the Olmsted Lock and Dam along the Ohio River for the 1987/88 (White unpubl.) and 1994/95 surveys.

Survey Year	Survey Totals	Number in One-Mile Interval	Percent of Total	Number in Six-Mile Interval	Percent of Total
1987/88	387	49	12.66	157	40.57
1994/95	129	5	3.88	43	33.33

A marginally significant reduction in the numbers of bald eagles within the six-mile interval (73%) was found when comparing the 1994/95 surveys with the 1987/88 surveys ($P=0.07$, Table 2). The densities of bald eagles within the six-mile segment were 43 and 157 for the 1994/95 and 1987/88 survey periods, respectively. An 18% reduction in proportional density of bald eagles occurred within the 6-mile interval in the 1994/95 surveys when compared with the 1987/88 surveys.

The distribution of bald eagles along the entire river study segment shifted in the upstream direction during the 1994/95 surveys as compared with the 1987/88 surveys. The mean location for bald eagles along the study segment during the 1987/88 preconstruction surveys was at river mile 963.5 (± 11.64 miles), one-half mile upstream from the site of dam construction (Fig. 2). The mean location for bald eagles along the study segment during the 1994/95 surveys was at river mile 962.5 (± 11.14 miles), one mile upstream from the 1987/88 distribution mean and one and one-half mile upstream from the site of dam construction (Fig. 3). The mean of the distributions for the 1987/88 and 1994/95 surveys was 0.75 miles downstream and 0.25 miles upstream, respectively, from the point where the upstream boundary of BCWMA meets the Ohio River shoreline (river mile 962.75).

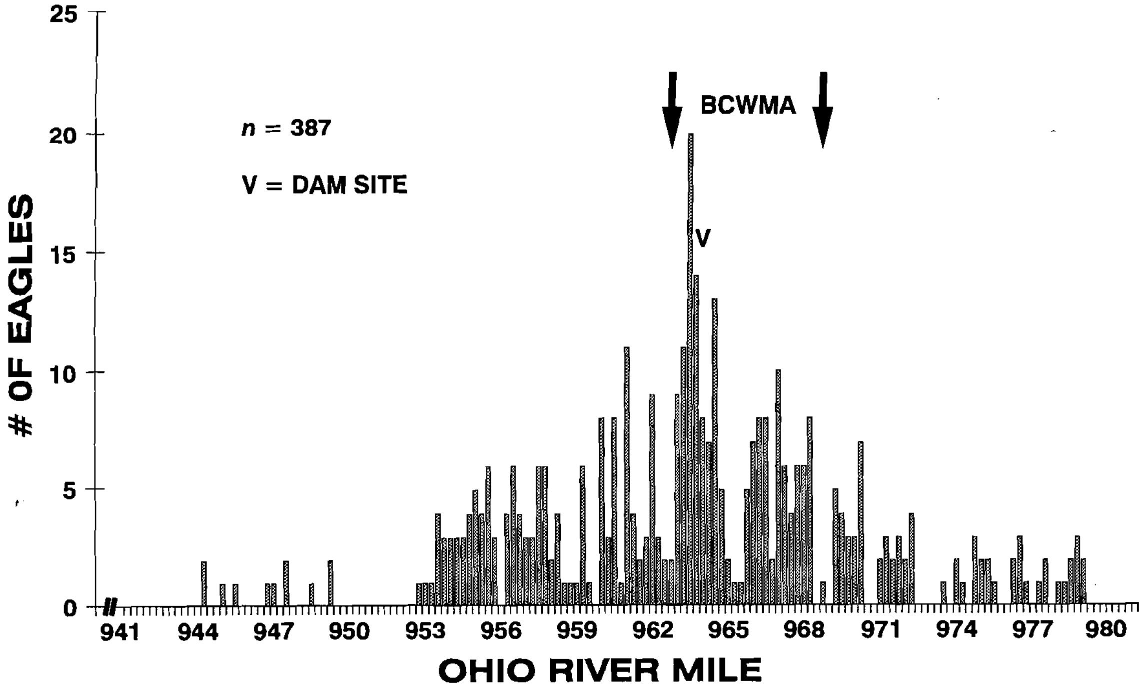

Figure 2. Distribution of quarter-mile densities of bald eagles as observed during aerial surveys conducted during the winter of 1987/88 (White unpubl.). The BCWMA shoreline boundaries (arrows) and dam construction site (v) are indicated as points of reference. "*n*" refers to the total number of bald eagles observed during survey period.

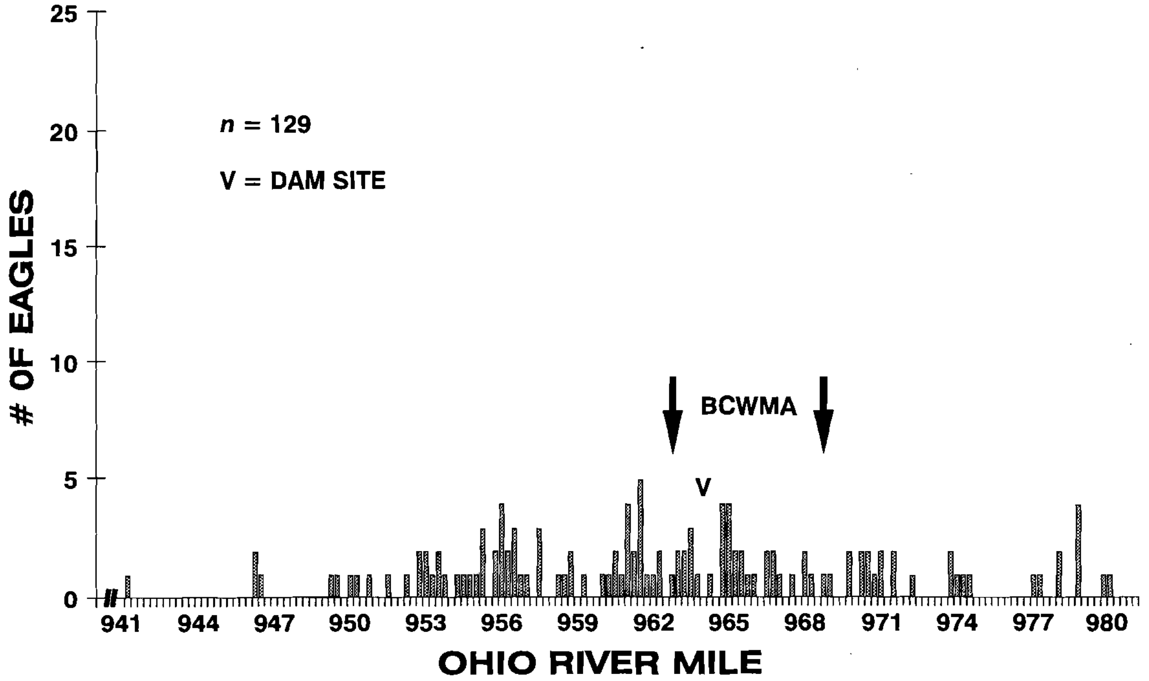

Figure 3. Distribution of quarter-mile densities of bald eagles as observed during aerial surveys conducted during the winter of 1994/95. The BCWMA shoreline boundaries (arrows) and dam construction site (v) are indicated as points of reference. "*n*" refers to the total number of bald eagles observed during the survey period.

The value of the D-statistic from the Kolmogorov/Smirnov test indicated a marginally significant shift in the 1994/95 distribution as compared to the 1987/88 distribution ($P=0.06$). We compared the cumulative percent frequency of bald eagles for the 1994/95 and 1987/88 survey periods in quarter-mile intervals (Fig. 4). The maximum distance between the two frequencies at any one river quarter-mile (D-max) was found to be a difference of 13.44%. D-max for rejection was 13.83%. The observed D-max value was found between river miles 961.5 and 962.0. During the 1987/88 surveys, 35.40% and 36.18% of the total number of bald eagles were observed at, or upstream from, river quarter-miles 961.5 and 961.75, respectively. During the 1994/95 surveys, 48.84% and 49.61% of the total number of bald eagles were observed at, or upstream from, river quarter-miles 961.5 and 961.75, respectively. The greater cumulative percent frequency of bald eagles calculated at river miles 961.5 and 961.75 for the 1994/95 surveys indicated a shift in the upstream direction as compared to the 1987/88 distribution.

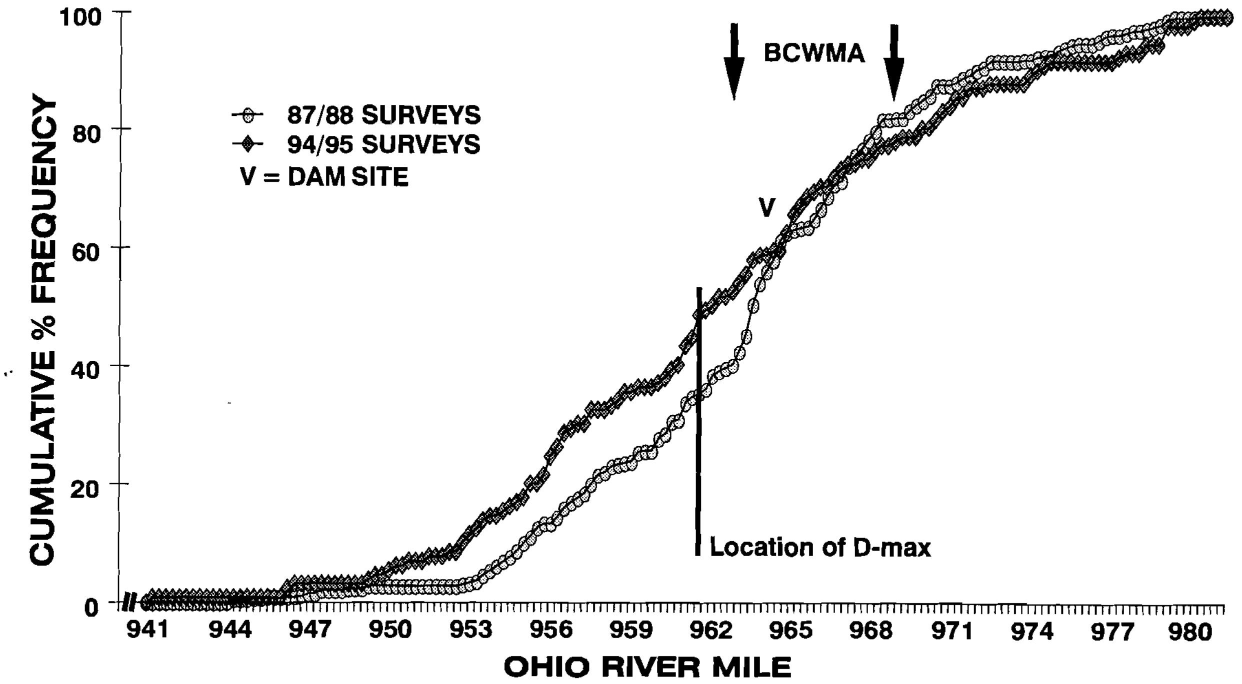

Figure 4. Cumulative percent frequency of bald eagles at each river quarter-mile for surveys conducted during the winters of 1987/88 (White unpubl.) and 1994/95. The D-max statistic, from the Kolmogorov/Smirnov test, indicates the location at which the difference in cumulative percent frequency was greatest between the two survey periods. The BCWMA shoreline area (arrows) and the dam construction site (v) are indicated as points of reference.

DISCUSSION

The density and distribution of bald eagles in the area of construction of the Olmsted Lock and Dam was reduced in 1994/95 as compared to 1987/88 (White unpubl.). We attributed the decline in density and distribution near the dam site to dam construction. It is likely that the impacts of dam construction were due to the intensity of construction-related disturbances as well as the novelty of the structure. Evidence for a causal relationship between dam construction and the abundance of bald eagles was the reduction in density of bald eagles near the dam and the increase in density of bald eagles away from the dam during the time of dam construction. Also, annual surveys of bald eagles at Kentucky Lake and Lake Barkley in Western Kentucky, ca. 85 km away from our study site, indicated that the density of bald eagles was 137% higher during the winter of 1994/95 as compared to the winter of 1987/88 (TVA unpubl.). Data from these surveys showed that bald eagle populations had been on the rise in nearby geographic regions.

The extension of the construction project and associated disturbances across the river, and directly into an area that bald eagles used frequently prior to dam construction, was likely to have increased the impact of disturbance on bald eagles in the area. Some researchers have suggested that visual buffers, a vegetative buffer for example, can lessen the impacts of disturbance and development on bald eagles (Stalmaster and Newman 1978, Paruk 1987).

The proportional densities of bald eagles were reduced in the one- and six-mile study intervals for the 1994/95 surveys as compared to the 1987/88 surveys (White unpubl.). The significant reduction in the proportional densities of bald eagles within the one-mile interval for the 1994/95 surveys is consistent with the distance-to-disturbance responses reported by Grubb *et al.* (1992). They observed alert responses when disturbance activities occurred within 500 m of bald eagles. A reduction in use of areas within 500 m from human-made structures by bald eagles was also reported by Buehler *et al.* (1991). A 500-m interval, extending both up- and downstream from the site of dam construction, would encompass ca. 62% of the one-mile study interval.

While the six-mile interval is not independent of the one-mile interval, it does extend away from the intensive disturbances found within the one-mile interval. Bald eagles on perches could probably avoid visual contact of dam construction in many areas of the six-mile interval, but bald eagles soaring over the treeline or the river itself could easily see the activities at the dam site. Numerous visible and audible disturbances were noted during construction of the dam, including frequent operation of vehicles and watercrafts, pedestrian movement, and operation of heavy equipment. The most notable disturbance was pile driving, which occurred routinely throughout the 1994/95 survey period. The sound of pile driving closely duplicates the sound of a firearm discharge or similar loud, abrupt noise which has been documented as disturbing to bald eagles (Stalmaster and Newman 1978, Grubb and King 1991, Grubb *et al.* 1992).

The shift in the distribution of bald eagles along the entire river study segment further supported our conclusion that dam construction affected use of the Ohio River by bald eagles. The mean of the distribution documented for the 1994/95 surveys moved from one-half mile upstream from the site of dam construction to a point one and one-half miles upstream from the site of dam construction, a change of one-mile in the upstream direction.

Human-related disturbance is often a determining factor in the abundance and/or distribution of bald eagles in an area (Buehler *et al.* 1991, Grubb *et al.* 1992). Bald eagles generally avoid areas where human activities and/or human developments occur (Buehler *et al.* 1991, Chandler *et al.* 1995). The greater decrease in proportional densities within the one-mile interval than in the six-mile interval agreed with studies that reported an inverse relationship between the magnitude of responses of bald eagles to their distance from disturbances (Buehler *et al.* 1991, Grubb *et al.* 1992).

Bald eagles have been shown to habituate to routine human-related activities and/or disturbances (Stalmaster and Newman 1978, Grubb *et al.* 1992). Also, some studies have disputed the long-term negative effects of dam construction and dam placement on bald eagles. While dam construction itself may be a serious disturbance, the long-term value of dam placement could be positive for bald eagles. Considerably more bald eagles have been found at river segments with dams than segments without dams along the Mississippi River (Paruk 1987). In the study by Paruk (1987), five of six river segments with dams were ranked in the top 8% for eagle use among the 143 river segments that were studied. The amount of woodland edge below dams was also found to be very important in determining distributions of bald eagles. The attractiveness of dams in Paruk's study area to bald eagles was believed to be the abundance of fish that were weakened and killed as they passed over or through the dam. Other researchers have also documented the importance of dams to wintering bald eagles (Southern 1963, Southern 1964, Steenhof *et al.* 1980).

If bald eagles do habituate to the Olmsted Lock and Dam, the dam could prove to be beneficial to bald eagles in the region in the long term, possibly even increasing the number of bald eagles in the area of the dam to higher densities than occurred during pre-construction times. We, therefore, recommend the continuation of research to examine both the short- and long-term impacts of dam construction and placement on bald eagles along the Ohio River between Paducah, Kentucky and Cairo, Illinois. We also recommend that surveys of bald eagles be conducted in other areas in the region that could be used as control areas for comparison purposes. Surveys conducted in these control areas would provide data on yearly fluctuations in densities and distributions of bald eagles in undisturbed areas.

ACKNOWLEDGMENTS

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SHORT-TERM VARIABILITY OF MACROINVERTEBRATE COMMUNITIES OF TWO HABITAT TYPES IN HOLLY FORK CREEK, HENRY COUNTY, TENNESSEE

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Over the past several decades there has been an increasing use of macroinvertebrates and other aquatic organisms for biomonitoring surface water quality (Rosenberg and Resh, 1993). Biological samples are usually described using one or more metrics, quantitative indices that relate relative abundances of taxonomic groups to community structure or pollution sensitivity (*e.g.*, abundance, richness, biotic index, *etc.*). These metrics are then used to analyze and assess the condition of the stream. (Norris and Georges, 1993). However, Voshell *et al.* (1989) revealed that 67% of the aquatic biomonitoring programs using benthic macroinvertebrates have time intervals of one month or greater between sampling dates. The largest percentage of these studies (40%) had a sampling interval of greater than one month to less than one year, many of which probably represent seasonal collections. Merritt *et al.* (1996) recommended that at least seasonal collections be made in faunal studies. Mackay and Kalff (1969) found significant differences in macroinvertebrate diversity between seasons and between habitat types in a Quebec stream. Robinson *et al.* (1993) also found seasonal differences among macroinvertebrate assemblages. Allan (1995), when discussing the structure of lotic communities, stated that we could "...expect that the same species, in roughly the same abundances, will be found in the same locale as long as environmental conditions do not change greatly".

Therefore, one collection per season may be sufficient to represent the macroinvertebrate community during each season as long as environmental factors remained within typical cycles for a given area. However, the possibility still exists that samples could be statistically different a week before or a week after the collection date. Short-term statistical differences could bias the overall stream assessment, and in turn, effect any proposed mitigation measures or regulatory actions.

Goals of this study were to 1) collect weekly macroinvertebrate samples over a three week period in a relatively simple habitat (sandy run) and a relatively complex habitat (gravel riffle), 2) use several community metrics to describe each macroinvertebrate sample, and 3) analyze the variability of each measurement among the three weeks for both habitats. The study was conducted in Holly Fork Creek, a stream characteristic of the West Sandy Creek watershed in northeast Henry County, Tennessee, during September, 1995.

Once a week five randomly selected, replicate samples were collected from both sites using a modified Hess sampler. Each sample was stored in 80% isopropanol and transported to the laboratory for processing. Insects were identified to family and other macroinvertebrates to lowest practical taxon. Because of the large number of organisms collected in the riffle samples, these were split using a Folsom Planktonic splitter. Macroinvertebrates from half of each riffle sample were identified and the number of each taxon doubled. Next, all samples were described using the metrics of abundance (individuals per sample), richness (taxa per sample), Pielou's evenness, Shannon-Weiner diversity, family-level biotic index (Hilsenhoff, 1988), and functional feeding group ratios (shredders, filtering collectors, gathering collectors, scrapers, and predators). We were primarily interested in abundance and richness measurements, metrics being analyzed for other studies in this stream. Resh and Jackson (1993) have suggested that richness can be one of the most reliable and consistent biomonitoring metrics. Abundance may also be a useful measurement, but under certain circumstances it could prove to be unreliable (like downstream from organic waste effluents). Also, abundance per sample has been shown to have sizable variability (Needham and Usinger, 1956).

In both habitats, abundance and richness were not significantly different among the three weeks (Fig. 1). Results from the other measurements varied (Table 1). At the sandy run, evenness, diversity, biotic index, and all five functional feeding groups did not vary significantly throughout the study period. Only two of the other measurements, percent of shredders and percent of scrapers, remained consistent at the gravel riffle.

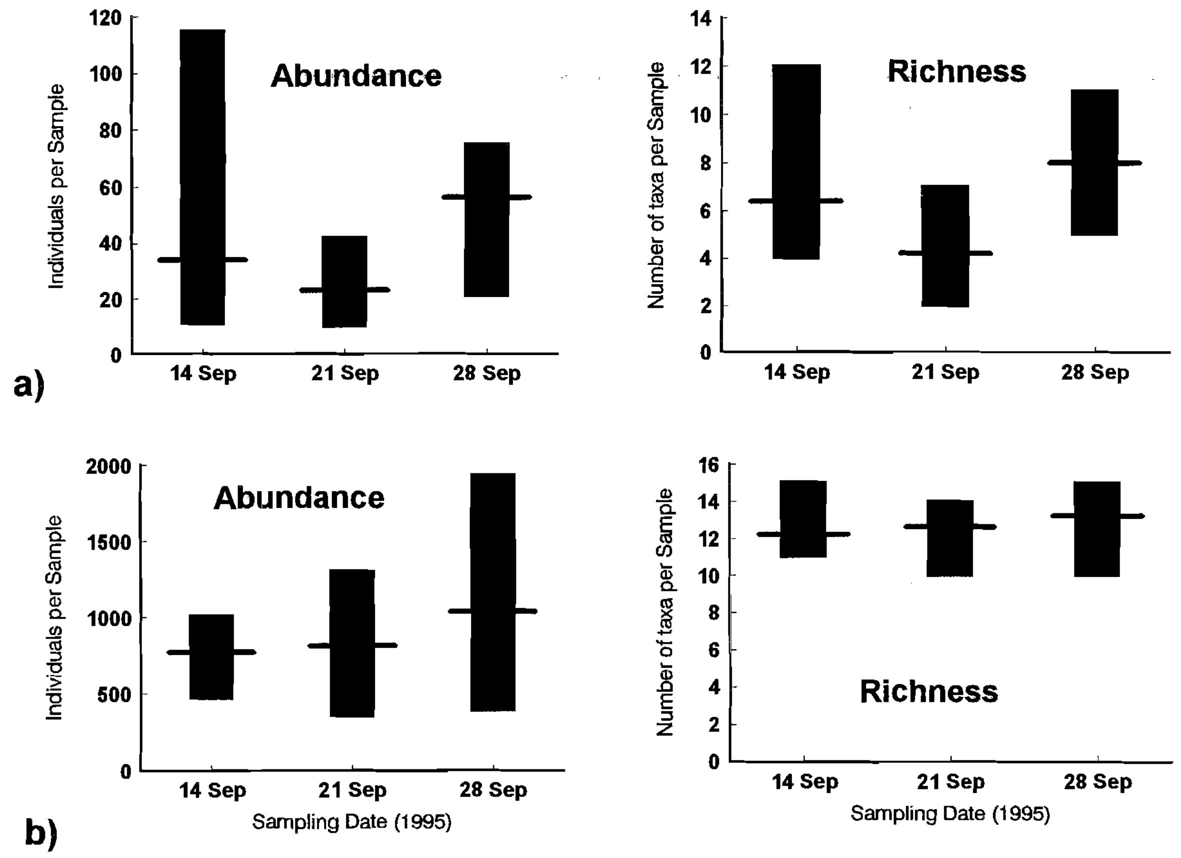

Figure 1. Range and mean of the abundance and richness of macroinvertebrate samples collected from a) a sandy run habitat and b) a gravel riffle habitat of Holly Fork Creek, Henry County, Tennessee, September 1995. There was no significant difference in abundance or richness among the three weeks at either habitat (Kruskal-Wallis analysis of variance, $p = 0.05$; n_1, n_2, $n_3 = 5$).

Table 1. Other comparisons among the three weeks for macroinvertebrates collected from two habitats of Holly Fork Creek, Henry County, Tennessee, September, 1995 (N = no significant difference, S = a significant difference; Kruskal-Wallis analysis of variance, $p = 0.05$, n_1, n_2, $n_3 = 5$).

Measurement	Sandy Run	Gravel Riffle
Pielou's Evenness	N	S
Shannon Diversity	N	S
Family-level Biotic Index	N	S
Functional Feeding Group Ratios		
Shredders	N	N
Scrapers	N	N
Filtering Collectors	N	S
Gathering Collectors	N	S
Predators	N	S

These results suggest that one collection over the three week period would have provided an accurate representation of the macroinvertebrate community in the sandy run, but might not in the gravel riffle. The precision of describing short-term community variability in the gravel riffle seems to be dependant on the type of metric(s) used. Although abundance and richness remained consistent during the study period, the relative contribution of the five most abundant taxa at the gravel riffle changed from week to week (Fig. 2). Abundance and richness are measurements that describe exactly what was collected. Diversity, evenness, and biotic index metrics area mathematical computations (Resh and Jackson, 1993). Therefore, these values along with the percentage of each functional feeding group are effected by the relative abundance of each taxon. This data indicates that consistently sampling similar abundances of specific taxa is much less likely than consistently sampling similar total abundances. In more physically and biologically complex habitats, such as a gravel riffle, it is less probable that you will consistently sample similar numbers of individuals within each taxon. This causes greater variation in metric computed from relational values compared to more absolute metrics such as taxa richness. These findings show the importance of understanding the limitations of the various measurements and how they may be affected by sample variation. However, collecting larger numbers of weekly samples, identifying organisms to generic or specific levels, and analyzing collections from different seasons could provide more conclusive results. Finally, it may be beneficial for monitoring programs, as time and funds allow, to collect a series of weekly samples at least once during each season. This would provide a better understanding of the temporal variability found in stream communities in different habitats.

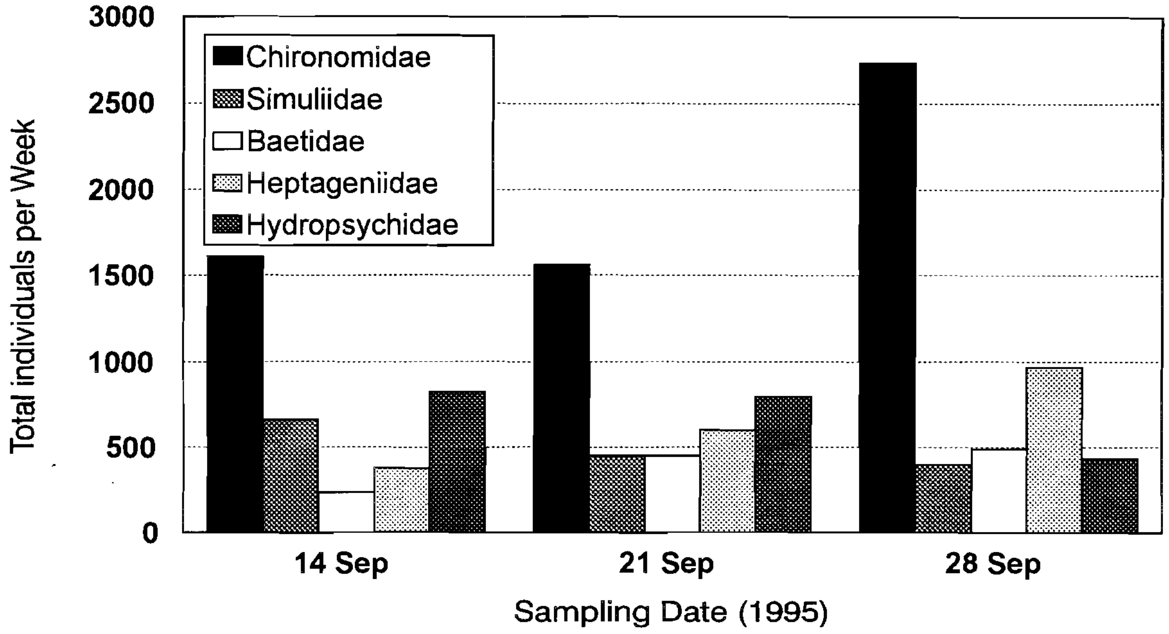

Figure 2. The five most prominent macroinvertebrate taxa collected in September 1995 from a riffle habitat of Holly Fork Creek, Henry County, Tennessee.

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THE DISTRIBUTION, HABITAT, AND SUBSPECIFIC STATUS OF THE PLAINBELLY WATER SNAKE (*NERODIA ERYTHROGASTER*) IN THE LOWER CUMBERLAND RIVER BASIN, TENNESSEE AND KENTUCKY

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ABSTRACT. To better define the distribution, habitat, and subspecific status of the plainbelly water snake (*Nerodia erythrogaster*) in the lower Cumberland River basin, we are seeking populations of the species along the Cumberland River from Old Hickory Dam near Nashville, Tennessee downstream to its confluence with the Ohio River at Smithland, Kentucky. Preliminary results show plainbelly watersnakes occur regularly in favorable wetlands in the river's floodplain and sparingly in adjacent uplands from Ashland City (Cheatham Co.), Tennessee to Barkley Dam (Lyon Co.), Kentucky. No records of the species have been obtained in the drainage above Ashland City or below Barkley Dam where floodplain wetlands are reduced and fragmented and historical collecting efforts have been minimal. Phenotypic characteristics of specimens from the region match most closely those described for the copperbelly watersnake (*N. e. neglecta*). However, they also show some minimal influence from the yellowbelly water snake (*N. e. flavigaster*). Research is ongoing in hopes of determining if the lower Cumberland River basin population of snakes is more similar to the previously reported intergrade (*N. e. neglecta* x *N. e. flavigaster*) population of northwestern Tennessee and southwestern Kentucky or if it is truly a good representative of the copperbelly subspecies.

AQUATIC MACROINVERTEBRATE SPECIES ASSEMBLAGES AT SELECTED SITES IN THE ABRAMS CREEK WATERSHED, GREAT SMOKY MOUNTAINS NATIONAL PARK: PHASE ONE OF A LONG-TERM STUDY

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ABSTRACT. Abrams Creek is a fifth order tributary of the Little Tennessee River (Chilhowee Reservoir), with a watershed almost entirely within the Great Smoky Mountains National Park (GSMNP). Macroinvertebrate communities were sampled at seven sites within the Abrams Creek watershed. Sites were sampled qualitatively and semi-quantitatively, three times annually (winter, spring, and fall), for two years (winter 1993-fall 1995). Excluding the Chironomidae, 347 total taxa in 88 families were identified, of which, the insect orders Ephemeroptera, Plecoptera, and Trichoptera (EPT) comprised 216 taxa in 29 families. Greatest taxa richness was observed among the Trichoptera (85 taxa, 18 families), with the Ephemeroptera (81 taxa, 11 families) and Plecoptera (50 taxa, 9 families) well represented. EPT taxa richness at each site varied from 99 to 134 taxa. Differences among sites in observed EPT richness was generally positively correlated with drainage area. However, Site 3, with the third largest drainage area but a more uniform substrate of finer particles, had the lowest EPT richness. Higher combined EPT richness was generally observed in spring samples, however, Plecoptera richness was greatest in winter samples with Trichoptera richness virtually equal in winter and spring. The North Carolina Biotic Index (NCBI) for mountain region streams was applied to semi-quantitative samples. All NCBI values among sites scored excellent. Among individual samples, Site 3, fall 1995, scored good, while all others scored excellent. When EPT taxa richness and NCBI scores are equally considered, all samples indicate excellent water quality at all sites. Lower indicator values at site 3, however, point out siltation effects probably due, in part, to erosion in Cades Cove, GSMNP.

A FIELD STUDY OF THE BLACK KINGSNAKE, *LAMPROPELTIS GETULA NIGRA*

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ABSTRACT. From 1990-1996, we conducted a mark-recapture study on *Lampropeltis getula nigra* (black kingsnake) inhabiting old-fields at the Clinch River Environmental site in Anderson County, Tennessee. This paper presents life history information previously not reported for this subspecies. Of 12 species of snakes found at the site, *L. getula nigra* made up 55% of 729 total captures. The number of individuals captured ranged from 28 in 1996 to 41 in 1992 (mean = 33). Thirty-two individuals were captured in more than one year. There was no difference between the number of males and females captured. Mean snout-vent lengths (SVLs) did not vary from year to year (except 1990 and 1994) indicating a relatively stable age structure. Mean SVLs and masses of males and females did not differ, but mature males (>60cm) had longer tails than females with equivalent SVLs. Recaptured *L. getula nigra* grew a mean of 1.4 cm/month (N=41). First and second year snakes showed the largest growth rate (mean = 2.6 cm/month), with growth rates decreasing noticeably thereafter, possibly indicating maturity. Allometric mass (g) - length (cm) relationships showed a significant correlation (r=0.98) with mass (g) = 0.005 SVL (cm)$^{2.92}$. Food items from unforced regurgitation included 4 snakes and 5 mammals, with individuals (N=4) over 60 cm regurgitating only *Microtus pinetorum*. Weight loss from regurgitation ranged from 8.4% to 30.9% of total body mass. For snakes found under wood and metal cover objects, the mean cloacal temperatures (26.5°C, N=36) was higher than air (24°C) and substrate (24.5°C) temperatures. Mean temperatures of males (25.6°C, N=18) and females (27.4°C) varied, but were not significantly different. At time of capture, no difference was found between wood and metal substrate temperatures. This may explain why there was no difference between the number of captures under wood versus those under metal. During a 26-hour survey of two male snakes implanted with temperature sensitive transmitters, body temperatures varied only 3.5°C and 7°C for an air temperature changes of 20°C. Seven individuals were radio-tracked a combined total of 413 times over a 3-year period. The mean home range (convex polygon method) was 23,260 m^2, with males having substantially larger home ranges than females. The mean distance per move for males was 1.6 times longer than moves recorded for females. On 176 of 381 (46%) tracking days individuals made no apparent move. This supports the hypothesis that individuals spend substantial time in small areas. Individual snakes frequently travel considerable distances only to return to these fixed areas. Tracked individuals were often active during the warmest part of the day; two individuals were observed feeding at mid-day when temperatures ranged from 25.7°C to 31.9°C. A rarely observed behavior, previously not described for *L. getula nigra*, was recorded during this study. When captured, certain individuals protruded a bright red cloaca and released cloacal contents, including variable amounts of blood, a behavior known as a cloacal autohemorrhaging. Twenty-eight individuals (71% of them females) had a total of 53 hemorrhaging events. Snakes demonstrating this response were at least a year old and ranged in SVL from 44 cm to 91 cm.

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HABITAT USE BY FIVE SYMPATRIC TURTLE SPECIES IN KENTUCKY LAKE

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ABSTRACT. A spotting scope was used to study habitat associations of five sympatric turtle species in a linear embayment of Kentucky Lake, an impoundment of the lower Tennessee River in western Kentucky. Counts of basking turtles were made on 182 occasions over three years. The least similar species in habitat use was the trionychid *Apalone mutica*, which was primarily confined to outer portions of the cove on two gravel beaches used for basking. Habitat electives of four emydids, which basked almost exclusively on logs and branches, demonstrated habitat preferences for progressively deeper waters further from the cove's creek inlet, in the order *Trachemys scripta, Pseudemys concinna, Graptemys pseudogeographica,* and *G. ouachitensis*. All species also showed some degree of habitat segregation between adults and juveniles. Only *T. scripta* is common in naturally lentic waters, while *Apalone*, *Graptemys*, and to a lesser degree *Pseudemys*, are strictly riverine taxa. These results suggest that phylogeny and historical habitat associations, rather than competitive interactions between close relatives, have been most important in determining community patterns in habitat use in this anthropogenically-modified habitat.

DYNAMICS OF THE AMPHIBIAN COMMUNITIES AT TWO SMALL PONDS IN LAND BETWEEN THE LAKES OVER THE PAST DECADE

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ABSTRACT. We analyzed data on amphibian captures and abiotic variables collected from 1 July 1987 through 31 June 1996 at two small ponds in the Tennessee portion of Land Between The Lakes. One objective was to make interpond comparisons between yearly changes in the following: 1) selected abiotic variables, 2) species richness, 3) community composition and similarity, and 4) activity levels. Another objective was to try correlating yearly changes in the community characteristics and activity at each pond with fluctuations in prevailing abiotic conditions. Abiotic variables studied included: air temperature and relative humidity; water level, temperature, pH, conductivity, and dissolved oxygen; soil temperature and moisture; and rainfall. Animals were captured in pitfall traps set along metal drift fences erected around each pond. Traps were checked and abiotic measurements taken every other day during spring, summer, fall, and the warmer parts of winter. During subfreezing weather, checks were conducted only once each week. Abiotic conditions at the two ponds were substantially different. Eight of the 10 variables sampled had significantly different overall means (*t*-test, $P < 0.05$). Overall captures totaled 46,104 (28,149 at the woodland pond and 17,955 at the field pond). Total captures per year at the woodland pond exceeded those at the field pond in all years except the first (1986-1987) when captures at the field pond were nearly twice those at the woodland pond. Average number of captures per pit (a more equitable comparison), was more balanced with each pond exceeding the other during 4 years and both being equal during 1 year. Mean annual captures per pit overall at the two ponds (880 and 898, respectively) was not significantly different (Wilcoxon Rank Sum Test, alpha level = 0.05). Total captures and average captures per pit varied yearly at both ponds, showing opposite trends the first 3 years and similar trends the last 6 years. Overall , frog and toad captures exceeded salamander captures by a large margin at both ponds amounting to 63% and 71% of the total, respectively. Total species richness over the entire 9-year period was equal at the two ponds (19 at each), yet it ranged yearly from 13 to 17 at the field pond and from 14 to 16 at the woodland pond. Frog species consistently outnumbered salamander species at both ponds during all years. Although differing slightly in which species were involved, the overall count at both ponds was 10 species of frogs and 9 species of salamanders. At the woodland pond, species richness per year averaged 9.1 for frogs (range 9-10) and 6.3 for salamanders (range 5-8). At the field pond the average was 9.0 for frogs (range 8-10) and 5.9 for salamanders (range 5-8). Of the 19 species recorded at each pond, six were dominant at the woodland pond, whereas eight dominated at the field pond. At both sites, 95% of the total captures were for one or another of the dominant species. Dominants (and the % of total captures each represented) at the woodland pond included the American Toad (33%), Spotted Salamander (31%), Southern Leopard Frog (13%), Green Frog (10%), Bullfrog (5%), and Zigzag Salamander (3%); at the field pond, the American Toad (33%), Spotted Salamander (15%), Eastern Newt (12%), Southern Leopard Frog (11%), Eastern Narrowmouth Toad (8%), Green Frog (7%), Bullfrog (5%), and Cope's Gray Treefrog (4%) were dominant. Correlation analyses (Spearman rank-order coefficient, r_s) between total yearly captures of species among the dominants at both ponds revealed that changes in activity levels were similar at both ponds for some but not others. These analyses also revealed a number of potential interspecific interactions within each pond. Correlation analyses between yearly counts and means of the abiotic variables sampled also revealed many significant relationships (both positive and negative). Results indicate major differences in the non-living component of the two pond ecosystems and lesser, but in some cases significant, differences in their amphibian communities. The findings also suggest that yearly shifts in composition, relative abundance, and levels of activity of each pond's resident amphibians are interrelated and probably influenced by both abiotic variables and interspecific interactions.

MONTHLY OBSERVATIONS OF NUMBER, SIZE, DISPERSION, ORIENTATION, AND MICROHABITAT OF THE VISIBLE INDIVIDUALS OF *EURYCEA LUCIFUGA* (CAVE SALAMANDER) IN SELECTED TENNESSEE AND KENTUCKY CAVES

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ABSTRACT. A year-long study of cave populations of *Eurycea lucifuga* was conducted from September 1994 through August 1995. Six caves (three in Montgomery County, Tennessee and three in Edmonson County, Kentucky) were studied. Abiotic conditions and physical descriptions of each cave and its adjacent epigean habitat were recorded. Individual cave salamanders encountered within the survey zone of each cave were counted, measured, and assessed for the following: distance from entrance, height above floor, side of cave found on, vertical and horizontal orientation, and microhabitat. Population changes recorded monthly throughout the year were nonrandom. In both regions populations peaked in spring, declined in summer, and then peaked again in either late summer or fall. After this secondary peak, numbers of visible individuals declined gradually to a low in January and February. Significant correlations were detected in both regions between monthly fluctuations in population size and monthly means of the following cave variables: relative humidity, air temperature, and available surface moisture. Of these factors, relative humidity correlated most strongly, followed in order by surface moisture and air temperature. There was no significant difference between the overall means for snout-vent-length of salamanders in the Tennessee versus Kentucky caves. Of the 421 individuals observed, 291 were located on walls, 129 on the floor, and only 1 on the ceiling. When observed on cave walls, salamanders were most often oriented horizontally (68%) with their directional headings (in or out) divided equally. Of those oriented vertically, 85% were observed with the head pointing upward. Surface moisture seemed to be the most important factor determining both dispersion and choice of microhabitat.

EVIDENCE FOR REPRODUCTIVE ISOLATION IN THE POLYMORPHIC MOLE SALAMANDER, *AMBYSTOMA TALPOIDEUM*

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ABSTRACT. Mole salamanders (*Ambystoma talpoideum*) are facultatively paedomorphic; some individuals transform into terrestrial "metamorphic adults" while others become sexually mature in an aquatic larval form termed "paedomorphic adults." This polymorphism provides an opportunity for reproductive isolation because both pre- and post-mating isolation mechanisms could be operating between morphs. We followed inter- and intramorph breeding interactions in two populations over a two year period. The two morphs were temporally segregated in that paedomorphs bred earlier in the season (Oct-Dec) than metamorphs (Dec-Jan). The morphs were also spatially segregated; metamorphs bred at shallower depths than paedomorphs. Finally, laboratory experiments revealed that intramorph matings were more common than intermorph matings. These data suggest that temporal, spatial, and behavioral separation could lead to reproductive isolation between morphs and the potential for sympatric speciation.

A COMPARISON OF TWO LIVE TRAP TECHNIQUES FOR CAPTURING SHREWS

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ABSTRACT. Two trapping techniques for shrews and other small mammals were compared at Land Between The Lakes (LBL), a 68,797-ha peninsula managed by the Tennessee Valley Authority. The study site was in Stewart County, the Tennessee portion of LBL. A 10 x 10-m trapping grid was established with alternating pitfall and live-trap stations. Pitfalls were 2.4-L plastic "cups" (14.3 cm top diameter, and 19.2 cm deep). The live traps were single-capture box traps based on a Soviet design and sensitive to only a few grams. Both trap types were baited with cat food and bread soaked in unrefined peanut oil. Traps were operated from February to August 1995, for a total of 29 trapping sessions. During each 12 to 18-h session, traps were checked every 3 hours. Weight and sex (when possible for shrews) were determined for captured animals and they were marked by toe-clipping. The only species of shrew captured was the northern short-tailed shrew (*Blarina brevicauda*). Shrews were caught in both trap types almost equally (58 in live traps and 52 in pitfalls). A total of 36 individuals was captured 110 times. *Blarina* abundance peaked in April, with 19 individuals known alive on the study grid. White-footed mice (*Peromyscus leucopus*) were taken only in live traps (67 individuals, 241 captures). Woodland voles (*Microtus pinetorum*) were taken in both pitfalls and live-traps but at low numbers (12 individuals, 28 captures; 15 captures were 1 individual). Trap-revealed microhabitat segregation and/or competitive interaction between *Blarina* and *Peromyscus* were not apparent. Home range values for *Blarina* are reported.

CONTRIBUTED PAPERS

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DIVERSITY AND DISTRIBUTION OF DENITRIFYING BACTERIA IN SOIL AND SUBSURFACE SEDIMENTS UNDER GRASSLAND AND CULTIVATED SOIL

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ABSTRACT. Microorganisms capable of dissimilatory nitrate reduction are important to the fate of nitrate in soil and groundwater. The influence of cultivation and environmental conditions associated with soil depth on the distribution of facultative nitrate-reducing bacteria was evaluated using more than 700 isolates obtained from the surface and subsurface of a grassland and a cultivated soil located near Manhattan, Kansas (USA). Most probable number (MPN) estimates indicated a higher total number of facultative nitrate-reducing bacteria in the cultivated than in the grassland soil. However, only 12 and 19% of the total facultative nitrate-reducing bacteria were denitrifiers at the prairie and agricultural site, respectively. The majority of isolates were ammonium producing nitrate reducers at both sites. *Pseudomonas fluorescens* represented the greatest number of isolates among facultative nitrate-reducing bacteria in the water-saturated zone and the most denitrifying strains. Environmental conditions associated with soil depth, especially organic carbon determined the species distribution. Repetitive sequence-based polymerase chain reaction using BOX A1R oligonucleotide primer, allowed measuring fine-structure diversity of closely related strains within *Pseudomonas* species in the collection of denitrifying bacteria obtained from prairie and agricultural site, from different depths, and at different times.

INTRODUCTION

Previous studies on the occurrence and activities of nitrate-dissimilating bacteria in soils have emphasized the potential roles of denitrifiers (Payne 1981, Knowles 1982, Parkin 1990) and other nitrate-dissimilators in N_2O production (Tiedje 1988), nitrate turnover (Tiedje 1988), and groundwater quality (Smith *et al.* 1994). However, relatively little is known of the bacterial population dynamics associated with denitrification, in part because it is difficult and time-consuming to characterize and differentiate the large number of strains required for such studies. Changes in the population dynamics of sub-soil microflora which arise in response to different nitrate levels due to application of fertilizers, may have a profound impact on local water quality. In 1994, nitrate levels exceeded EPA (Environmental Protection Agency) standards for primary drinking water sources in about 25% of the wells sampled across Kansas (Siefker and Elkins 1994). Using both molecular and conventional methodologies, the main objective of the present study was to assess the population of denitrifying bacteria of a pristine Kansas grassland soil and underlying subsurface sediments. A comparative site planted with wheat was also characterized to determine if distribution of genetic diversity of denitrifying bacteria of the cultivated and non-cultivated soils was different.

MATERIALS AND METHODS

Collection and characterization of soils

Soil samples were collected from two sites (separated by approximately 1 km), at the Konza Prairie Research Natural Area, a 3,500-ha area dedicated to tallgrass prairie ecological research near Manhattan, Kansas. Samples were collected from two boreholes, each drilled to bedrock in grassland and agricultural sites in the Kings Creek valley, where clay-based unconsolidated sediments overlie the limestone bedrock (Dodds *et al.* 1996). The grassland site has been in pasture since 1939 and was used for livestock grazing as recently as 1980 (Dodds *et al.* 1996). About 50% of the grass is big bluestem (*Andropogon gerardii*), a dominant grass in the tallgrass prairie. The agricultural site is 1 km downstream on Kings Creek was planted with soybean and wheat. Properties of soils and subsurface sediments are presented in Table 1. Nitrogen fertilizer was applied at a rate 50 kg N/ha in March 1993.

Table 1. Properties of soils and subsurface sediments

Site and location	Depth (m)	pH (soil:water)	Organic C (g/kg)
Grassland, surface	0 - 0.1	6.3	3.11
Grassland, vadose	2.2 - 2.8	7.9	0.07
Grassland, water saturated	6.5 - 7.1	7.9	0.10
Cultivated, surface	0 - 0.2	5.8	1.39
Cultivated, vadose	2.7 - 3.3	8.0	0.16
Cultivated, water saturated	7.7 - 8.3	7.8	0.36

Data obtained from Dodds *et al.*, 1996.

The soil type at both sites was Reading silt loam (mixed, mesic, Typic Argiudoll). The average annual precipitation is 82.5 cm with heaviest rainfalls occurring in May, June and July. Soils were sampled from two cores from each site in April 1993 using a split spoon sampler with a sterilized polycarbonate inner liner in 60 cm increments to a depth of 7.6 and 10.2 m in the prairie and cultivated sites, respectively. The water table occurred at approximately 4.3 m (Dodds *et al.* 1996). Surface soils from both sites were sampled again in April 1995 and were obtained from a depth of 0-10 cm. Samples were stored at field water content in sterilized mason jars at 4°C.

Isolation and characterization of isolates

General aerobic bacteria were enumerated by standard plate count techniques (Wollum 1982). Microorganisms with nitrate dissimilative abilities were enumerated by the most probable number (MPN) method (Tiedje 1982). Cultures from the MPN Hungate tubes with N_2O production were presumed to contain denitrifying bacteria and were streaked onto half-strength tryptic soy agar plates supplemented with 5mM KNO_3 and incubated under anaerobic conditions. Colonies of different morphology were selected from each plate and isolates cultivated in nitrate-supplemented TSB preserved at -80°C in 15% glycerol. All isolates were characterized according to morphology, motility, Gram-reaction, pigment production, oxidase test, catalase reaction, and the ability to grow at 37°C and 42°C on tryptic soy agar (Smibert and Krieg 1981).

The ability of bacterial strains to utilize carbohydrates, organic acids, and amino acids was evaluated by BIOLOG (BIOLOG Inc., Hayward, CA) following the manufacturer's instructions. The results were recorded both visually and automatically in a Titertek Multiskan Microplate Reader (Flow Laboratories Inc., McLean, VA) at 590 nm. Data were compared to carbon utilization patterns from strains with known taxonomic descriptions in the BIOLOG database. *Pseudomonas fluorescens* ATCC 33512 and *Pseudomonas mephitica* ATCC 33665 were used as reference strains to provide assurance that the BIOLOG system was working as expected. Identification of total cellular fatty acids was performed by Analytical Services Inc. (Willispon, VT).

DNA fingerprints for each strain were generated from isolated genomic DNA. Total genomic DNA was prepared by a modified miniprep method for bacterial genomic DNA (Ausubel *et al.* 1992). The cetyltrimethyl-ammonium bromide was not included, and 95% ethanol was used instead of isopropanol. DNA was quantified spectrophotometrically (Sambrook *et al.* 1989). To generate a genomic DNA fingerprint, repetitive extragenic palindromic polymerase chain reaction (rep)-PCR was used (DeBruijn 1992, Louws *et al.* 1994). The primer, BOX A1R, corresponding to the BOXA subunit of the BOX element (Martin *et al.* 1992) (5' -CTACGGCAAGGCGAC GCTGACG- 3') was synthesized by the Biotech Facility at Kansas State University. PCR amplifications were performed in an automated thermal cycler (MJ Research, Inc., Watertown, MA) using published parameters (Louws *et al.* 1994). Amplified PCR products were separated by gel electrophoresis on 1.5% agarose gels in Tris-acetate/ EDTA electrophoresis buffer (Sambrook *et al.* 1989). Fingerprints generated from different strains were compared visually and scored for presence and absence of bands. PCR reactions were repeated three times.

Analysis of Denitrifiers

Gas samples (0.5 ml) withdrawn from the MPN bottles were analyzed for N_2O by gas chromatography. For determination of N_2O, a Shimadzu 8AIT gas chromatograph (Pittsburgh, PA) equipped with a thermal conductivity detector and Porapak Q column was used; column temperature was 50°C, the injection port temperature was 70°C, and the detector temperature was 70°C. NO_3- and NH_4^+ were determined colorimetrically (Morgan 1930, Daniels *et al.* 1994). When pure bacterial culture was grown with 5mM KNO_3, N_2O constituted 80-90% of the N-products recovered for each denitrifying strain, and there was no detectable nitrate at the end of growth. Denitrification was confirmed by the lack of gas production in the nitrate-free controls. Denitrifying bacteria possessing N_2O reductase were distinguished by the presence of significantly less or no N_2O accumulation in the absence of C_2H_2. Nitrate-reducing bacteria were distinguished by the absence of N_2O. Ammonium-producing nitrate reducers (APNR) were distinguished by the presence of NH_4^+ in the culture and the absence of significant amounts of N_2O. The absence of NO_3- in the culture indicated total dissimilation of NO_3-. Isolates were designated nondissimilatory isolates if they did not consume NO_3- or produce detectable amounts of N_2O in both media. All tests were performed on each of the 1,243 isolates. Tests for denitrifiers were repeated twice. *Pseudomonas fluorescens* ATCC 33512 was included as a representative N_2O-producing denitrifying bacteria.

Data analysis

In addition to using data for identification purposes, data from carbon utilization profiles and fatty acid profiling were used to assess relationships between strains. The data were converted to binary, i.e., the 95 carbon utilization profiles were coded as 1 (positive) or 0 (negative) for each character state. Redundant characters in carbon utilization profiles were excluded resulting in 74 characters analyzed. Binary data from carbon utilization and fatty acid profiles also were analyzed as a combined data set. Binary data for fatty acids were converted by scoring for the presence (1) or absence (0) of each fatty acid for population comparison purposes. A similarity matrix was generated from binary data with NTSYS-pc v. 1.8 (Rohlf 1993) using Jaccard's coefficient of similarity (Sneath and Sokal, 1973). The clustering of strains was performed on the similarity coefficients according to the unweighted average pair-group method (Sneath and Sokal 1973). Clusters were displayed in the form of a dendrogram.

The genetic diversity (*H*) of denitrifying strains was calculated as $H=[n/(n-1)](1-x_i^2)$, where x_i is the frequency of the *i*th BOX-PCR type in any one grouping, or the average frequency of the *i*th BOX-PCR type in the entire population, *n* is the number of strains examined, and n/ (n-1) is a correction factor for bias for small sample size (Nei 1978).

RESULTS AND DISCUSSION

Enumeration and depth distribution of culturable microflora in grassland and agricultural soils

The numbers of facultative nitrate reducing bacteria obtained from the grassland and agricultural surface soils were similar (Table 2). In contrast, facultative nitrate-reducing bacteria were distinctly more numerous in vadose and water-saturated zone at the agricultural site (Table 2). Surprisingly, a very low percentage of total number of isolates were denitrifying bacteria from surface soils at both sites (Table 2). The majority of facultative nitrate-reducing bacteria were ammonium-producing nitrate reducers (APNR) at both sites. Similar numbers of facultative nitrate reducing bacteria, denitrifying bacteria, and APNR were obtained in surface soils in April 1995 (data not shown). The proportion of denitrifying bacteria among the total NO_3- dissimilative strains and total number of bacteria increased with depth (Table 2). For both grassland and agricultural soils, the proportion of APNR decreased with depth (Table 2).

Table 2. Cellular fatty acid composition (%) of *P. fluorescens*, *P. putida* and *P. mephitica* KS isolates

Isolate[a]	$C_{10:0}$	$C_{10:0\ 3OH}$	$C_{12:0}$	$C_{12:0\ 2OH}$	$C_{12:0\ 3OH}$	$C_{14:0}$	$C_{16:0}$	$C_{16:1w7c}$	$C_{17:0\ cyclo}$	$C_{18:0}$	$C_{19:0}$
KS1ps	-	4.29	4.11	1.46	-	0.76	37.04	43.41	3.54	-	-
KS12pws	0.51	4.15	3.76	1.75	-	0.80	37.62	44.66	1.81	-	-
KS31av	-	4.74	4.55	1.59	-	-	32.93	47.18	-	-	-
KS45aws	0.37	-	3.74	1.51	-	0.61	37.96	43.23	-	-	-
KS72pws	-	3.49	3.15	3.65	3.87	0.28	31.30	26.66	4.98	1.40	-
KS8pws	-	3.04	2.90	3.87	3.59	0.55	30.06	28.09	3.03	1.35	-
KS14pws	-	2.91	2.93	3.77	3.53	0.53	30.88	26.92	4.45	1.31	-
KS17pws	-	2.86	2.97	3.78	3.42	0.56	30.95	26.89	4.90	1.27	-
KS78as	-	9.72	3.24	4.38	9.08	1.05	20.95	24.06	1.85	-	-
KS65av	-	4.21	3.26	4.52	3.98	/	28.56	36.86	1.93	0.77	-
KS75pv	-	6.54	2.77	3.76	6.39	0.42	31.16	27.08	4.45	0.85	-
KS41pv	1.01	6.27	2.71	4.27	6.00	0.34	28.47	28.11	3.46	0.75	-
KS42pv	0.93	6.11	2.76	4.34	5.75	0.35	27.68	29.43	2.93	0.68	-
KS39av	-	3.70	3.30	3.57	3.63	0.42	32.99	19.36	18.01	1.20	2.81
KS40av	0.14	3.88	3.70	3.75	4.07	0.51	31.08	19.18	19.60	1.01	2.40
P.f.[b]	-	3.13	4.39	3.18	3.72	-	23.59	32.18	1.30	0.62	-
P.m.[c]	-	3.87	3.67	1.71	-	0.86	34.51	48.70	1.73	-	-

[a] as (agricultural site, surface); av (agricultural site, vadose); aws (agricultural site, water saturated zone)
ps (prairie, surface); pv (prairie, vadose); pws (prairie, water saturated zone)

[b] *P. fluorescens* ATCC 33512

[c] *P. mephiticia* ATCC 33665

"-" denote not present

Phylogenetic characterization of denitrifying bacteria

Utilizing the MPN enrichment method, 1243 bacterial isolates were obtained from the grassland and the cultivated surface and subsurface environments. All isolates were selected on tryptic soy agar. Taxonomic identification of denitrifying bacteria and APNR was achieved with both biochemical and physiological tests. *Pseudomonas* species were distinguished from enteric bacteria based on two tests: gas was not produced from glucose in oxidative/fermentative medium and the oxidase test was always positive. Forty six denitrifying strains were selected for analysis of carbon source utilization profiles by BIOLOG. These strains were representative of the zones sampled relative to the morphological and biochemical diversities of the denitrifying isolates. All denitrifying strains were identified to the genus level as *Pseudomonas* utilizing carbon source utilization profiles by BIOLOG analysis. Because final identification of denitrifying strains was not possible based solely on carbon utilization profiles, fatty acid analysis was also performed on fifteen strains.

Fatty acid analysis yielded identifications for 10 of 15 strains tested with a very good match to the data base. However, if a strain was grown on different media, it was sometimes identified as two different species by fatty acid analysis. For example, the two ATCC reference strains were not identified correctly. *P. mephitica* ATCC 33665 was not in the database of fatty-acid profiles and was identified as *Janthinobacterium lividum*. Although *P. fluorescens* was in the database, *P. fluorescens* ATCC 33512 was identified as *Pseudomonas cichorii*. All denitrifying strains were identified to the genus level as *Pseudomonas*.

Two- and 3-hydroxy fatty acids can be used to assign *Pseudomonas* strains to six major groups, each containing subgroups (Stead 1992). Group 1 strains contain $C_{10:0\ 3\text{-}OH}$, $C_{12:0\ 2\text{-}OH}$, and $C_{12:0\ 3\text{-}OH}$ (Stead 1992). The major fatty acids in all Kansas strains obtained from different soil sites and depths were $C_{16:0}$ and $C_{16:1w7c}$ (Table 2), followed by $C_{12:0}$ and $C_{12:0\ 2OH}$. All *P. fluorescens* and *P. putida* strains additionally contained $C_{10:0\ 3OH}$ and $C_{12:0\ 3OH}$, whereas no *P. mephitica* strain contained $C_{12:0\ 3OH}$. Only *P. putida* KS 39av and KS 40av contained $C_{19:0cyclow8c}$. Based on the presence of 2- and 3-hydroxy acids, all strains are likely in group 1. All fluorescent pseudomonads belong to subgroup 1a (Stead 1992). *Pseudomonas fluorescens* KS strains and *P. putida* KS strains grouped with subgroup 1a.

Grouping of strains obtained after combining carbon utilization and fatty acid data agreed well with grouping based on each separate method. The combined BIOLOG and fatty acid analyses consistently differentiated *P. fluorescens* strains. Identification of bacterial strains by BIOLOG and fatty acid profile analysis was limited by strains and species presently represented in the database. Both systems performed reasonably well when combined for identification of *Pseudomonas* rRNA group I (Palleroni 1984). More than 50% of the denitrifiers frequently encountered in soils are from rRNA group I of *Pseudomonas*, and most of those pseudomonads are fluorescent (Gamble 1977, Tiedje 1988).

Genetic diversity of selected denitrifying fluorescent *Pseudomonas* strains

Rep-PCR was used to assess the diversity of total of 292 denitrifying strains (156 from grassland and 136 from cultivated sites). Rep-PCR has been shown to be reliable means to characterize and group bacterial strains (DeBruijn 1992, Louws *et al.* 1994 Vera Cruz *et al.*

1995). Unidentified bacteria from soil samples can be grouped on the basis of their rep-PCR fingerprinting patterns (DeBruijn 1992). Each colony type yielded few different BOX-PCR types, e.g. within colony type 1 three BOX-PCR types were distinguished, within colony type 2, 11 BOX-PCR types were distinguished, and within the third colony type, 13 BOX-PCR types were distinguished. On the basis of occurrence of BOX-PCR types , 22 different BOX-PCR types were observed in 279 *P. fluorescens* strains tested. The two *P. putida* strains each had unique but similar BOX-PCR types. *Pseudomonas mephitica,* which was detected in low numbers (10^2 - 10^4), revealed three different BOX-PCR types for 11 strains.

The frequency of BOX-PCR types was different in grassland compared to cultivated sites (Figs.1 and 2). The dominant BOX-PCR type in the grassland was 7 (type strain KS8pws) and it was detected at a frequency of 39% within the group of denitrifying strains obtained from the grassland site. The dominant BOX-PCR type at the cultivated site was BOX-PCR type 8 (type strain KS75pv) and it was detected at a frequency of 42% in the denitrifying strains from the cultivated site. BOX-PCR patterns were used to estimate genetic diversity of the population of denitrifying bacteria. The mean genetic diversity (H_T) of the selected denitrifying population in both the grassland and cultivated sites combined was estimated to be 0.80. However, calculated genetic diversities between grassland (H=0.81) and cultivated sites (H=0.78) were not significantly different. Kennedy and Smith (1995) also found no differences in diversity when prairie and cultivated sites were compared. In their study, diversity in heterotrophic bacterial communities (based on ability to utilize different substrates, ability to grow in the presence of heavy metals, polyethylene glycol or antibiotics) were compared. Another study (Lal 1991) found higher diversity at a prairie site.

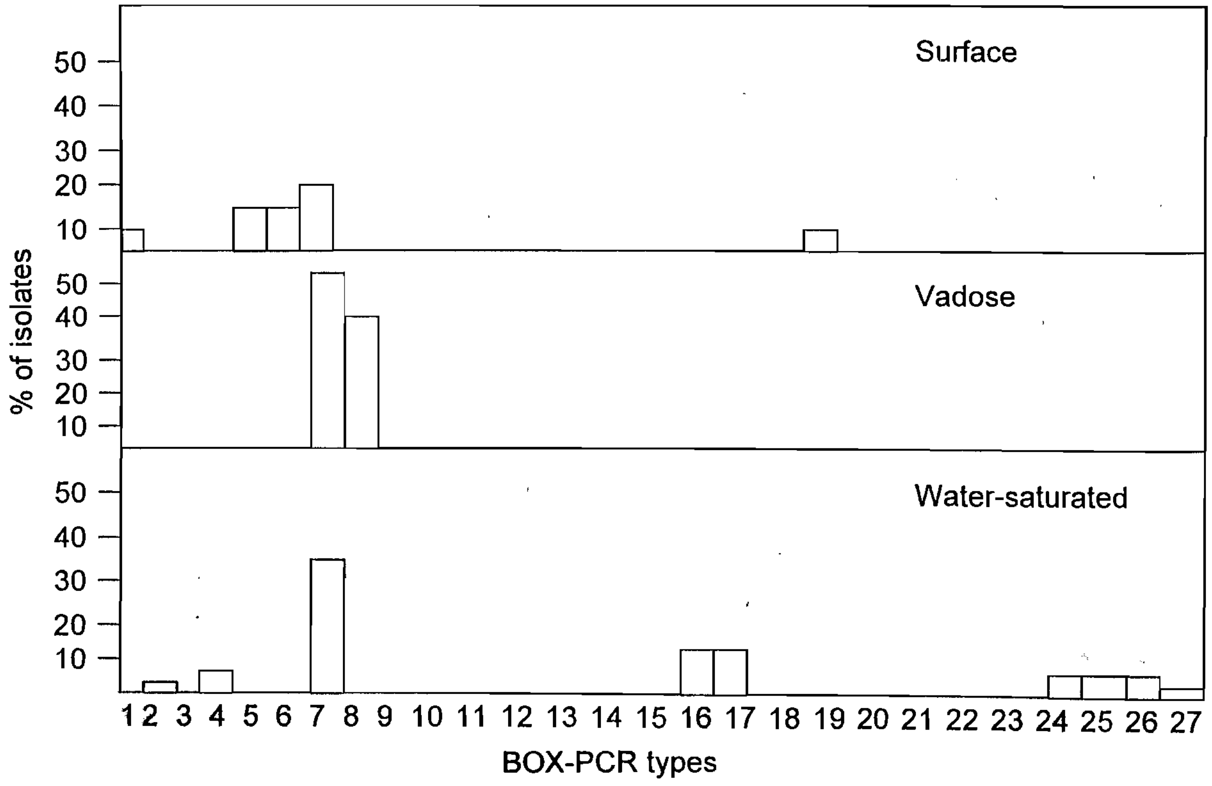

Figure 1. Frequency and distribution of BOX-PCR types at the grassland site.

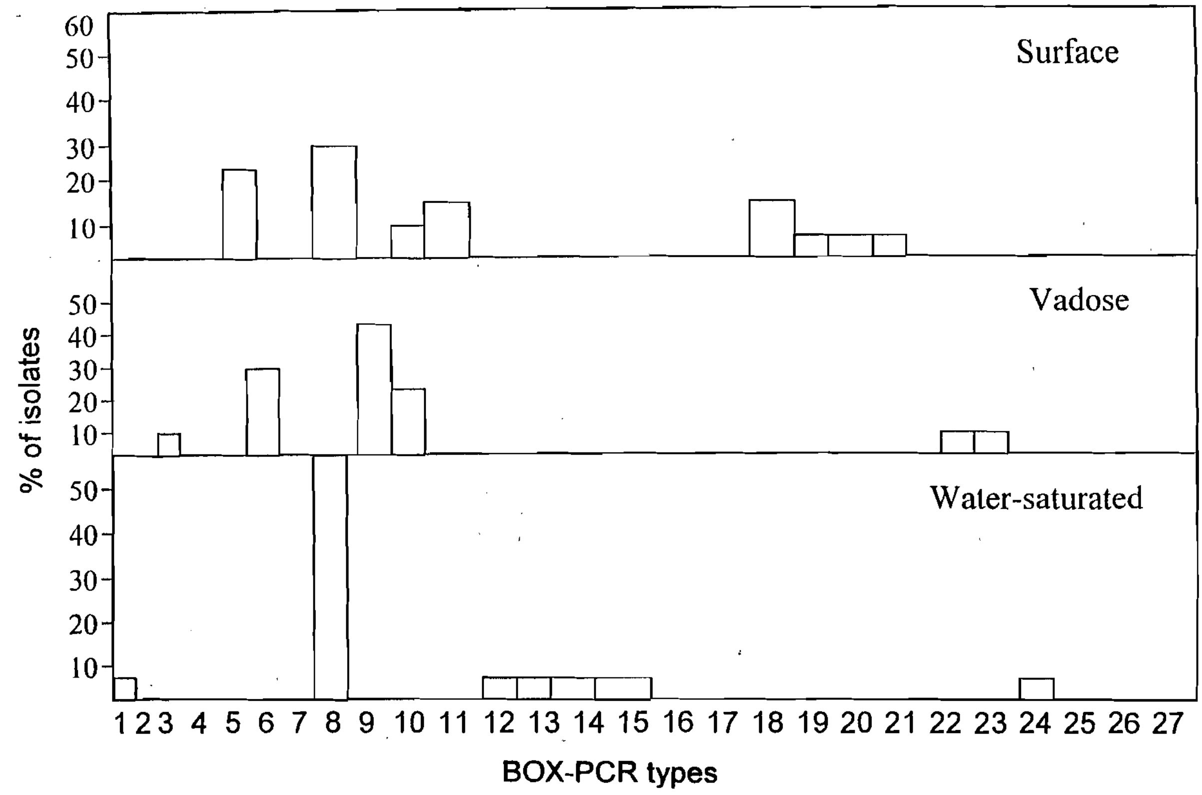

Figure 2. Frequency and distribution of BOX-PCR types at the cultivated site.

A marked difference in genetic diversity was found between strains obtained from different depths (when strains were grouped according to depth). The genetic diversity was estimated to be significantly greater near the soil surface (H=0.90) than the genetic diversity of the total population (H=0.80). The change in genetic diversity throughout the profile was affected by soil depth and, therefore, by different environmental conditions (Dodds *et al.* 1996). Only two BOX-PCR types were observed in the vadose zone at the grassland site (Fig. 1). The lowest number of denitrifying bacteria also was enumerated in the vadose zone at the grassland site (Table 1).

Previous studies have demonstrated that surface soils harbor denitrifying microbial communities (Clays-Josserand *et al.* 1995, Gamble *et al.* 1977, Knowles 1982), and that most heterotrophic bacteria from such habitats are fluorescent *Pseudomonas* spp. The present study extends these observations to terrestrial subsurface habitats. The occurrence of denitrifying *Pseudomonas* species at both surface and subsurface depths of grassland and agricultural soils demonstrated that this genus was widespread in these ecosystems. Pseudomonads have a diverse range of metabolic capacities (Palleroni *et al.* 1984), and their activity in subsurface soils likely affects the fate of organic contaminants and nitrate in ground water. Although the soil profiles at both sites were not anaerobic (Dodds *et al.* 1996), the fluctuating water table at approximately 4.4 m may impede the diffusion of oxygen enough to increase the frequency of microniches in soil for denitrification and denitrifier populations in the saturated zone of the soil profile.

The present results shows that the application of fertilizer at 50 kg N/ha increased the total population of facultative nitrate reducers but did not have any affect on species distribution of selected denitrifying strains in grassland and agricultural soils. The present results are reflecting population profiles of denitrifying bacteria at early spring, but that might change during the year and with higher input of fertilizers.

CONCLUSIONS

This study shows that (i) the proportion of denitrifying bacteria and APNR was affected at different depths by different environmental conditions, especially organic carbon at both sites, (ii) most heterotrophic denitrifying bacterial communities from surface and subsurface depths of these Kansas grassland and cultivated soils are composed predominantly of fluorescent *Pseudomonas* species, (iii) among APNR bacterial communities, *Bacillus* and *Enterobacter* species dominated on the surface, and (iv) *Pseudomonas* species were the predominant bacteria among APNR in water-saturated zone at both the grassland and cultivated sites.

Sotomayor (1996) had shown that these soils had the potential for denitrification in April 1993. Although the soil NO_3^--N content was significantly higher in the cultivated site (maximum value of 10 mg NO_3^--N kg^{-1} at 0.8 m) than the grassland site (soil NO_3^- -N content less than 1 mg NO_3^--N kg^{-1} throughout the profile) (Sotomayor 1996), NO_3^- use does not appear to be an important selector of denitrifying or APNR populations (Tiedje 1988). In fact, these populations are successful when NO_3^- is very low or absent (as in sediment or grassland). Tiedje (1988) postulated that the major influence on the population distribution of denitrifying bacteria is their ability to compete for carbon substrates.

Since the ability to denitrify is present in phylogenetically diverse groups of eubacteria (Woese 1987, Zumft 1992) denitrifiers have therefore diverse substrate requirements and it is unlikely that any particular medium would satisfy the specific requirements of all (Capone 1997). The most common culturable denitrifying bacteria are *Pseudomonas* species, such as *P. fluorescens* (Gamble *et al.* 1977, Tiedje, 1988), *P. aeruginosa*, and related pseudomonads (Madigan *et al.* 1997). Pseudomonads have a diverse range of metabolic capacities (Palleroni 1984) which could affect their survival in oligotrophic environments. Additionally, these organisms have the capacity for long-term survival without O_2 or NO_3- and appear to be capable of providing for their maintenance by carrying out low level fermentation (Jorgensen and Tiedje 1993).

Two population studies done with soils using MPN methodology have both shown that APNR were more numerous than denitrifier populations (Smith and Zimmerman 1981, Tiedje 1982). Additionally, the results of Wagner *et al.* (1996) suggest that the reduction of NO_3^- to NH_4^+ may occur in Kansas grassland soils. Enterobacteriaceae are the most commonly encountered APNR and are favored in environments high in organic carbon such as the gastrointestinal tract (Cole, 1990) and rhizosphere of grasses and cereals (Pedersen *et al.* 1978, Haahtela *et al.* 1981, Belly *et al.* 1983, Kleeberger *et al.* 1983, Subba Rao 1983, Vaisanen *et al.* 1985, Jagnow 1988, Halda *et al.* 1991). The number of *Enterobacter* sp. isolates distinctly decreased in the water saturated zone, where organic carbon is also low (Table 1). In our study, all isolated *Bacillus* strains were APNR. The domination of *Bacillus* sp. in the surface soils is not surprising as it can be quite numerous due to the persistence of the endospore. Besides *Bacillus*, other bacteria with oxidative metabolism were characterized as APNR in these soils (*P. fluorescens*, *P. putida*, *P. corrugata*, *P. marginalis* and few unidentified isolates which likely belong to *Pseudomonas* spp. and *Xanthomonas* spp.). It is becoming increasingly clear that bacteria with oxidative metabolism are also capable of dissimilating of NO_3- to NH_4^+ (Samuelsson 1985, Clays-Josserand *et al.* 1995, this study).

In the present investigation, the distribution of selected denitrifying bacteria and APNR in grassland and agricultural soils were analyzed in spring. Rep-PCR provided fine-structure analysis of denitrifying strains obtained from different depths, different ecosystems and at different times; it is evident that differences in the distribution of denitrifying bacteria occur at the strain level. Changes in the distribution of facultative nitrate-reducing bacteria between two ecosystems remains to be analyzed during the year and with higher input of fertilizers.

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STATUS, PROBLEMS, AND FUTURE PROJECTIONS FOR THE OBION CREEK FLOODPLAIN, HICKMAN COUNTY, KENTUCKY

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ABSTRACT. The Commonwealth of Kentucky provides stewardship of over 3,200 acres of bottomland hardwood and cypress swamp wetlands within the floodplain of Obion Creek in Hickman and Carlisle Counties, Kentucky. Flooding by Obion Creek is perceived as potentially threatening State Highway 307, agricultural production, and public wetland resources. However, conflicting land-use interests and the lack of understanding of the surface hydrology in the project area have prevented a consensus approach to the management of Obion Creek flooding. The objective of this project was to provide base-line data to facilitate discussion among private, local, state, and federal interests regarding the management of Obion Creek and associated wetlands. Construction of a pre-1930 drainage ditch within the Obion Creek floodplain, along with associated agricultural land clearing, led to the diversion of water out of natural stream channels and into the ditch. Reduced water velocity in the natural channels allowed certain reaches to accumulate sediment. The lack of maintenance caused the dug ditch to eventually become filled with woody debris, trash, and sediment. Presently, large reaches of the ditch are non-functional and water that once flowed within the ditch cuts through the bank and flows overland at several locations, creating a braided stream type of system with areas of elevated erosion. Because of geologic and topographic features of the Obion Creek drainage basin, only extensive dredging and channelization will alleviate all natural flooding, but only at the expense of sacrificed wetland habitat. A major problem is State Highway 307, which spans the entire stream valley and functions as a dam. Preliminary recommendations include minor clean-outs of the ditch above and below highway 307, improvement of bridges to increase conveyance of water during flood-flow conditions, and the development of a long-term plan to restore the natural channels and flow-path of Obion Creek to increase natural conveyance of water.

INTRODUCTION

Problem

The Commonwealth of Kentucky provides stewardship of approximately 3,200 acres of bottomland hardwood and cypress swamp wetlands within the floodplain of Obion Creek in Hickman and Carlisle Counties, Kentucky. Flooding by Obion Creek is perceived as potentially threatening State Highway 307 and timber and agricultural production within the project area. Conflicting land-use interests among private, local, and state entities and the lack of knowledge of the surface hydrology in the project area have prevented a consensus approach to management of flooding in the Obion Creek floodplain.

Objective

The broad objective of this project was to provide base-line data to facilitate discussion among the private, local, state, and federal interests with regard to management of Obion Creek and associated wetlands. The specific objectives of this study were to:

1) describe wetland resources within the project area prior to channelization of Obion Creek and construction of State Highway 307

2) determine the ecological status including habitats, vegetation and wetland functions within the project area

3) determine current hydrologic problems resulting from man-made or natural perturbations in Obion Creek that result in increased flooding

4) provide future projections of the project area ecology given continuation of current hydrologic conditions

Background

Vegetative and hydrologic characteristics prior to settlement

Historical maps show that Obion Creek had but one channel within the project area. Further, from comparison of the old maps with current topographic and soils maps it appears that the constructed ditch was dug south of the natural Obion Creek channel east of HWY 307 and north of the natural Cypress Creek channel west of HWY 307. Abandoned stream channels and what appear to be oxbows can be seen on aerial photographs.

Because Obion Creek is a tributary of the Mississippi River, it would have experienced annual backwater flooding along its lower reaches extending into the upper reaches depending upon the river elevation. Retention of headwater floods by expansive bottomland forests would have reduced and desynchronized subsequent downstream flood peaks and helped remove sediment from floodwater prior to reaching the Mississippi River. Retention of backwater floods by the bottomland forest would have reduced the sediment load and nutrient content of water returning to the streams and rivers and improved water quality downstream. The accumulation of deposited sediments over thousands of years created rich bottomland soils responsible for some of the most productive agriculture in the United States..

Prior to settlement, the project area likely included two major wetland habitats. A deepwater swamp, consisting of large tracts of immense cypress trees (*Taxodium distichum*), probably existed within the shallow streams, old creek meanders, oxbows, and low areas with ponded soils (Mhoon soils). Remnants of old second growth cypress trees can be seen in some of these habitats. The permanent standing water in these deepwater swamp areas would have prevented the establishment and survival of most bottomland hardwood trees. However, just upland of the swamps vast bottomland hardwood forests would have existed within the floodplain.

The original extent of the bottomland hardwood forest habitat was probably contiguous with the current extent of non-ponded hydric soils within the project area. Hydric oaks including overcup oak (*Quercus lyrata*), swamp chestnut oak (*Q. michauxii*), willow oak (*Q. phellos*), and shingle oak (*Q. imbricaria*), were likely among the dominant trees in the original bottomland forest. Upland forest trees would have been absent from the forested wetland due to the hydric soils.

History of stream alterations to Obion Creek

As the value of agricultural land increased and the availability of more suitable drier soils decreased, pressure to farm lower and wetter soils increased. Eventually the need for additional farmland and a need to reduce flood damage within the floodplain created a need to reduce the extent of annual headwater and backwater flooding.

The first alteration of Obion Creek began in 1916 and involved clearing a 10 mile portion of the upper end of the creek (Table 1). In the late 1920's, Obion Creek was dredged beginning near Pryorsburg and ended west of the present location of HWY 307. The work was halted before completion because of a lack of funding during the Great Depression. Channelization of Obion Creek stopped short of providing a connection with the natural channel further downstream. The purpose of the channel was to increase the conveyance of floodwater out of the wetlands into the channel and to downstream areas, and reduce the duration and frequency of flooding on the bottomland so that more acreage could be converted to agriculture. Early success of the project is indicated by the conversion of large tracts of bottomland forests on hydric soils into farmland.

Important ecological functions of bottomland hardwood wetlands

Bottomland hardwood wetlands are known to perform several important ecological functions (Mitsch and Gosselink, 1993). Prior to 1940 most bottomland hardwood wetlands were considered to be "waste lands" devoid of any value to society. Later, however, these wetlands were shown to provide many functions valuable to society that greatly enhance its quality of life. Recognition of this lead to the purchase of thousands of acres of bottomland hardwood wetlands by state and federal agencies for conservation and preservation for future generations. Important wetland functions include habitat for wildlife including deer, turkey and waterfowl, important breeding areas for fish, production of invertebrates important for fish and wildlife food, removal of sediments and pollutants from surface waters, and recreation and educational use (Mitsch and Gosselink, 1993).

Functions that bottomland hardwood wetlands perform can be classified into four general groups: 1) physical, 2) chemical, 3) biological, and 4) recreation/education (Adamus *et al.*, 1991). Important physical functions include sediment retention, floodflow alteration, and on-site erosion control. Bottomland hardwood wetlands have the capacity to retain suspended sediments because the velocity of floodwaters that enter the wetland are greatly reduced, which causes suspended sediments including sand, silt and clay to be deposited in the wetland. The ability of a bottomland hardwood wetland to provide flood control to downstream areas is related to the size of the Manning's number and the ability of the flood basin to store floodwater. The large Manning's number (an estimate of the friction a surface offers to the movement of water) associated with these wetlands is primarily responsible for the reduction in the velocity of water as it spreads over the wetland. Features of the wetland that contribute to the large Manning's number include: large tree trunks, fallen trees, branches and twigs, litter, and small variations in topography.

Table 1. Chronological history of alteration of creeks in the Obion Creek project area locality.

DATE	EVENT
1916	10 mile stretch of Obion Creek in the upper end of the project area cleared.
about 1924	First attempts at channelization of three creeks (Obion, Mayfield, Bayou du Chein) were unsuccessful.
late 1920's	Obion Creek and Bayou du Chein channelization by using a floating dredge began. Dredging stopped during the Depression.
1927	First reaches of Mayfield Creek channelized.
1937	Mayfield Creek channelization completed.
mid 1940's	KY HWY 307 built.
about 1950	Beavers introduced to Murphy Pond by Kentucky Wildlife Dept. The dams caused flooding along Obion Creek which led to the "Larkins Land Use Debate" a few years later.
1957	Obion Creek Watershed Conservancy District formed.
1958	Authorization for studies and planning for the West Kentucky Tributaries Project - Obion Creek began.
1965	Congress authorized the Obion Creek flood control improvement project in the Flood Control Act of 1965.
late 1960's	Soil Conservation Service channelized Little Creek.
1975	Murray State University obtained Murphy Pond. Murphy Pond's nickname was "Little Okefenokee."
1976	Memphis District Corps of Engineers completed an environmental impact statement after 11 years of project design and study.
1978	Final Environmental Impact Statement Supplement filed for West Kentucky Tributaries Project to meet EPA concerns.
1979	Obion Creek Watershed Conservancy District got a permit to clean out Obion Creek beginning at the Purchase Parkway to KY HWY 307.
1980	Obion Creek cleaned out from Pryorsburg (Purchase Parkway area) to a very short distance west of KY HWY 307.
1990	Obion Creek cleaned out from KY HWY 307 for a good distance past the powerline that parallels KY HWY 307 to the east. Blockages consisted of several feet of trash, sticks, and logs.

Bottomland hardwood wetlands also have the capacity to retain floodwater, and thereby reduce the height and desynchronize downstream flood peaks. This function protects downstream areas from flooding at the expense of on-site flooding in the wetland. It is estimated that the wholesale destruction of bottomland hardwood wetlands associated with the Mississippi River and its tributaries has contributed to the need for higher levees.

Bottomland hardwood wetlands also function to remove dissolved nitrogen and phosphorus from surface waters (Mitsch and Gosselink, 1993). These two nutrients are responsible for the eutrophication of surface waters and greatly contribute to the degradation of water quality. Bottomland hardwood wetlands remove nutrients through plant, algal, and bacterial uptake, and also by the conversion of nitrogen to gaseous forms which leave the wetland. These wetlands help improve the water quality of downstream creeks and rivers by reducing eutrophication.

Bottomland hardwood wetlands are extremely important for providing recreation. Hunting, fishing, hiking, camping, canoeing, and nature watching are all potentially available in these wetlands. They can also provide unique educational opportunities since identification of animal tracks, plants, and observation of how wetlands function is not easily taught in classrooms.

Effect of stream channelization on wetland ecology

Humans have a long history of impacting rivers. As early as 3200 B. C. drainage and water supply modifications were applied to the Yellow River in China (Drower, 1954). Also many centuries ago, embankments were built on rivers in England prior to the 11th century for control of flooding and to provide additional agricultural land (Cole, 1976). Little (1973) estimated that over 53 million hectares of wetlands have been drained as a result of river channelization in the United States. Related to river channelization are estimates that about 7% of the continental United States surface area is within a 100 year floodplain (Goddard,1976).

Recent research has shown that channelization can greatly alter river and wetland ecology (Brookes, 1988). The physical effects of channelization of streams can be explained by the change in any one of several stream variables including: channel width, depth and slope, boundary roughness, and the size and concentration of sediment load (Brookes, 1988). Most streams that are candidates for channelization have stream variable values that result in too much water remaining on the surrounding land, i.e. have flooding problems. Alteration of the above stream variables leads to a system (channelized river) that is out of equilibrium with its watershed. After channelization the river system will attempt to reach equilibrium unless considerable energy is invested in channel maintenance.

Rivers and streams in lower portions of watersheds with fine soils naturally meander or "walk" across the landscape, mostly because of a reduction in channel gradient. Also, it is natural for most rivers and streams to overflow their banks at least annually. Expansive plant communities have evolved and depend on periodic flooding for establishment of seedling trees. Channelization reduces flooding into adjacent wetlands which leads to increased sediment load in the river and formation of bars and other depositional features that require frequent and costly dredging. Streams that are naturally stable and have meandering paths will always be unstable after channelization and require extensive channel maintenance (Brookes, 1988).

Because of the natural connectivity that exists in river systems, impacts to the river and its floodplain are not restricted to the impact site (Mrowka 1974). Impacts are potentially transmitted downstream over a much wider area than that of the initial impact area. Therefore, land managers and politicians must take a broader view of the effects of stream alterations to include potential impacts to downstream areas. Unfortunately, this perspective has been lacking in most stream improvement activities in the past.

MATERIALS AND METHODS

Field techniques used for this study involved establishment of a transect in each of the two tracts of the Kentucky Department of Fish and Wildlife Resources (KDFWR) Obion Creek Wildlife Management Area. Azimuths for the Mathis and Wallace Tract transects were determined by examination of topographic maps to include an adequate representation of each tract (Fig. 1). The transect in the Kentucky Nature Preserves (KNP) tract follows the channelized Obion Creek, going east from Hwy 307, and returns along the north side of the channel (Fig. 1).

Study plots were established at 244 m intervals along each transect for use in vegetation sampling. For convenience, distances were paced off, counting 0.61 m per step. All transects were flagged. The plot center was placed 50 m off the transect at a random azimuth so the plot would not get trampled with future work on the transect. The 50 m was measured with a standard 50 m measuring tape. The plot centers were marked with conduit and a survey flag. Five plots were to be placed in the Mathis Tract, but only three were installed because two would have been located in agriculture fields. The Wallace Tract had nine plots installed and the KNP Tract had sixteen plots installed, eight along each side of the channelized Obion Creek.

Vegetation sampling at each plot was performed to provide a plant inventory of the bottomland hardwood forest and also to determine how wetland vegetation is distributed throughout the wetland. Plant species within a 20 m diameter circle around the plot center were recorded. Height of water marks and/or sediment deposits on trees were measured or visually estimated to estimate maximum potential depth of flooding at each plot. Plant species identification was done by use of standard field guides and taxonomic keys. Indicator status, a determination of habitat preference, was obtained from the National List of Plant Species that Occur in Wetlands: Northeast (Region 1) (Reed, 1988).

Three groundwater recording piezometers from Remote Data Systems, Inc. were installed in the Wallace tract to measure height of groundwater and depth of surface water in the wetland. An 2.4 m piezometer (WL80) was installed on the peninsula west of the Cypress Creek bridge on HWY 307 to a depth of 1.5 m. A 1.2 m piezometer (WL40) was installed at plot 2 to a depth of 0.9 m. The same type of piezometer was installed at plot 4, to a depth of 0.6 m. Sand was placed around each well point to prevent clay from clogging the water level sensing apparatus. Native clay was packed in around the top of each piezometer. Each well was programmed to record water levels every three hours. Data was downloaded from each well at convenient intervals.

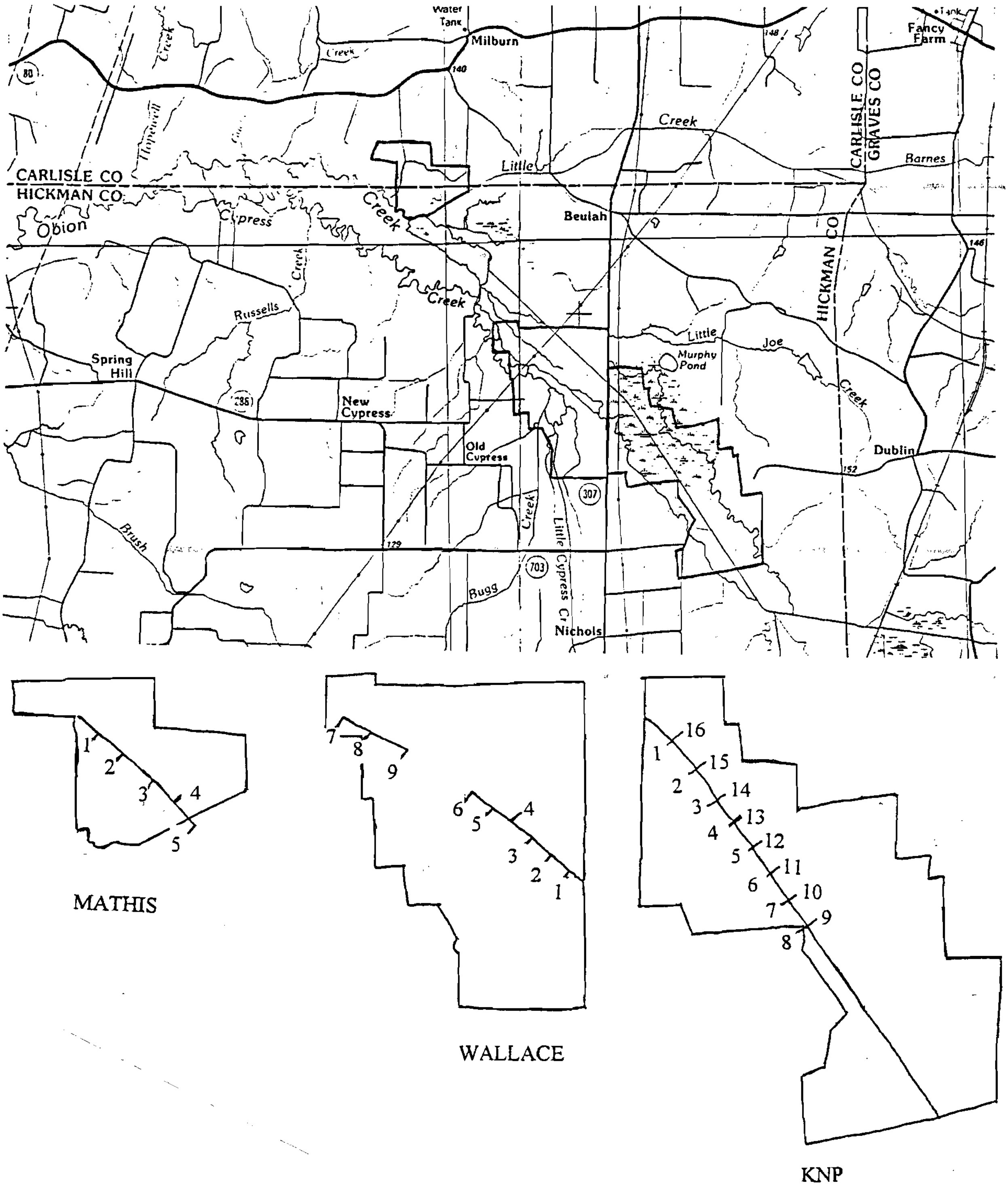

Figure 1. Location of transects and study sites in the Kentucky Department of Fish and Wildlife Resources (KDFWR) Wallace and Mathis tracts of the Obion Creek Wildlife Management Area and the neighboring Kentucky Nature Preserves (KNP) tract.

Library techniques used for the Obion Creek study included a preliminary literature search of the history of the Obion Creek floodplain. Old maps, documents, books, and photographs as well as current aerial photography were obtained from the KDFWR, regional National Resource Conservation Service (NRCS) offices, and the Waterfield and Pogue Libraries at Murray State University. Verbal historical descriptions from individuals in the mentioned agencies were also received. The above information was used to create a timeline of Obion Creek floodplain events (Table 1). Soil maps showing the location of hydric soils in Hickman County were obtained from the NRCS office in Clinton.

RESULTS AND DISCUSSION

Geology and Soils of the Project Area

The Obion Creek floodplain is characterized by two important features that help to explain the extensive flooding within the project area. First, the width of the creek valley measured at the 400 ft. contour line is greatly constricted downstream of the project area near Hopewell Creek (Fig. 2). Second, the stream gradient becomes much flatter within the project area compared to sites upstream and downstream. These two characteristics create geomorphological conditions that greatly reduce the conveyance of water through the project area. That the project area experiences extensive flooding is partially a result of natural geomorphological conditions that lead to the development of hydric soils and extensive wetland habitats. The extent of hydric soils in the project area is greatest where the stream gradient is the lowest (Fig. 3).

Soils within the project area are predominantly hydric (Table 2). The presence of hydric soils within the project area is a strong indication that at one time bottomland hardwood forests were prevalent in the area. The fact that some of the farmland surrounding the project area is on hydric soils suggests that the original extent of the bottomland hardwood forest wetland extended much further than its current distribution.

Effect of Previous Channelization of Obion Creek on Vegetation and Hydrology

Channelization was likely effective for some time and conveyed water off the wetland. As a result, large areas were made available for the expansion of agriculture and the invasion of more xeric plant species into what used to be bottomland forest. Conversion of wetlands to farmlands was probably preceded by logging of harvestable timber. The new agricultural lands were probably farmed until channel degradation lead to increased flooding. There is evidence that individual land owners constructed small ditches to increase conveyance of water from lands near Obion Creek. When farms were abandoned because of increased flooding, bottomland wetland vegetation began to return to the area.

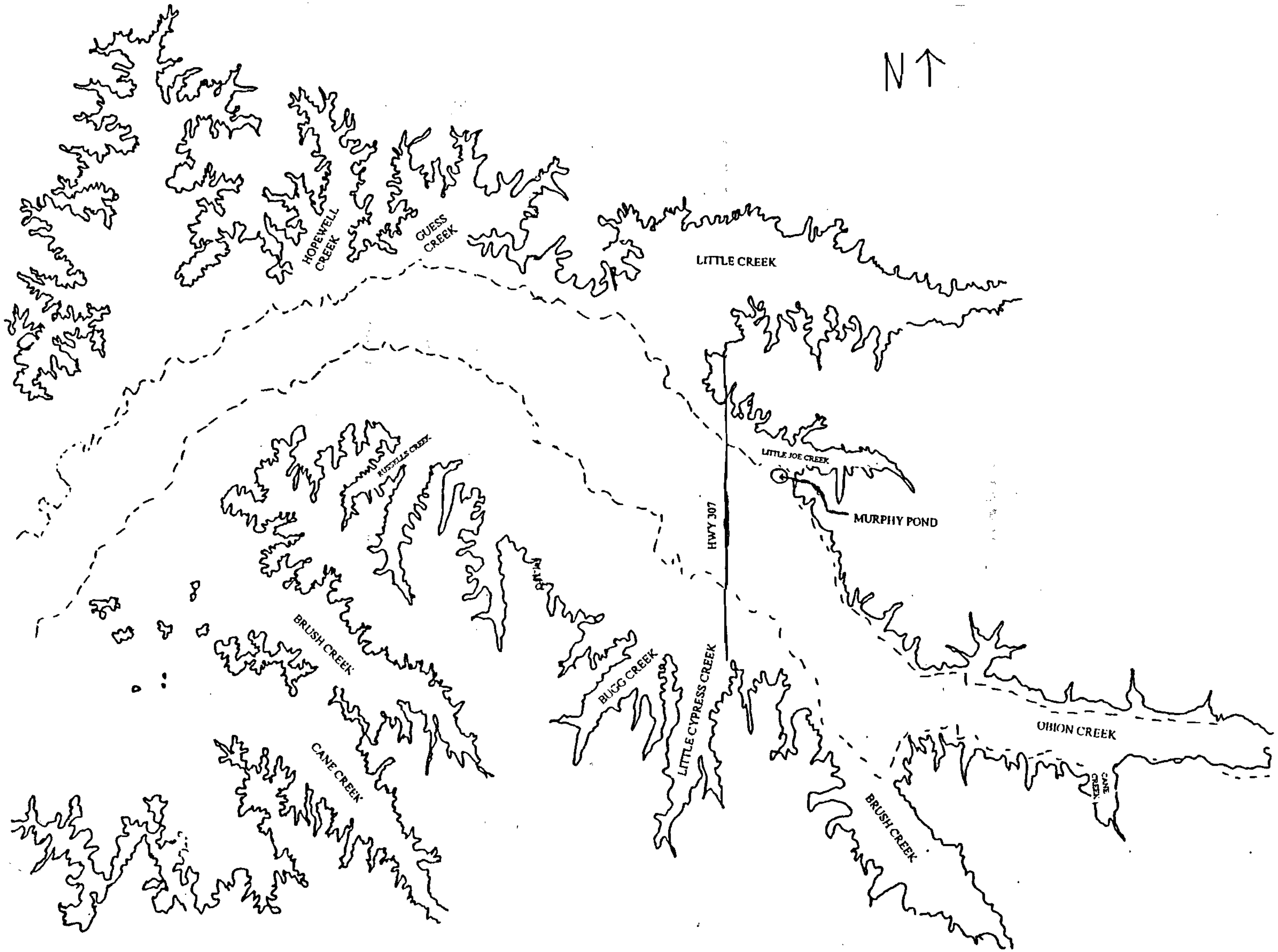

Figure 2. Width of the Obion Creek valley (dashed line) in the 400 ft contour interval (solid line). The stream channel narrows past Hopewell Creek, downstream of the project area.

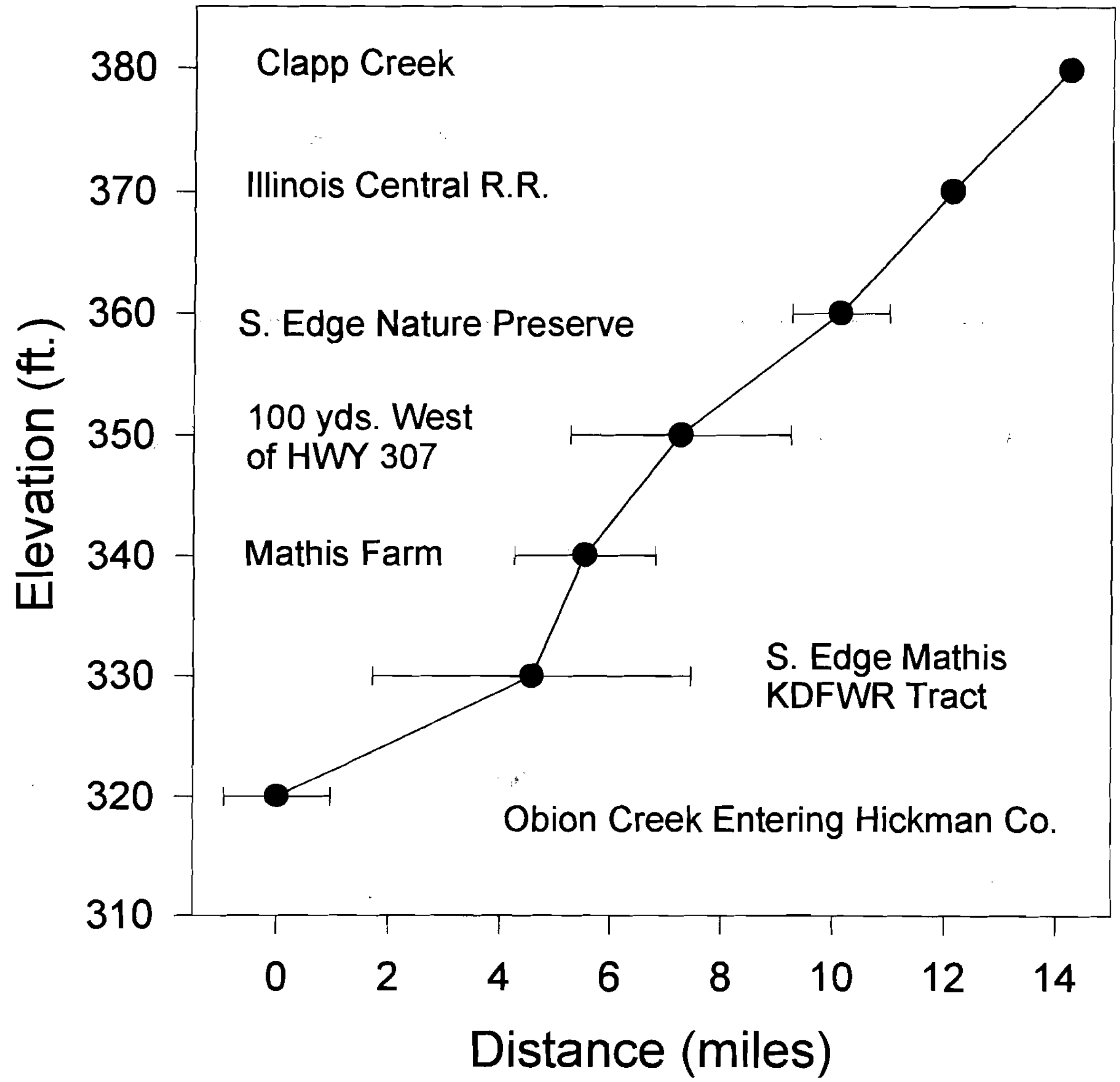

Figure 3. Elevation of Obion Creek beginning where it enters Hickman County, Kentucky and ending near Clapp Creek upstream from the project area. The horizontal bars represent the extent of hydric soils perpendicular to Obion Creek.

Of noteworthy interest is the area northeast of the KY HWY 307/Obion Creek bridge that is owned by the KNP and Murray State University. The area is known as Murphy Pond and has numerous groundwater seeps and potentially springs. Alteration of the groundwater table by channel construction in this area could indirectly impact Murphy Pond. Although there is concern over sedimentation from Obion Creek entering Murphy Pond from increased flooding there are not data available to document this problem. Historically, it is likely that water entered Murphy Pond from Obion Creek during floods, and that at one time Obion Creek flowed through what is now Murphy Pond. Aquatic and riverine systems all experience sediment deposition during their natural succession which normally requires hundreds of years. Murphy Pond should be studied from a groundwater hydrology perspective prior to any stream channelization in the area. When the channelization was effective in conveying water off the bottomland, Murphy Pond may have diminished in size temporarily, perhaps inviting logging.

Table 2. Soil type with abbreviation in parenthesis and potential maximum depth of flooding at each site along transects established in the two tracts of the KDFWR Obion Creek Wildlife Management Area and the one transect of the Kentucky Nature Preserves tract.

TRACT	SITE	SOIL TYPE	APPROXIMATE DEPTH OF FLOODING (in)
MATHIS	1	Convent-Adler silt loams (Cn)	Agriculture field
	2	Mhoon silt loam (Mo)	18
	3	Convent-Mhoon silt loams (Ct)	Agriculture field
	4	Mhoon silt loam (Mo)	12
	5	Convent-Mhoon silt loams (Ct)	24
WALLACE	1	Convent-Mhoon silt loams (Ct)	16
	2	Convent-Adler silt loams (Cn)	20
	3	Convent-Mhoon silt loams (Ct)	8
	4	Convent-Mhoon silt loams (Ct)	12
	5	Convent-Mhoon silt loams (Ct)	24
	6	Mhoon silt loam (Mo)	18
	7	Convent-Mhoon silt loams (Ct)	24
	8	Convent-Mhoon silt loams (Ct)	18
	9	Convent-Mhoon silt loams (Ct)	18
KENTUCKY NATURE PRESERVES	1	Convent-Adler silt loams (Cn)	0
	2	Convent-Adler silt loams (Cn)	0
	3	Convent-Adler silt loams (Cn)	0
	4	Convent-Adler silt loams (Cn)	0
	5	Convent-Adler silt loams (Cn)	8
	6	Convent-Adler silt loams (Cn)	18
	7	Convent-Adler silt loams (Cn)	12
	8	Convent-Adler silt loams (Cn)	12
	9	Convent-Adler silt loams (Cn)	12
	10	Convent-Adler silt loams (Cn)	12
	11	Convent-Adler silt loams (Cn)	16
	12	Convent-Adler silt loams (Cn)	15
	13	Convent-Adler silt loams (Cn)	15
	14	Convent-Adler silt loams (Cn)	18
	15	Convent-Adler silt loams (Cn)	20
	16	Convent-Adler silt loams (Cn)	20

Vegetative and Hydrologic Status of the Project Area

When each of the plant species observed in the project area was assigned a regional wetland indicator status, a general wetness factor was determined for each site (Table 3). Determination of jurisdictional wetland boundaries requires application of a complete delineation method. Wetness factor values less than 1.0 indicate that more of the species are upland than wetland, and suggest that the area may be drier than areas with a higher wetness value. Larger wetness factor values indicate that more of the species are wetland than upland and that the area is likely a wetland. Of the 30 sites studied, 2 were agricultural, and only 1 had a wetness value less than 1.0. Twenty-seven sites had values ≥ 1.0 (Table 3). These data suggest that most of the project area is probably wetland.

Table 3. Number of plant species of each indicator status, the resulting wetness factor, and probability of of occurrence of each indicator status in wetlands for sites established in the two tracts of the KDFWR Obion Creek Wildlife Management Area and the Kentucky Nature Preserves tract.

		NUMBER OF SPECIES					WETNESS FACTOR
TRACT	SITE	OBL	FACW	FAC	FACU	UPL & -X-	(OBL + FACW) ÷ (FACU + UPL)
MATHIS	1	-	-	-	-	-	Agriculture field
	2	1	3	5	2	1	1.33
	3	-	-	-	-	-	Agriculture field
	4	1	7	6	2	1	2.67
	5	1	6	2	2	1	2.33
WALLACE	1	0	4	5	6	0	0.67
	2	1	4	6	3	1	1.25
	3	2	3	4	5	0	1.00
	4	7	4	3	3	1	2.75
	5	3	6	7	0	0	∞
	6	5	3	5	1	1	4.00
	7	2	4	3	2	4	1.00
	8	4	5	4	1	2	3.00
	9	2	5	6	2	0	3.50
KENTUCKY NATURE PRESERVES	1	0	6	4	1	1	3.00
	2	0	4	5	0	1	4.00
	3	0	8	7	1	0	8.00
	4	1	5	6	1	2	2.00
	5	0	5	5	4	1	1.00
	6	0	6	6	2	0	3.00
	7	0	6	6	4	0	1.50
	8	0	5	0	1	1	2.50
	9	1	2	4	1	1	1.50
	10	1	4	4	3	0	1.67
	11	1	3	8	1	0	4.00
	12	3	5	4	0	2	4.00
	13	0	4	7	3	1	1.00
	14	0	6	8	4	2	1.00
	15	2	4	6	2	2	1.50
	16	1	8	10	2	1	3.00
PROBABILITY (%) OF INDICATOR STATUS OCCURRING IN WETLANDS		>99	67-99	34-66	1-33	<1	

The average wetness factor for sites 1-8 on the south side of the channel in the KNP Tract was 30% less than for sites 9-16 on the north side of the channel. These data agree with those from the hydric soils maps that show the distribution of the wettest hydric soil (Mhoon) to be restricted to the area north of the channel.

The vegetation in the project area changes from deepwater cypress swamp to bottomland hardwood depending on proximity to one of the many channels in the project area. Many large cypress trees with buttressed trunks occur within the channels of the streams. Along the natural levees of the creeks are more xeric species including sweetgum (*Liquidambar styraciflua*), red maple (*Acer rubrum*), and box elder (*A. negundo*).

Common tree species found in the bottomland forest are box elder, red maple, green ash (*Fraxinus pennsylvanica* var *subintegerrima*), sweetgum, and swamp chestnut oak. Frequent but less common species include river birch (*Betula nigra*), sycamore (*Platanus occidentalis*), overcup oak, willow oak, and American elm (*Ulmus americana*). The understory species are predominantly ironwood (*Carpinus caroliniana*), possum-haw (*Ilex decidua*), winged elm (*U. alata*), and slippery elm (*U. rubra*).

The herbaceous understory species are numerous. Commonly found are false nettle (*Boehmeria cylindrica*), wild oats (*Chasmanthium latifolium*), jewelweed (*Impatiens capensis*), lance-leaved loosestrife (*Lysimachia lanceolata*), smartweed (*Polygonum* sp.), poison ivy (*Rhus radicans*), blackberry (*Rubus allegheniensis*), arrowhead (*Sagittaria latifolia*), and lizard's tail (*Saururus cernuus*).

The tree mortality area in site 4 of the KDFWR Wallace Tract is topographically lower than the area near the dug channel and may represent the location of an old meander of Obion Creek. A large cypress tree stump with regrowth was observed in the area indicating that cypress trees were once in the immediate vicinity. The observation of many small cypress tree saplings suggest the area is suitable for the development of a deepwater cypress swamp, similar to areas within the existing Obion Creek stream channels.

Problems Associated with the Project Area

Altered hydrology

It appears that the channelized portion of Obion Creek within the KDFWR Wallace and KNP tracts is located on land of slightly higher elevation compared to land northeast and southwest of the channel. In fact, the channel appears to have been constructed between two streams (Cypress and Obion Creeks) in an attempt to facilitate drainage of both systems. This conclusion is strengthened by field observations of surface hydrology which show that floodwater that overflows the channel within the project area does not return to the dug channel but continues overland until it enters topographically lower natural drainage systems (Fig. 4). Further, the soils in which the channel was constructed are Convent-Adler hydric soils, which have the greatest depth to the water table (drier soils). Soils to the northeast and southwest of the ditch in the project area include the wetter hydric soils Mhoon, and Convent-Mhoon. Apparently, the original ditch was located in the worst possible location for effective land drainage. The rationale for such an engineering blunder may have been a gamble to achieve drainage of two systems by construction of a single deep ditch. This strategy may have worked for some time after ditch construction, but original surface water likely returned to the two stream system after the ditch became filled with sediment.

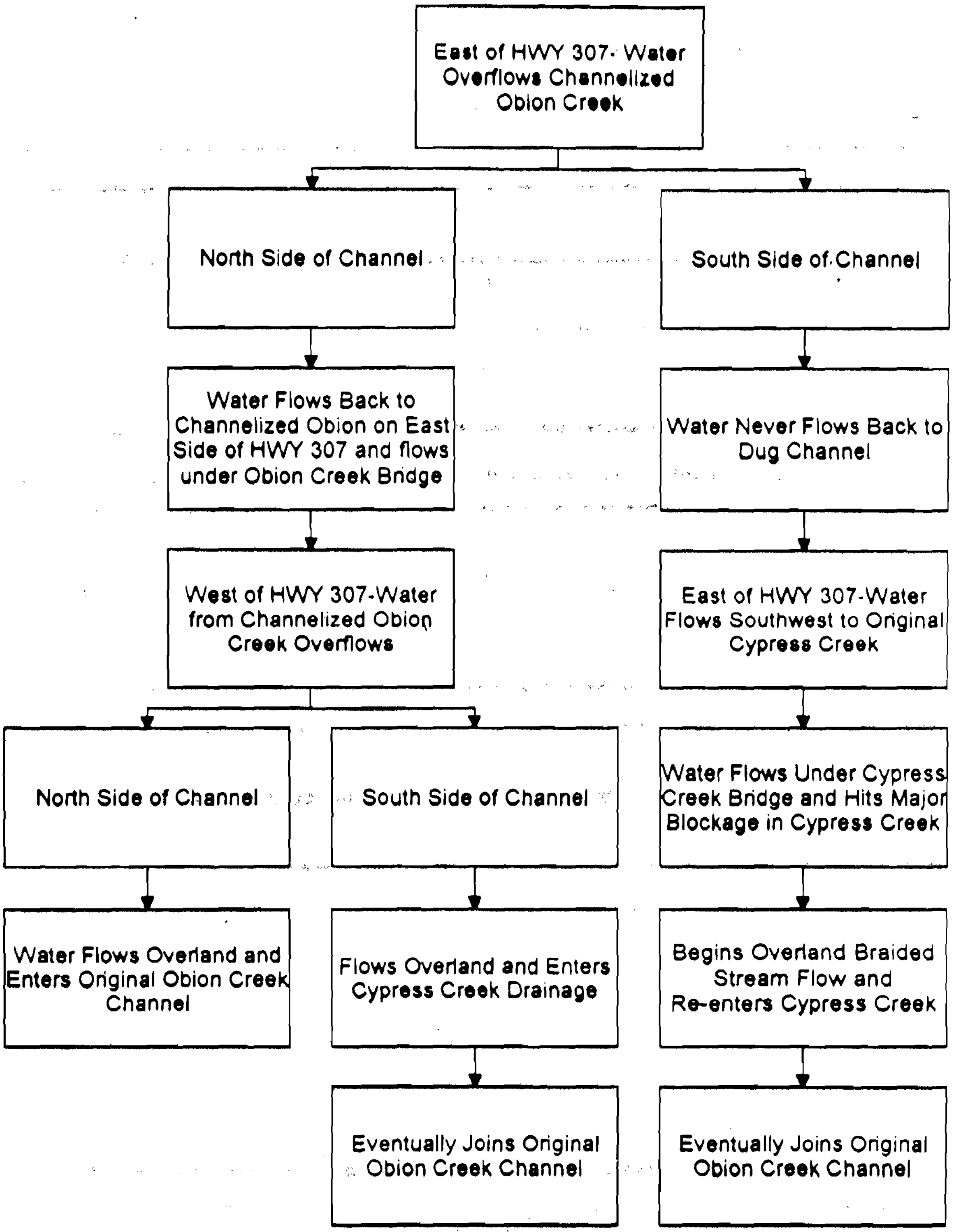

Figure 4. Present surface hydrology during flooding of the channelized Obion Creek.

The most permanent and hydrologically destructive event in the project area was the construction of HWY 307 that created a dam across the entire stream valley and prevented the establishment of original surface hydrology when the dug ditch became non-functional. As a result unstable surface drainage patterns currently exist in the KDFWR Wallace and KNP tracts. We observed that during flood events the ditch overflows its banks onto adjacent land and does not immediately return to the ditch (Fig. 4).

Tree mortality

There are at least three locations in the project area where tree mortality is evident. All three sites are located within the KDFWR Wallace Tract. The first is located at site 4, the second is in the NW corner of the Wallace Tract at site 7, and the third location is on the west side of HWY 307 north of the ditch.

The dead timber in site 4 is located in a low area of Convent-Mhoon hydric soils where water that spills over the south side of the ditch flows southwest towards Cypress Creek. Water enters this mortality area during both base and flood flows, and is therefore continually wet (Fig. 5). The tree mortality in this area is not a result of beaver activity, but is a result of disturbed surface hydrology. The tree mortality area is bounded by a functional reach of Cypress Creek on the south and west. Dead trees observed in the area include red maple, river birch, persimmon (*Diospyros virginiana*), red ash (*Fraxinus pennsylvanica*), and overcup oak (Table 4). Living trees that showed signs of stress included red maple, silver maple (*Acer saccharinum*), northern catalpa (*Catalpa speciosa*), green ash, red ash, sweet gum, and slippery elm. Trees in the area that were healthy and showed no signs of stress included box elder, red maple, ironwood, buttonbush, green ash, possum-haw, swamp chestnut oak, willow oak, and bald cypress.

Water levels in this area recorded from Nov. 23, 1995 through May 9, 1996 show that the mortality area was continually flooded except for the first month when the water table was no more than 4 in. below ground (Fig. 5). The hydrograph data also show several flood events which occurred in the Cypress Creek location throughout the study period. These data demonstrate typical bottomland hardwood forest wetland hydrology in Cypress Creek and the non-stressed bottomland habitat. The lower water levels in the non-stressed habitat are due to a slightly higher elevation in this area. The data suggest that floodwater from Cypress Creek enters the non-stressed and tree mortality sites.

Timber mortality in site 7 appears to have occured some time ago. Surface ponding of water was not observed in the area at any time during the project. It is likely that at one time beaver activity created ponded conditions which lead to the death of the trees. Trees in this area do not appear to be under stress at this time.

Dead timber along HWY 307 is located in a low area of Convent-Mhoon hydric soil that receives water from Little Joe Creek and from a small privately dug ditch located at the southern edge of the Burgess farm and the northern edge of KNP land. The water flows beneath the first bridge encountered traveling south on HWY 307 in the project area. Because of natural topography, the water entering this area does not flow south to the dug ditch. Instead, it flows northwest until it reaches the original Obion Creek channel.

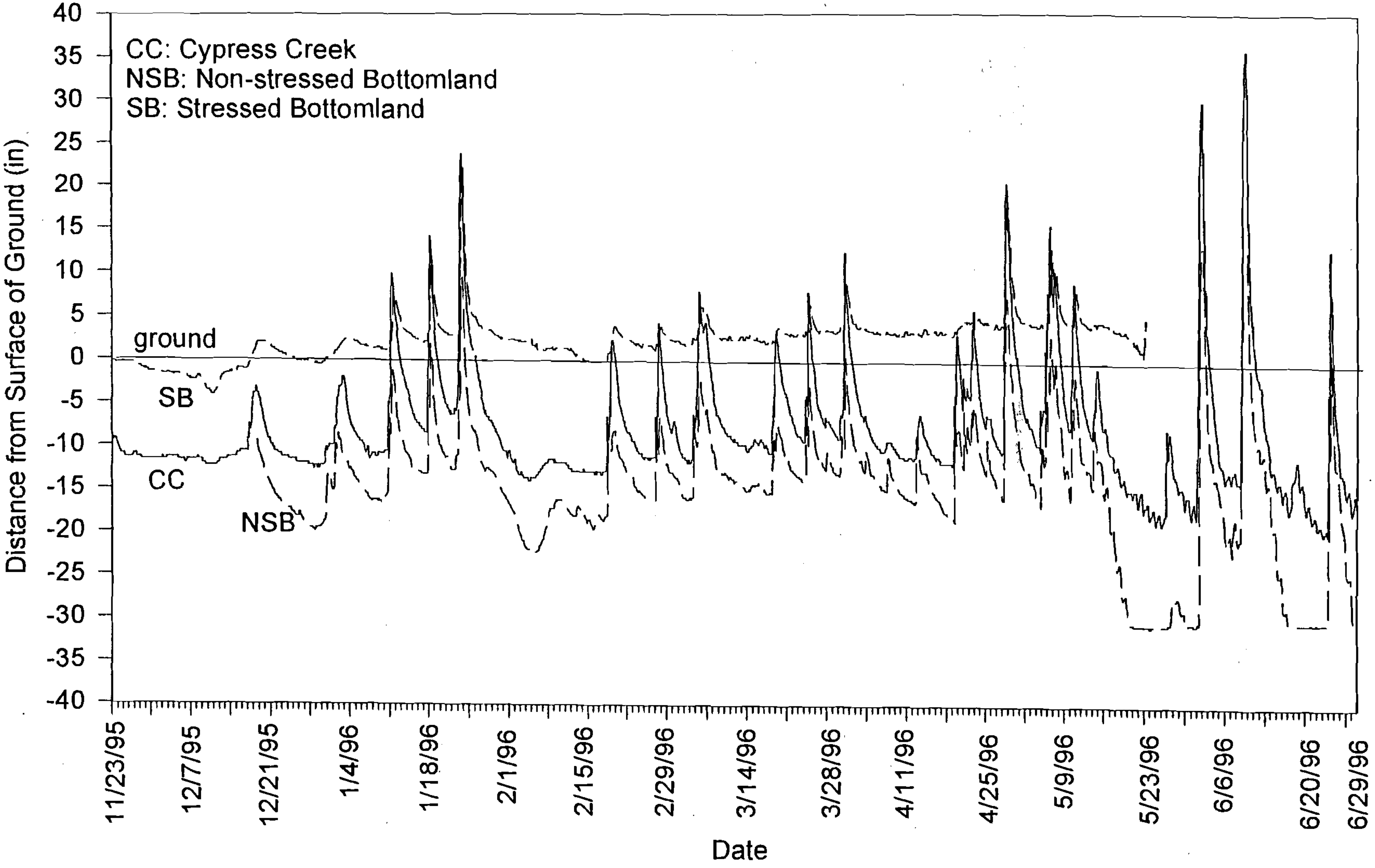

Figure 5. Height of groundwater and/or surface water at three sites in the Wallace Tract of the KDFWR Obion Creek Wildlife Management Area measured from 11/23/95 to 6/29/96.

Table 4. Health status of trees and shrubs observed in and around the tree mortality area located in site 4 of the Wallace Tract of the KDFWR Obion Creek Wildlife Management Area.

SPECIES	COMMON NAME	HEALTH STATUS		
		HEALTHY	STRESSED	DEAD
Acer negundo L.	Box Elder	X		
Acer rubrum L.	Red Maple	X	X	X
Acer saccharinum L.	Silver Maple		X	
Betula nigra L.	River Birch			X
Carpinus caroliniana Walter	Ironwood	X		
Catalpa speciosa Warder	Northern Catalpa		X	
Cephalanthus occidentalis L.	Buttonbush	X		
Diospyros virginiana L.	Persimmon			X
Fraxinus pennsylvanica Marshall var. *subintegerrima* (Vahl) Fern.	Green Ash	X	X	
Fraxinus pennsylvanica Marshall	Red Ash		X	X
Ilex decidua Walter	Possum-haw	X		
Liquidambar styraciflua L.	Sweet Gum		X	
Quercus lyrata Walter	Overcup Oak			X
Quercus michauxii Nutt.	Swamp Chestnut Oak	X		
Quercus phellos L.	Willow Oak	X		
Taxodium distichum (L.) Rich.	Bald Cypress	X		
Ulmus rubra Muhl.	Slippery Elm		X	

The presence of tree mortality in the project area is apparently restricted to the above areas. It does not appear that the bottomland hardwood trees in other areas within the project area are threatened or stressed. It appears that current hydrologic conditions are not a threat to bottomland hardwood trees outside of the three above mentioned areas.

Flooding onto HWY 307

We did not observe water on HWY 307 during the project. However, we have observed sediment on the road indicating that floodwaters were on the road. We have also received personal communication from several people indicating that HWY 307 is occasionally flooded just north of the Obion Creek bridge. The flooding of HWY 307 is presently restricted to a single location and is a direct result of the hydrologic problems caused by the presence of HWY 307 in the floodplain and inadequate conveyance of water through the Obion Creek bridge.

Future Projections for the Project Area if Current Conditions Continue

Three major trends are predicted to occur if current conditions continue in the project area. First, two out of the three areas that are now experiencing hardwood mortality will develop into cypress swamp habitat or freshwater marsh habitat with loss of standing hardwood timber. Second, portions of previously farmed hydric soils will revert to bottomland hardwood wetland habitat. Third, floodwater will more frequently flow onto portions of HWY 307.

The first trend is similar to the natural events that occur within bottomland hardwood wetlands. Low gradient creeks and rivers naturally exhibit changing flow paths that create permanently ponded sites that were once annually flooded hardwood sites, and drier annually flooded sites that were once permanently flooded sites. We observed no evidence that the entire project area is converting into a cypress swamp. In fact, we observed several areas in which regeneration of hydric oaks is occurring. Although the overall health of the bottomland hardwood wetland is not threatened, there are small locations within the project area that are experiencing hardwood tree mortality. We believe that the prolonged ponding presently resulting in tree mortality is caused by site-specific effects that are not present project-wide.

The second trend represents a potential economic loss. Certain small sections of previously and presently farmed areas in Convent-Mhoon silt loams and the lower parts of Convent-Adler silt loams that have surface drainage connections to Obion Creek are the most likely areas to revert to bottomland hardwood wetlands. However, landowners could obtain an economic benefit of this "natural" reversion to bottomland hardwood habitat if they were to establish mitigation banks where "shares" of the actively managed bottomland hardwood wetland habitat could be sold to those needing mitigation land. It should be recognized that much of the area was originally wetland habitat that became available for agriculture only after the construction of drainage ditches.

The third trend of increased flooding on portions of HWY 307 will continue and is a result of poor civil engineering planning. Highway 307 spans the entire Obion Creek valley and essentially functions as a dam. There may not be sufficient area for the conveyance of water beneath the bridges on HWY 307 in the project area during flood events. Further, the failure to maintain even minimal clean-out on both sides of the bridges and the alleged presence of pilings under the bridges greatly contributes to the current flooding of HWY 307. Unless the responsible local and state agencies begin routine bridge maintenance, flooding onto HWY 307 will become more severe.

SUMMARY AND RECOMMENDATIONS

Geologic and topographic features of the Obion Creek drainage basin result in unavoidable flooding of hydric soils and wetlands in the project area. Current hydrologic problems in and around the project area have resulted in excess unnatural flooding. However, complete removal of flooding will degrade extremely valuable habitat.

The surface hydrology within the project areas has been greatly modified away from natural conditions by the construction of HWY 307 and the drainage ditch. Ditch construction ultimately resulted in the loss of effective drainage of the area when it became filled. While the ditch was functional, water velocity in Obion Creek north of the ditch and in Cypress Creek south of the ditch was greatly decreased. As a result, sediment and debris accumulated in the streambeds. When the ditch became filled with sediment and water began to flow overland, the original Obion and Cypress Creek streams could not convey the water because portions were non-functional. As a result water currently flows overland in several places creating a braided stream system resulting in excessive erosion and flooding. The presence of HWY 307 creates a dam effect across the entire stream valley, forcing water to move across the land in a destructive manner.

The presence of dead timber does not indicate that the project area is converting away from a bottomland hardwood forest into a cypress swamp. The tree mortality areas are caused by site-specific factors not active in the entire project area. The project area is not in danger of losing more than a minimal amount of its hardwood timber.

Flooding of HWY 307 will continue unless some type of channel work is completed. Agricultural lands near the project area will be lost to increased flooding and will revert back to bottomland hardwood wetlands unless flooding is reduced. A major channelization project, however, will result in the loss of current bottomland hardwood wetlands by dredging, filling, lowering of water tables, and the stimulated conversion of wetlands to agricultural lands. Strategic minimal channel clearing may provide a modicum of flood relief without destroying valuable habitat.

The management plan that is most likely to be supported by the various resource/conservation agencies, and therefore most likely to be funded, is one that emphasizes the restoration of Obion and Cypress Creeks to their natural flow path rather than channelization to provide flood control. An approach should be taken similar to that for the Kissimmee River in central Florida. The Kissimmee River was originally straightened and channelized to provide flood control. However, the project ultimately resulted in severe degradation of downstream water quality. During the 1980's a plan was approved and funded that began restoration of the original meandering flow-path of the river without jeopardizing flood control. The result was that the resource and conservation agencies supported the plan. It is the opinion of the authors, that although re-channelization of Obion Creek would certainly reduce flooding, it would also result in unacceptable losses to wetland and wildlife habitat. Mitigation of wetland losses would be expensive and could greatly exceed any benefits associated with agricultural gains. Further, periodic expensive maintenance including snagging, clearing, and dredging would be required to maintain a functional channel.

The following recommendations represent a beginning point for discussion by affected parties:

1) Abandon the original extensive Obion Creek channelization plans.
2) Consider minimal strategically placed channel clearing.
3) Develop plans that partially alleviate flooding by stream restoration.
4) Restore the original channels of Obion and Cypress Creek within the project area.
5) Re-engineer Hwy 307 to facilitate conveyance of water where the natural channels of Obion and Cypress Creeks cross.
6) Develop maintenance plans that will remove debris from around bridges in the project area.

7) Emphasize the importance of the area as one of the last remaining bottomland hardwood wetlands of the Mississippi Embayment in Kentucky.
8) Make the project a demonstration project designed to provide a modicum of flood control along with habitat development.
9) Explore the possibility of developing a mitigation bank program.

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USING MACROINVERTEBRATE INDICATORS TO MONITOR THE PERFORMANCE OF AGRICULTURAL BEST-MANAGEMENT PRACTICES

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ABSTRACT. Water chemistry samples and habitat and biotic surveys have proven to be useful tools in assessing the ecological integrity of freshwater aquatic systems. Faculty and students from Western Kentucky University (WKU) have been sampling Buck Creek, a stream bordering a large swine operation, to determine if runoff from the fertilized fields is affecting the ecological integrity of the stream. We performed a qualitative habitat assessment and collected macroinvertebrate samples in Buck Creek and an un-impacted reference stream, May's Branch, during June and October of 1995 and 1996. Traveling kick net samples were taken along at least two transects in riffle and in pool habitats in Buck Creek upstream and downstream of the fertilized fields at the swine operation. Similar samples were collected in the reference stream, May's Branch. All samples were preserved using 75% ETOH. Samples were analyzed using a stereomicroscope and the macroinvertebrates were identified to the lowest practicable taxon. Data analysis included standard and a principal component analysis. Principal component analysis indicates that the riffle communities downstream of the fertilized fields in Buck Creek were significantly different from all other samples. Biometric scores supported the findings of the PCA, but seemed to indicate that there was no significant impairment of water quality.

INTRODUCTION

In order to determine ecological integrity of freshwater aquatic systems, government and private monitoring organizations employ water chemistry analysis, as well as habitat and biotic surveys. The latter method, particularly benthic macroinvertebrate bioassessment protocols, enables the detection of site specific environmental stress. Macroinvertebrate communities in impacted watersheds are often subjected to stressors such as temperature extremes, mine tailings effluents, inorganic and organic contaminants, or agricultural waste runoff. Certain measures of community structure, such as overabundance of tolerant macroinvertebrates or the absence of sensitive species, may indicate diminishing ecological integrity due to anthropogenic impacts. Intensive livestock rearing facilities produce large quantities of waste and often must adopt best-management practices (BMPs) to reduce impacts on local biotic communities. The efficiency and effectiveness of BMPs in reducing nonpoint source run-off into streams may be evaluated using benthic macroinvertebrate indicators.

Although a variety of bioassessment protocols have been established for benthic macroinvertebrate sampling within the last decade (Plafkin *et al.* 1989, Klemm *et al.* 1990, Kentucky Division of Water 1993, Lenat and Barbour 1994), stream disturbances have been evaluated by determining the integrity of macroinvertebrate communities since the late 1960s (Berkman *et al.* 1986). Wohl *et al.* (1995) found distinct patterns between macroinvertebrate species distribution in Appalachian streams and habitat attributes, thereby demonstrating a relationship between environmental parameters and invertebrate community structure. Pollutants are environmental parameters largely influenced by or originating from anthropogenic practices and can affect invertebrates either directly by physiological responses or indirectly by alterations in habitat (Lemly 1982). For example, Lemly (1982) established that variation of benthic insect communities was correlated with sedimentation combined with nutrient enrichment. Berkman *et al.* (1986) tested and established the validity of utilizing benthic macroinvertebrates as bioindicators of environmental stress from agricultural practices.

A large swine operation in Franklin, Kentucky, has installed a large, 16 cell constructed wetland on their property. Waste water from the swine operation is passed though these cells to reduce nutrient levels and then the processed filtrate is spread as a fertilizer onto adjacent cattle pasturage twice a year. Even though nutrient levels in the filtrate are reduced, these applications still result in considerable nutrient loading to the fields (David Stiles, personal communication). There was concern that there might be significant nutrient run-off from the fields into Buck Creek, the major stream draining the watershed (cattle do not have direct access to the creek). In 1995-1996, benthic macroinvertebrates were sampled in Buck Creek and a reference stream as part of a larger water quality assessment project to test whether the nutrient loadings to the downstream site of Buck Creek were severely impairing the stream. The macroinvertebrate communities in Buck Creek and May's Branch will allow us to draw inferences about the ecological integrity of the stream and determine if further control measures are necessary to protect the ecological integrity of Buck Creek.

METHODS

Buck Creek is a third order, perennial stream as it passes though the swine operation. Sampling sites in Buck Creek were chosen based on run-off patterns and the positions of effluent ditches from the surrounding fields and constructed wetland; the upstream (no impact) sites were positioned several hundred yards upstream from the effluent ditches while the downstream sites were located just below the effluent ditches. While fish collections have been made on Buck Creek since 1993, no macroinvertebrate collections were made until the spring of 1995.

May's Branch was selected as a reference reach in the spring of 1995. Data from reference streams are often useful in bioassessment studies because they provide a measure of sample variability due to biological or temporal factors that are not directly connected to anthropogenic impact. For example, macroinvertebrate communities may differ between upstream and downstream stations due to changes in habitat which are the result of physicochemical variation naturally occurring along the length of a stream, not the result of impacts. Unfortunately, there is no "pre-impact" data available from either stream, but if we assume that differences between the upstream and downstream communities in May's Branch are the result of "natural effects", we can infer that larger differences between the upstream and downstream macroinvertebrate communities in Buck Creek may be the result of anthropogenic impacts. May's Branch is about 8.5 km east of Buck Creek and lies in the same drainage basin. This reference stream, however, becomes a fourth order stream between the upper and lower stations. This situation may confound the data analysis, but there are few streams in this drainage with geomorphometric features similar to Buck Creek that are not heavily impacted by agricultural activities or brine run-off from old wells. May's Branch was the best reference stream available for the purposes of this project, and we believed it might provide useful comparative data despite its limitations.

Both Buck Creek and May's Branch were surveyed in May of 1995 to establish baseline physical parameters for the macroinvertebrate bioassessment. Two riffle and two pool areas (=sites) were chosen in each upstream and downstream portion of both streams. The physical environment in the sites was assessed using Kentucky Division of Water (KDOW) protocols (Kentucky Division of Water 1993). Briefly, this includes qualitative assessments of riparian vegetation composition and condition, phytoplankton and periphyton abundance, and stream substrate structure. Current velocities were taken at each site using a Gurley current meter.

Macroinvertebrate samples were taken in riffles and pools using the modified traveling kick net (TKN) method (Plafkin *et al.* 1989). A D-frame net (35x33 cm, 600 μm mesh) was dragged upstream for 1 meter over a 60 second time period while the operator vigorously kicked the substrate to dislodge resident macroinvertebrates. The macroinvertebrates were swept by the current into the net and were then washed from the net into a white enamel pan where the larger specimens were separated out from the detritus and other material using fine forceps. The remaining contents of the pan were then passed and washed through a #30 sieve (600 μm mesh) to remove those organisms which may have been missed in the initial processing. At least two and usually three TKN samples were taken in each riffle and pool site using this method (total of 2 pools/riffles* 2/3 transects=4-6 samples per upstream and downstream area). Samples were not pooled. KDOW methods also require selected sampling of depositional habitats (snags, leaf packs, etc.), but these special habitats were almost completely absent in these streams. Leaf packs have been observed in this stream in the fall, but samples were scheduled specifically to avoid periods of litter fall, since the litter would interfere with the fish collections also taking place in this system. Pools, which were sampled using the same TKN methods, were the only significant depositional habitats in these streams. All macroinvertebrates were placed in labeled Whirl-pak bags in 90% alcohol for transportation to the laboratory. Macroinvertebrates were identified to the lowest practicable taxon (always to family, usually to genus/species) using an Olympus stereomicroscope and standard taxonomic references (e.g. Merritt and Cummins 1996, Brigham *et al.* 1982) and the advice of local experts familiar with the fauna (primarily Dr. Rudy Prins, WKU).

Taxonomic data was analyzed using the Principal Components Analysis (PCA) module of the statistical package SYSTAT. The entire data set (both streams) was analyzed first, followed by within-stream analyses. The purpose of these analyses was to determine if the downstream riffle and pool areas in Buck Creek had a different community composition than the upstream sites in Buck and/or both sites in May's Branch. The data were then evaluated using a series of biological metrics recommended by KDOW: total number of individuals (TNI), taxa richness, Ephemeroptera/Plecoptera/Trichoptera (EPT) index, EPT:Chironomidae ratio and the Jaccard index. The first two metrics are self-explanatory. The EPT index measures the number of distinct taxa from each of these three insect orders that are present. Members of these orders are generally intolerant of poor water quality and are often used as indicator species. The EPT:Chironomidae ratio compares the number of intolerant EPT taxa with the generally more tolerant chironomid taxa found at the same station. Thus, higher ratios indicate better water quality. The Jaccard coefficient is an index of similarity based on the presence and absence of taxa, in which scores vary from 0 to 1, increasing as the similarity of a site to its reference station increases. This ratio is calculated as $c/(a+b+c)$, where $a=$ the number of taxa found in sample A but not B, $b=$ the number of taxa found in sample B but not A, and $c=$ the number of taxa common to both samples.

The PCA and biological metrics scores together, along with the physical assessment, were used to determine if the downstream site in Buck Creek was significantly different from the upstream site or the reference stream sites.

RESULTS

The physical assessment of the two streams indicated that they were very similar in terms of canopy cover and phytoplankton in riffle areas (Table 1). Substrate was similar between the two streams in riffle areas, although there was more sedimentation evident in the downstream areas of May's Branch. A significant percentage of the exposed stream bed in upstream May's Branch was exposed limestone, which provides little suitable habitat for many macroinvertebrates. Average current velocity and alga cover were different between the two sites; filamentous algae was very common in downstream Buck Creek during all sample periods and uncommon elsewhere in the streams. Average current velocities were much higher in May's Branch than in Buck Creek. This is primarily the result of a series of small waterfalls in both portions of May's Branch which increased water velocities. These differences in the physical structure among riffle sites may confound the analysis of the macroinvertebrate data.

Table 1. Physical assessment of Buck and May's Branch riffle sites using Kentucky Division of Water metrics. 1995 data only.

Parameter	Method	Buck Riffle	Mays Riffle
Current velocity	Pygmy	0.22 m s^{-1}	0.78 m s^{-1}
Substrate	transect, mean	60% exposed bedrock, 40% mixed pebble/gravel	50 % exposed bedrock, 30% pebble gravel, 10% sediment
Canopy (spring)	Estimation	70% cover	50% cover
Condition		perennial	perennial
Alga cover	quadrat	< 5% up riffle 25-30% down riffle (Cladophora)	< 5 %
Phytoplankton	KDOW Index	1	1

An additional complicating factor was the loss of some data for the May's Branch downstream pool sites in 1995. Inadequate preservation in the field resulted in the samples being destroyed by fungal, and presumably bacterial, action. As a result, the pool data comparisons are not as complete in terms of community representation as the riffle community samples.

The PCA analysis revealed that macroinvertebrate data points in the downstream riffles of Buck Creek (Fig 1a) fell outside the data cloud formed by the other Buck Creek areas along the two PCA axes, indicating that macroinvertebrate community structure in this area was different than that in other areas. Similarly, the May's Branch upstream riffles separated from the data cloud in the analysis (Fig 1b), indicating macroinvertebrate community structure in the upstream riffles was different from that in other areas of the reference stream.

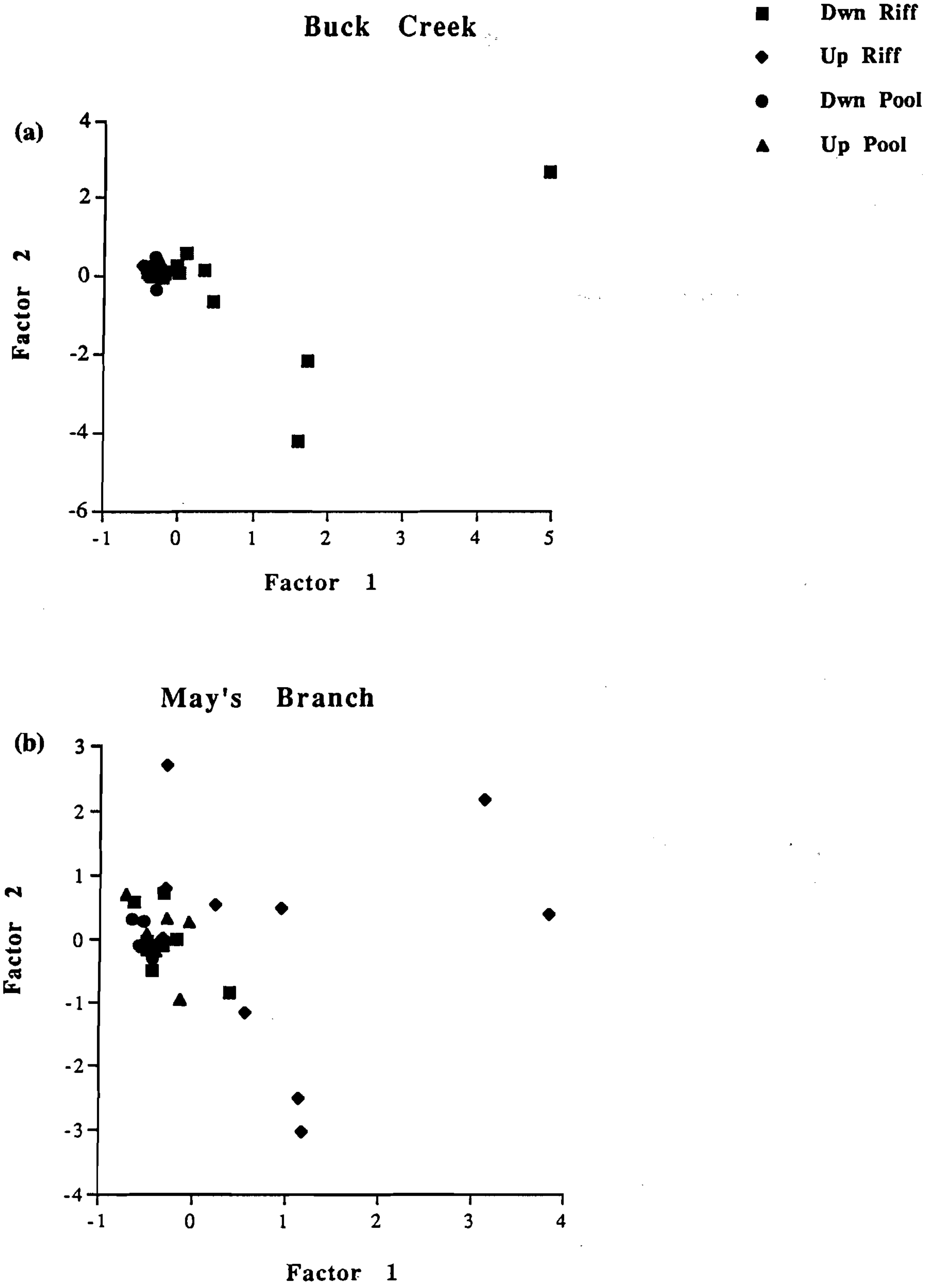

Figure 1a-b. Results of Principal Components Analysis for macroinvertebrate communities in Buck Creek and May's Branch. (a) Data from Buck Creek, (b) Data from May's Branch.

The biometrics were quite variable in their scores for the pool sites and somewhat less so for the riffle sites (Tables 2 & 3). Pool sites had generally lower numbers of individuals and lower taxa richness, EPT scores and Jaccard coefficients than riffle habitats in the same reach. Because of this, and the loss of some pool data mentioned above, we will focus our analysis on the riffle reaches of Buck Creek and May's Branch.

The downstream Buck riffles showed higher numbers of individuals and greater taxa richness compared to the upstream riffles; the opposite was true for riffles in May's Branch. EPT taxa were found in all habitats and the EPT:Chironomidae ratios were high in all of the riffles sampled. Jaccard coefficients between reference and impacted riffles, however, were rather low (all< 0.60).

Table 2. Result of biometrics for upstream and downstream pool sites in the impacted stream (Buck Creek) and the reference stream (May's Branch) for 1995 and 1996 sample periods.

Site	Date	Taxa Rich.	TNI	EPT	EPT:Chiron.	Jaccard
Buck up	May '95	1	3	1	1:0	0.08
Buck dwn	May '95	13	53	6	6:1	NA
Mays up	May '95	8	53	3	3:1	*
Mays dwn	May'95	NA	NA	Na	NA	*
Buck up	Sept. '95	2	2	1	1:0	0.09
Buck dwn	Sept '95	17	3	3	3:0	0
Mays up	Sept'95	11	36	5	5:1	*
Mays dwn	Sept '95	2	2	0	0:1	*
Buck up	May '96	7	19	3	3:0	0
Buck dwn	May '96	10	26	4	4:1	0.38
Mays up	May '96	6	20	1	1:0	*
Mays dwn	May '96	8	15	5	5:0	*
Buck up	Sept. '96	1	3	1	1:0	0.11
Buck dwn	Sept '96	3	5	2	2:1	0.33
Mays up	Sept '96	9	22	5	5:1	*
Mays dwn	Sept '96	5	13	3	3:1	*

Table 3. Result of biometrics for upstream and downstream riffle sites in the impacted stream (Buck Creek) and the reference stream (May's Branch) for 1995 and 1996 sample periods.

Site	Date	Taxa Rich.	TNI	EPT	EPT:Chiron.	Jaccard
Buck up	May ‘95	9	36	3	3:1	0.13
Buck dwn	May ‘95	17	515	4	4:1	0.11
Mays up	May ‘95	19	76	8	8:1	*
Mays dwn	May'95	4	56	2	2:1	*
Buck up	Sept. ‘95	8	47	6	6:1	0.19
Buck dwn	Sept ‘95	16	135	3	3:1	0.19
Mays up	Sept'95	14	105	6	6:1	*
Mays dwn	Sept ‘95	8	71	4	4:1	*
Buck up	May ‘96	11	27	6	6:1	0.32
Buck dwn	May ‘96	17	208	6	6:1	0.47
Mays up	May ‘96	14	76	3	3:0	*
Mays dwn	May ‘96	18	56	8	8:0	*
Buck up	Sept. ‘96	11	47	4	4:0	0.38
Buck dwn	Sept ‘96	12	145	6	5:1	0.60
Mays up	Sept ‘96	11	105	3	3:0	*
Mays dwn	Sept ‘96	14	71	5	5:1	*

DISCUSSION

One of the most useful aspects of bioassessments and biometrics is the potential for biotic communities to reveal subtle impacts in the environment through changes in macroinvertebrate community structure. The purpose of this project was to determine if applying biofiltered effluent on fields was having a deleterious effect on Buck Creek. Based on these results, there does appear to be impact, but perhaps not impairment, on Buck Creek downstream riffles.

Several lines of evidence support this conclusion. First, the PCA analysis indicates that macroinvertebrate communities in the downstream riffle portions of Buck Creek are different than the upstream riffles. Taxa richness and total numbers of individuals are higher in the downstream riffles than they are in the upstream riffles. This increase in numbers may be the result of nutrient enrichment. Studies have shown that stream periphyton can be nutrient limited (Stockner and Shortreed 1978; Shortreed and Stockner 1983) wherein low levels of nutrient input may enhance periphyton growth and thus the resource base for macroinvertebrates. In addition, these downstream riffles are the only areas were filamentous algae are common. These algae are often indicative of nutrient enrichment. The impact of nutrient run-off did not, however, result in a shift in community composition of species more tolerant of poor water quality (e.g. Chironomidae). There was no consistent pattern of loss of EPT species downstream and EPT:Chironomidae ratios remained high at all Buck Creek sites. It is likely that run-off from the fields is affecting the stream, but not significantly impacting water quality. Cooperators on this project have taken, but not yet analyzed, nutrient samples for 1995 and 1996. These water chemistry samples will be very helpful in further interpretation of the macroinvertebrate community patterns and assessing the likely impact of run-off on the stream biota.

Community patterns seen in May's Branch differed from those in Buck Creek. Taxa richness and total numbers of individuals were greater upstream than downstream in 1995, yet the opposite was true for 1996 samples. This variation in community composition coupled with the physical differences already mentioned limits the usefulness of May's Branch as a reference site. In addition, considerable sedimentation (Table 1) was observed in the downstream areas of May's Branch, which may also affect macroinvertebrate colonization, further confounding the comparison between Buck Creek and May's Branch.

Our data indicate that run-off flowing from the swine operation to downstream Buck Creek is affecting this ecosystem's macroinvertebrate community structure, but no severe impairment is indicated. Correlation with water chemistry data is necessary to confirm that applying biofiltered water to pasture lands of the farm is not having a negative impact on downstream Buck Creek. May's Branch is of limited usefulness as a reference stream and perhaps should not be sampled in future.

Since the conclusion of 1996 sampling, a low-water ford has been constructed across Buck Creek bisecting the upstream and downstream stations. This bridge has significantly altered the downstream habitat (shifted flow patterns; created a new, deeper pool just downstream of the bridge, etc.). As a result, additional work performed on this stream will have to take into account the hydrologically and biologically altered environments. We do recommend that the monitoring of Buck Creek continue, however. Macroinvertebrate bioassessment of Buck Creek has given the owners of the swine operation valuable insights into the effects of their operation on this watershed. Biological indicators have provided them a cost-effective and scientifically sound ecological impact assessment approach thereby allowing them to be both environmentally conscious corporate citizens and maintain a profitable operation in a competitive agribusiness market.

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THE EFFECTS OF DUNBAR CAVE STATE NATURAL AREA WATER ON THE SURVIVORSHIP AND REPRODUCTION OF *CERIODAPHNIA DUBIA* (CLADOCERA: DAPHNIIDAE)

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ABSTRACT. The Dunbar Cave State Natural Area is a source for both ground water and surface water as evidenced by sinkholes in the area, streams within the cave, and Swan Lake surrounding the cave. The proximity of the sinkholes and Swan Lake provide an avenue for pollutants to enter the cave water system. In 1988, The Federal Cave Resource Protection Act was created to provide inventories, scientific studies, resource assessment and management plans to protect caves from human input and other environmental contaminants. This study was conducted to determine if there are indications that pollutants from the environment have reached the cave and surrounding water. Aquatic toxicity testing is one of the more significant methods used to study and assess water quality. To assess the quality of the water, 10 replicates of *Ceriodaphnia dubia* were exposed to a control, and three different concentrations of the water collected from four different sites. Two sites were from within the cave and two sites were from Swan Lake. The endpoints measured were survivorship and reproductive success. The data show that survivorship for organisms exposed to cave water was less than that for the controls, while survivorship for organisms exposed to the lake water was approximately equal to that for the control. Reproduction was significantly less than the control for organisms exposed to the cave water, and significantly greater than the control for those exposed to Swan lake water. These data indicate the presence of some factor(s) that alter the natural ecology of *Ceriodaphnia*.

SPATIAL AND TEMPORAL VARIATIONS IN STREAM FISH COMMUNITIES ADJACENT TO A UNIQUE AGRARIAN ENTERPRISE

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ABSTRACT. An intensive swine rearing production facility in south central Kentucky has adopted the practice of irrigating concentrated animal waste effluents onto pasture lands at rates of 52 to 95 kg N/ha, 12 to 15 kg P/ha, and 91 to 95 kg K/ha per application, four times annually. The wastes are taken from the second of a two cell, in-series lagoon system and applied to the land. Buck Creek, an Order III tributary to the Trammel Fork of Drake's Creek, lies adjacent to the treated land and receives runoff via two effluent ditches. Two stream sampling stations were established on Buck Creek, Station I upstream from the uppermost effluent source and Station II below the lowermost effluent. Samples were made in the spring and fall from Fall 1992 to Spring 1995 using standard electrofishing methods. A total of 6,753 fish representing 23 species, including one hybrid, were taken in the study. Species occurrences at both stations in both seasons were similar. The largescale stoneroller minnow and southern redbelly dace were the major herbivores present (34.2% of total), bluntnose minnow the major omnivore (11.1%) and the creek chub, northern studfish, and orangethroat darter the major carnivores (34.3%). Significantly more fish were taken at Station II (59% vs 41%) and in the Fall (53% vs 47%). Significantly more carnivorous species occurred at Station I than Station II. Principal component analyses suggested strong seasonal, station, and year effects on patterns of fish community composition (60.2% of total variation). The amount of variance explained by each of the three composite variables were generally similar, season effects 26% of the total, stations effects 20%, and year effects 14.5%. Seasonal effects were manifest primarily on striped shiner, green sunfish, splendid darter, greenside darter, rainbow darter, and fantail darter all of which were more abundant in the spring; station effects were dominated primarily by bluntnose minnow, striped shiner, and green sunfish which occurred mostly in the downstream station; year effects identified the first year as qualitatively different in species composition and level of variability from the second two years and were influenced mostly by orangefin darters and southern redbelly dace and northern studfish. A second stream, Mays Branch, an Order III stream 6.5 miles to the east of Buck Creek and not influenced by anthropogenic effects, was sampled in Fall 1994 and Spring 1995 and included in a separate analysis for comparison purposes. Both Mays Branch samples clustered with the upstream data from Buck Creek; no interstation effects in Mays Branch were observed as in Buck Creek, though principal axes from both analyses were highly correlated. This suggested that the species composition in the downstream Buck Creek station is impacted by factors not operating at the other three stations. Based on the known external influences acting on the downstream Buck Creek station, this study concludes that agricultural runoff contributes significantly to the interstation variation in that system.

SEDIMENTATION IN THE LOWER REACHES OF KENTUCKY LAKE, 1946-1995

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ABSTRACT. Eight transects in the lower portion of the mainstem of Kentucky Lake from Governor Ned R. McWherter Bridge to Kentucky Dam were established by the Tennessee Valley Authority (TVA) in 1946 and last resurveyed by TVA in 1961. Murray State University researchers revisited the transects in 1995 to determine recent rates of sedimentation. Seven new transects were also set in embayments as embayment sites in the study area were lacking. Deposition was measured at each TVA transect using a Lowrance Model X-16 chart recorder and a Trimble Pathfinder Pro-XL GPS. Data were then entered into a database and manipulated using ARC/INFO GIS software to produce updated transects and calculate deposition. When reviewing sedimentation at each transect, transects located downstream from two major embayments, Jonathan Creek and Blood River, showed a tendency toward an increased rate of deposition. A rather dramatic increase in rate was evident for the 1951-1956 time period for all transects. The 1961-1995 period showed a gradual rate of increase. Volume of deposition was also calculated and yielded a high rate of sedimentation between 1951 and 1956. An overall increase in rate of deposition by reach occurred between 1961 and 1995 for six of eight reaches. The average annual rate of sedimentation by reach from 1946-1995 varied from 53 to 119 acre-feet/mile/year. Total accumulation from 1946-1995 was 162353.2 acre-feet. The capacity of the reservoir decreased at a nearly linear rate of approximately 3300 acre-feet/year between 1946 and 1995. If this rate were extended, the life of the lower reachers of Kentucky Lake would be 370 years.

SEDIMENT-WATER CHEMICAL EXCHANGE IN KENTUCKY LAKE RESERVOIR

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ABSTRACT. Benthic chambers have been used to make direct measurements of sediment-water chemical exchanges of nitrogen, phosphorus, silicon, and dissolved oxygen in Kentucky Lake Reservoir, the largest impoundment of the Tennessee River system. Reservoir sediments are characterized by high accumulation rates (several cm per year) and low organic carbon and nitrogen contents (≈ 1.0% and 0.1%, respectively). Sediment-water chemical fluxes have been found to be strongly correlated with water temperature. Despite the low organic matter concentrations, fluxes of ammonia from the sediments are as high as ≈ 12 millimoles N/m^2/day. Sedimentary fluxes of nitrogen and phosphorus may be the primary source of nutrients utilized by primary producers during the summer months. One reason for the high sediment-water nutrient fluxes may be that the water column is usually well-oxygenated despite the 30°C water temperature through much of the summer season. Related ongoing studies are attempting to relate these chemical fluxes to microbial activity in the sediments, and to better define patterns of organic matter accumulation.

STRUCTURE AND FUNCTION OF MICROBIAL COMMUNITIES IN KENTUCKY LAKE SEDIMENTS

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ABSTRACT. Sediment microbial communities are major contributors to the cycling of biogeochemically important nutrients across the sediment-water interface. It has been technically difficult to measure microbial diversity or observe specific activities of microbial populations *in situ*. It is estimated that only 2% of bacteria in a soil sample form colonies on bacteriological media. Nucleic acid hybridization with specific probes and amplification by PCR can be utilized to identify and quantify microbes from rDNA. Many of these methods have proven problematic when working with complex environmental samples, such as sediment. We have developed methods to measure the microbial diversity of the sediments of Kentucky Lake by analysis of amplified rDNA. Sediment was suspended in Tris lysing buffer and the cells disrupted by freezing and thawing. The sample was treated with phenol/chloroform and the DNA precipitated with ethanol. At this point the DNA was clean enough for PCR amplification and was used as template for PCR reactions using universal primers designed to amplify rDNA. The amplified rDNA was then subjected to restriction endonuclease analysis to measure the diversity of Kentucky Lake sediment. Presently, we are comparing sites in Kentucky Lake, different in macrofauna, and monitoring for fluctuations in genotypic diversity that result from changes in temperature, oxygen availability, and nutrient availability. Additionally, we are working on the methodology to detect the expression of genes that encode the enzymes necessary for important biogeochemical metabolic pathways. We have searched the Genbank® database for DNA sequences that encode dinitrogenase reductase (nitrogen fixation), nitrite reductase (denitrification), carbamoyl-phosphate synthetase (ammonia utilization), ammonia monooxygenase and hydroxylamine oxidoreductase (nitrification), and ATP sulfurylase (sulfate reduction). Deduced sequences will be used as primers in PCR reactions to amplify mRNA. These data will allow us to identify the conditions under which certain metabolic pathways are active.

EFFECT OF LAND-USE ACTIVITY ON DENITRIFICATION POTENTIAL OF WETLAND SOILS

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ABSTRACT. The effect of varied land-use activity upon denitrification potential of bottomland hardwood wetland soils is not well understood. It is important to understand how land-use activities affect wetland functions such as denitrification so that reasonable predictions can be made concerning the effect a change in land-use activity may have on wetland functioning. Four sites in the Obion Creek floodplain were selected for study: Murphy Pond, a deepwater cypress swamp (DCS); a bottomland hardwood wetland with natural hydrology (BHWN); a bottomland hardwood wetland with altered (increased depth and duration of flooding) hydrology (BHWAlt); and a section of bottomland hardwood wetland converted to agricultural fields (AG). Eight 5 cm deep by 4 cm wide sediment cores were collected at each site four times during 1996 using a 15 cm long by 4 cm wide piece of PVC pipe. The pipes were sealed with rubber stoppers at the bottom and top and transported to the lab in an ice chest. To determine the effect of overlying litter upon denitrification potential, four cores received *in-situ* litter, while four cores were litter-free. Water from Cypress Creek was collected during each sampling trip and amended with sodium nitrate ($NaNO_3$) (10 mg/L), and chloramphenicol (1 mg/L) to prevent microbial growth, and vigorously bubbled with nitrogen gas (N_2) to achieve anaerobic conditions. Each core was filled with 120 ml of prepared water. The tops of the pipes were sealed with a solid rubber stopper and water samples were extracted at set time intervals and analyzed for nitrate concentration. Rates of nitrate disappearance were then determined and expressed on the basis organic carbon content of the sediment and/or litter. These experiments were performed between January and September when ambient temperatures were 10, 15, 20, and 25°C. Comparisons were made between with-litter and without-litter treatments, between sites, and between dates (temperatures). The presence of litter stimulated nitrate disappearance at all sites except at DCS. Experiments are in progress to elucidate the absence of a litter-effect at DCS. The DCS site exhibited the lowest denitrification rates while the AG and BHWAlt sites exhibited the highest. Denitrification was positively correlated with temperature. In conclusion, if the BHWN site is taken as the natural condition, then conversion of bottomland hardwood forests to agricultural fields or excessive flooding of bottomland hardwood forests during the growing season do not appear to reduce denitrification potential.

BIOLOGICAL INDICATORS OF WATER QUALITY AT DUNBAR CAVE STATE NATURAL AREA, CLARKSVILLE, TENNESSEE

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ABSTRACT. For many years, fecal coliform and fecal streptoccal densities have been used as indicators of water quality both on the state and federal level. Recently, many researchers in the United States have encouraged studies to investigate the relationship between poor water quality and amphibian decline. This study uses both bacteria and amphibians as biological indicators of water quality at Dunbar Cave State Natural Area (DCSNA) in Clarksville, Tennessee. For the amphibian portion of the study, experimental containers housing eggs of the Cope's Gray Treefrog (*Hyla chrysoscelis*) were positioned at sites within DCSNA. Two sites common with the amphibian study and two additional sites within the cave were assessed for fecal coliform and fecal streptococci using a standard membrane filter technique. Our bacterial data show that three of the four sites exceeded EPA standards at least once during the study period. In addition, our amphibian data show a reduced survivorship (6.5%) for eggs incubated at DCSNA as compared to controls (43.5%). These data demonstrate the need for further monitoring of the water quality at DCSNA.

EFFECT OF TAXONOMIC LEVEL OF IDENTIFICATION ON RAPID BIOASSESSMENT RESULTS

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ABSTRACT. Current U.S. EPA guidelines, "Rapid Bioassessment Protocols (RBPs)," suggest eight numerical indices of community structure and function (i.e. metrics) be used to evaluate water quality. The RBPs are suggestions only and actual methods of collecting, processing, and analyzing biological data vary between individuals and agencies. The level of taxonomic identification varies greatly between studies as does assumptions about which kinds of taxa to include in an assessment study. The US EPA has sponsored research to test the effects of these sources of variation, including taxonomy, on assessment accuracy. Results from a limited number of studies suggest that RBP methodology is robust to variations in user technique and taxonomy. However, a review of hypothetical errors suggests, and the US EPA concurs, that further testing, validation, and refinement of RBP methods may be necessary. This paper discusses hypothetical effects of differing levels of taxonomic identification on RBP metrics and compares them to preliminary RBP data collected as part of the West Sandy Creek Project in Henry County Tennessee. Because published RBP studies that use family level taxonomy usually do not include taxonomic checklists identifying the taxa to lower levels of taxonomy, it is difficult to test the validity of these RBP assessments independently. The EPA RBPs were intentionally designed to be flexible to facilitate their implementation in a diverse range of habitat conditions; however, their exits a continuing need for additional definition of some parameters of RBPs if researchers working in different habitats and political jurisdictions are to be able to compare results and have confidence in their validity. The limited RBP data presented here generally confirm that RBP methodology is robust to differing levels of taxonomic identification, but there is sufficient variation to justify additional review.

DENSITY-DEPENDENT PHYSIOLOGICAL PLASTICITY IN AQUATIC PLANTS

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ABSTRACT. The survival and growth of individual plants can be negatively affected by increasing population density. This density-dependent effect is partially explained by a negative relationship between population density and the availability of resources. Although population level density-dependent effects have been demonstrated, no such documentation exists for density-dependent physiological response in higher plants. There are, however, no *a priori* reasons why increase in population density, with concurrent reduction in resource availability, within the lifespan of an individual plant might not also effect changes in physiology; perhaps in ways that increase resource acquisition, survival and even fecundity. The identification of individual (phenotypic) physiological plasticity in response to changes in population density could provide an important mechanism useful in explaining plant response to density-dependent resource depletion. Further, understanding the mechanisms responsible for these density-dependent responses could lead to novel genetic manipulations that could increase plant production under stressful conditions. The objective of this paper is to provide evidence for the existence of density-dependent physiological response to resource depletion in two submersed aquatic angiosperms. Field data indicated that the photorespiratory state exhibited by the two submersed aquatic angiosperms, *Hydrilla verticillata* and *Myriophyllum spicatum*, was influenced by population density. Subsequent laboratory experiments demonstrated that plants grown under higher densities exhibited lower CO_2 compensation points, and higher photosynthetic rates under low levels of dissolved inorganic carbon (DIC). The population density effect appears to be mediated by depletion of DIC at the higher densities. These data represent the first direct confirmation that physiological response in plants is density-dependent. Knowledge that physiological response of plants can change with population density should lead to interesting research on the mechanisms of competitive dominance and superiority.

OPTIMUM TEMPERATURE FOR PHOTOSYNTHETIC CARBON ASSIMILATION IN KENTUCKY LAKE FOLLOWS SEASONAL CHANGE IN AMBIENT TEMPERATURE

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ABSTRACT. Laboratory studies have shown that optimum temperatures for both carbon assimilation and growth rates of individual algae species can vary with culture temperature. Few studies, however, have investigated the optimum temperature of carbon assimilation of natural freshwater phytoplankton communities and changes with seasonal temperature. Although there exists a relationship between seasonal acclimation of carbon assimilation and temperature in marine macroalgal species, we could not find similar data for natural populations of freshwater phytoplankton. Early studies of natural phytoplankton populations suggest that adaptation of photosynthesis to seasonal change in temperature does not occur. Given that the optimum temperature of carbon assimilation can vary markedly among algal species and provenances, and that laboratory studies indicate acclimation of optimum temperatures of photosynthesis to growth temperature, we hypothesized that the optimum temperature of carbon assimilation of natural phytoplankton communities in temperate lakes should, in fact, change with season. When carbon assimilation by natural phytoplankton assemblages collected from Kentucky Lake, Kentucky during 1995 was measured in the laboratory at 5, 10, 15, 20, 25, and 30°C, the optimum temperature shifted from 5° for the winter population to over 30°C for the summer population. Arhhenius plots of carbon assimilation for summer and winter phytoplankton exhibited membrane phase-transition temperatures of 20° and 10°C, respectively. Q_{10} values for summer and winter phytoplankton were 3.61 and 1.60, respectively. These data plus the observation that carbon assimilation of the winter phytoplankton measured at 5° was almost 70% greater than carbon assimilation of the summer phytoplankton at 5°C, suggest that adaptations which allow for greater carbon assimilation during colder temperatures preclude equivalent or greater carbon assimilation at warmer temperatures. It appears that the same phytoplankton community cannot maintain optimal carbon assimilation rates at both cold and warm temperatures. These data may be useful to modelers who wish to develop more robust and precise models of freshwater primary productivity by alerting them of the need to acquire data for different temperature response equations of seasonal phytoplankton populations.

SURFACE-SUBSURFACE PROCESSES IN AGRICULTURAL VS. FORESTED STREAMS: INITIAL STUDIES

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ABSTRACT. The hyporheic ecotone, the biologically and chemically active interface between groundwater and surface water, functions as a sink and source of dissolved organic matter and nutrients to maintain stream productivity. Increased sedimentation coupled with highly variable discharge and nutrient inputs in agricultural basins may impair hyporheic functions, explaining differences in productivity between more pristine and human-dominated basins. Most of our present knowledge of hyporheic ecotones comes from a very limited number of high gradient, relatively pristine streams in summer months at base flow. The objective of this research has been to characterize the function of hyporheic ecotones in pristine versus agricultural streams. Research focuses on 3rd order reaches of two basins, one a forested ecosystem (Panther Creek), the other an agricultural basin (Ledbetter Creek). Selected studies also are occurring in 1st and 2nd order tributaries of both basins. The overall objectives are being met by 1) determining surface, groundwater, and hyporheic dynamics, 2) following changes in surface and subsurface conditions during and after seasonal sedimentation events (i.e., storms), and 3) comparing spatially and temporally selected chemical and biological processes which may be directly affected by hyporheic storage and release, e.g., methane production, benthic algal structure and function, and bacterial abundance, activity and diversity.

CONTRIBUTED PAPERS

SESSION III: BOTANY

Saturday, March 1, 1997

Moderator:

Edward W. Chester
Austin Peay State University

Editor:

Edward W. Chester
Austin Peay State University

Editorial Assistants:

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and

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CHARACTERIZATION OF SOME REMNANT BOTTOMLAND FORESTS OF THE LOWER CUMBERLAND RIVER IN TENNESSEE AND KENTUCKY:

2. THE ST. STEVENS SITE IN LYON COUNTY, KENTUCKY

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ABSTRACT. The results of phytosociological analyses within a 10-ha bottomland forest on the west side of Barkley Lake (the impounded Cumberland River) in Lyon County, Kentucky, are presented. The forest, St. Stevens Woods, is within Land Between The Lakes, a public use area managed by the Tennessee Valley Authority (TVA) since 1963. The forest was designated a TVA Ecology Study Area in 1973. All taxa (30 species, 830 stems) with dbh ≥2.54 cm were measured by species in 16 0.04 ha circular plots. Shrubs and woody seedlings (725 stems) were counted in 0.004 ha plots at the center of the larger plots. An importance value (IV) was determined for each species by summing relative density, relative basal area, and relative frequency (maximum value = 300) for the canopy (dbh ≥10.16 cm) and sapling\small tree stratum (dbh 2.54-10.15 cm). For the shrub\woody seedling stratum (dbh <2.54 cm), a modified IV (maximum 200) was determined by adding relative density and relative frequency. *Liquidambar styraciflua* (IV = 61.29), *Quercus pagoda* (55.69), and *Nyssa sylvatica* (41.63) dominate the canopy, accounting for almost 53% of IV. The sapling and small tree stratum is dominated by *Asimina triloba* (IV = 68.39), *Acer rubrum* (41.00), *Acer saccharum* (25.40), *Liquidambar styraciflua* (23.62), *Carpinus caroliniana* (21.85), and *Ulmus rubra* (19.46); these taxa account for almost 67% of IV. *Lindera benzoin* (IV = 48.70) and *Asimina triloba* (40.98) make up 45% of IV in the shrub and woody seedling stratum. These data from St. Stevens Woods add to our data base on remnant bottomland forests of the lower Cumberland River in Tennessee and Kentucky.

INTRODUCTION

This is the second paper in our series presenting the results of vegetational and floristic studies of three remnant bottomland forests (Figure 1) along the lower Cumberland River, south and east of Barkley Dam in Kentucky and Tennessee. The series was introduced, literature surveyed, the region described, and the first study site characterized in our initial paper (Chester and Schibig 1993). We noted then that a considerable forested floodplain existed along the lower Cumberland River in Tennessee and Kentucky at the time of settlement. Most of those forests had been removed by the late 1800s and the rich lands converted to agriculture (Sudworth 1897). In addition, Barkley Dam, at River Mile 30.6 south of the confluence with the Ohio River, was closed in 1966, inundating most of the floodplains southward through Kentucky and into Tennessee. Today, all of this forest type has disappeared except for a few remnants (Smalley 1980).

This paper provides an analysis of the second study site that we have designated St. Stevens Woods due to its proximity to the St. Stevens Cemetery and former church by the same name. The third site, Long Pond Slough, is described in the following paper.

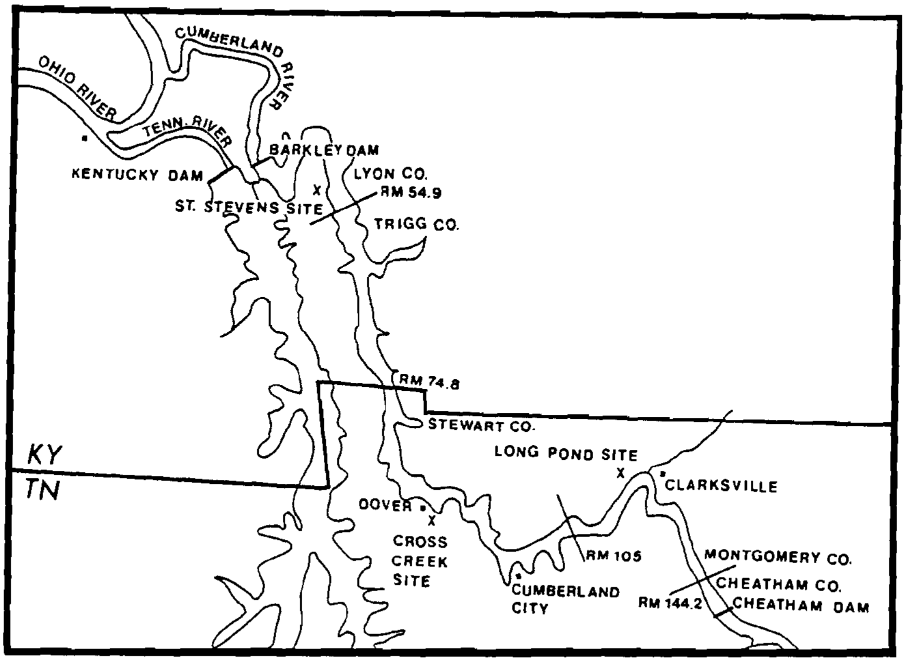

Figure 1. Location of the Long Pond, Cross Creeks, and St. Stevens bottomland forest sites on the lower Cumberland River, Tennessee and Kentucky.

THE STUDY AREA

Location and Description

St. Stevens Woods is a 10 ha tract in Land Between The Lakes (LBL), Lyon County, Kentucky (Figures 1, 2). The site is on the west side of the Cumberland River (Barkley Lake) at River Mile 47.3; Clay Creek Bay (River Mile 46.8) is to the north, Mammoth Furnace Creek Bay (River Mile 49.2) is to the south, and St. Stevens Cemetery and former church site is one-fourth mile to the south. The woodland is centered at 37°00'20" north latitude and 88°04'10" west longitude on the Eddyville, Kentucky, 1967, USGS topographic quadrangle. The 375-foot contour line encircles the area (Figure 3). Barkley Reservoir borders the woods on the east, where normal summer pool is 359 feet above sea level. North and south boundaries are footslopes of surrounding secondary forests; the western boundary is secondary succession-young timber of bottomland fields that were in tilth prior to TVA stewardship. A small, usually summer-dry creek meanders through the woods and overflows during heavy rains. Much of the area may be flooded temporarily (no more than a few days) during reservoir high-water periods (winter-spring) of occasional years.

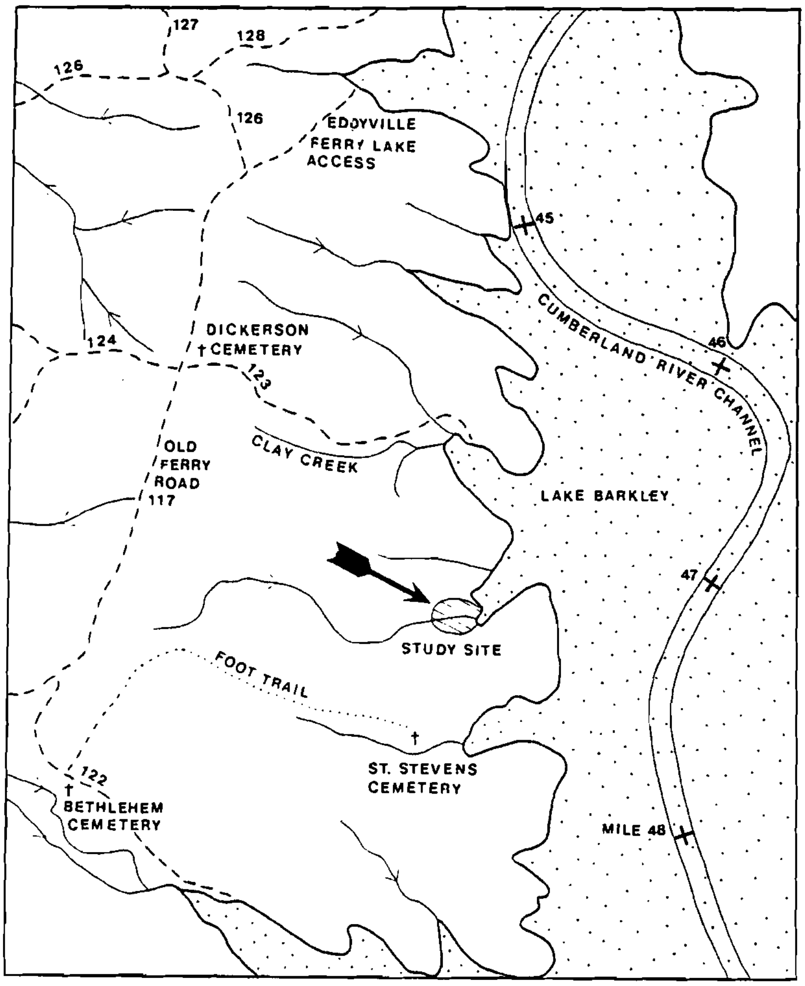

Figure 2. Location of the St. Stevens bottomland forest site, Lyon County, Kentucky.

The site is in the Cumberland-Tennessee Rivers Section of the Major Soil Associations of Kentucky. Soils of this dissected area have generally developed in thin loess which lies over gravel and chert beds; most are low in fertility, droughty, and inferior for agriculture (Bailey and Winsor 1964). Bottomland soils have formed in alluvial sediments derived from erosion of the uplands and consist of clay and siliceous fragments; bedrock of LBL is dominantly cherty limestone of the Mississippian System (Harris 1988). Soils of the study site are Newark silt loam, a deep, somewhat poorly drained, nearly level (0-2 percent slope) type of flood plains and upland depressions. The Newark soil has moderate permeability, is fertile, with moderate amounts of organic matter. Available water capacity is high and the soil is subject to occasional flooding from December to May, and even in summers where there are depressions. The water table is at a depth of 6 to 18 inches when not flooded; the soil is best suited for woodland use (Humphrey 1981).

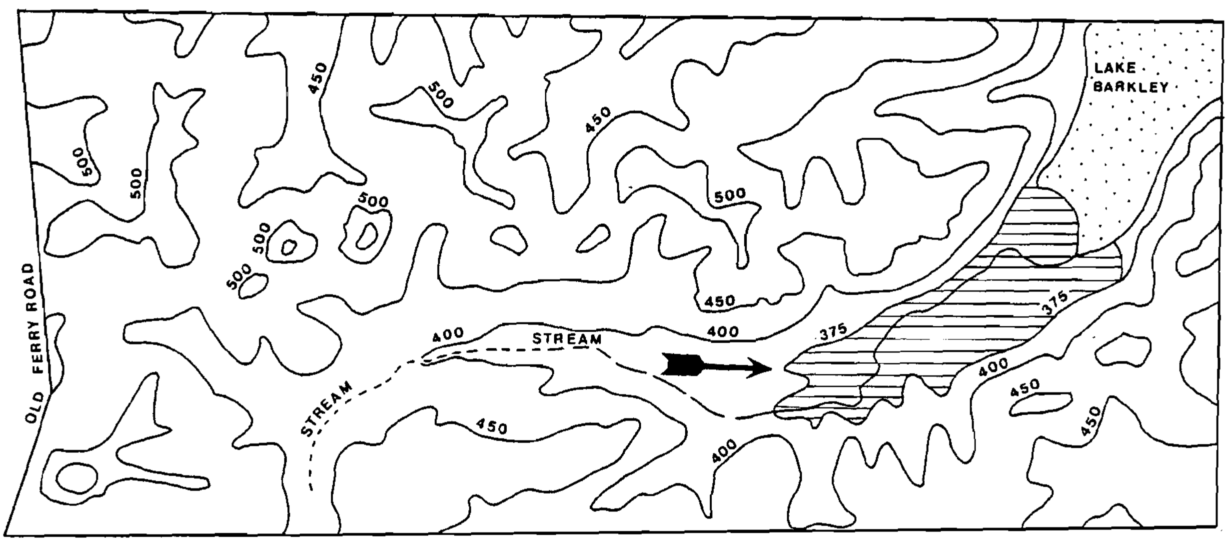

Figure 3. Topographic details of the St. Stevens bottomland forest site, Lyon County, Kentucky.

History

Land Between The Lakes is a 170,000-acre outdoor recreation and environmental education area in southwestern Central Kentucky and northwestern central Tennessee that has been under management by the Tennessee Valley Authority since 1963. Prior to then, LBL consisted of numerous small farms, communities, a National Wildlife Refuge, and corporately-owned woodlands. The study site was in private ownership before 1963 and usage of the woodlands is unknown; however, the area was heavily timbered to provide charcoal for the 1800s iron industry, which had several blast furnaces within a few miles of the site, and certainly timber was removed. The woodland has been virtually untouched since 1963.

In 1972, LBL began identifying a network of Ecology Study areas, selected because of their characteristic natural features or their potential as demonstration areas, such as erosion control areas or areas to study the effects of fire on forest communities. Ecology Study Areas now total 1,170 acres on 34 sites (TVA 1993). One of the sites selected in 1972 was Forest Study Area Number 3, Maple Swamp. The site was described as (TVA internal memo, 6-28-1973):

> A 25-acre tract of bottomland hardwood with approximately 11,200 board feet of sweet gum, cherrybark oak, white oak, and yellow poplar per acre with a very dense understory of ironwood, greenbrier, hazelnut, spicebush, sweet gum, yellow poplar and oaks. The stand is composed of large mature trees.

METHODS

Sixteen 0.04 ha (0.1-acre) circular plots, representing about 6.4% of the area, were established along two paralleled compass lines which ran lengthwise through the forest. Plots were centered at 50 meter intervals along the compass lines and were permanently marked with PVC pipe, witness trees, and compass bearings. Within each plot all trees with a diameter breast height (dbh, about 4.5 feet about ground level) of 2.5 cm (1 inch) were recorded by species and measured to the nearest 0.25 cm (0.1 inch). These data were used to calculate standard parameters as outlined by Barbour *et al.* (1987). Statistics determined include density (number/ha), basal area (m^2/ha), and frequency (percent of plots with the species). Relative values of density, basal area, and frequency also were determined and the three relative values summed to give an importance value with a maximum of 300.

At the center of each 0.04 ha plot, a circular plot of 0.004 ha (0.01 acre) was nested and shrubs and tree seedlings with dbh's <2.54 cm counted by species or in some cases by genus only. Density and frequency values (absolute and relative) were determined and summation of the two relative values gave an importance value with a maximum of 200.

Several reconnaissance and surveying trips were made to the area from 1989-present. All quantitative data were taken on 14 and 23 May 1990. Taxonomic determinations and nomenclature generally follow Gleason and Cronquist (1991).

RESULTS AND DISCUSSION

Size-Class Distribution

A total of 830 stems with dbh's ≥2.54 cm was measured. The 30 species represented are listed alphabetically, with the number of each species, average diameter per species, and size class distribution, in Appendix 1. The majority of stems (576 = 69.4%) are in the 2.54-10.15 cm (1-3.9 inches) dbh size class. The 254 stems with dbh of ≥10.16 cm make up 30.6% of stems. The average diameter of all stems is 12.57 cm (4.95 inches). For stems ≥10.16 cm, the average is 30.04 cm (11.83 inches). For the four dominant canopy species (*Liquidambar styraciflua, Quercus pagoda, Nyssa sylvatica, Acer rubrum*), the dbh average for all stems is 37.86 cm (14.91 inches). When the arbitrary size class of 50.8 cm (20 inches) is chosen to indicate "large trees," three taxa of *Quercus* and *Liquidambar styraciflua* clearly dominate this aspect of the forest. The largest tree measured was a *Quercus pagoda* with a dbh of 92.46 cm (36.4 inches). The large tree category includes: *Acer rubrum* (1), *Carya ovata* (2), *Carya tomentosa* (1), *Celtis laevigata* (1), *Liquidambar styraciflua* (17), *Liriodendron tulipifera* (1), *Nyssa syyvatica* (1), *Quercus alba* (3), *Quercus imbricaria* (1), *Quercus pagoda* (17), and *Ulmus rubra* (1).

Canopy Species

Twenty-two species with dbh ≥10.16 cm (4 inches) were measured. Appendix 2 provides data on the 254 stems sampled, including ranking by IV and percent of total IV. The data show that two species, *Liquidambar styraciflua* (20.43% of IV) and *Quercus pagoda* (18.56%)

dominate. However, *Nyssa sylvatica* (13.88%), *Acer rubrum* (9.30%), *Acer saccharum* (5.69%), *Carya ovata* (4.41%), *Liriodendron tulipifera* (4.23%), and *Ulmus alata* (3.73%) are important contributors to the community. Three species (*Asimina triloba, Cercis canadensis, Carpinus caroliniana*) more commonly found in the understory appear insignificantly in the canopy (total of 4.61% of IV). Genera represented by more than one species include *Quercus* (5 species, 22.8 % of IV), *Acer* (2 species, 14.99%), *Carya* (3 species, 8.01%), and *Ulmus* (2 species, 6.38%). Only one canopy species was seen that was not sampled; a few large *Betula nigra* trees grow in shallow water and swampy conditions near the confluence of the creek and the bay.

Saplings and Small Trees

Appendix 3 gives data on the 24 species, represented by 576 stems, that were measured in this stratum (dbh 2.54-10.15 cm). Saplings and small trees found that did not appear in the canopy include *Carya laciniosa, Cornus florida, Corylus americana, Crataegus viridis, Fraxinus americana, Ilex decidua, Lindera benzoin,* and *Viburnum rufidulum.* Canopy species that did not appear in this stratum are *Quercus alba, Quercus bicolor, Quercus imbricaria, Quercus pagoda, Quercus palustris,* and *Sassafras albidum.* Appendix 3 indicates clear dominance by *Asimina triloba* (22.80% of IV), which occurred throughout and often in dense stands. Other typical understory species of importance were *Carpinus caroliniana* (7.28%), and *Ilex decidua* (4.28%). *Acer rubrum, Acer saccharum, Liquidambar styraciflua, Ulmus rubra, Ulmus alata, Celtis occidentalis, Liriodendron tulipifera,* and *Carya ovata*, all canopy species, provide over 51% of total IV in this stratum. The absence of oaks is noticeable and potentially significant for future canopy structure.

Shrubs and Woody Seedlings

Data for shrubs and woody seedlings (dbh <2.54 cm) are given in Appendix 4. Identifications were to genus only for *Carya, Fraxinus,* and *Ulmus*; oaks were grouped into the "whites" and "red-blacks." A total of 725 stems was counted. *Lindera benzoin* (24.35% of IV) and *Asimina triloba* (20.49%) are the clear dominants. As in the saplings and small trees strata, few oaks were seen.

Woody Vines

Woody vines were not sampled. Common taxa observed were crossvine (*Bignonia capreolata*), wild grapes (*Vitis* spp.), greenbriar (*Smilax rotundifolia*), poison ivy (*Rhus radicans*), and Virginia creeper (*Parthenocissus quinquefolia*).

SUMMARY

This paper represents the second in our series on bottomland forests of the lower Cumberland River basin in Tennessee and Kentucky. Data on the Long Pond Slough site in Montgomery County, Tennessee, are presented in a companion paper. In addition, we are summarizing published and unpublished data on the herbaceous flora of bottomland forests and will present these results in a future paper.

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Appendix 1. Average dbh (cm) and size class distribution for all stems sampled (830) with dbh ≥2.54 cm.

Taxa	No.	Avg. DBH	Size Classes & Number of Stems in Each								
			2.54-10.15	10.16-20.31	20.32-30.47	30.48-40.63	40.64 - 50.79	50.80-60.95	60.96-71.11	71.12-81.27	81.28-91.43
Acer rubrum	120	9.18	85	25	8	1	-	1	-	-	-
Acer saccharum	66	8.58	46	18	1	-	1	-	-	-	-
Asimina triloba	190	4.33	187	3	-	-	-	-	-	-	-
Carpinus caroliniana	46	7.01	37	9	-	-	-	-	-	-	-
Carya cordiformis	8	19.49	3	2	1	1	1	-	-	-	-
Carya laciniosa	7	4.61	7	-	-	-	-	-	-	-	-
Carya ovata	21	18.82	12	2	1	2	2	2	-	-	-
Carya tomentosa	3	31.75	1	-	-	1	-	1	-	-	-
Celtis laevigata	7	32.51	2	1	1	-	2	-	-	1	-
Celtis occidentalis	17	7.04	14	3	-	-	-	-	-	-	-
Cercis canadensis	2	7.88	1	1	-	-	-	-	-	-	-
Cornus florida	4	6.09	4	-	-	-	-	-	-	-	-
Corylus americana	7	2.58	7	-	-	-	-	-	-	-	-
Crataegus viridis	2	3.05	2	-	-	-	-	-	-	-	-
Fraxinus americana	6	3.35	6	-	-	-	-	-	-	-	-
Fraxinus pennsylvanica	8	4.86	7	1	-	-	-	-	-	-	-
Ilex decidua	23	3.65	23	-	-	-	-	-	-	-	-
Lindera benzoin	3	2.88	3	-	-	-	-	-	-	-	-
Liquidambar styraciflua	99	21.01	41	25	10	4	2	10	5	2	-
Liriodendron tulipifera	30	12.92	17	9	2	1	-	-	-	1	-
Nyssa sylvatica	44	27.89	4	10	9	13	7	1	-	-	-
Quercus alba	3	61.13	-	-	-	-	-	1	2	-	-
Quercus bicolor	1	42.42	-	-	-	-	1	-	-	-	-
Quercus imbricaria	1	64.01	-	-	-	-	-	-	1	-	-
Quercus pagoda	26	61.98	-	1	-	5	3	-	6	8	3
Quercus palustris	1	49.53	-	-	-	-	1	-	-	-	-
Sassafras albidum	1	29.97	-	-	1	-	-	-	-	-	-
Ulmus alata	37	8.97	26	6	4	1	-	-	-	-	-
Ulmus rubra	46	8.02	40	3	1	1	-	-	1	-	-
Viburnum rufidulum	1	3.30	1	-	-	-	-	-	-	-	-
TOTALS	830	12.57	576	119	39	30	20	16	15	12	3

Appendix 2. Data for trees (≥10.16 cm dbh), ranked by I.V. (254 stems).

Species	No. stems	Avg. DBH (cm)	Density (No./ha)	Rel. Density	Basal Area (m^2/ha)	Rel. Basal Area	No. Plots	Freq.	Rel. Freq.	I.V. (300)	% of I.V.
Liquidambar styraciflua	58	31.78	89.55	22.84	10.15	24.94	15	93.8	13.51	61.29	20.43
Quercus pagoda	26	61.98	40.14	10.24	13.36	32.85	14	87.5	12.60	55.69	18.56
Nyssa sylvatica	40	30.19	61.76	15.75	5.03	12.37	15	93.8	13.51	41.63	13.88
Acer rubrum	35	18.00	54.04	13.78	1.71	4.21	11	68.8	9.91	27.90	9.30
Acer saccharum	20	16.10	30.88	7.87	0.81	1.99	8	50.0	7.20	17.06	5.69
Carya ovata	9	36.83	13.90	3.54	1.75	4.29	6	37.5	5.40	13.23	4.41
Liriodendron tulipifera	13	22.59	20.07	5.12	1.24	3.06	5	31.3	4.51	12.69	4.23
Ulmus alata	11	19.44	16.98	4.33	0.59	1.45	6	37.5	5.40	11.18	3.73
Carpinus caroliniana	9	12.31	13.90	3.54	0.17	0.42	5	31.3	4.51	8.47	2.82
Celtis laevigata	5	41.91	7.72	1.97	1.36	3.33	3	18.8	2.71	8.01	2.67
Ulmus rubra	6	27.39	9.26	2.36	0.82	2.00	4	25.0	3.60	7.96	2.65
Carya cordiformis	5	28.60	7.72	1.97	0.60	1.47	4	25.0	3.60	7.04	2.35
Quercus alba	3	61.13	4.63	1.18	1.37	3.36	2	12.5	1.80	6.34	2.11
Asimina triloba	3	12.70	4.63	1.18	0.06	0.15	3	18.8	2.71	4.04	1.35
Carya tomentosa	2	43.56	3.09	0.79	0.47	1.16	2	12.5	1.80	3.75	1.25
Celtis occidentalis	3	11.68	4.63	1.18	0.05	0.12	2	12.5	1.80	3.10	1.03
Quercus imbricaria	1	64.01	1.54	0.39	0.50	1.22	1	6.3	0.91	2.52	0.84
Quercus palustris	1	49.53	1.54	0.39	0.30	0.73	1	6.3	0.91	2.03	0.68
Quercus bicolor	1	42.42	1.54	0.39	0.22	0.54	1	6.3	0.91	1.84	0.61
Sassafras albidum	1	29.97	1.54	0.39	0.11	0.27	1	6.3	0.91	1.57	0.52
Cercis canadensis	1	10.16	1.54	0.39	0.01	0.03	1	6.3	0.91	1.33	0.44
Fraxinus pennsylvanica	1	10.16	1.54	0.39	0.01	0.03	1	6.3	0.91	1.33	0.44
TOTALS	254	30.04	392.14	100.00	40.64	100.00		694.40	100.00	300.00	100.00

Appendix 3. **Data for saplings and small trees (2.54-10.15 cm dbh), ranked by I.V. (576 stems).**

Species	No. stems	Avg. DBH (cm)	Density (No./ha)	Rel. Density	Basal Area. (m^2/ha)	Rel. Basal Area	No. Plots	Freq.	Rel. Freq.	I.V. (300)	% I.V.
Asimina triloba	187	4.20	288.73	32.47	0.463	23.90	16	100.0	12.02	68.39	22.80
Acer rubrum	85	5.55	131.24	14.76	0.363	18.73	10	62.5	7.51	41.00	13.67
Acer saccharum	46	5.31	71.02	7.99	0.177	9.14	11	68.8	8.27	25.40	8.47
Liquidambar styraciflua	41	5.77	63.30	7.12	0.188	9.73	9	56.3	6.77	23.62	7.87
Carpinus caroliniana	37	5.72	57.13	6.42	0.168	8.66	9	56.3	6.77	21.85	7.28
Ulmus rubra	40	5.11	61.76	6.94	0.140	7.25	7	43.8	5.27	19.46	6.49
Ulmus alata	26	4.54	40.14	4.51	0.079	4.06	10	62.5	7.51	16.08	5.36
Ilex decidua	23	3.65	35.51	3.99	0.040	2.08	9	56.3	6.77	12.84	4.28
Celtis occidentalis	14	6.04	21.62	2.43	0.071	3.64	6	37.5	4.51	10.58	3.53
Liriodendron tulipifera	17	5.53	26.25	2.95	0.072	3.70	4	25.0	3.01	9.66	3.22
Carya ovata	12	5.31	18.53	2.08	0.046	2.35	6	37.5	4.51	8.94	2.98
Fraxinus pennsylvanica	7	4.25	10.81	1.22	0.017	0.87	6	37.5	4.51	6.60	2.20
Carya laciniosa	7	4.61	10.81	1.22	0.020	1.04	5	31.5	3.76	6.02	2.01
Fraxinus americana	6	3.35	9.26	1.04	0.009	0.46	4	25.0	3.01	4.51	1.50
Cornus florida	4	6.10	6.18	0.69	0.021	1.07	3	18.8	2.26	4.02	1.34
Corylus americana	7	2.58	10.81	1.22	0.006	0.28	3	18.8	2.26	3.76	1.25
Nyssa sylvatica	4	4.83	6.18	0.69	0.013	0.69	3	18.8	2.26	3.64	1.21
Lindera benzoin	3	2.88	4.63	0.52	0.003	0.16	3	18.8	2.26	2.94	0.98
Celtis laevigata	2	9.02	3.09	0.35	0.020	1.01	2	12.5	1.50	2.86	0.95
Carya cordiformis	3	4.32	4.63	0.52	0.007	0.38	2	12.5	1.50	2.40	0.80
Crataegus viridis	2	3.05	3.09	0.35	0.002	0.12	2	12.5	1.50	1.97	0.66
Carya tomentosa	1	8.13	1.54	0.17	0.008	0.41	1	6.3	0.76	1.34	0.45
Cercis canadensis	1	5.59	1.54	0.17	0.004	0.20	1	6.3	0.76	1.13	0.38
Viburnum rufidulum	1	3.30	1.54	0.17	0.001	0.07	1	6.3	0.76	1.00	0.33
TOTALS	576	4.87	889.34	100.00	1.938	100.00		832.10	100.00	300.00	100.00

Appendix 4. Data for shrubs and woody seedlings (<2.54 cm dbh), ranked by I.V. (725 stems).

Taxa	No. Stems	Density (No./ha)	Rel. Density	No. Plots	Freq.	Rel. Freq.	I.V. (200)	% I.V.
Lindera benzoin	261	4027.75	36.00	16	100.00	12.70	48.70	24.35
Asimina triloba	205	3163.56	28.28	16	100.00	12.70	40.98	20.49
Carya spp.	23	354.94	3.17	13	81.25	10.32	13.49	6.75
Fraxinus spp.	26	401.23	3.59	12	75.00	9.52	13.11	6.56
Nyssa sylvatica	33	509.26	4.55	10	62.50	7.94	12.49	6.25
Ulmus spp.	25	385.80	3.45	9	56.25	7.14	10.59	5.30
Liriodendron tulipifera	13	200.62	1.79	6	37.50	4.76	6.55	3.28
Liquidambar styraciflua	18	277.78	2.48	5	31.25	3.97	6.45	3.23
Sassafras albidum	40	617.28	5.52	1	6.25	0.79	6.31	3.16
Carpinus caroliniana	8	123.46	1.10	6	37.50	4.76	5.86	2.93
Acer saccharum	14	216.05	1.93	5	31.25	3.97	5.90	2.95
Quercus (reds-blacks)	6	92.59	0.83	6	37.50	4.76	5.59	2.80
Ilex decidua	15	231.48	2.07	4	25.00	3.17	5.24	2.62
Corylus americana	13	200.62	1.79	3	18.75	2.38	4.17	2.09
Acer rubrum	7	108.02	0.97	3	18.75	2.38	3.35	1.68
Celtis occidentalis	6	92.59	0.83	3	18.75	2.38	3.21	1.61
Symphoricarpos orbiculatus	3	46.30	0.41	2	12.50	1.59	2.00	1.00
Cornus florida	2	30.86	0.28	2	12.50	1.59	1.87	0.94
Prunus serotina	4	61.73	0.55	1	6.25	0.79	1.34	0.68
Aralia spinosa	1	15.43	0.14	1	6.25	0.79	0.93	0.47
Cercis canadensis	1	15.43	0.14	1	6.25	0.79	0.93	0.47
Quercus (whites)	1	15.43	0.14	1	6.25	0.79	0.93	0.47
Totals	725	11,188.21	100.00		787.50	100.00	200.00	100.00

CHARACTERIZATION OF SOME REMNANT BOTTOMLAND FORESTS OF THE LOWER CUMBERLAND RIVER IN TENNESSEE AND KENTUCKY:

3. THE LONG POND SLOUGH SITE IN MONTGOMERY COUNTY, TENNESSEE

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ABSTRACT. In 1972, a secondary but relatively undisturbed bottomland forest surrounding Long Pond Slough, an old meander channel of the Cumberland River in Montgomery County, Tennessee, was sampled. The data have not been published and the forest was selectively harvested soon after sampling. The random pairs sampling technique was used to measure 428 trees with a diameter breast height (dbh) of at least 10.2 cm. The sampling yielded 30 taxa representing 18 genera. Average dbh for all stems was 23.60 cm. Importance values (IV = 300) indicated dominance by a mixture of mesic-hydric species, including *Ulmus rubra* (15.57% of IV), *Celtis laevigata* (14.53%), *Carya cordiformis* (13.33%), *Quercus shumardii* (8.17%), *Celtis occidentalis* (7.71%), *Carya laciniosa* (7.46%), *Quercus macrocarpa* (4.89%), *Fraxinus americana* (4.87%), *Acer saccharinum* (4.19%), and *Fraxinus pennsylvanica* (3.84%). These ten species accounted for 84.56% of IV. Genera represented by more than one species included *Quercus* (7 species, 16.51% of IV), *Carya* (3 species, 22.74%), *Celtis* (2 species, 22.24%), *Fraxinus* (2 species, 8.71%), and *Acer* (3 species, 6.66%). No quantitative information was obtained on subcanopy species.

INTRODUCTION

This is the third paper in our series presenting the results of vegetational and floristic studies of remnant bottomland forests along the lower Cumberland River, south and east of Barkley Dam in Kentucky and Tennessee. Locations are shown in Figure 1 of the second paper of the series presented in this volume. We here give the results of an analysis of a bottomland forest that surrounded Long Pond Slough (LPS) in Montgomery County, Tennessee, when the sampling data were obtained in 1972. The woodland was selectively harvested shortly thereafter.

THE STUDY AREA

Location and Description

LPS is a 12-hectare wetland on the floodplain of the lower Cumberland River (Barkley Reservoir) in Montgomery County, northwestern Middle Tennessee. The Slough lies approximately 10 km west of Clarksville, Tennessee, centered at 87°26'00" W longitude and 36°30'10" N latitude on the New Providence, 1957, and Palmyra, 1958, USGS topographic quadrangles. It is within the Western Highland Rim Subsection, Highland Rim Section, of the Interior Low Plateau Physiographic Province (Fenneman 1938). The site appears to be an old river meander channel that contains permanent water. Such slow-flowing, shallow swamps-marshes historically have been referred to as sloughs in the southeastern United States (Mitsch and Gosselink 1986). LPS is now a designated Tennessee wetland with more than one-half of the site owned and managed by the Tennessee Wildlife Resources Agency as part of a program to acquire targeted wetlands across the state (Tennessee Environmental Policy Office 1996).

Long Pond Slough is on an alluvial terrace and includes an elongated pond of 6 ha. The permanent water is surrounded by a narrow band of woodlands where conditions range from emergent marsh to swamp and bottomland hardwood forest (Figure 1). At midpoint of the pond, the eastern edge is about 500 m west of the Cumberland River while the western edge is about 150 m east of footslopes of adjacent uplands. Cultivated fields (corn, soybeans, tobacco) and/or pastures completely surround the wetland, which is rarely visited except by hunters (deer, small game, waterfowl). The elevation is 114 m above sea level or 4.6 m above normal summer pool elevation of Barkley Reservoir. Water levels of the slough are maintained by run-off from adjacent lands and by occasional flooding from the river; yearly and sometimes multi-yearly river overflow (backwater) occurred before construction of Barkley Dam in 1966. Underground springs also may be significant since the water level drops only slightly in dry years. LPS drains from the south end where beaver dams also effect water levels.

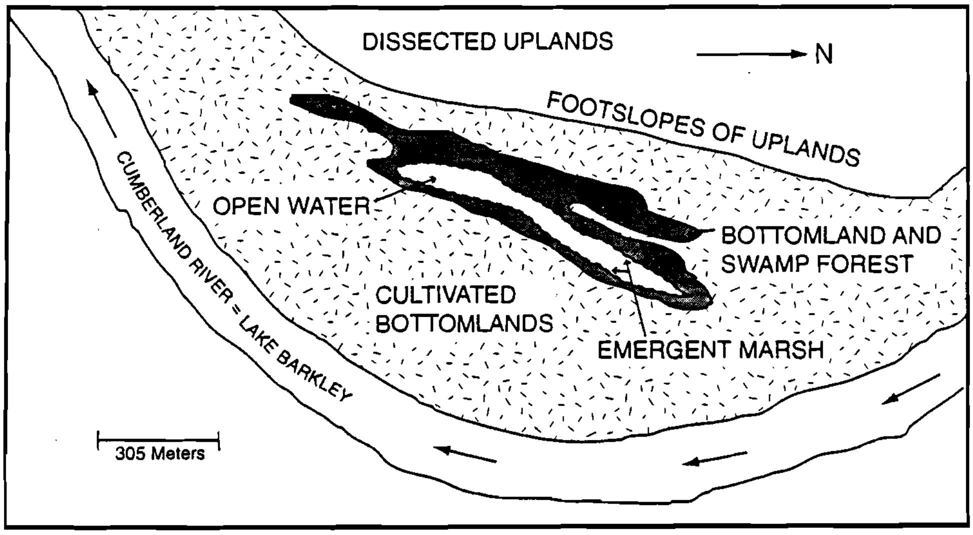

Figure 1. Topographic map of Long Pond Slough, Montgomery County, Tennessee, redrawn from aerial photograph in Lampley *et al.* (1975).

The substrate is Quaternary (Pleistocene and Recent) alluvium consisting of unconsolidated silt, sand, clay and gravel up to 15 m in thickness (Marsh 1969, Marsh and Marcher 1975). This substrate lies within a bedrock valley developed in the St. Louis and Warsaw Limestones of middle Mississippian age (Quarterman and Powell 1978).

Soils of three series occur in the area (Lampley *et al.* 1975). Newark silt loam (Newark Series) on the west side of LPS is a poorly drained soil of first bottoms. It mostly occurs in narrow bands with slopes of 0-2%, has slight-medium acidity, and the natural fertility is high. Ponding is common, the water table is high, and it is not well suited to row crops. Lindside silt loam (Lindside Series) occupies the east side. This nearly level soil (slopes less than 2%) has medium to neutral acidity, high natural fertility, and occurs on first bottoms. It is moderately well drained and suitable for row crops. Soils of the Arrington Series surround the area just outside of the study zones. This is the deep, occasionally flooded but well drained and highly productive soil of floodplains. Slopes are less than 2% and almost all Arrington soils are in tilth.

The climate of the area is warm-temperate and characteristic of a humid-mesothermal type (Thornthwaite 1948). The growing season often exceeds 200 days and extends from mid-April to mid-late October. Soils normally freeze to a depth of several cm each winter but rarely remain frozen for more than a few days. It is not uncommon for the standing water of LPS to freeze completely, with partial or complete thawing usually within five days. Yearly rainfall averages 120-125 cm; late winter-spring are typically the wettest seasons and autumn the driest; an average winter has several small snowfalls totaling 25-35 cm but no measurable snowfall occurs some winters (Chester *et al.* 1995).

LPS lies within the diverse Western Mesophytic Forest Region of Braun (1950); this transition region is characterized by a wide variety of forest types and the codominance of several species. All area forests are second-growth and dominated by several species of four major genera: *Acer, Carya, Quercus*, and *Ulmus* (Chester *et al.* 1995).

The vascular flora of LPS and the surrounding area was studied by Dodson (1973) and incorporated into a thesis. Additional floristic studies between 1973-1996 were combined with the Dodson (1973) data and the known vascular flora presented in an annotated list of 251 species (Chester and Dodson 1996). Plant community types were summarized as: (1) vegetated open water, (2) emergent marsh, (3) swamp, and (4) bottomland forest. The bottomland forest community occupies a narrow strip surrounding areas of permanent inundation. Flooding at depths ranging from a few cm to a m or more and for periods of 1-3 days is commonplace in winter and spring. The soil is usually exposed in summer and fall although the soil may be saturated. Standing water is frequently present in depressions during the growing season. The very existence of the forest attests to the wetness of soil since it would have been long since cleared if not too wet for spring cultivation. This forest community was sampled by Dodson (1973) but the results were not published. The purpose of this report is to present the results of that study. The data are especially important since the forest was selectively and heavily harvested soon after this study.

METHODS

The forest was sampled during the summer of 1972 by Frank Dodson, Richard Jensen, and Joe Schibig, using the random pairs method developed by Cottam (1947) and Cottam and Curtis (1949, 1955, 1956), and Cottam, Curtis, and Hale (1953), as summarized by Phillips (1959). A single line transect was taken around the periphery of the standing water within forested areas not considered swamp forest. At each of 214 points, each spaced 6.2 meters apart, the two nearest trees with diameters at breast height (dbh) of at least 10.2 cm were recorded by species and dbh taken to the nearest 0.25 cm.

The data were used to calculate for each species relative (percent) density (= number of individuals of a species/number of individuals of all species X 100), relative (percent) frequency (= number of points of occurrence for a species/number of points of occurrence of all species X 100), and relative (percent basal area (= basal area of species in square meters/total basal area of all species X 100). An importance value was obtained by summing the relative values (maximum = 300). Nomenclature has been upated to correspond to that of Wofford and Kral (1993).

RESULTS AND DISCUSSION

Size Class Distribution

The 428 trees sampled included 30 taxa representing 18 genera. Appendix 1 gives an alphabetical listing of all taxa with the number of each, average diameter per species, and size class distribution. Nearly one-half of stems sampled (210 of 428 = 49.07%) were in the 10.16-20.31 cm (4.0-8.0 inches) category. Average dbh for all stems was 23.60 cm. Average dbh for dominant taxa were: *Carya cordiformis* (21.84 cm), *C. laciniosa* (18.49), *Celtis laevigata* (23.37), *C. occidentalis* (23.32), and *Quercus shumardii* (35.53). The "large tree" category (dbh 50.8 cm = 20 inches and above) included *Acer saccharinum* (2 stems), *Carya cordiformis* (1), *Fraxinus americana* (1), *Platanus occidentalis* (1), *Quercus macrocarpa* (1), *Q. shumardii* (4), and *Ulmus rubra* (3).

Canopy Species

Appendix 2 provides data on the 428 stems sampled, including ranking by IV and percent of total IV. The data indicate that this forest consisted of a mixture of mesic-hydric species. Three taxa, *Ulmus rubra* (15.57% of IV), *Celtis laevigata* (14.53), and *Carya cordiformis* (13.33) accounted for nearly one-half of IV (43.43%). Three other species, *Quercus shumardii* (8.17%), *Celtis occidentalis* (7.71), and *Carya laciniosa* (7.46) accounted for an additional 23.34%. *Quercus macrocarpa* (4.89%), *Fraxinus americana* (4.87), *Acer saccharinum* (4.19), and *Fraxinus pennsylvanica* (3.84) contributed an additional 17,79%. These ten species accounted for 84.56% of IV. Genera represented by more than one species included *Quercus* (7 species, 16.51% of IV), *Carya* (3 species, 22.74%), *Celtis* (2 species, 22.24%), *Fraxinus* (2 species, 8.71%), and *Acer* (3 species, 6.66%). Thus, at the generic level this forest was dominated by *Carya, Celtis*, and *Quercus*.

Subcanopy Species

Small trees, saplings, shrubs, woody seedlings, and woody vines were not sampled. However, dense thickets of *Arundinaria gigantea, Asimina triloba, Lindera benzoin*, and *Smilax rotundifolia* occur throughout.

SUMMARY

This paper completes a three-part effort on our part to document the composition of remnant bottomland forests of the lower Cumberland River basin. Additional field work on other remnants will depend upon availability of sites and time contstraints of the authors. Work is underway that will summarize data on the herbaceous flora of these forests.

ACKNOWLEDGMENTS

Appreciation is extended to the Martin and Armistead families for granting us unrestricted access to Long Pond Slough through their property. David Johnson, Austin Peay State University Media Services, kindly prepared the figure.

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Appendix 1. Number of stems, average dbh (cm), and size class distribution for 428 stems sampled in the Long Pond Slough bottomland hardwood forest.

Taxa	No. Stems	Avg. dbh	10.16-20.31	20.32-30.47	30.48-40.63	40.64-50.79	50.80-60.95	60.96-71.11	71.12-81.-27	81.28-91.43
Acer negundo	8	27.25	2	3	2	1	-	-	-	-
Acer saccharinum	15	28.83	7	2	2	2	1	1	-	-
Acer saccharum	2	23.62	1	1	-	-	-	-	-	-
Asimina triloba	1	10.92	1	-	-	-	-	-	-	-
Carpinus caroliniana	7	13.21	7	-	-	-	-	-	-	-
Carya cordiformis	61	21.84	31	17	-	2	1	-	-	-
Carya laciniosa	38	18.49	27	6	4	1	-	-	-	-
Carya ovata	9	20.37	6	1	2	-	-	-	-	-
Celtis laevigata	66	23.37	30	20	12	4	-	-	-	-
Celtis occidentalis	35	23.32	16	12	3	4	-	-	-	-
Cercis canadensis	2	13.97	2	-	-	-	-	-	-	-
Diospyros virginiana	1	19.30	1	-	-	-	-	-	-	-
Fraxinus americana	21	22.20	12	4	3	1	1	-	-	-
Fraxinus pennsylvanica	18	21.46	8	9	1	-	-	-	-	-
Gleditsia triacanthos	3	23.19	1	1	1	-	-	-	-	-
Juglans nigra	4	22.68	1	3	-	-	-	-	-	-
Liquidambar styraciflua	1	24.64	-	1	-	-	-	-	-	-
Morus rubra	2	18.92	1	1	-	-	-	-	-	-
Ostrya virginiana	1	10.41	1	-	-	-	-	-	-	-
Platanus occidentalis	5	28.50	3	-	-	1	1	-	-	-
Populus deltoides	3	38.53	-	-	2	1	-	-	-	-
Quercus imbricaria	1	36.07	-	-	1	-	-	-	-	-
Quercus lyrata	2	26.04	-	2	-	-	-	-	-	-
Quercus macrocarpa	20	24.84	9	4	6	-	1	-	-	-
Quercus michauxii	1	29.72	-	1	-	-	-	-	-	-
Quercus palustris	7	21.59	3	3	1	-	-	-	-	-
Quercus rubra	3	29.39	2	-	-	-	1	-	-	-
Quercus shumardii	25	33.53	9	3	5	4	2	-	2	-
Robinia pseudoacacia	3	26.26	-	2	1	-	-	-	-	-
Ulmus rubra	63	24.79	29	21	6	4	1	-	1	1
TOTALS	428	23.60	210	117	62	25	9	1	3	1

Appendix 2. **Composition and structure of the canopy, Long Pond Slough bottomland hardwood forest community, based on 428 stems sampled.**

Taxa	No. Stems	% of Stems	Total BA (M^2)	Average BA (M^2)	% of BA	No. Points	Rel. Freq.	IV 300	% of IV
Ulmus rubra	63	14.72	4.10	0.07	17.31	58	14.68	46.71	15.57
Celtis laevigata	66	15.42	3.31	0.05	13.98	56	14.18	43.58	14.53
Carya cordiformis	61	14.25	2.74	0.04	11.57	56	14.18	40.00	13.33
Quercus shumardii	25	5.84	2.92	0.12	12.33	25	6.33	24.50	8.17
Celtis occidentalis	35	8.18	1.80	0.05	7.60	29	7.34	23.12	7.71
Carya laciniosa	38	8.88	1.22	0.03	5.15	33	8.35	22.38	7.46
Quercus macrocarpa	20	4.67	1.17	0.06	4.94	20	5.06	14.67	4.89
Fraxinus americana	21	4.91	1.04	0.05	4.39	21	5.32	14.62	4.87
Acer saccharinum	15	3.50	1.31	0.09	5.53	14	3.54	12.57	4.19
Fraxinus pennsylvanica	18	4.21	0.71	0.04	3.00	17	4.30	11.51	3.84
Acer negundo	8	1.87	0.51	0.06	2.15	8	2.03	6.05	2.02
Carya ovata	9	2.10	0.35	0.04	1.48	9	2.28	5.86	1.95
Quercus palustris	7	1.64	0.27	0.04	1.14	7	1.77	4.55	1.52
Platanus occidentalis	5	1.17	0.45	0.09	1.90	5	1.27	4.34	1.45
Carpinus caroliniana	7	1.64	0.10	0.01	0.42	7	1.77	3.83	1.28
Populus deltoides	3	0.70	0.35	0.12	1.48	3	0.76	2.94	0.98
Quercus rubra	3	0.70	0.29	0.10	1.22	3	0.76	2.68	0.89
Juglans nigra	4	0.93	0.17	0.04	0.72	4	1.01	2.66	0.89
Robinia pseudoacacia	3	0.70	0.17	0.06	0.72	3	0.76	2.18	0.73
Gleditsia triacanthos	3	0.70	0.14	0.05	0.59	3	0.76	2.05	0.68
Quercus lyrata	2	0.47	0.11	0.06	0.46	2	0.51	1.44	0.48
Acer saccharum	2	0.47	0.09	0.05	0.38	2	0.51	1.36	0.45
Morus rubra	2	0.47	0.06	0.03	0.25	2	0.51	1.23	0.41
Cercis canadensis	2	0.47	0.03	0.02	0.13	2	0.51	1.11	0.37
Quercus imbricaria	1	0.23	0.10	0.10	0.42	1	0.25	0.90	0.30
Quercus michauxii	1	0.23	0.07	0.07	0.30	1	0.25	0.78	0.26
Liquidambar styraciflua	1	0.23	0.05	0.05	0.21	1	0.25	0.69	0.23
Diospyros virginiana	1	0.23	0.03	0.03	0.13	1	0.25	0.61	0.20
Asimina triloba	1	0.23	0.01	0.01	0.04	1	0.25	0.52	0.17
Ostrya virginiana	1	0.23	0.01	0.01	0.04	1	0.25	0.52	0.17
TOTALS	428	99.99	23.68	1.64	99.98	395	99.99	299.96	99.99

VEGETATION RESULTS FROM EARLY LAND SURVEYS RECORDED IN REGISTER'S BOOKS, CAMPBELL COUNTY, TENNESSEE, 1806-1833

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ABSTRACT. Metes and bounds property transfer surveys from three Register Books were used to reconstruct forest composition in Campbell County, Tennessee, for the 1806-1833 period. Percentage species or species group composition agreement between the early surveys and modern inventories was relatively good. Oak, oak-other hardwoods, or oak-hickory forests probably prevailed on most upland area. Non-forested corners occurred rarely. Results suggest that surveys were chiefly from the Ridge and Valley part of the county. A large increase in percentages of pine taxa occurred between the time of the surveys and the modern inventories.

INTRODUCTION

Vegetation cover of the landscape at or near the time of settlement by Europeans or European-Americans is of interest to field scientists. Information of this type is used by historians (Williams 1989), paleoecologists (Delcourt *et al.* 1986), pedologists (Jenny 1980), anthropologists (Chapman and Shea 1981), vegetation biomass modelers (Waring and Schlesinger 1985), and vegetation ecologists (DeSelm 1994) who interpret present vegetation in terms of known environmental and historical factors (Mueller-Dombois and Ellenberg 1974).

Congressional Land Survey records have been used extensively to delimit midwestern vegetation (as Iverson *et al.* 1989). Similar surveys have been used in the Southeast, as in Alabama (Jones and Patton 1966), Florida (Delcourt and Delcourt 1977), Georgia (Plummer 1975), Kentucky (Bryant and Martin 1988), Louisiana (Delcourt 1976), and Tennessee (DeSelm 1994). These rectilinear surveys, with their north-south and east-west lines and regularly spaced landscape/tree/other vegetation observations, contrast with metes and bounds surveys where the records have less chronological and geographic pattern. Metes and bounds surveys, because of the absence of continuity and pattern, have been little used in studies of early settlement vegetation. Examples of usage may be found in DeSelm (1995) and DeSelm and Rose (1995).

This paper reports vegetation results gleaned from metes and bounds surveys in Campbell County, Tennessee, for 1806-1833 (Figure 1). The study area centers at about 36°22'N, 84°7'W and is included in major parts of the Block, Duncan Flats, Ivydell, Jacksboro, Jellico East, Jellico West, Lafollette, Pioneer, and Well Spring, Tennessee, U.S. Geological Survey 7.5 minute quadrangles. I report here the average forest composition seen by the surveyors and compare that information with that from more modern inventories.

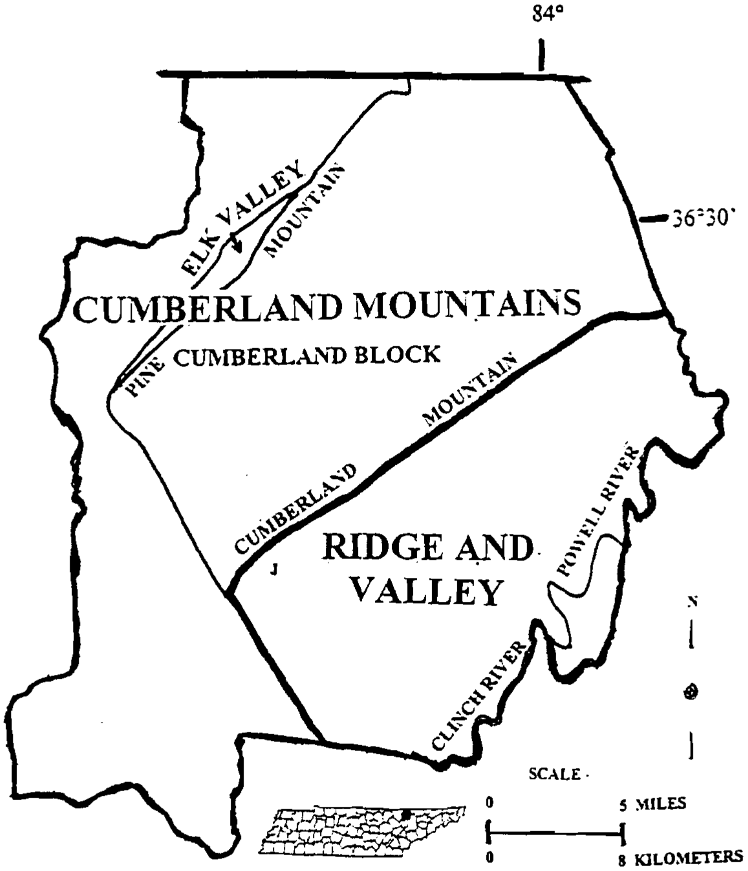

Figure 1. Map of Campbell County, Tennessee. J is location of Jacksboro. Separated are the Ridge and Valley and Cumberland Mountain parts of the county (Wilson *et al.* 1956). Base from Tennessee Department of Transportation map of Campbell County, 1991, scale 1/125,000.

CHARACTER OF THE SURVEYED AREA

The county straddles the Ridge and Valley Province and the Cumberland Mountain Section of the Appalachian Plateaus Province (Fenneman 1938). Mountain elevations vary from about 275 m to >1007 m; Ridge and Valley elevations vary from about 275-427 m. Drainage is partly to the south to the Clinch and Powell Rivers (here as Norris Lake), which cross or border the southern part of the county and run north to the Cumberland River.

The Cumberland Mountains part includes the Cumberland Block bordered by Cumberland Mountain and Pine Mountain with Elk Valley just to the north; other mountains lie to the west. Bedrock consists of nine mapped groups of geologic beds, each comprised of several members of sandstone, shale, and coal beds. Most bedrocks are horizontally disposed except on Cumberland and Pine Mountains where they may be nearly vertical (Wilson *et al.* 1956). Alluvium covers the valley floors over the sandstone and shale. Alluvium also covers the Elk Valley floor but several other bedrocks, including limestone and shale, outcrop on the Valley edges (Englund 1968).

Soils of the mountain area are mapped as the Bouldin-Rock Outcrop-Ramsey and Muskinghum-Gilpin-Jefferson State soil associations. They are hilly and steep, well drained, loamy and stony, acid soils classed as Typic Paleudults, Lithic and Typic Dystrochrepts, and Typic Hapludults (Springer and Edler 1980).

The Ridge and Valley area is characterized by northeast-southwest trending low ridges and wide valleys. The bedrocks are mapped as dolomite or dolomitic limestone beds (most of the area), limestone and shale beds, and several formations consisting of mixed limestone, siltstone, sandstone, and shale; sometimes dolomite is interbedded (Rodgers 1953).

Soils of the Ridge and Valley area are mapped as the Talbott-Rock Outcrop-Etawah and Fullerton-Dewey State soil associations. The first association is on undulating to hilly land. The soils have shallow to deep profiles, are well-drained, clayey or loamy, with some limestone outcrops. The second association is on rolling to hilly land. Soils have deep, well-drained, cherty and clayey profiles and lie over dolomitic limestone. The series are Typic Hapludalfs or Typic Paleudults (Springer and Elder 1980).

The flora of the area is well known (Wofford and Kral 1993). Studies of the forest vegetation include the general statements of Braun (1950), DeSelm (1984), Stephenson *et al.* (1993), and Hinkle *et al.* (1993). The vegetation of the Ridge and Valley part is mapped (Tennessee Valley Authority 1941) as yellow pine-hardwood over most of the area, with smaller areas of cedar-hardwood, upland hardwood, and oak-chestnut types. The Tennessee Valley Authority (1963) classes over two-thirds of their sample plots as upland hardwood, with less of the shortleaf and Virginia pine types, yellow pine hardwood, northern hardwoods, cove hardwoods, cedar hardwoods, and cedar-pine hardwoods. In the Tennessee Valley Authority (1967) study, elm-ash-maple, oak-hickory (replacing upland hardwood), black locust, beech-birch-hard maple (replacing northern hardwoods), yellow poplar, northern red oak-basswood-ash (replacing cove hardwoods), and hemlock hardwood types were also classed from their plot data. Martin (1971), in a study in nearby Ridge and Valley counties, classed over four dozen types from his sample data. Barrens occur occasionally in the Cumberland Plateau and in the limestone areas of the Ridge and Valley (DeSelm 1992, 1993; Ridenour 1941).

The study area was visited or occupied by Native American cultures at least 10,000 years before present (Archaic culture and the Paleoindian hunters earlier). Later cultures built villages along major streams, and the uplands were used especially for hunting and food gathering (Hudson 1976).

White settlement began about 1795 in the Powell Valley with the purchase of land by Henderson & Company. Settlement of Henderson & Company land and peripheral land, some held by survey and some by tomahawk rights, preceded the flurry of land purchase transactions and land occupations after the opening of the Registers Office in Jacksboro in 1806 (McDonald 1993). Forests were cleared, some land was drained in the valleys, and row crops were cultivated. Slopes were logged for farm timber, and the forests were grazed and often burned (surface fires) in the spring (DeSelm 1993).

METHODS

Three Register (of Deeds) Books (Campbell County 1806-1810, 1817-1820, 1820-1826) have been examined. They were copied (typed) by the Works Progress Administration 1937-1938; books A and C were made available at the Special Collections Library, The University of Tennessee, Knoxville. Book D is available from Mountain Press. These books contain hundreds of property transfers with some land transfer statements recording one or more trees at each angle call per survey. A total of 452 surveys were used, with 3212 stems (trees or sometimes a shrub) cited. The citation of the tree names at corners makes compilation of average forest composition possible.

Surveyors generally recorded a tree, a stream or river, or a topographic feature such as a ridge or hollow at each corner. The botanical qualifications of the surveyors are unknown. A stake was recorded at about one-fourth of the corners. Surveyors used the compass and measured distances in poles or chains and links. No point-to-tree distances or tree diameters were given. No attempt has been made to find surveyors lines on the ground, and for the most part, their specific locations are unknown.

Some surveys consisted entirely of staked corners that included city lots in Jacksboro. A few other surveys, especially large ones, used topographic features only and often referred to private plat maps. The fact that these surveys are, for the most part, placed adjacent to already settled and at least partly developed ("improved") land is suggested by the starting points on existing property lines of then current owners. Also, surveys often crossed roads and trails to homes, and some referred to "a stake in a field." Occasional surveys mentioned the non-native peach. Some surveys duplicated corner trees and these have been eliminated when recognized.

RESULTS

The surveys record some streams by names that are currently known and some that cannot be verified in modern records. The surveyor's topographic vocabulary included bluff, branch, cave, cliff (clift), creek, fork, hill, hollow, knob, ridge, river, sink, and spring. Trees were recorded by name, although sometimes with descriptors such as double, large, sapling (saplin), small, sprout, or stump. "Dedwood" was recorded in three surveys; it is interpreted to mean stump or snag. Plants named were generally trees which grow to overstory size, but a few understory tree names occur (as dogwood, *Cornus florida,* and holly, *Ilex* spp.). Plumbush (*Prunus* sp.), probably a shrub, also is named. An individual survey crossed landforms and various soil series and thus is not expected to represent a single plant community. However, some surveys included trees that indicate the presence of upland oak, mesic ravine, or river border communities.

Table 1 (appended) contains the probable scientific name corresponding to the surveyors plant names—spelling variations are included. Note the high percentage of oaks (*Quercus* spp., 39.8%), maples (*Acer* spp., 7.7%), and hickories (*Carya* spp., 8.4%) in the forests of the period. The ratio of oaks to hickories is over 4.7 to 1, and the ratio of oaks to pines exceeds

28.4 to 1. The high percentages of white oak (*Quercus alba*) and black oak (*Q. velutina*) suggests the occurrence of the white oak-black oak type as seen by Martin (1971) or separate types dominated by each of these taxa, both also seen by Martin (1971), Hinkle (1975, 1978, 1989), and Wade (1977). Hickories (*Carya* spp.) are important associates of oaks (as seen by Martin 1971), but pines (*Pinus* spp.) in this sample are insignificant (1.4%, ranking only thirteenth.). Post oak (*Quercus stellata*) ranks at a little over half as important as black oak, indicating its importance in the oak types (as seen by Martin 1971). Mesic forests represented by beech (*Fagus*), sugar maple (*Acer saccharum*), tulip poplar (*Liriodendron*), black walnut (*Juglans nigra*), and ash (*Fraxinus* spp.) reflect forests of ravines and lower north- and east-facing slopes. "McClary's sugar camp" and other sugar camps suggest local sugar maple abundance. Taxa of deeper ravines or protected slopes, such as buckeye (*Aesculus* spp.), basswood (*Tilia* spp.), and hemlock (*Tsuga*) are much less common. Mesic communities representing these types were seen by Martin (1971), Hinkle (1975), and Smith (1977). Stream and river-border taxa were reported occasionally and include boxelder (*Acer negundo*), red maple (*Acer rubrum*), hackberry (*Celtis* spp.), sweetgum (*Liquidambar*), sycamore (*Platanus*), and elm (*Ulmus* spp.). The true identity of water white oak and swamp oak are not known.

Comparison of the early surveys results with later inventory data appears in Table 1 (appended). Taxa which usually increase in abundance with disturbance (*e.g.*, red maple, hickories, tulip poplar, and pines) can be seen to do so. The increase in pines may be due to or the result of planting, invasion of old fields, and logging (Smith 1968). The increase in black locust is due to disturbance and planting. The increases in pin (scarlet) and chestnut oaks may be related to the less than full knowledge of oak species by the surveyors. Species whose relative abundance have decreased are sugar maple, chestnut (*Castanea dentata*), beech (*Fagus*), and white oak. These changes are probably the result of conversion of mesic and dry-mesic forests to agricultural uses. The decrease in chestnut is due to chestnut blight (Hepting 1971).

Non-forest vegetation was rarely seen in the surveys. The prominent use of stakes at survey corners is interpreted as a convenience for the surveyor rather than an absence of trees. The citing of bushes (actual or tree sprouts) at corners may mean tree absence or tree damage but probably means that a tree was not conveniently close to the corner.

Glades are part of two surveys. Adjoining the land of William H. Smith, the survey extends to "a stake in a glade;" the survey also mentions white oak and post oak nearby. In another survey, the description "beginning at a pine near Sampson David's line at the lower end of a glade extending to a black oak. . . ." is used. Whether or not these glades were in fact old fields is not known. Eroded or infertile cleared fields were abandoned in the nineteenth century (Killebrew *et al.* 1874) and commonly seen by the surveyors. It seems probable that these sites were cedar-pine glades or barrens best known from the Ridge and Valley part of the county (DeSelm 1993, DeSelm and Murdock 1993).

DISCUSSION

Reconstruction of vegetation cover at or near the time of white settlement in East Tennessee has been hampered by the lack of Congressional type rectilinear land survey data. The use of metes and bounds data in this study is the third attempt to reconstruct early forest composition in East Tennessee (see also DeSelm 1995, DeSelm and Rose 1995).

The survey data leave much to be desired. Of the 62 taxa reported, only 42 can be assigned to a modern species. Several genera (Table 1, appended) contain unknown species or groups of species (this assumes the surveyors could distinguish between, *e.g.*, the red oaks). *Quercus shumardii* was probably included in red or black oak; it was not described until 1860 (Little 1979). Martin (1971) recorded 23-40 overstory and understory tree taxa from old growth forest community types in nearby counties. On the other hand, the Tennessee Valley Authority study (1963) reports only 10 taxa to the species level and several groups: red oaks, hickories, other soft woods, and other soft-textured and hard-textured hardwoods. The 1967 Tennessee Valley Authority report is similar in this respect. Further, both Tennessee Valley Authority reports exclude non-commercial tree species and cull trees. Clearly the Martin studies (Martin 1971, 1978, Martin and DeSelm 1976) are the most comparable in species number used, whereas the forestry studies (Tennessee Valley Authority 1963, 1967; Cowan 1946) are most similar in random selection of trees and stands.

The number of community types (variant or variant groups) (Martin 1971) in nearby Ridge and Valley counties is 54. These vary from many kinds of oak forests on ridges and open slopes, pine forests chiefly on ridges, tulip poplar forests of open slopes and coves, mixed forests of lower slopes and coves, and bottomland swamp forests. The Tennessee Valley Authority (1963, 1967) group their data into 6-7 community types. Communities can scarcely be discerned from the survey data, although upland white oak and white oak-black oak or oak-hickory types are suggested by joint occurrences at survey corners. The mixed mesic forests are suggested by co-occurrences of beech and sugar maple. Swamps along streams with red maple, hackberry, sweetgum, sycamore, and elm are mentioned. However, most types described by Martin (1971) and the Tennessee Valley Authority (1963, 1967) are not distinguishable in the data.

In the surveys used in this study, the low percentage of pine, chestnut oak, hemlock (common in mountain hollows) and white pine, as well as the presence of cedar, and of glades, suggests that these surveys were chiefly from Ridge and Valley locations where the original settlements had been made. The Cumberland Mountains part of the county was surveyed to a much lesser extent. The two Tennessee Valley Authority studies (1963, 1967) were from the same part of the county (Tennessee River Valley) and are similar. They also are similar to the survey results in general. The biggest exception is pine, which has only 1.2% in the surveys, 18.8% and 21.9% in the 1960s (TVA data), and 28.3% in Cowan (1946). The Cowan report includes trees from both the Ridge and Valley and Cumberlands. This represents several hundreds of percent increase in pine between the end of the surveys (1833) and the Cowan report (1946). Heavy logging, increase in edge due to forest fragmentation, invasion of old fields, and planting have all contributed to the increase in the importance of pine (Smith 1968).

Most surveys of the kind discused in this paper are deficient in one or more ways. These deficits include (1) a lack of knowledge of locations of most surveys, (2) a lack of information on the starting points on property boundaries (which may have been disturbed), (3) the fact that some survey lines pass through disturbed areas along roads, (4) the unknown taxonomic expertise of the surveyors, (5) the possible non-random choice of corner trees, (6) the use of small trees and shrubs, and (7) the lumping of taxa by surveyors and modern inventory takers. In spite of these deficiences, the metes and bounds survey results constitute the only record of the vegetation present near the time of settlement in this part of Tennessee. Thus, they contribute greatly to historical botanical knowledge.

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APPENDIX

Table 1. Plant taxa seen in the early surveys as percent, with percentages from three later inventories.

Taxa	**% of Total Surveys 1806-1833**	**Cowan[1] 1946**	**TVA[2] 1963**	**TVA[3] 1967**
Acer rubrum (maple)	2.5		3.1	5.3
Acer negundo (box elder)	0.1			
Acer saccharum (sugar tree, shugar tree)	5.1			2.7
Acer, all maples	7.7	2.8		8.0
Aesculus octandra (buckeye)	1.1			
Alnus serrulata (alder)	0.1			
Amelanchier spp. (sarvis, service tree)	0.2			
Asimina triloba (poppaw, pappaw, pawpaw)	0.2			
Betula spp. (burch, birch)	0.3			
Carya spp. (hickory)	7.8			
Carya tomentosa (black hickory)	0.6			
Carya, all hickories	8.4	10.3	12.8	12.4
Carpinus caroliniana (hornbean)	6.3			
Castanea dentata (chestnut)	2.5			
Celtis spp. (hackberry)	0.2			
Cercis canadensis (redbud)	<0.1			
Cornus florida (dogwood)	6.8			
Crataegus/Prunus (white thorntree, thorntree)	0.2			
Crataegus/Viburnum (hawbush)	0.1			
Diospyros virginiana (persimmon)	0.4			
Fagus grandifolia (beech, beach)	7.1	3.4	1.9	0.7
Fraxinus spp. (ash)	1.4			1.7
F. quadrangulata (blue ash)	<0.1			
Ilex spp. (holly)	0.2			
Juniperus virginiana (ceder, ceadar, sedar, bull cedar)	0.6	0.7		
Juglans cinerea (white walnut)	1.0			
Juglans nigra (black walnut)	1.4		1.5	
Kalmia latifolia (laurel)	0.1			
Lindera benzoin (spicewood)	<0.1			
Liquidambar styraciflua (sweetgum)	0.6			
Liriodendron tulipifera (poplar)	5.5	6.9	8.8	8.8
Magnolia acuminata (cucumber)	0.3			
Morus rubra (mulberry)	0.4			
Nyssa sylvatica (blackgum)	2.6	0.7	3.5	2.5
Nyssa/Liquidambar (gum)	0.4			
Ostrya virginiana (ironwood)	0.7			
Oxydendron arboreum (sourwood, sowerwood)	1.7			

Table 1. Continued.

Taxa	% of Total Surveys 1806-1833	Cowan[1] 1946	TVA[2] 1963	TVA[3] 1967
Pinus spp. (pine)	1.2			
P. strobus (white pine)	0.2	0.7		
P. yellow		28.3	21.9	18.8
Platanus occidentalis (sycamore, cicamore)	0.9	0.7		
Prunus persica (peach)	0.1			
Prunus serotina (cherry tree)	0.2			
Prunus spp. (plum, plumbush)	0.1			
Quercus spp. (oak)	0.3			
Q. alba (white oak)	24.5		5.5	10.0
Q. bicolor (swamp white oak)	<0.1			
Q. coccinea (scarlet, pin oak)	<0.1		1.8	4.3
Q. falcata (Spanish oak)	2.2			
Q. montana (chestnut oak)	0.4		8.8	10.8
Q. rubra (red oak)	2.1			
Q. stellata (post oak)	3.7			
Q. velutina (black oak)	6.6			
Q. velutina, Q. rubra, Q. falcata	*10.9*		*9.6*	*10.0*
swamp oak	<0.1			
sweet acorn tree	0.1			
water oak	<0.1			
water white oak	0.1			
Quercus (all white oaks)	24.5	8.3	5.5	20.8
Quercus (all red oaks)	10.9	29.7	11.4	14.3
Quercus (all oaks)	39.8	38.0	25.7	35.1
Quercus and *Pinus*	41.0	67.0	47.6	53.9
Quercus and *Carya*	48.2	48.3	38.5	47.5
Robinia pseudo-acacia (locust)	0.1			2.3
Salix babylonica (weeping willow)	<0.1			
Sassafras albidum (sassafras)	0.3			
Tilia heterophylla (lynn, linn, lyn)	1.3			
Tsuga canadensis (spruce pine)	0.8			
Ulmus spp. (elm, ellum)	0.8			
Ulmus americana (white elm)	0.1			
Viburnum prunifolium (black haw)	<0.1			

[1] Percent volume (Cowan 1946)
[2] Percent of trees ≥ 5 inches (Tennessee Valley Authority 1963)
[3] Percent of trees ≥ 5 inches (Tennessee Valley Authority 1967)

VEGETATION STUDIES OF BARRENS IN NORTHWESTERN ALABAMA

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ABSTRACT. In a study of the flora and vegetation of five northwestern Alabama limestone prairie barrens, two were selected for study by the quadrat method. Nearly 50% of the known flora was included in these samples. Two of the eight rare-in-Alabama taxa, *Eriogonum longifolium* var. *harperi* and *Mirabilis albida*, occurred. At both sites, sample sets were obtained on three topographic units: low valley flats, ridge footslopes, and ridge sideslopes. Nearly 50% more taxa occurred on the steep sideslopes than on the footslopes or valley flats in spite of the shallower soil of the sideslopes and characteristic rock ledges. Decreasing richness downslope suggests that some factor, as past stock grazing and present-day deer grazing and browsing, has influenced species survival in the lower, more accessible vegetation.

INTRODUCTION

The limestone prairie barrens of northwestern Alabama are part of a system of grassy, prairie-like vegetation described as widespread in the uplands of the southeastern United States (DeSelm 1986, DeSelm and Murdock 1993). Alabama barrens were observed by early travelers (Gosse 1959, Griffith 1969) and by the surveyor Edmund Gaines in 1807-08 (Stone 1971). Later, agricultural scientists saw what they called prairies (Smith 1883) and "black limy prairie-like lands" (McCalley 1896). Plot sampling in Alabama grasslands was reported by Schuster and McDaniel (1973) and DeSelm (1993). Other studies on the landscape units studied here are the barrens flora (Webb *et al.* 1997), the glade flora (Baskin *et al.* 1995), and *Astragalus* distribution (Webb *et al.* 1992). Perennial grass cover distinguishes barrens from the rocky glades (Quarterman *et al.* 1993).

It is the purpose of this study to present details of the vegetation and site characteristics of this area unique to Alabama and to compare these results with those of the western Highland Rim (WHR) of Tennessee (DeSelm 1988, 1995, DeSelm and Chester 1993). Nomenclature generally follows Gleason and Cronquist (1991) where species authorities may be found.

THE STUDY AREA

Of the five barrens sites originally examined for floristic study (Webb *et al.* 1997), two were selected for detailed sampling: the Littleville and Cedar Creek sites. These lie within 200-220 m elevation in the Highland Rim Section of the Interior Low Plateaus Province (Sapp and Emplaincourt 1975). Topography is hilly, but bedrock is flat-lying Mississippian limestones underlain by fissures, cracks, and caves (Adams *et al.* 1926, Szabo *et al.* 1988). Soils are mapped as the Colbert series or Rockland in both Colbert County (Bracken and Gray 1939) and Franklin County (Sherard *et al.* 1965) and are shallow, stony, and clayey. The study area lies within the Western Mesophytic Forest Region (Braun 1950) or the Oak-Hickory-Pine Forest Region (Skeen *et al.* 1993); both studies describe the oak and oak-pine forests and note upland grassland present.

Northwestern Alabama was the living and hunting area of a long succession of Native American cultures beginning ca. 10,000 years before present (YBP) (Swanton 1946, Hudson 1976). These cultures are all thought to have used fire as a management tool (Williams 1989). European settlement began in the 1806-1832 period (Abernathy 1922) when areas with gentle topography were cleared for row crops. Most of the rest of the landscape was grazed by domestic stock until the end of the open range period (ca. 1940s) (Smith 1883, McCalley 1896, McWilliams 1992). Additional information about the study area is included in Webb *et al.* (1997).

METHODS

Reconnaissance study of several barrens began in 1972 and continued until 1992. Each barren site consisted of an open valley flat (0-5% slope), the footslope (11-20% slope), and steep sideslope (32-70% slope) of the adjacent ridge. Plot sampling was conducted on each landform at the Littleville (34°35'22"N, 87°39'50"N) and Cedar Creek (34°33'25"N, 87°59'05"N) sites in August 1988, at the time of peak community biomass and species richness. Twenty 0.5 x 1.0 m (0.5 m^2) plots were placed at one meter intervals on each landform/site. Percentage cover was estimated for bedrock, gravel, bare soil, tree litter, and each plant taxon. Slope angles and aspects were recorded. In the center of each plot, a steel rod was inserted into the soil to the depth of maximum rock resistance. The rock was believed to be bedrock, but in some plots it may have been colluvial profile stone.

In each set of 20 plots, frequency of each species was calculated, summed, and relative frequency calculated. Cover estimates were added, and relative cover/species was calculated. Relative frequency and relative cover were summed to obtain the Importance Value (IV = 200) for each species. Sorenson's Species-Presence Index of Similarity (Mueller-Dombois and Ellenberg 1974) was used to compare data between sites and with the WHR.

RESULTS AND DISCUSSION

A comparison of the total (plot) floras of the two study areas with sample floras from the WHR reveals a Sorenson Index of 61.0%. Littleville and Cedar Creek are similar at 67.8%. The vegetation was dominated by perennial grasses as it appeared aspectually. Characterized by species, five of six sample plot sets were dominated by *Schizachyrium scoparium*; the steep sideslope at Littleville was dominated by *Sporobolus clandestinus*. In five plot sets, the second dominant was a graminoid species: *Sporobolus clandestinus*, *Schizachyrium*, *Carex* or *Bouteloua* (Tables 1, 2, appended). On the low flat at Cedar Creek, *Solidago nemoralis* was the second dominant. These sites were much less uniform in dominants than the xeric grasslands of the WHR (DeSelm 1988, DeSelm and Chester 1993).

At Littleville, the three parts of the topographic gradient (Table 1, appended) illustrated both the continuity of species and species groups across the gradient and the uniqueness of some species' distribution. In spite of their proximity (the topographic units were only a few meters apart), the floras of the topographic units were only similar (Sorenson's Index) in the range of 59.3-68.4). Species richness varied: sideslopes=SS (46 taxa) > low flats=LF (34 taxa) > footslopes=FS (30 taxa). The most taxa occurred on the SS with intermediate cover of exposed rock, gravel and soil, and mean soil depth (Table 3, appended). Unique taxa (Oberholster and Hilton 1996) occurred upslope (FS and SS). Total plant cover and total graminoid cover are arrayed LF > SS > FS. High cover occurs upslope (SS) where rock, gravel, and soil, as well as shallow bedrock outcrops, are most exposed (Table 3, appended). High cover also occurs downslope (LF) on deeper soils.

At Cedar Creek, the topographic unit floristic similarities ranged from 53.9-56.3. Richness again varied as SS (55 taxa) > LF (37 taxa) > FS (34 taxa). Richness peaked on SS with shallow rock and intermediate exposure of rock, gravel, and soil (Table 3, appended). State listed taxa again occurred on the upper slopes (FS, SS). Total cover and total graminoid cover varied as SS > LF > FS. As with richness, maximum covers (on SS) occur with shallow soil and intermediate rock, gravel, and soil exposure.

Although the quadrated flora is only about half of the total flora, frequencies nonetheless follow Raunkiaer's expected distributions: class A (1-20%) > B (21-40%) > C (41-60%) > D (61-80%) < E (81-100%). Class D (1.2% of the flora) and Class E (2.4% of the flora) indicate few dominant taxa and low homogeneity (Oosting 1956, Raunkiaer 1934). Few taxa in the higher abundance classes, only 18 at Littleville and 16 at Cedar Creek (29 total taxa), occurred across all three parts of the topographic gradient. Of the across-the-gradient taxa, only *Gaura filipes* followed the trend of most cover on deepest, least rocky soil, and least cover on the most shallow, most rocky soil. This suggests that other factors beyond profile depth and stoniness may be influencing available soil moisture (Brady 1974), and hence controlling the cover trend. It seems possible that grazing/browsing of both past stock and of deer at present may well influence individual species and genet distribution directly by selective consumption, by increasing competitive ability of less palatable taxa (Weaver and Clements 1938), and by modifying soil conditions by compaction and erosion (DeSelm 1988). The grazing/browsing mechanism may explain decreased species richness downslope--the steep upper slopes being less accessible to large animals. Browsing of small woody plants and the presence of droppings also suggest current activities of deer.

Scanning of Tables 1 and 2 (appended) shows the numerous taxa with 1% cover—the lowest percentage cover recorded. It seems likely that use of fractional cover percentages would have resulted in more taxa with apparent cover trends (cf. DeSelm 1994, Finn 1968). The use of 1% rather than a fractional percent cover exaggerates the importance of the scattered forb taxa. This could result in typing vegetation as Forb-Grass cover—referred to as Grass-Forb in the WR (DeSelm 1994).

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APPENDIX

Table 1. Plot sampling results at the Littleville barren site. Abbreviations are: Frequency (F) and Cover (C). IV-200 is the sum of Relative Frequency and Relative Cover.

	Slope Position		
Character	**Lower Flat** **F-C**	**Footslope** **F-C**	**Steep Sideslope** **F-C**
Rock cover %	0-0	10-1	100-8
Gravel cover %	25-10.0	100-85.9	100-36.3
Soil cover %	75-10.7	0-0	0-0
Tree litter %	0-0	0-0	15-6.3
Mean soil depth (cm)	15.8	6.5	8.1
Taxa	**F-C-IV200**	**F-C-IV200**	**F-C-IV200**
Agave virginica			25-1.0-.040
Asclepias tuberosa	5-1.0-.012		
A. viridiflora			15-1.0-.028
Aster hemisphericus	50-1.0-.051	65-1.0-.097	20-1.0-.034
A. laevis	40-1.0-.042		15-1.0-.028
A. patens	10-1.0-.017	5-1.0-.030	30-1.0-.046
A. pratensis	90-1.1-.086	40-1.2-.074	90-1.0-.121
Bouteloua curtipendula	10-1.0-.017	20-1.5-.058	15-18.0-.178
Carex cf. *umbellata*	10-1.0-.017		35-3.1-.070
Ceanothus americanus	15-1.7-.026		
Celtis tenuifolia			5-1.0-.015
Composite, unknown	5-1.0-.012	5-1.0-.030	15-1.0-.036
Dalea candida			10-1.0-.047
D. purpurea	55-1.1-.056	5-1.0-.030	30-1.1-.047
Desmodium ciliare	25-1.0-.029	5-1.0-.030	25-1.0-.040
Erigeron strigosus		15-1.0-.041	
Eriogonum longifolium var. *harperi*		45-2.3-.105	10-1.0-.021
Euphorbia corollata		90-1.3-.132	5-1.0-.015
Forb, unknown		10-1.0-.035	
Galactia volubilis	75-1.0-.072	5-1.0-.030	80-1.0-.108
Gaura filipes	5-1.0-.012	30-1.7-.074	25-1.0-.040
Gramineae, annual, unknown	45-3.3-.064	95-1.3-.137	
Grindelia lanceolata		45-1.1-.076	30-1.0-.046
Helianthus occidentalis	15-1.0-.021	20-1.0-.046	5-1.0-.015
Heliotropium tenellum		5-1.0-.030	10-1.0-.021

Continued:

Table 1. Continued.

Houstonia purpurea var. *calycosa*	55-1.0-.055	10-1.0-.035	15-1.0-.028
Hypericum sphaerocarpum		55-1.0-.085	50-1.0-.071.0
Juniperus virginiana	15-6.3-.063		5-1.0-.015
Lespedeza virginica			5-1.0-.015
Liatris aspera	90-1.2-.086		35-1.0-.052
L. squarrosa	70-1.0-.068	25-1.0-.052	30-1.0-.046
Linum medium	15-1.0-.021	20-1.0-.046	15-1.0-.028
Lithospermum canescens	20-1.0-.025		5-1.0-.015
Lobelia spicata			10-1.0-.021
Monarda fistulosa			5-1.0-.015
Nostoc sp.		5-4.0-.101	5-1.0-.015
Onosmodium virginianum		5-1.0-.030	5-1.0-.028
Phlox amoena	55-1.0-.046	5-1.0-.030	35-1.0-.052
Physostegia virginiana	80-1.0-.076	55-1.0-.085	60-1.0-.084
Ratibida pinnata	10-1.0-.017		
Rudbeckia fulgida	5-1.0-.012		
R. hirta	5-1.0-.012		
Ruellia humilis		65-1.2-.102	40-1.0-.059
Salvia pitcheri			20-1.0-.034
Schizachyrium scoparium	100-75.1-.678	90-5.5-.232	100-16.2-.267
Scleria oligantha	25-1.0-.029		
Senecio anonymus			5-1.0-.015
Silphium asteriscus	10-1.0-.017	10-1.5-.047	15-1.0-.028
S. pinnatifidum	25-5.0-.060		
Sisyrinchium albidum			5-1.0-.015
Smilax bona-nox			5-2.0-.024
Solidago nemoralis		40-1.4-.078	
S. rigida	20-1.0-.025	5-1.0-.030	5-1.0-.015
Sorghastrum nutans	15-1.3-.023		5-1.0-.015
Sporobolus asper	20-1.0-.025		
S. clandestinus	80-6.6-.120		95-31.8-.398
Toxicodendron radicans			5-1.0-.015
Tragia cordata			20-1.2-.036

Table 2. Plot sampling results at the Cedar Creek barren site. See Table 1 for abbreviations.

	Slope Position		
Character	**Lower Flat F-C**	**Footslope F-C**	**Steep Sideslope F-C**
Rock cover %	80-6.0	75-7.1	90-15.6
Gravel cover %	95-9.2	100-58.8	60-17.3
Soil cover %	0-0	0-0	45-8.6
Tree litter %	10-6.0	10-3.0	45-26.8
Mean soil depth (cm)	17.5	13.5	12.1
Taxa	**F-C-IV200**	**F-C-IV200**	**F-C-IV200**
Acalypha graciliens			10-1.0-.012
Agalinis tenuifolia		5-1.0-.016	
Agave virginica		5-1.0-.016	40-1.0-.047
Asclepias viridiflora		5-1.0-.016	5-1.0-.012
Aster hemisphericus		85-1.0-.092	15-1.0-.022
A. laevis	5-1.0-.016		80-1.3-.089
A. patens	95-1.2-.123	10-1.0-.021	45-1.0-.052
A. pratensis		20-1.0-.031	
Bignonia capreolata			5-1.0-.012
Blephilia ciliata	5-1.0-.016		5-1.0-.012
Bouteloua curtipendula		60-4.2-.104	40-20.3-.179
Bryophyte, unknown			5-3.0-.026
Carex cf. *umbellata*	5-25-.293		
Ceanothus americanus			35-2.6-.053
Celtis tenuifolia			20-19.0-.150
Centrosema virginiana			5-1.0-.012
Composite, unknown			10-2.5-.027
Crotalaria sagittalis	5-1.0-.016		
Dalea candida	15-1.0-.028		
D. purpurea	5-1.0-.016		
Desmodium ciliare		15-1.0-.037	25-1.0-.039
Diodia teres		45-1.0-.054	10-1.0-.017
Eriogonum longifolium var. *harperi*		50-2.0-.070	
Euphorbia corollata	10-1.0-.022	55-1.0-.064	10-1.0-.017
E. maculata			30-1.0-.037
Fimbristylis puberula			25-8.2-.081
Forb, unknown			5-1.0-.012
Galactia volubilis	55-1.0-.074		50-1.1-.058
Galium pilosum	5-1.0-.016		10-1.0-.017

Continued:

Table 2. Continued.

Gaura filipes	35-1.0-.051	40-2.0-.061	15-1.4-.025
Gramineae, annual, unknown	50-7.8-.135	40-2.1-.062	10-1.0-.010
Helianthus hirsutus		10-1.0-.021	35-1.0-.042
Houstonia purpurea var. *calycosa*	100-1.0-.127	70-1.1-.083	20-1.0-.027
Hypericum sphaerocarpum	30-1.2-.047	55-1.0-.064	25-1.0-0.032
Isanthus brachiatus		25-1.0-.035	
Juniperus virginiana	10-1.5-.027		
Kuhnia eupatorioides	20-1.0-.033	5-1.0-.017	50-1.0-.057
Legume, unknown			5-1.0-.012
Liatris aspera	85-2.2-.121	30-1.3-.043	30-2.0-.044
L. squarrosa			15-1.0-.022
Linum medium	20-1.0-.033	10-1.0-.021	
Lithospermum canescens	10-1.0-.022	10-1.0-.021	15-1.7-.027
Lobelia spicata	25-1.0-.039	25-2.0-.035	10-1.0-.017
Mirabilis albida			5-1.0-.012
Onosmodium virginianum			10-1.5-.020
Panicum commutatum			20-1.0-.027
Passiflora lutea			5-1.0-.012
Physostegia virginiana	5-1.0-.016	40-1.0-.050	5-1.0-.012
Polygala boykinii	5-1.0-.016		5-1.0-.012
Prunella vulgaris	15-1.0-.028		
Quercus muehlenbergii			10-4.0-.037
Rhus aromatica			5-4.0-.032
Rhynchosia tomentosa		5-1.0-.016	40-1.8-.052
Rosa carolina	5-1.0-.016		
Rudbeckia fulgida	5-1.0-.016	5-1.0-.016	
R. hirta	10-1.0-.022	5-1.0-.016	
Ruellia humilis	20-1.0-.033	40-1.1-.051	50-1.3-.059
Salvia pitcheri			10-1.0-.017
Schizachyrium scoparium	100-52.0-.625	95-19.7-.316	100-21.3-.247
Scleria oligantha			10-3.0-.031
Senecio anonymus	5-1.0-.016		
Silphium asteriscus	5-1.0-.016	20-1.0-.031	
S. terebinthinaceum		25-1.8-.044	
Sisyrinchium albidum	15-1.0-.028		
Smilax bona-nox	15-1.0-.028		15-1.6-.026
Solidago nemoralis	100-4.9-.165	60-1.4-.072	20-1.0-.027
Solidago sp.	5-1.0-.016		5-1.0-.012
Sorghastrum nutans	15-2.0-.038	5-2.0-.028	15-7.0-.063
Sporobolus asper	5-1.0-.016		5-1.0-.012
Toxicodendron radicans	5-1.0-.016		15-1.0-.022
Tragia cordata			15-1.0-.022
Viola pedata	35-1.0-.051	85-1.1-.093	10-1.0-.017
Vitis sp.			5-2.0-.019

Table 3. Sums of percent covers of exposed rock plus gravel plus soil, total plant cover, total graminoid cover and taxon richness. Soil depth is expressed as 100 minus percent average maximum depth (25 cm at 100 %).

	Site					
	Littleville/position			Cedar Creek/position		
	LF	FS	SS	LF	FS	SS
∑ Rock + Gravel + Soil (%)	20.7	86.9	44.3	15.2	65.9	41.5
Soil depth	63.2	26.0	32.4	70.0	54.0	48.4
∑ of above	83.9	112.9	76.7	85.2	119.9	89.9
Number of taxa	34	30	46	37	34	55
Total Cover (%)	126.6	46.3	112.4	101.8	86.8	144.3
Total perennial graminoid cover (%)	87.0	7.0	70.1	55.0	50.9	61.8

WESTERN AND CENTRAL-SOUTHEASTERN ELEMENTS IN THE FLORA OF THE SOUTHERN RIDGE AND VALLEY

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ABSTRACT. The eastern portions of the ranges of 26 western and local central-southeastern xerophytic, heliophytic herbs have been mapped from herbarium and literature records. These ranges pose problems in their geographical and historical interpretation. It is likely that the taxa migrated to the Ridge and Valley from the west, but neither the routes nor mechanisms of movement are known. Ranges are individualistic but are classed here into a few types based on distances between their different geographic parts.

INTRODUCTION

In a study of the flora and vegetation of the barrens and glades of the southern Ridge and Valley (Lee County, Virginia, to St. Clair County, Alabama), the authors noted several taxa that also are present in barrens and floras to the west (DeSelm 1988, 1989a,b, 1990, 1993, 1992a,b, DeSelm and Chester 1993, DeSelm *et al.* 1994, Webb *et al.* 1997). These species occurred in the southern Ridge and Valley, chiefly in southeast Tennessee, northwest Georgia, and/or northeast Alabama. Few occurred in the Ridge and Valley northward into upper East Tennessee, Virginia or West Virginia. The several taxa selected to illustrate the ranges of those reaching the study area are mainly western or central-southeastern xerophytic, heliophytic herbs characteristic of prairies, barrens, and limestone outcrops. The argument could be made that they evolved outside the Ridge and Valley, near the center of their current ranges, and have migrated to the Ridge and Valley. For example, Baskin and Baskin (1986) note that certain western genera have cedar glade species in the Central Basin: *Astragalus, Dalea, Echinacea, Lesquerella, Pediomelum, Penstemon, Talinum,* and *Onosmodium.* Bridges and Orzell (1986) mapped the ranges of several punitive western taxa ranging eastward to Middle Tennessee.

Several western taxa, in addition to those to be discussed here, reach the Ridge and Valley; these include *Astranthium integrifolium* and *Oenothera triloba.* Three presumed western tree taxa reach the Ridge and Valley: *Fraxinus quadrangulata, Gleditsia triacanthos* (Little 1971), and *Prunus munsoniana* (Little 1977). Western shale barrens taxa, like *Astragalus distortus* (Keener 1983), serpentine barrens taxa (Wherry 1963) (see distributions illustrated in this paper), and salt marsh taxa, like *Scirpus robustus* (Ogle 1981), are long-range disjuncts into the Ridge and Valley.

Descriptions in the literature of the range of certain species suggest that long-range dispersion (as in *Solidago ptarmicoides*) has occurred. The time of arrival, migration impetus (though past climatic changes and modern regional droughts), and mechanisms (e.g., tornadic winds, animal movement, Native American activities, or even the actions of European-Americans) are little known. Long-range dispersal or movement by short saltation "hops" (see papers cited by Harper 1977) may have occurred. The location of most taxa in the Central Basin, exposed only during the Pleistocene, indicates probable post-Tertiary distribution.

The possibility of late glacial low temperature Boreal Forest prevalence in eastern United States from Central Alabama northward (Delcourt and Delcourt 1987) poses problems for species persistence and movement. When did the taxa arrive? Was there persistence southward and migration north during the Holocene? What part did the Tennessee River valley and adjacent hills play as refugia or migration paths? These questions will be addressed later.

THE STUDY AREA

The Ridge and Valley Physiographic Province is a linear region extending from the St. Lawrence River lowland southward to central Alabama (Fig. 1). The bedrock is of Paleozoic age. At its southern terminus it touches the Coastal Plain of Alabama 48 km north of the Black Belt (Fenneman 1938, Szabo *et al.* 1988) with its prairie history (Jones and Patton 1966). From southern Pennsylvania southward it is bounded on the east by the Blue Ridge or Piedmont and on the west by the Appalachian Plateaus Province (southward the Cumberland Mountains and Plateaus).

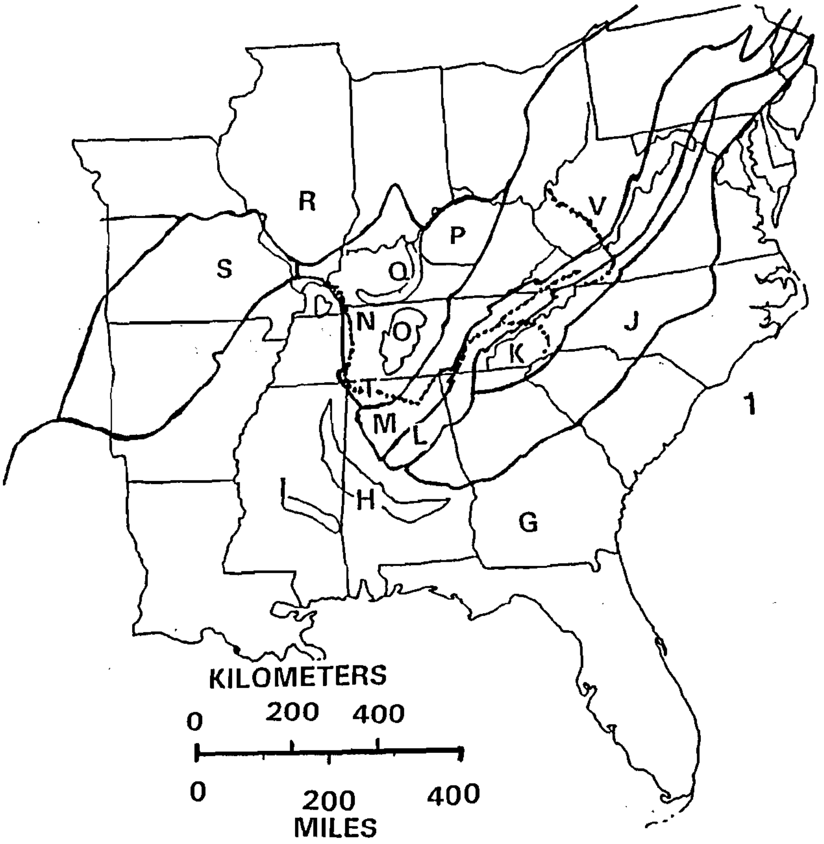

Figure 1. Physiographic provinces and subprovince or vegetation areas: G - Coastal Plain, H -Black Belt, I - Jackson Prairie, J - Piedmont, K - Blue Ridge, L - Ridge and Valley, M - Appalachian Plateaus, N - Interior Low Plateaus, O - Central Basin, P - Kentucky Bluegrass, Q - Kentucky Barrens, R - Central Lowland, S - Interior Highlands; Rivers (dotted): T - Tennessee River (Holston and French Broad rivers upstream), V - Kanawha and New rivers (Fenneman 1938, DeSelm 1959, DeSelm and Murdock, 1993, DeSelm and Schmalzer 1982).

The western boundary of the Ridge and Valley, along most of its length, is the escarpment border of the Appalachian Plateau rising to 600 to over 900 m, with a rolling upland of about 300-600 m, and with Cumberland Mountain peaks to nearly 1100 m. The surface geologic beds are sandstone and shale overlying limestone. In the deeper valleys, as the Tennessee River in southeast Tennessee and northern Alabama, the limestone beds are exposed extensively and lie adjacent to the limestones of the Interior Low Plateaus (Wilson *et al.* 1956, Hardeman 1966). The Ordovician limestones of the Central Basin, where many species discussed here also occur, were exposed during the Pleistocene (Thornburg 1965).

Extending northeast and southwest in the Ridge and Valley are more or less parallel dolomitic or sandstone ridges separated by shale or limestone (or sometimes dolomitic) valleys or rolling landscape. The land surface was modified in Pleistocene times from surfaces exposed in late (Wright 1934, 1936) to early (King 1949) Tertiary time. In a study of the area's cedar-pine barrens and glades, DeSelm (1993) found that most of this vegetation occurred on the karstic Chickamauga limestone although a few sites occurred on calcareous shales (Conasauga and Ottossee) and on the Knox group (dolomite) (see Hardeman 1966, Rodgers 1953, Calver *et al.* 1963, Butts and Guildersleeve 1948, Cardwell *et al.* 1968, and Szabo *et al.* 1988 for maps of these strata). Soils of these sites were shallow, stony, clayey and often drain through bedrock cracks and fissures. Soils are usually classed as Udults in Rock Outcrop, Colbert, Conasauga, or Talbott series (U.S. Soils Conservation Service 1970, Springer and Elder 1980).

Vaiksnoras and Palmer (1973) found that 10.9% of the East Tennessee months of May through August had moderate, severe, or extreme droughts. Also between 1952 and 1956 there were 48 consecutive months of meteorological drought.

The fossil evidence suggests a variable climate during the Tertiary (Graham 1964, Wolfe 1978). Emeliani (1966) postulates eight cool/warm periods in the last 425,000 years of the Pleistocene. Climatic fluctuations, lowering of landform, and stream terrace deposition occurred (Fenneman 1938). In the last Pleistocene full glacial, apparently spruce-pine forest occupied much of the upland as far south as about central Alabama (Delcourt *et al.* 1983, Delcourt and Delcourt 1987). However, the flora of alvars of Michigan (Herendeen 1985) suggests that some barren/glade taxa could exist alongside boreal taxa. The Hypsithermal, a Holocene warm/dry period centering during the period 8,000-4,000 years BP (Delcourt 1979, Delcourt and Delcourt 1987, Delcourt *et al.* 1983), was a time of Middle Tennessee cedar glade expansion (Delcourt *et al.* 1986), just as the Prairie Peninsula became established in the Middle West (Webb *et al.* 1983). Low elevation natural openings where heliophiles might survive include sites with soil shallow to bedrock (DeSelm 1993, DeSelm and Murdock 1993), river and stream borders (Hupp 1983), and cliffs, debris slides, and flood zones (Clark 1987, Clark *et al.* 1987). Climatic actions may have provided both migration impetus and a mechanism via occasional tornado winds (Vaiksnoras 1971). The effects of the Tertiary-Pleistocene large mammal bestiary (Semken 1983) is unknown, but these and Holocene herd mammals may have carried propagules and opened existing vegetation, making it more susceptible to invasion.

Native American village-centered civilizations, beginning ca. 10,000 years BP, made trail, (Haywood 1823, Myer 1928), village, and field openings (Steiner and DeSchwelinitz's observations in 1799 in Williams 1928) by direct action and made other changes using fire as a game and vegetation management tool (Swanton 1946, Lewis and Kneberg 1958, Williams 1989).

Europeans initially settled the study area during the period 1790 to 1837. Clearings for buildings, roads, and fields greatly increased edges, and roads and field borders provided open migration routes between similar habitats. The landscape was further opened to heliophiles by stock grazing and burning the pastures and woods to increase forage yield—these practices lasted until the end of open range, ca. 1940 in Tennessee. Destructive agricultural practices, especially on slopes, often left fields unusable for row crops, and they were subsequently abandoned or were used for pasture (Killebrew *et al.* 1874, Killebrew 1878), and at least their edges often served as temporary refugia for heliophiles (DeSelm *et al.* 1969, Crosby 1972).

METHODS AND MATERIALS

Twenty-six taxa, whose centers of distribution are western or are in the central-southeast and that also occur in Ridge and Valley barrens and glades were chosen for study. Included are 20 taxa protected or watched as rare or unusual in Alabama, Georgia, or Kentucky as well as nine in Tennessee (Nordman 1996). Distribution records were obtained from ALU, AUA, EKU, IBE, JSU, MISSA, and TENN. Some private collections were seen. Literature records consulted for species as appropriate were Andreas (1989), Braun (1943, 1967), Brown and Brown (1984), Brown and Athey (1992), Clewell (1985), Cooperrider (1982), Cusick and Silberhorn (1977), Deam (1940), Evans (1978), Fisher (1988), Freeman *et al.* (1979), Harvill *et al.* (1992), Jones and Coile (1988), MacRoberts (1989), Mahler (1970), Medley (1992), Mohlenbrock and Ladd (1978), Radford *et al.* (1968), Smith (1988), Steyermark (1963), Strausbaugh and Core (1978), Wherry *et al.* (1979), Wharton and Barbour (1991), Whetstone (1981), Wofford and Evans (1979), and Wunderlin (1982).

The taxa used in this study (distribution maps appended) are:

Agalinis auriculata (Michx.) Blake (*Tomanthera*, *Gerardia*)
Asclepias hirtella (Pennell) Woods.
A. viridis Walt. [*Asclepiadora viridis* (Walt.) Gray]
Aster pratensis Raf. (*A. sericeus* Vent.)
Bouteloua curtipendula (Michx.) Torr.
Clematis versicolor Small ex Rydb.
Dalea candida Wild. [*Petalostemum candidum* Michx.]
D. gattingeri (Heller) Barneby [*Petalostemum gattinger* (Heller) Heller]
Desmanthus illinoensis (Michx.) Mac Mill. ex B.L. Robins. & Fern.
Heliotropium tenellum (Nutt.) Torr.
Isoetes butleri Engelm.
Leavenworthia exigua Rollins
L. torulosa Gray
Liatris cylindracea Michx.
Monarda citriodora Cerv. ex Lag.
Onosmodium molle Michx. ssp. *occidentale* (Mack.) Cochrane

Ophioglossum engelmannii Prantl
Pediomelum subacaule (T. and G.) Rydberg (*Psoralea subacaulis* T. and G.)
Pycnanthemum pilosum Nutt.
Sedum pulchellum Michx.
Silphium pinnatifidum Ell.
S. radula Nutt. (*S. asperimum* Hook.) - submerged in *S. asteriscus* L. in Steyermark (1963)
Solidago ptarmicoides (Nees) Boivin [*Aster ptarmicoides* (Nees) T. and G.]
Sporobolus heterolepis Gray
S. compositus (Poir.) Merr. var. *drummondii* (Trin.) Kartesz & Gandhi
S. ozarkanus Fern.

Nomenclature essentially follows Kartesz (1994); journal abbreviations follow Lawrence *et al.* (1968). Some often-used terms are abbreviated. They are: BB = Black Belt; CB = Central Basin, CP = Coastal Plain, CPM = Cumberland Plateau and Mountains, HR = Highland Rim (Interior Low Plateaus), JP = Jackson Prairie area, KB = Kentucky Barrens area, RV = Ridge and Valley, TNR = Tennessee River.

RESULTS

Some of the western taxa that occur in the RV appear to have reached there by long distance dispersal. These include nine taxa with range gaps of about 250-500 km. Three of these taxa reach the RV but do not occur on the CP or only peripherally so. *Isoetes butleri* (Fig. 2) occurs in shallow limestone-derived soils of the ILP, on the TNR, and rarely in the Alabama RV (cf. A. M. Evans, pers. comm.).

Sporobolus ozarkanus (Fig. 3) occurs in the Interior Highlands and its periphery; it occasionally occurs in the ILP and CPM and eastward in the RV.

Sporobolus heterolepis (Fig. 4) exhibits long-range gaps eastward, ca. 200 km from the western to eastern ILP and 350 km from the ILP to the RV. The Georgia RV station was seen by Cronquist (1949) and is substantiated by Jones and Coile (1988) and DeSelm (1993). It is also known from the adjacent Blue Ridge (Mansberg and Wertworth 1984) and across a 500 km range gap from Ohio to the eastern Pennsylvania serpentine barrens (Massey *et al.* 1983, Tyndall and Farr 1990, pers. comm. T. Rawinski and T. Wiebolt).

Six taxa with large range gaps also occur on the CP. *Solidago ptarmicoides* (Fig. 5) exhibits a 500 km range gap between the Interior Highlands populations and those in the RV. In the east there is a 150 km gap between northwest Georgia and the Piedmont of South Carolina (cf. Nelson 1989).

Sporobolus drummondii (Fig. 6) has a 400 km range gap from the Interior Highlands to the ILP, thence a gap of 200 km to the RV. The occurrence of two ILP and three RV stations on the TNR should be noted.

Clematis versicolor (Fig. 7) (Dennis 1976), a species with a plumose style, has a dicentric range with a 300 km gap between the Interior Highlands populations and those of the ILP. It occurs, with small gaps, from the CB to the HR and CPM to the RV.

Agalinis auriculata (Fig. 8) is a hemiparasite which grows attached to the roots of composites in open, shallow soil (Cunningham and Parr 1990). It occurs in the Prairie Peninsula area. In the Southeast it is known from the BB, an historic station in West Tennessee, in the Sequatchie Valley of the CPM, and in the RV at Oak Ridge National Laboratory. A farther outlier station occurs on the Piedmont of South Carolina (Nelson 1989). Northward a 300 km range gap occurs between the eastern Ohio populations and these of the Pennsylvania RV, thence a 150 km gap to the serpentine barrens of eastern Pennsylvania. It was known to John Clayton in the Delaware River Valley before 1760 (Pennell 1935).

Aster pratensis (Fig. 9) has extensive western distribution with a 300 km gap to populations in the ILP. Eastward populations are rare but occur in the CPM and RV.

Heliotropium tenellum (Fig. 10) has extensive populations in the Interior Highlands and Gulf Coastal Plain. A 250 km range gap exists between the western and ILP populations. The nearest population to the RV is on the TNR in the ILP; the gap between them is ca. 50 km.

Six taxa exhibit ranges with 150-200 km gaps between eastern and western population or sometimes within the eastern (east of the Mississippi River) range. The western populations in the Interior Highlands and Gulf Coastal Plain of *Silphium radula* (Fig. 11) extend east into Mississippi and Alabama on the CP. The eastern upland populations extend from the ILP to the CPM and RV.

Asclepias hirtella (Fig. 12), its seed with coma, has CP, Interior Highlands, and Interior Lowlands distribution in the west, extending with the Prairie Peninsula to Ohio. Southeastward its distribution in the ILP is only occasional, but it also occurs in the HR, CPM, and RV.

The distribution of *Pycnanthemum pilosum* (Fig. 13) occurs widely westward from the Coastal Plain, Interior Highlands, Interior Lowlands and Prairie Peninsula into Ohio. There is a gap of approximately 200 km from the ILP to the RV.

The distribution of *Dalea candida* (Fig. 14) (cf. Baskin and Baskin 1982) is wide and extends from the Coastal Plain to the Interior Lowlands. Gaps within the ILP are less than 100 km, and gaps from the HR to the RV also are about 100 km. The easternmost ILP station, at the tunnel at Cowan, Tennessee, was reported by Gattinger (1901) and was substantiated by Thomas Patrick (pers. comm.) The pollen type occurred in the *Quercus-Pinus* zone (300 cm depth) at Mingo Pond (Delcourt 1979), which is 17.7 km west of Cowan.

Liatris cylindracea has an Interior Highlands and Prairie Peninsula distribution (Fig. 15). It reaches the ILP partly on the TNR and occurs in the CPM also on the TNR. The gap into the ILP is about 200 km but eastward to the RV gaps are shorter. This species has a pappus dispersal mechanism.

Onosmodium molle ssp. *occidentale* (Fig. 16) has wide though generally sparse distribution in the west. It occurs in the southern Illinois bridge and on the TNR in the western ILP. The gap to the RV is 150 km; in the RV it occurs from northwest Georgia to southwestern Virginia (Baskin *et al.* 1986).

Three taxa exhibit generally smaller (100-200 km) gaps between populations. *Sedum pulchellum* (Fig. 17) exhibits eastern and western (Interior Lowlands especially) populations including the southern Illinois bridge. According to Baldwin (1943), the western populations are diploid, the Kentucky populations tetraploid, the Alabama plants tested were diploid, but the Tennessee populations were diploid, tetraploid and hexaploid—Tennessee being the center of diversity of the derived ploides.

Ophioglossum engelmanii (Fig. 18) also exhibits small gaps with widespread western populations in the Coastal Plain, Interior Highlands, and Interior Lowlands. It occurs in the southern Illinois bridge and on shallow limestone-derived soils eastward in the ILP and on the TNR in the CPM and RV. Note its northward extension in the RV (cf. Baskin *et al.* 1974).

Bouteloua curtipendula (Fig. 19), a western prairie dominant (Weaver 1954) with many related taxa in the west (Hitchcock and Chase 1950), exhibits a nearly 100 km gap between the southern Illinois bridge and the nearest Kentucky ILP population. It occurs on the BB, along the TNR in northern Alabama, and into eastern Tennessee. Note its extension northward to Pennsylvania in the RV.

The distribution of two taxa with western distributions exhibit a southern concentration. *Monarda citriodora* (Fig. 20), with sparse occurrences, exhibits a 150 km gap in the CP and a 300 km gap between the CP and the ILP or RV. *Monarda* is an escape in Illinois (Mohlenbrock 1975) and is adventive in Kentucky (Medley 1992). Note the 300 km gap to South Carolina (cf. Jones 1976).

Asclepias viridis (Fig. 21) has populations in the Interior Lowlands. Gaps from the west to the northern ILP are more than 200 km, whereas the populations in the southern end of the RV are only 70 km from those just north of the BB.

Desmanthus illinoensis (Fig. 22) exhibits a distribution nearly continuous from the west eastward into the RV. Collections have been made eastward into eastern Pennsylvania, eastern Virginia, central and eastern South Carolina, and the Piedmont of Alabama. It may be that the range of this species has been influenced by man's movements.

In addition to the foregoing taxa, a few narrow endemics characteristic of the central-southeast are useful for this study. These include a barrens species and four cedar glade taxa. The barrens were examined by DeSelm (1986) and DeSelm and Murdock (1993) (also see the Barrens Symposium, Castanea 59[3], 1994). The cedar glade flora and vegetation has been examined extensively (Quarterman 1950, Baskin and Baskin 1986, 1985, 1988, 1989) (see also The Cedar Glade Symposium, ASB Bull. 33[4] 1986).

Silphium pinnatifidum (Fig. 23) occurs in grassy barrens in the ILP, rarely in the CPM, and in the RV. Range gaps in the ILP are ca. 150 km south of the KB, but populations are few.

Pediomelum psoralioides (Fig. 24) (cf. Kral 1983) and those taxa following are typically limestone glade species (Somers *et al.* 1986), but they occur also in rocky barrens in the RV (DeSelm 1993). The range gap from the CB or TNR to the RV is 100-150 km across or through the Cumberland Plateau.

Dalea gattingeri (Fig. 25) has a center of abundance in the glades of the Central Basin of Tennessee, but it occurs also in the BB, on the TNR in northern Alabama, and in the RV. The range gaps from the CB or from the TNR to the RV are about 100 km across or through the Cumberland Plateau. The population at the southern end of the RV is near one in the BB.

Our species of *Leavenworthia* are thought to have evolved in the Central Basin after the arrival from Texas (?) of a founder species *L. crassa* (Rollins 1963). *L. exidua* (Fig. 26) (Bates 1985) has moved west to the TNR from the Basin and across or through the CPM to the RV of northwestern Georgia.

Leavenworthia torulosa (Fig. 27) (cf. Baskin and Baskin, 1977, Cranfill *et al.* 1985) has moved north from the Basin to the KB, south into the TNR hills, and east into the RV through or over the imposing CPM barrier.

DISCUSSION

Since the time of Asa Gray, students of the southeastern flora have been interested in disjunction of species and genera (and families) such as those between the southeast and Europe and Asia (Gray 1846, Sharp 1972, Li 1952), the southeast and western United States (Wood 1970), and the southeast and Mexico (Dressler 1954). Shorter disjunctions are discussed or mapped in this paper. Other taxa such as *Calamovilfa arcuata* (Rogers 1972) are no less interesting; this species occurs in Oklahoma and the CPM of Tennessee. The timing and possible routes of dispersal of species and genera of especially arboreal taxa has been stimulated by the success of palynologists who interpret these facts from the stratigraphic record (cf. Delcourt and Delcourt 1987). Here, clearly shown, are the changes in pollen and spore numbers showing the movements of plant taxa onto not only the deglaciated areas to the north but also such changes over the rest of eastern and central United States.

The time required for migration of prairie species has been examined by Webb *et al.* (1983). Changes in the isofrequency contours of five percent prairie forbs from Illinois to Ohio, 10,000 to 9,000 yr B.P., required movement of about 150 m/year. Changes in the 10% isofrequency contour of prairie forbs from central Minnesota to Ohio 10,000-8,000 yr B. P. required movement of about 240 m/year. The 10% isofrequency contour took 2000 years to reach Ohio where it lasted until 6000 yr B.P., suggesting a longer period of prairie extension in the upper Midwest (4000 years, Minnesota) than in the eastern end of the Prairie Peninsula (2000 years, Illinois, Indiana, Ohio).

Neither for the Prairie Peninsula prairie flora, nor for the species of the present study, is it known whether long, intermediate, or short distance individual movements have been responsible for species migrations. Species with adhering or wind dispersed seed or fruit, *Clematis* (style plumose), *Aster*, *Liatris*, *Solidago* (pappus), and *Asclepias* (seed with coma) occur. Spikelets of grasses, such as those of *Bouteloua,* may be scabrous and adhering. Small seed (several taxa) and aerially produced spores (*Ophioglossum*) may be subject to wind movement. The achenes of *Silphium* spp. and the rhizomes of *Dalea* may have been used as food by Native Americans. This record of morphology as possible aids to dispersal is not impressive; using only coma, pappus and style morphological adaptation, 19% of the taxa are included. Considering plant parts as food in addition, 42% of the taxa have possible dispersal aids. These taxa are scattered among gap sizes and centers of greatest density location types.

The most frequent species locations near the RV are populations in the CB of the ILP. On a straight line from the eastern edge of the CB to the western edge of the RV, the distance is about 118 km. A migration time of 2000 years would require dispersal at 59 m/year. The CB to RV route via the Elk and Tennessee River (limestone) valleys is at least 304 km. In the same 2000 years, at least 152 m/year dispersal is required. Routes from farther west require more time or larger "hops."

Evidence for a distinct mid-Holocene Hypsithermal here, in contrast to the Midwest, is less convincing. Grass assemblages in the forest cover is interpreted from the pollen flora at 30,000-24,000 yr B.P. at Nonconnah Creek in West Tennessee (Delcourt *et al.* 1980). At Mingo Pond on the HR, representatives of the barrens flora were present before 12,500 yr B.P. (Delcourt 1979). At Anderson Pond on the HR, an increase in grass pollen centering on the 9500 yr B.P. period and a slightly warmer, drier period 8000-5000 yr B.P. was postulated (Delcourt 1979). A decrease in effective precipitation is inferred for the period 10,000-8,400 yr. B.P. at Cahaba Pond, St. Clair County, Alabama in the RV (Delcourt *et al.* 1983). Pollen evidence for enlargement of the Kentucky Barrens was inferred from pollen evidence for the period after 3900 yr. B.P., "rather than during the classic Prairie Period of the Hypsithermal Interval" (Wilkins *et al.* 1991).

Warm or dry climatic fluctuations may increase the size of xerophytic plant communities, increasing the numbers of individual plants and thus making more propagules available to disperse. Drought may also enlarge the potential target areas increasing the probability of the area receiving dispersing propagules. In studies of two limestone prairie-barren areas in the ILP (western Highland Rim of Tennessee) (DeSelm 1988) and northwestern Alabama (Webb *et al.* 1997), over twice as many western taxa occurred in the Alabama barrens as in those in Tennessee. The expanse of Rockland and Colbert soils in Alabama averaged 150% of the area of the same soils in the Tennessee barrens area.

Warm or dry climatic fluctuations also increase the probability of fires starting and spreading--after a lightning strike--by its influence on plant and litter moisture content (Wright and Bailey 1982). Drought with fire makes more open forest available to dispersing heliophytes. Open and edge areas may have attracted populations of large mammals whose modification of vegetation on buffalo trails and at springs were well known in early Tennessee history (Haywood

1823).

For the taxa studied here, there were two large barriers to eastward migration for western taxa and one large barrier for the western or central-southeast taxa. These barriers were the Gulf Coastal Plain (including the Mississippi River Alluvial Plain) and the Cumberland Plateau.

The surfaces of the Gulf Coastal Plain are covered chiefly by alluvium or loess and are mostly areas of gentle topography with relatively fertile soils. They were well forested at the time of settlement but with a few modern barrens known (DeSelm 1989a), and grasslands interpreted in the late Pleistocene pollen record (Delcourt *et al.* 1988). These surfaces are used at least to a small extent by 76% of the studied taxa (the central-southeastern taxa excluded); of these, 56% also occur in the southern Illinois bridge as well as certain other surfaces. Similarly, most taxa (95%) (southeastern taxa excluded) use the Interior Lowlands to the north and 47% of these also occur in the bridge. Taxa using the bridge are chiefly intermediate, short, and continuous range taxa (90% of these taxa use the bridge). The southern Illinois bridge is an important phytogeographic feature. The several taxa mapped with populations in the bridge area may well have used it as a dispersal route to the east and west.

The second barrier is the Cumberland Plateau and Mountains with its elevation and cap of acid sandstones and shales. Such surfaces, and soils derived from them, are avoided by calciphiles. None of the taxa discussed here occur on the open sandstone flat rocks of the Plateau surface examined by Perkins (1981), but some taxa occur in CMP barrens or forest borders as previously mapped.

Underlying the sandstone and shale are many meters of upper Mississippian limestone, which meet the limestones and dolomites of the RV to the east and limestones of the HR and CB westward. Piercing this massive barrier is the Tennessee River valley with Mississippian age limestones bordering its route. The occurrence of some stations of the study taxa in the north-flowing western Tennessee River valley and its west-flowing Alabama section has been illustrated. This wide valley extends eastward into the CPM of Tennessee where, east of the Sequatchie Valley, it enters a 27.4 km long narrow gorge. Straight across Waldens Ridge, the distance is only 12.9 km. Ridge to ridge the gorge is only about 3.2 km wide. A study of the biota of the gorge section (Tennessee Natural Heritage Program 1984) did not reveal populations there of the studied taxa. Thus while 35% of the taxa occur at least sparingly on the CPM surface and 86% of the taxa have populations in the TNR valley west of the gorge, none is known in the gorge itself, making it an important part of the CPM barrier. The gorge continues to be an important site for continued floristic study.

SUMMARY AND CONCLUSIONS

The data used in this paper were acquired from various sources, including published works. Some of the data may have species identification problems, and some species with problems of systematic interpretation are included. Time of dispersal of the taxa is unknown though most taxa have populations in the CB which was not excavated until Pleistocene times. Western taxa have not evolved described varieties or subspecies in the eastern part of their ranges, suggesting a geologically short time of residence and time since dispersal. Mechanisms of dispersal are unknown, but a few taxa may have been aided by morphological adaptations, and a few may have been used as food by Native Americans. One or more taxa might have spread through actions of European-Americans. Various Pleistocene or Holocene climatic shifts may have provided impetus for movement.

Based on map information, the taxa can be grouped into several classes based on distances between the geographic parts of their ranges. The groups are the Long-Range Gap Group (250-500 km), Intermediate Range Gap Group (150-200 km), Short Range Gap Group (100-200 km), and the Continuous Range Taxon. Two taxa may be dispersing north from southern populations. Five taxa are central-southeastern United States endemics which have rare populations in the RV.

Physical barriers to movement include the glacial till plains Interior Lowland, the East and West Gulf Coastal Plain, and the Mississippi Alluvial Plain. The gap between these northern and southern areas is only a few km wide and here is called the southern Illinois bridge. Several taxa occur on the bridge and may have used it as a route east or west in the past. The Cumberland Plateau, with its elevation above the HR and RV and its cap of sandstone and shale geologic beds giving rise to acid soils, is a partial barrier. A few taxa occur on the Plateau surface and many taxa occur along the Tennessee River on the upper Mississippian strata to the Sequatchie Valley. However, no populations of the study taxa are known in the Walden Ridge Tennessee River Gorge section of the Plateau. The mechanism and route of dispersal of these taxa through or over the Plateau remain subjects of future study.

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APPENDIX: DISTRIBUTION MAPS

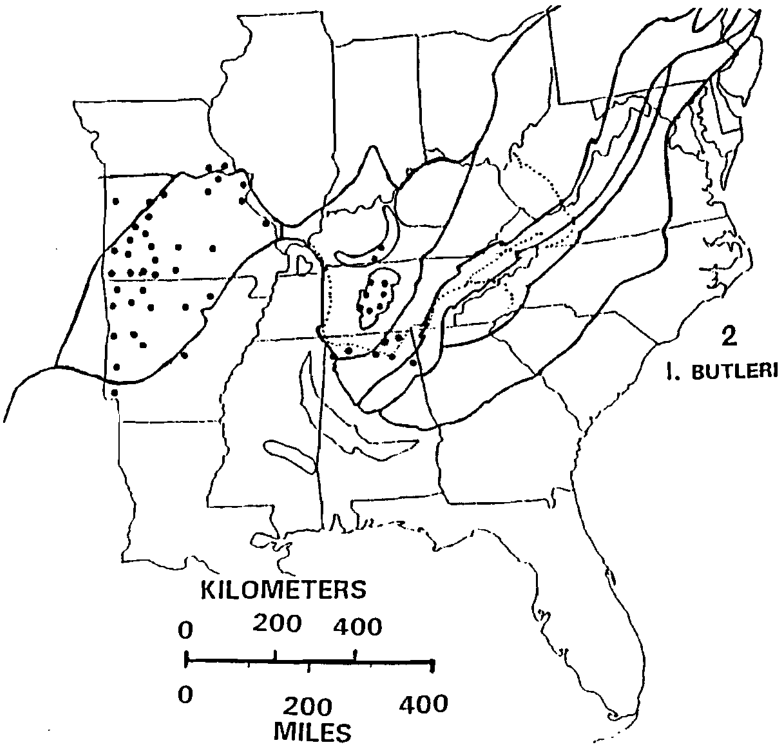

Figure 2. Eastern range of *Isoetes butleri*.

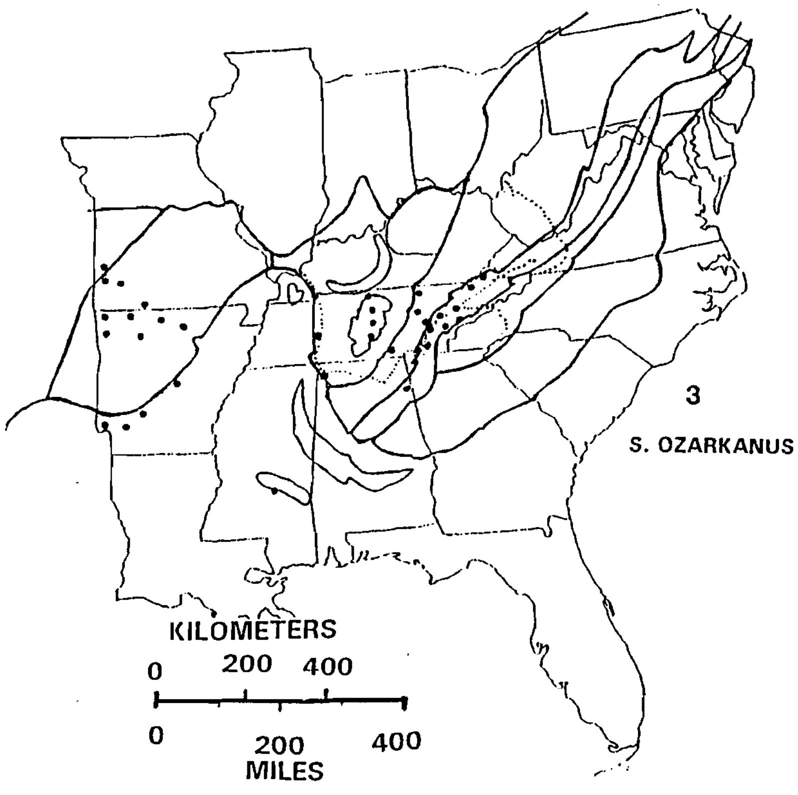

Figure 3. Eastern range of *Sporobolus ozarkanus*.

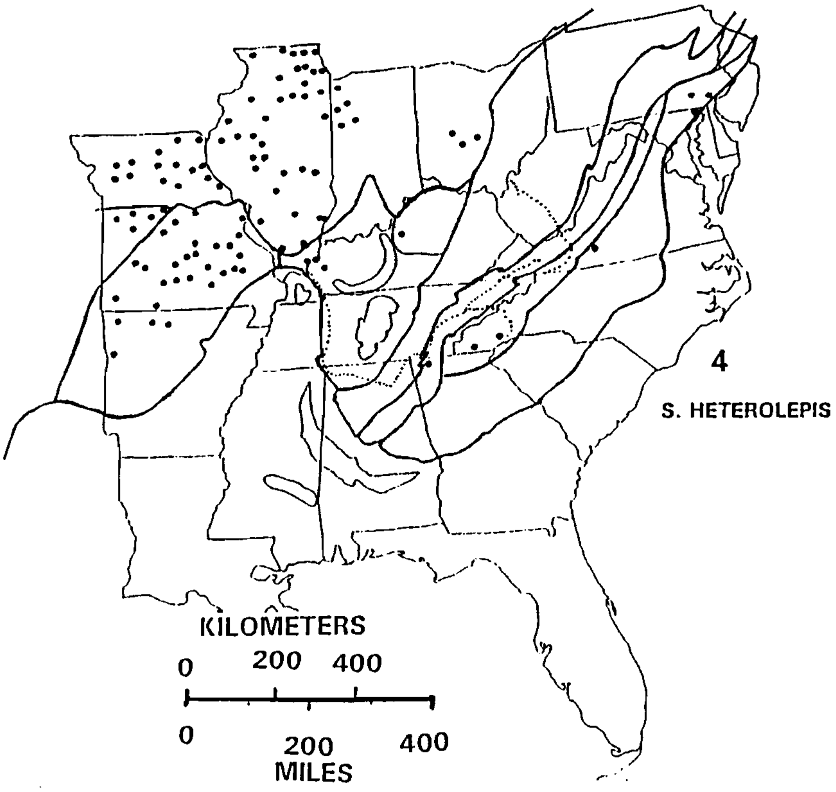

Figure 4. Eastern range of *Sporobolus heterolepis*.

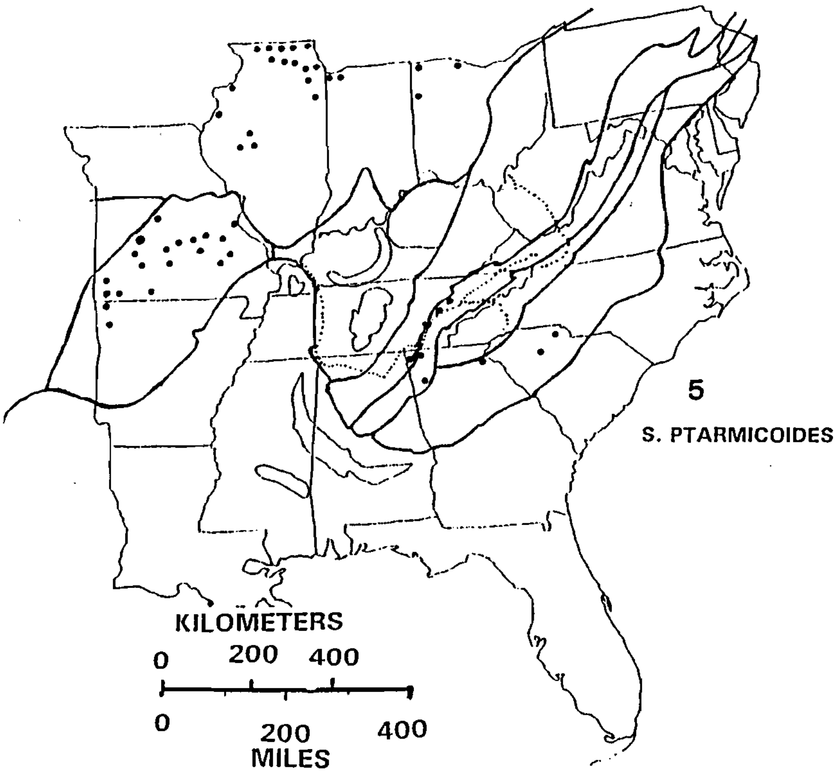

Figure 5. Eastern range of *Solidago ptarmicoides*.

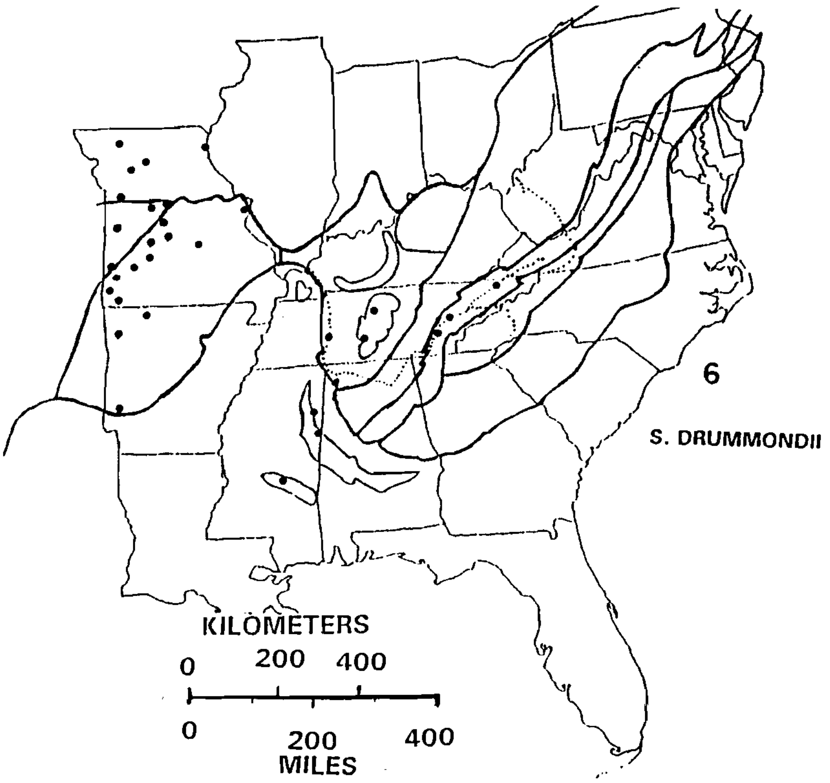

Figure 6. Eastern range of *Sporobolus drummondii.*

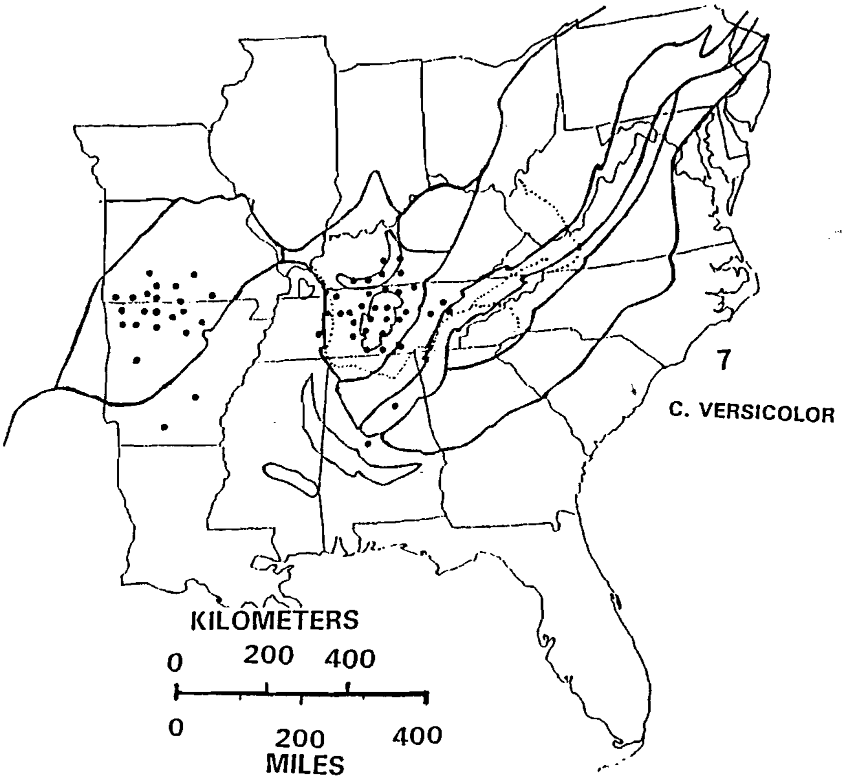

Figure 7. Eastern range of *Clematis versicolor.*

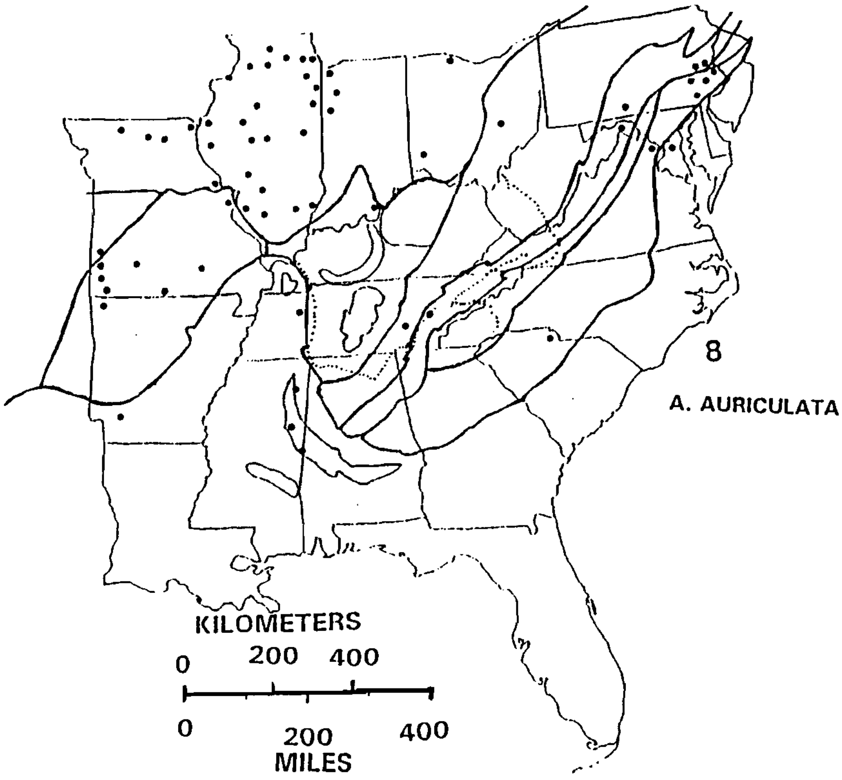

Figure 8. Eastern range of *Agalinis auriculata*.

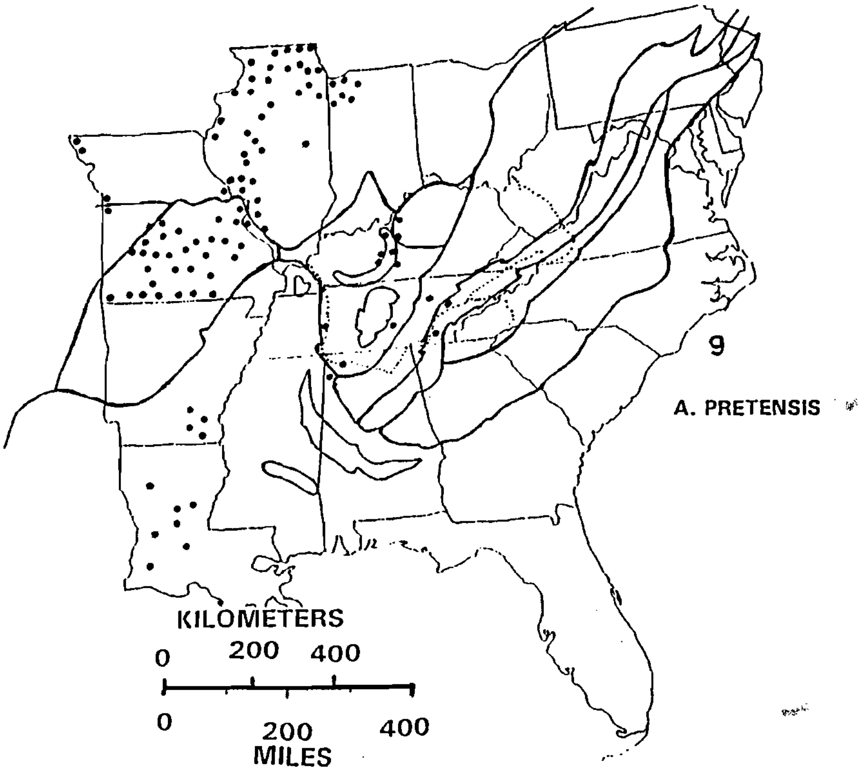

Figure 9. Eastern range of *Aster pratensis*.

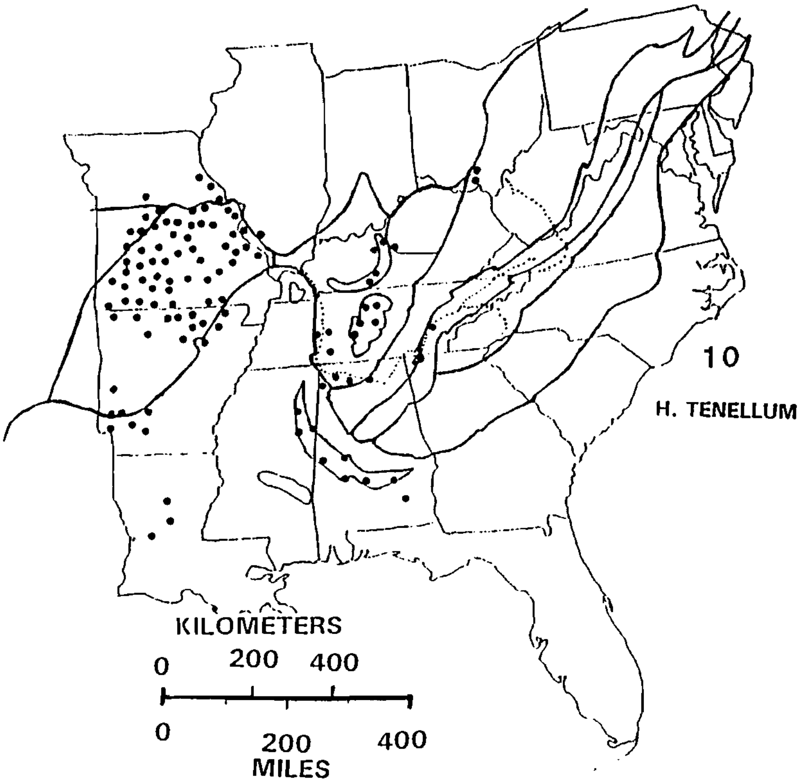

Figure 10. Eastern range of *Heliotropium tenellum*.

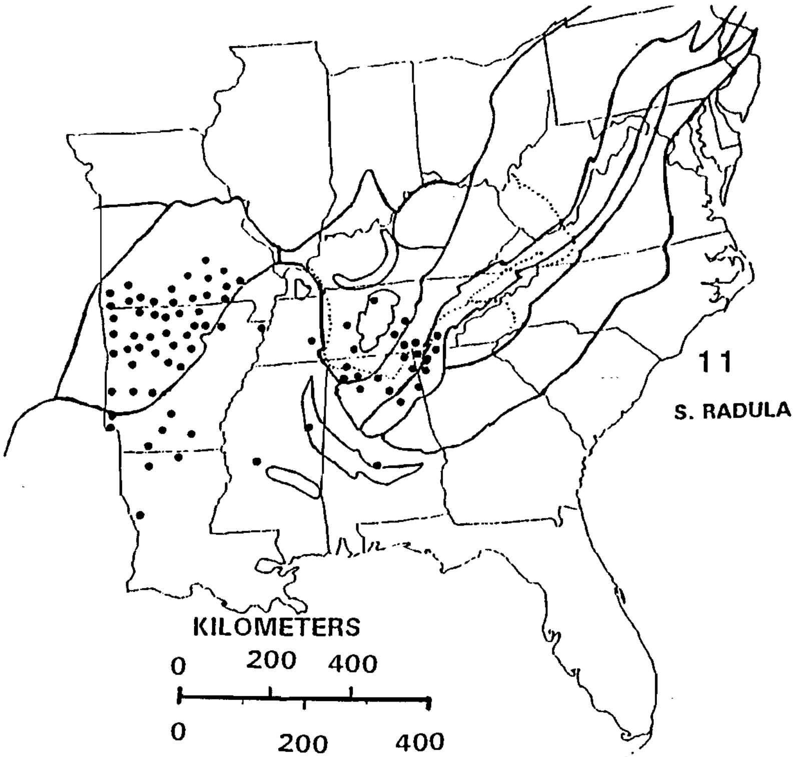

Figure 11. Eastern range of *Silphium radula*.

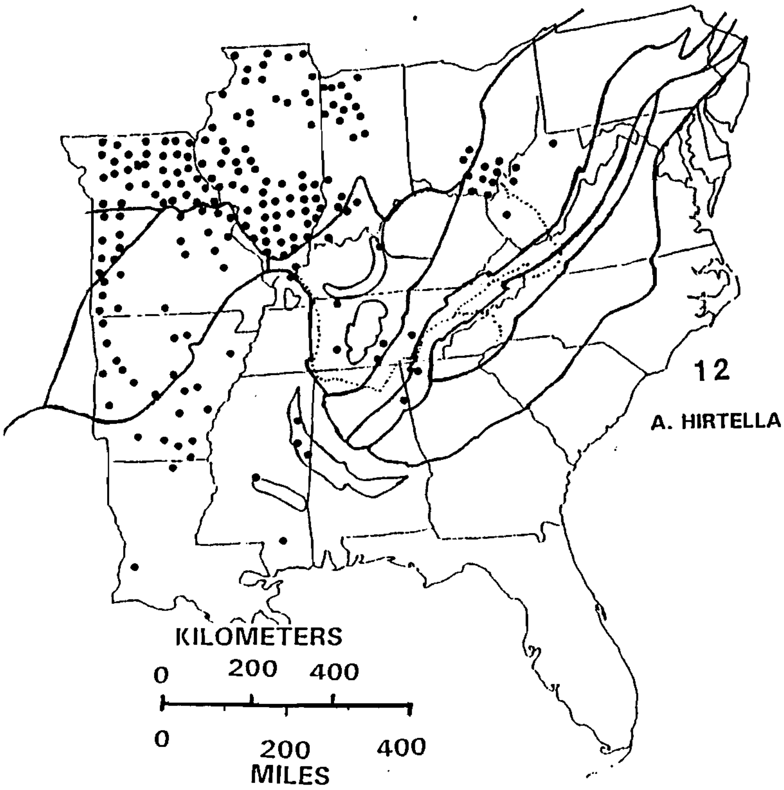

Figure 12. Eastern range of *Asclepias hirtella.*

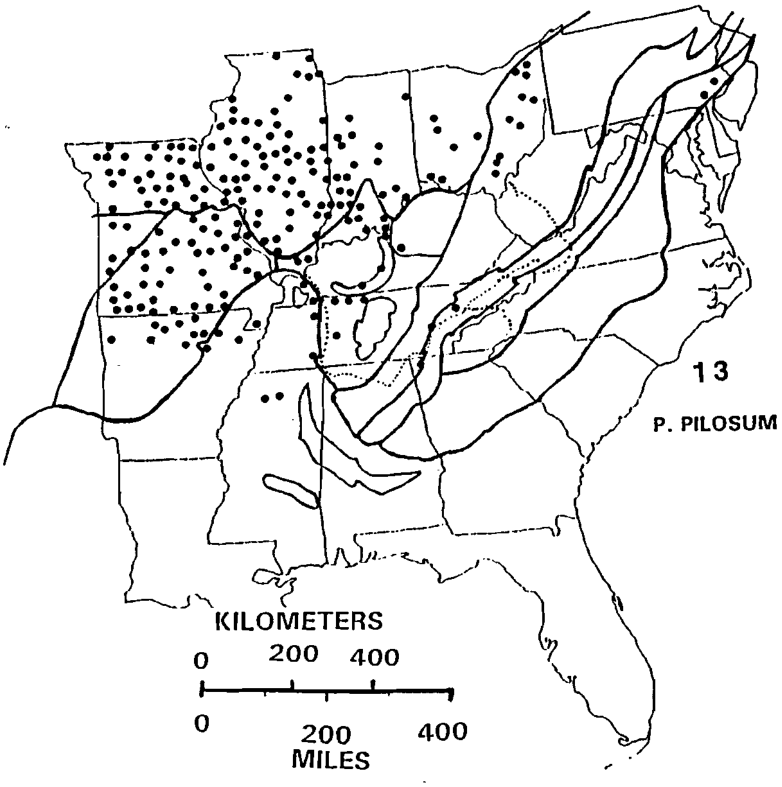

Figure 13. Eastern range of *Pycnanthemum pilosum.*

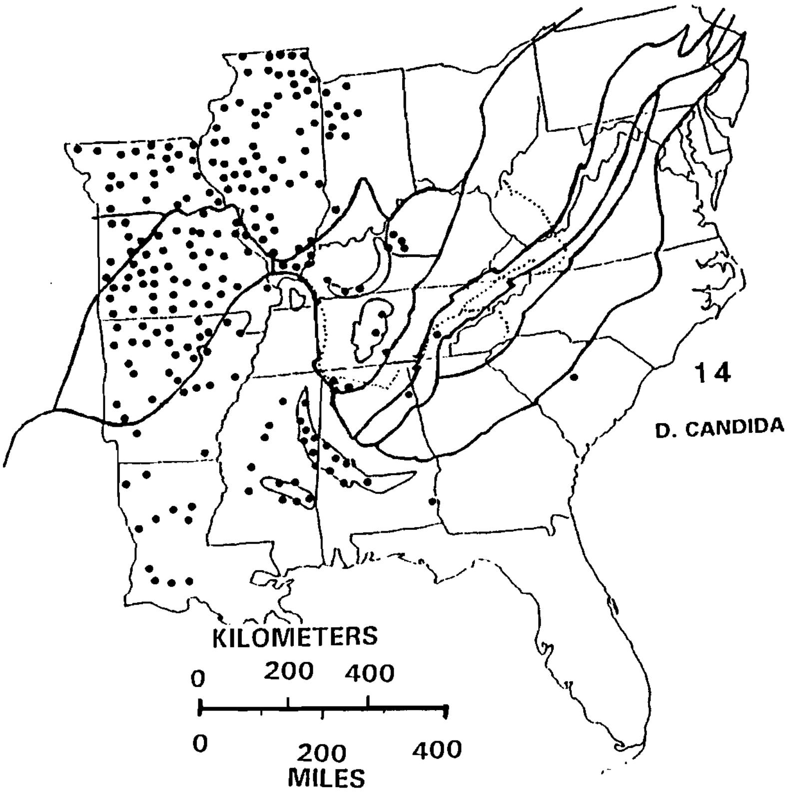

Figure 14. Eastern range of *Dalea candida*.

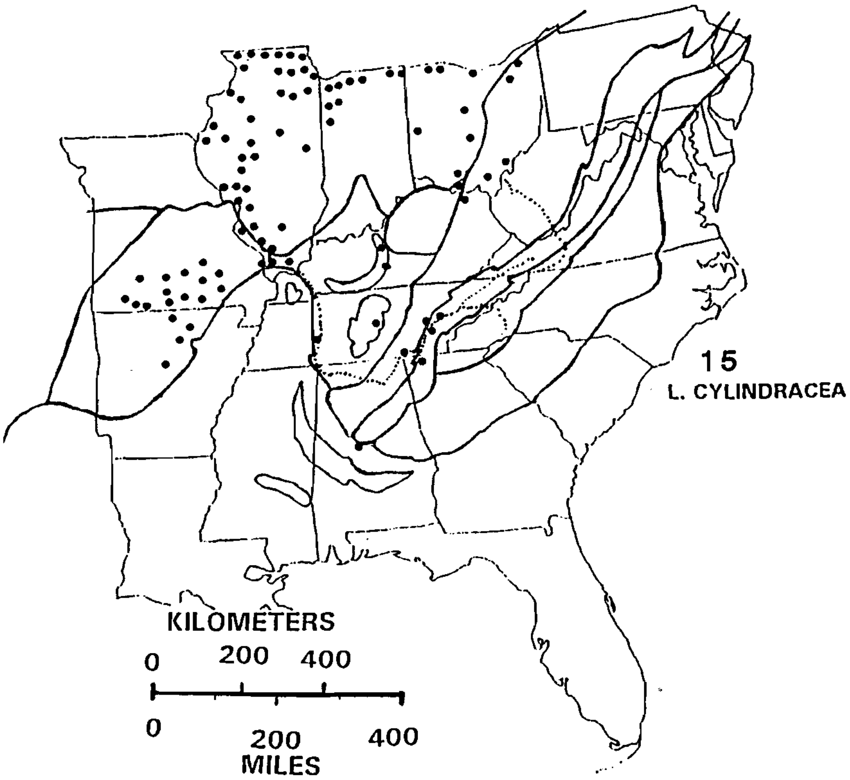

Figure 15. Eastern range of *Liatris cylindracea*.

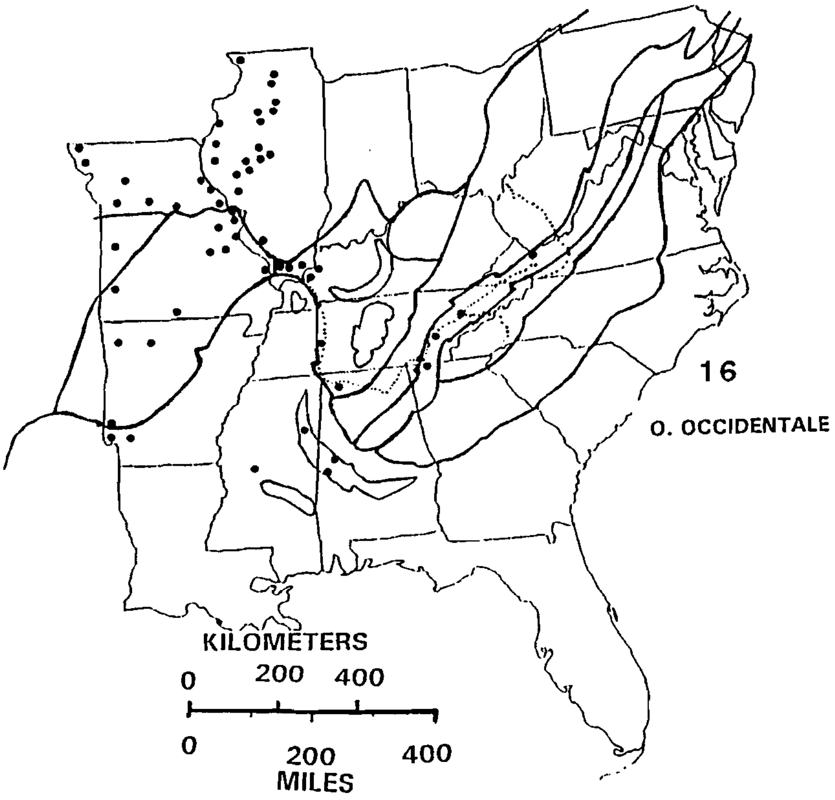

Figure 16. Eastern range of *Onosmodium occidentale*.

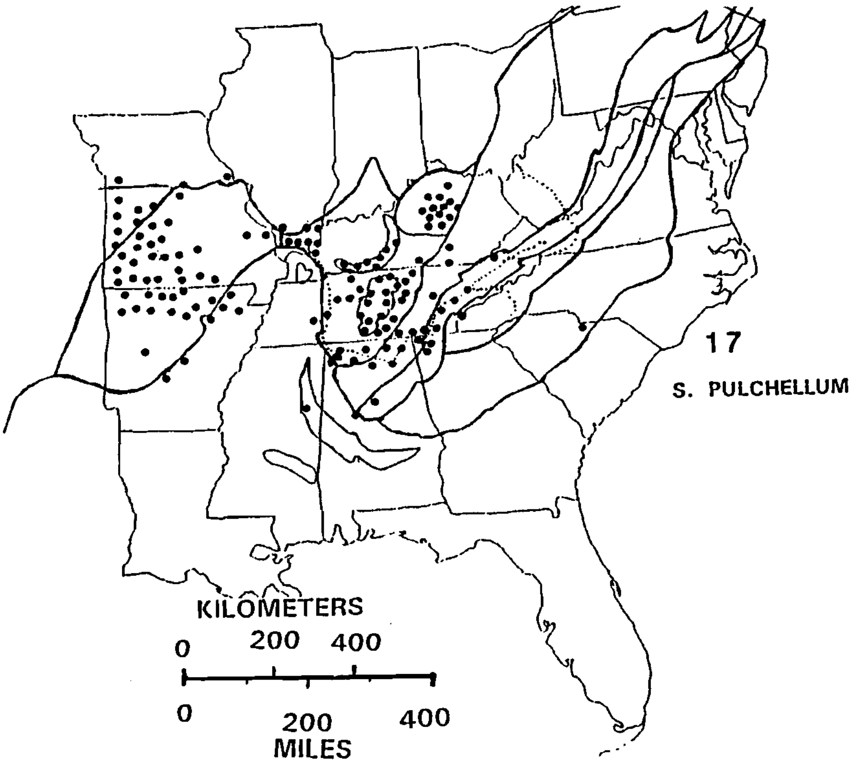

Figure 17. Eastern range of *Sedum pulchellum*.

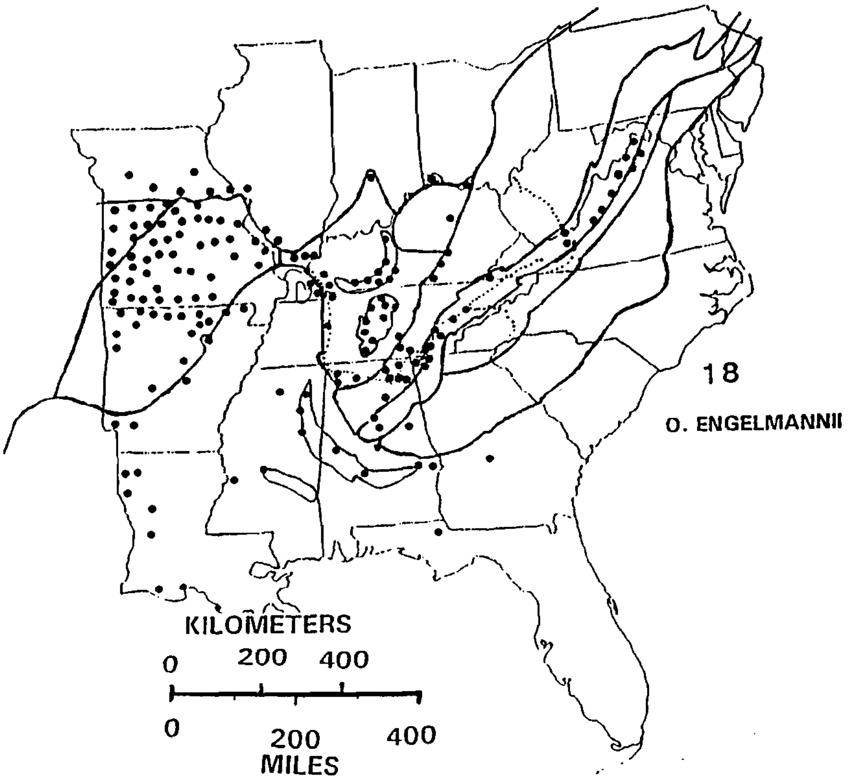

Figure 18. Eastern range of *Ophioglossum engelmannii.*

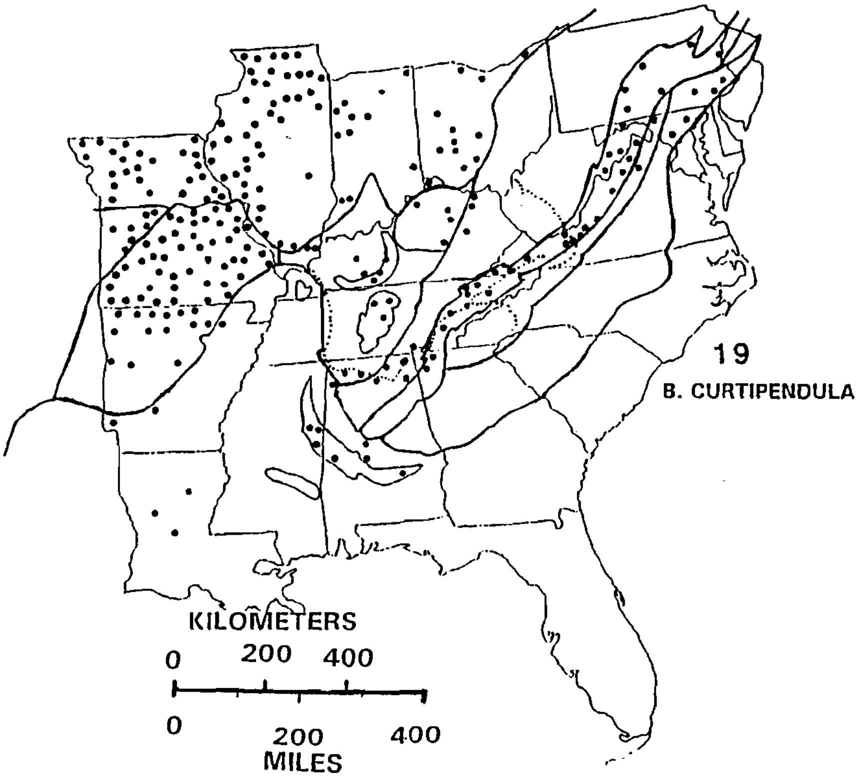

Figure 19. Eastern range of *Bouteloua curtipendula.*

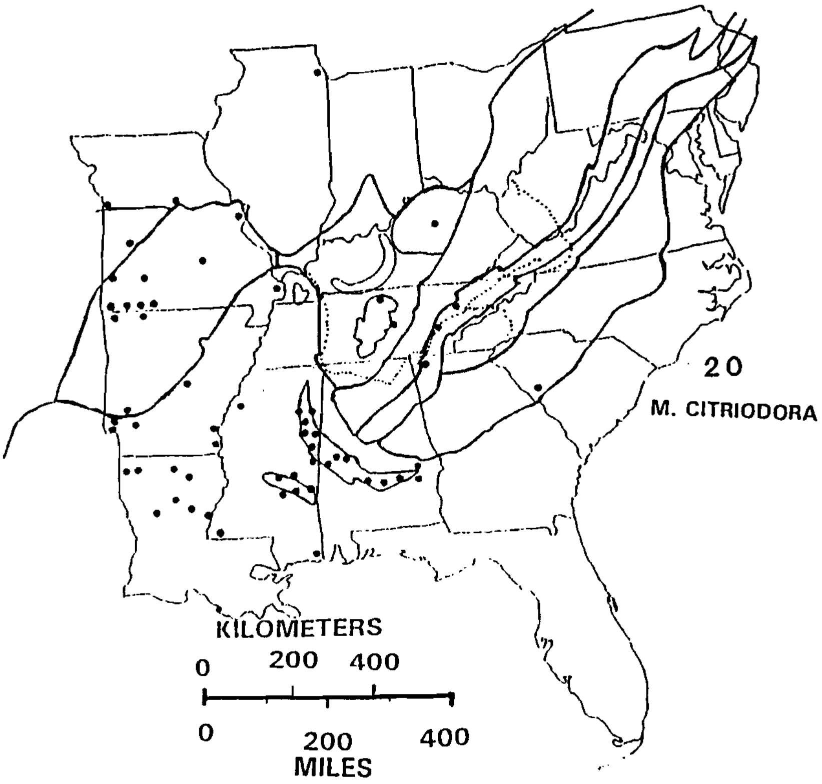

Figure 20. Eastern range of *Monarda citriodora*.

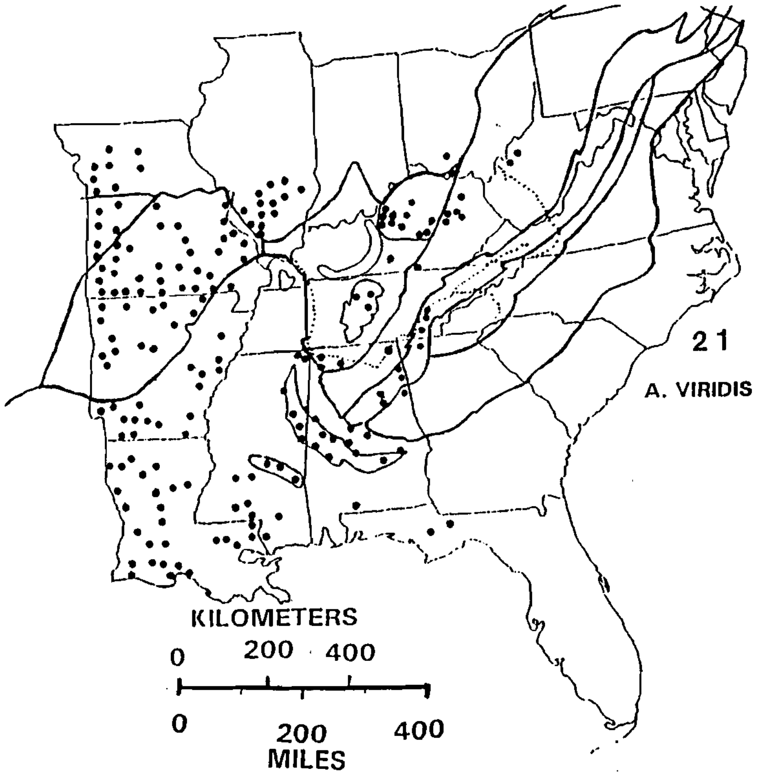

Figure 21. Eastern range of *Asclepias viridis*.

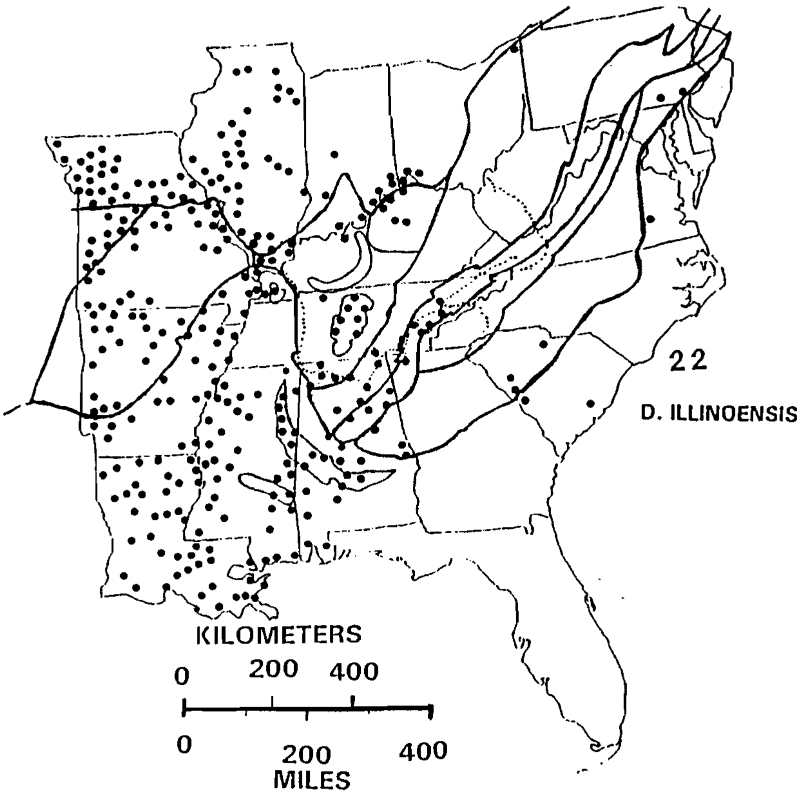

Figure 22. Eastern range of *Desmanthus illinoensis*.

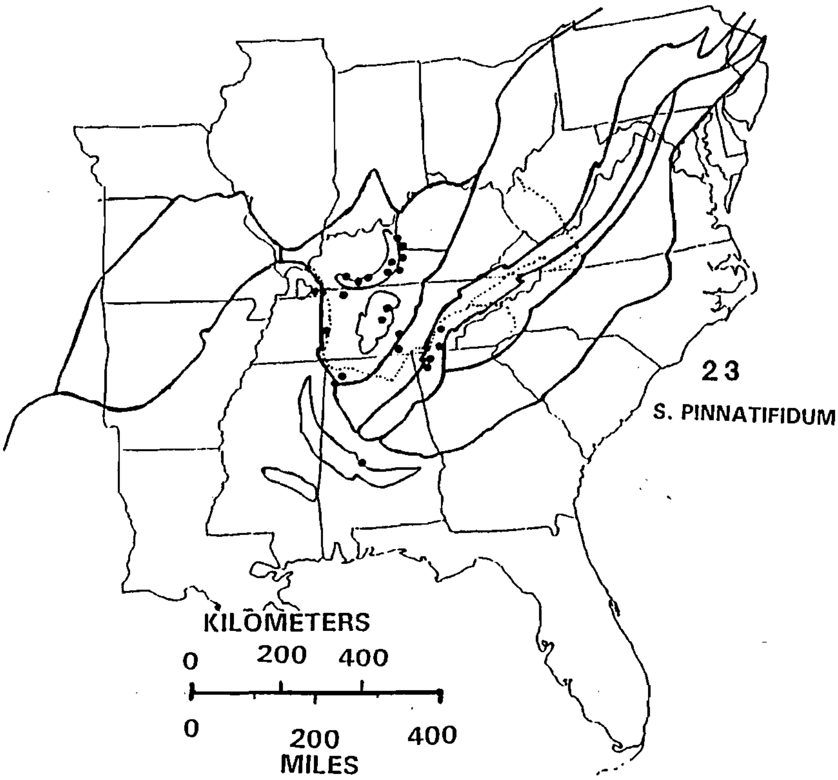

Figure 23. Range of *Silphium pinnatifidum*.

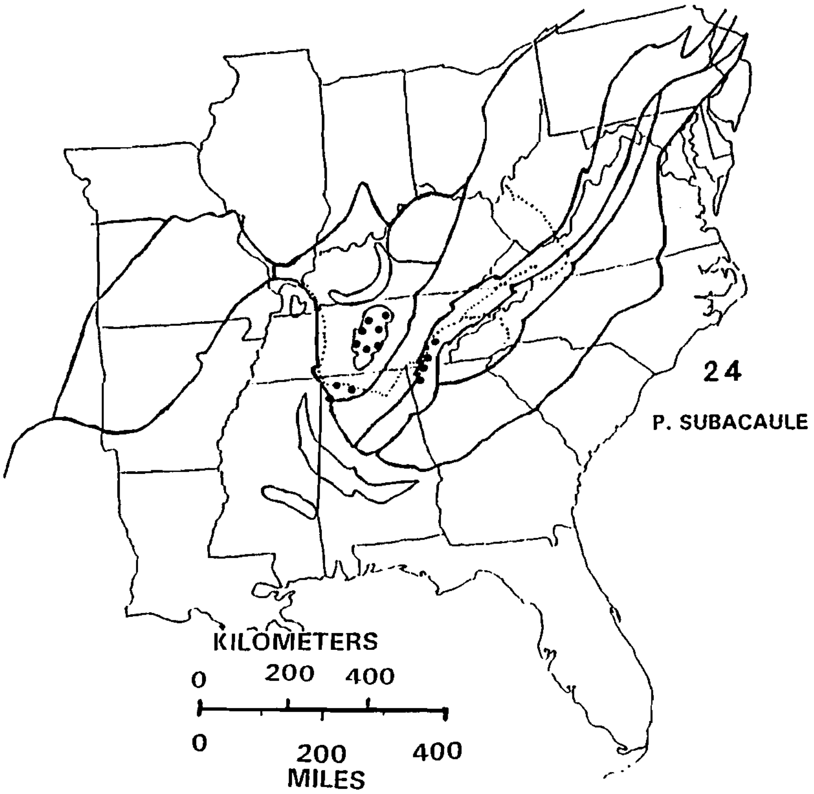

Figure 24. Range of *Pediomelum subacaule*.

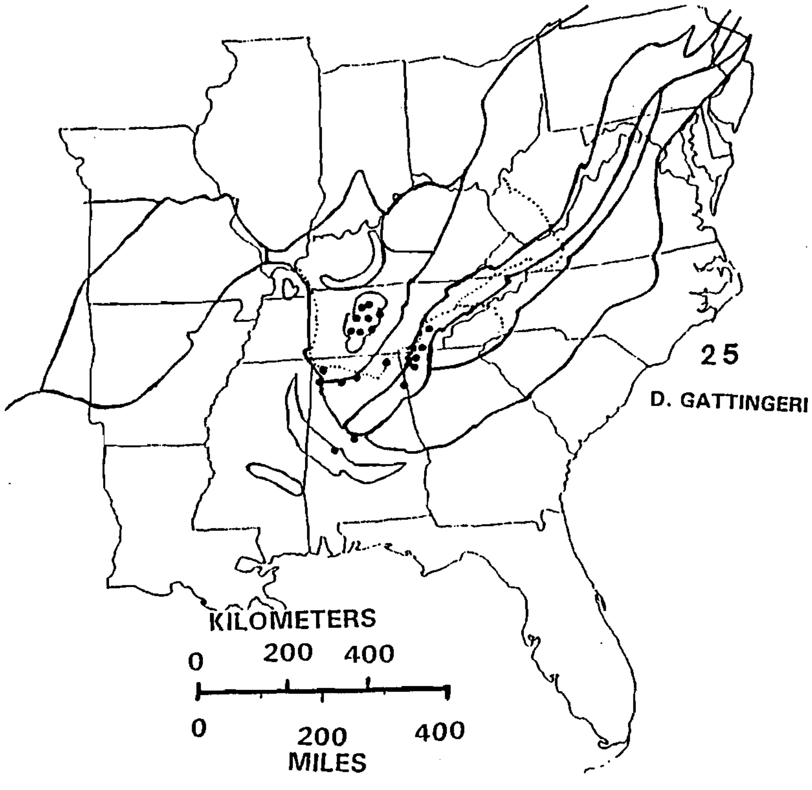

Figure 25. Range of *Dalea gattingeri*.

and the age of the forest overstory. Community species richness (diversity) is not a constant value for a specific site condition (xeric, mesic, etc.) but is influenced by overstory composition (which determines level of shade and litter depth) and time since stand establishment (*e.g.*, young open stands vs. medium age closed stands vs. old stands with gaps). Data collected in a study of partial (shelterwood) cuts in forest stands indicate that herbaceous diversity (species number and cover) increases when canopy gaps are created by removing a small number of trees. This increase is related to the increased light level at the forest floor. The data is consistent with that (pre- and post-sample data) from experimental plots (burned, cut, burned and cut). However, with the development of dense seedling and sapling strata beginning at about eight years post harvest, the diversity of the herbaceous layer is substantially diminished. As these young stands begin to naturally thin with age, there may be a slow recovery of the herbaceous understory.

5. Finally, based on a comparison of species richness between LBL and the Shawnee National Forest (Illinois), the herbaceous stratum is still recovering from major disturbances that began with iron smelting in the early 1800s and continued with grazing and wildfire into the 1950s. The numerous small farmers of that era often used the woods for grazing domestic livestock, particularly swine, who seriously damaged the forest floor and associated herbs.

SECOND ORDER RESEARCH RESULTS

The term "second order" is used to indicate the importance of the scientific results and practical implications over and above first order results that usually are generated in research. These advances in research may be more important than the first order results which are restricted to the study area. The context here can be clarified by answering the question of how the results have contributed to: (1) an improvement in methodology and data analysis that will advance research and assist other researchers, and (2) our understanding of forest ecosystem function in general not only at LBL but in other regions and in a scientific and applied sense.

Two advances from the LBL research can be identified.

1. Extremely different community/site relationships appear if forest overstory (tree) data for compositionally stable (climax, terminal) forest stands are analyzed separately from data for unstable (successional) stands. In order to understand the relationships, data sets for stable and unstable forest stands must be analyzed independently. For example, in analysis using indirect ordination (a common analytical procedure), forest stands may be sequenced along one axis and tree data plotted on this axis to form a coenocline, or the stands may be sequenced along several axes. In theory, each axis may represent a complex environmental gradient (soil moisture, nutrients, pH, organic matter, depth of the A horizon, aspect, slope steepness, surface temperature, etc.), so the location of stands based on tree species composition should permit an identification of community/site relationships. However, if data sets are combined, relationships become obscure. For example, stable and successional stands dominated by relatively pure white oak are likely to appear near each other on the soil moisture gradient although the former is typically situated on a hot, dry south or southwest slope, and the latter on a cool, moist north slope or stream terrace. In this situation, the results are ambiguous and the interpretation is at best tentative and probably open to considerable error.

2. The LBL forest data set was used as an example of parallel analysis. Parallel analysis was used to compare 29 analyses from 22 published journal articles. The comparison indicated that a particular method, parallel analysis, was the most efficient, consistent, accurate and objective in determining the significance of and identifying the threshold for extracting principal components.

In addition, spatial fire temperature data were used to develop a new permutation analysis of the two-term local variance (TTLV) analysis technique, a frequently used pattern analysis technique. The new permutation identified a weakness in the method.

RESEARCH AWARDS

For his research on LBL forests and environment, Dr. Scott B. Franklin received the 1991 Eugene T. Odum Award from the Southeastern Section of the Ecological Society of America during a joint meeting with the Association of Southeastern Biologists at Boone, NC. The paper presented at the meeting for the award was:

Franklin, S. B., J. S. Fralish, and P. A. Robertson. 1991. Ordination of compositionally-stable forest communities of Land Between The Lakes, KY and TN.

LONG TERM MONITORING

Long-term monitoring and periodic remeasurement of the plots will continue by scientists at Southern Illinois University, Carbondale, Illinois, and the University of Memphis, Memphis, Tennessee. Long-term monitoring (multiple remeasurements) provides the opportunity to examine ecosystem change and response that may not be apparent or identified by a single measurement.

RELATED RESEARCH

Although completed before this project began in 1986, Schibig and Chester, Volunteer State Community College, Gallatin, Tennessee (Schibig) and Austin Peay State University, Clarksville, Tennessee (Chester), studied the pine and mixed hardwood-pine community located on Devil's Backbone at the southern end of LBL. Their plots were permanently marked for remeasurement and long term study. This research is reported in:

Schibig, L. J. and E. W. Chester. 1988. Vegetational and floristic characterization of a mixed hardwoods-shortleaf pine stand in Stewart County, Tennessee. Journal of the Tennessee Academy of Science 63:83-88.

Dr. Stanley Harris (now Emeritus) of the Geology Department, Southern Illinois University, Carbondale, Illinois, summarized the geological information; although his work on the geology was not part of the forest ecology project, it was closely aligned with our work. His work is reported as:

Harris, S. E., Jr. 1988. Summary review of geology of Land Between The Lakes, Kentucky and Tennessee. Pp. 23-83 *in:* D. H. Snyder (ed.). Proceedings of the First Annual Symposium on the Natural History of Lower Tennessee and Cumberland River Valleys. Center for Field Biology, Austin Peay State University, Clarksville, Tennessee.

ACKNOWLEDGMENTS

The Center for Field Biology, Austin Peay State University, Clarksville, Tennessee, and the Department of Forestry and the Department of Plant Biology, Southern Illinois University, Carbondale, Illinois, have generously supported this project, graduate students and student workers. During the early years of the project, the Land Stewardship Unit at Land Between The Lakes (TVA), Golden Pond, Kentucky, also extensively supported this project by providing interns to assist in data collection, housing for researchers, interns, and student workers, information and maps of potential research areas, and field personnel for installation of experimental plots on fire and timber harvesting. We thank Larry Doyle, Beth Wellbaum, Gail O'Neil, Eric Schmeckpeper, Nick Watson, and Leamon Lyons of Land Stewardship for their assistance.

Dr. Philip Robertson, Department of Plant Biology, Southern Illinois University, Carbondale, Illinois, had a major contribution to the research not only in analysis and publication but also through his assistance as a member of the guidance committees for graduate students within the Department of Forestry.

Several other researchers have contributed their expertise to the development of the Forest Ecology Project at LBL. The methodological expertise of Dr. David J. Gibson, Department of Plant Biology, Southern Illinois University, Carbondale, Illinois, and the statistical assistance of Dr. John T. Pohlmann, Department of Educational Psychology, Southern Illinois University, Carbondale, Illinois, were important in the development of a major manuscript. Dr. David Sharpe, Department of Geography, directed the Ph.D. dissertation of Zhao Yang in a modeling study in Blockhouse Watershed, LBL.

Fred B. Crooks provided exceptional support with data collection and summarization during the first two years of the project. A number of people, some as student workers and some as LBL Interns, assisted with the data collection both in the field and laboratory. These students were Lucy Rudowicz, Wendy Smith, Charles Conner, Larry Mahler, Trevor Cottle, Michael Kelly, Sue Peterson, Pam Snyder, Gena Howe, Matt Peterson, Dave Philips, Tim Phelps, and Ken Werner.

APPENDIX A. COMPLETED THESES AND DISSERTATIONS

Wellbaum, E. M. 1989. Site, stand and tree characteristics associated with oak decline and mortality at Land Between The Lakes, KY and TN. Master of Science Thesis. Department of Forestry, Southern Illinois University, Carbondale, Illinois.

Franklin, S. B. 1990. The effect of soil and topography on forest community composition at Land Between The Lakes, KY and TN. Master of Science Thesis. Department of Forestry, Southern Illinois University, Carbondale, Illinois.

Kettler, S. M. 1990. The effect of soil and topography on forest successional patterns at Land Between The Lakes, KY and TN. Master of Science Thesis. Department of Forestry, Southern Illinois University, Carbondale, Illinois.

Yang, Z. 1993. Analysis of alternative designs for buffer zones around conservation areas with a spatial decision support system (SDSS). Ph.D. Dissertation. Department of Geography, Southern Illinois University, Carbondale, Illinois.

Snyder, P. R. 1995. Forest regrowth in 10-12 year old clearcuts at Land Between The Lakes, Kentucky and Tennessee. Master of Science Thesis. Department of Forestry, Southern Illinois University, Carbondale, Illinois.

Franklin, S. B. 1996. A community view of disturbance and vegetation dynamics. Ph.D. Dissertation. University of Joensuu, Joensuu, Finland.

Franklin, S. B. 1996. Disturbance effects on upland *Quercus* community dynamics at Land Between The Lakes, Kentucky and Tennessee. Ph.D. Dissertation. Department of Plant Biology, Southern Illinois University, Carbondale, Illinois.

Close, D. D. 1996. Evaluation of herbaceous diversity and differential species in mature forest stands at Land Between The Lakes, Kentucky and Tennessee. Master of Science Thesis. Department of Forestry, Southern Illinois University, Carbondale, Illinois.

APPENDIX B. BOOK CHAPTERS

Fralish, J. S., S. C. Franklin, P. A. Robertson, S. M. Kettler, and F. B. Crooks. 1993. An ordination of compositionally stable and unstable forest communities at Land Between The Lakes, Kentucky and Tennessee. Pp. 247-267 *in*: J. S. Fralish, R. P. McIntosh, and O. L. Loucks (eds.). John T. Curtis: Fifty Years of Wisconsin Plant Ecology. Wisconsin Academy of Science, Arts and Letters, Madison, Wisconsin.

Fralish, J. S. 1997. Community succession, stability and diversity in the central hardwood forest. *in*: M. W. Schwartz (ed.). Conservation in Highly Fragmented Landscapes. Chapman & Hall, New York. (Scheduled for release late 1997).

Fralish, J. S., S. B. Franklin, and D. D. Close. In press. The open woodland communities of southern Illinois, western Kentucky and west Tennessee. *in:* R. C. Anderson, J. S. Fralish, and J. M. Baskin (eds.). The Savanna, Barren and Rock Outcrop Communities of North America. Cambridge University Press, New York, New York.

APPENDIX C. JOURNAL ARTICLES

Fralish, J. S. and F. B. Crooks. 1989. Forest composition, environment and dynamics at Land Between The Lakes in northwest middle Tennessee. Journal of the Tennessee Academy of Science 64:107-11.

Franklin, S. B., P. A., Robertson, J. S. Fralish, and S. M. Kettler. 1993. Overstory vegetation and successional trends of Land Between The Lakes, U.S.A. Journal of Vegetation Science 4:512-520.

Franklin, S. B. 1994. Late Pleistocene and Holocene vegetation history of Land Between The Lakes, Kentucky and Tennessee. Transactions of the Kentucky Academy of Science 55:6-19.

Franklin, S. B., D. J. Gibson, P. A. Robertson, J. T. Pohlmann, and J. S. Fralish. 1995. Parallel analysis: a method for determining significant principal components. Journal of Vegetation Science 6:99-106. (Based on the forest site data collected at LBL).

Franklin, S. B., P. A. Robertson, and J. S. Fralish. 1997. Small-scale fire temperature patterns in upland *Quercus* communities. Journal of Applied Ecology. (In press).

Campbell, J. C., S. B. Franklin, D. J. Gibson, and J. Newman. Permutation of two-term local quadrat variance analysis: general concepts of interpretation of peaks. Journal of Vegetation Science. (Accepted for publication).

APPENDIX D. REVIEWED PROCEEDINGS ARTICLES

Fralish, J. S. and F. B. Crooks. 1988. Forest communities of the Kentucky portion of Land Between The Lakes: A preliminary assessment. Pp. 164-175 *in:* D. H. Snyder (ed.). Proceedings of the First Annual Symposium on the Natural History of Lower Tennessee and Cumberland River Valleys. Center for Field Biology, Austin Peay State University, Clarksville, Tennessee.

Yang, Z. and D. M. Sharpe. 1991. Design of buffer zones for conservation areas and a prototype spatial decision support system (SDSS). Pp. 60-70 *in*: Proceedings of the American Congress on Surveying and Mapping: GIS/LIS. Atlanta, Georgia.

Fralish, J. S. and P. R. Snyder. 1993. Forest regrowth in 10-12 years old clearcuts at Land Between The Lakes, Kentucky and Tennessee. Pp. 179-194 *in*: S. W. Hamilton, E. W. Chester and A. F. Scott (eds.). Proceedings of the Fifth Annual Symposium on Natural History of Lower Tennessee and Cumberland River Valleys. Center for Field Biology, Austin Peay State University, Clarksville, Tennessee.

Franklin, S. B. and J. S. Fralish. 1994. The chestnut oak and post oak woodlands of Land Between The Lakes, Kentucky and Tennessee. Pp. 341-346 *in*: J. S. Fralish, R. C. Anderson, J. E. Ebinger and R. Szefoni (eds.). Proceedings of the Second North American Conference on Savannas and Barrens. Environmental Protection Agency, Great Lakes National Program Office, Chicago, Illinois.

Franklin, S. B., J. S. Fralish, and P. A. Robertson. 1995. The effect of prescribed burning on fuels and soil nutrients of upland *Quercus* communities. Pp. 191-214 *in*: S. W. Hamilton, D. S. White, E. W. Chester, and A. F. Scott (eds.). Proceedings of the Sixth Annual

Symposium on the Natural History of the Lower Tennessee and Cumberland River Valleys. The Center For Field Biology, Austin Peay State University, Clarksville, Tennessee.

Fralish, J. S., S. B. Franklin, and D. D. Close. 1997. The long term forest ecology research program at Land Between The Lakes, Kentucky and Tennessee. Proceedings of the Seventh Annual Symposium on the Natural History of the Lower Tennessee and Cumberland River Valleys. The Center For Field Biology, Austin Peay State University, Clarksville, Tennessee. (In Press).

APPENDIX E. PAPERS AND ABSTRACTS

Fralish, J. S. and F. B. Crooks. 1988. Forest communities of the northern portion of Land Between The Lakes, TVA. Paper presented at the annual meeting of the Association of Southeastern Biologists. Abstract: ASB Bulletin 35:36.

Fralish, J. S. and F. B. Crooks. 1988. Forest communities of the Kentucky portion of Land Between The Lakes. Pp. 164-175 *in*: D. H. Snyder (ed.). Proceedings of the First Annual Symposium on the Natural History of Lower Tennessee and Cumberland River Valleys. The Center for Field Biology, Austin Peay State University, Clarksville, Tennessee.

Crooks, F. B. and J. S. Fralish. 1988. Diameter, height and age relationships for selected *Quercus* at Land Between The Lakes. Pp. 76 *in*: D. H. Snyder (ed.). Proceedings of the First Annual Symposium on the Natural History of Lower Tennessee and Cumberland River Valleys. The Center for Field Biology, Austin Peay State University, Clarksville, Tennessee.

Fralish, J.S. and F. B. Crooks. 1989. Forest Communities of Land Between The Lakes in northwest middle Tennessee. Paper presented at the Second Annual Symposium on the Natural History of Lower Tennessee and Cumberland River Valleys. The Center for Field Biology, Austin Peay State University, Clarksville, Tennessee.

Rudowicz, L. and J. S. Fralish. 1989. Forest communities of xeric sites at Land Between The Lakes, Kentucky and Tennessee. Paper presented at the annual meeting of the Association of Southeastern Biologists, Biloxi, Mississippi. Abstract. ASB Bulletin 36:113.

Kettler, S. and J. Fralish. 1989. Forest succession patterns at Land Between The Lakes, KY and TN. Paper presented at the annual meeting of the Association of Southeastern Biologists, Charlotte, North Carolina. Abstract. ASB Bulletin 36:112.

Franklin, S. and J. Fralish. 1989. Forest Communities of xeric-mesic and mesic sites at Land Between The Lakes, KY and TN. Paper presented at the annual meeting of the Association of Southeastern Biologists, Charlotte, North Carolina. Abstract. ASB Bulletin 36:112-113.

Kettler, S., J. Fralish, and F. Crooks. 1990. Forest succession and site index patterns at Land Between The Lakes, KY and TN. Paper presented at the annual meeting of the Association of the Southeastern Biologists, Baltimore, Maryland. Abstract. ASB Bulletin 37:74.

Franklin, S., J. Fralish, and F. Crooks. 1990. The effect of soil and topography on forest stand composition and growth at Land Between The Lakes, KY and TN. Paper presented at the

annual meeting of the Association of the Southeastern Biologists, Baltimore, Maryland. Abstract. ASB Bulletin 37:74.

Rudowicz, L., J. Fralish, and F. Crooks. 1990. Forest understory vegetation at Land Between The Lakes, KY and TN. Paper presented at the annual meeting of the Association of the Southeastern Biologists, Baltimore, Maryland. Abstract. ASB Bulletin 37:74-75.

Franklin, S., J. Fralish, and F. Crooks. 1990. Community-site relationships at Land Between The Lakes, KY and TN. Pp. 103 *in*: S. W. Hamilton and M. T. Finley (eds.). Proceedings of the Third Annual Symposium on the Natural History at Lower Tennessee and Cumberland River Valleys. The Center for Field Biology, Austin Peay State University, Clarksville, Tennessee.

Kettler, S., J. Fralish, and F. Crooks. 1990. Forest succession and site index patterns at Land Between The Lakes, KY and TN. Abstract. Pp. 105 *in*: S. W. Hamilton and M. T. Finley (eds.). Proceedings of the Third Annual Symposium on the Natural History at Lower Tennessee and Cumberland River Valleys. The Center for Field Biology, Austin Peay State University, Clarksville, Tennessee.

Kettler, S., J. Fralish, and F. Crooks. 1990. Forest succession and site index patterns at Land Between The Lakes, KY and TN. Paper presented at the annual meeting of the Association of the Southeastern Biologists, Baltimore, Maryland. Abstract. ASB Bulletin 37:74-75.

Fralish, J. S. 1991. A provisional ecological land classification system for Land Between The Lakes, KY and TN. Paper presented at the annual meeting of the Association of the Southeastern Biologists, Boone, North Carolina. Abstract. ASB Bulletin 38:116.

Franklin, S., J. S. Fralish, and P. Robertson. 1991. Ordination of compositionally-stable forest communities of Land Between The Lakes, KY and TN. Paper presented at the annual meeting of the Association of the Southeastern Biologists, Boone, North Carolina. Abstract. ASB Bulletin 38:116.

Robertson, P., J. S. Fralish, S. Franklin, and S. Kettler. 1991. Forest vegetation of Land Between The Lakes, KY and TN in relation to physical and chemical soil-site variables. Paper presented at the annual meeting of the Association of the Southeastern Biologists, Boone, North Carolina. Abstract. ASB Bulletin 38:116.

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Franklin, S. B., P. A. Robertson, J. S. Fralish, and S. M. Kettler. 1992. Mulitvariate analysis of the overstory vegetation of Land Between The Lakes, KY and TN. Pp. 103 *in*: D. H. Snyder (ed.). Proceedings of the Fourth Annual Symposium on the Natural History of the Lower Tennessee and Cumberland River Valleys. The Center for Field Biology, Austin Peay State University, Clarksville, Tennessee.

Franklin, S. B. 1992. A vegetation history of Land Between The Lakes. Paper presented at the annual meeting of the Association of the Southeastern Biologists, Tuscaloosa, Alabama. Abstract. ASB Bulletin 39:98-99.

Franklin, S. B. 1993. From Pleistocene to Present: A vegetational history of Land Between The Lakes, Kentucky and Tennessee. Pp. 195 *in*: S. W. Hamilton, E. W. Chester and A. F. Scott (eds.). Proceedings of the Fifth Annual Symposium on the Natural History at Lower

Tennessee and Cumberland River Valleys. The Center for Field Biology, Austin Peay State University, Clarksville, Tennessee.

Snyder, P. R. and J. S. Fralish. 1993. A study of oak re-establishment in clearcut forest at Land Between The Lakes, KY and TN. Paper presented at the annual meeting of the Association of the Southeastern Biologists, Virginia Beech, Virginia. Abstract. ASB Bulletin 40:126.

Franklin, S. B., P. A. Robertson, J. S. Fralish, and S. M. Kettler. 1993. Stratum analysis for separating successional from compositionally stable stands. Paper presented at the annual meeting of the Association of the Southeastern Biologists, Virginia Beech, Virginia. Abstract. ASB Bulletin 40:127.

Franklin, S. B., B. J. Gibson, P. A. Robertson, J. T. Pohlman, and J. S. Fralish. 1994. Parallel analysis: a method for determining significant factors. Paper presented at the annual meeting of the Association of the Southeastern Biologists, Orlando, Florida. Abstract. ASB Bulletin 41:97

Synder, P., and J. Fralish. 1994. A study of oak re-establishment in clearcut forest at Land Between The Lakes, KY and TN. Paper presented at the annual meeting of the Association of the Southeastern Biologists, Orlando, Florida. Abstract. ASB Bulletin 41:135.

Franklin, S. , P. Robertson, and J. Fralish. 1995. Small scale fire temperature heterogeneity in an upland hardwood forest. Paper presented at the annual meeting of the Association of the Southeastern Biologists, Knoxville, Tennessee. Abstract. ASB Bulletin 42:110.

Close, D. D. and J. S. Fralish. 1996. Analysis of the herbaceous stratum within forest communities at Land Between The Lakes, KY and TN. Paper presented at the annual meeting of the Association of the Southeastern Biologists, Statesboro, Georgia. Abstract. ASB Bulletin 43:129.

Franklin, S. B. 1996. Effect of fire on upland white oak communities, Land Between The Lakes. Abstract. Transactions Illinois State Academy of Science 89 (Supplement):46.

Franklin, S. B. 1996. Effect of fire on while oak community structure, Land Between The Lakes. Transactions of the Kentucky Academy of Science 55:6-19.

Franklin, S. B. 1997. The effects of prescribed burning on upland *Quercus* forest vegetation, Land Between The Lakes. Proceedings of the Seventh Annual Symposium on the Natural History of the Lower Tennessee and Cumberland River Valleys. The Center For Field Biology, Austin Peay State University, Clarksville, Tennessee. (In Press).

Close, D. D. and J. S. Fralish. 1997. Herbaceous dominance types and species response to an environmental gradient for undisturbed forest stands at Land Between The Lakes, KY and TN. Proceedings of the Seventh Annual Symposium on the Natural History of the Lower Tennessee and Cumberland River Valleys. The Center For Field Biology, Austin Peay State University, Clarksville, Tennessee. (In Press).

Close, D. D. and J. S. Fralish. 1997. Herbaceous dominance types and species response to an environmental gradient for undisturbed forest stands at Land Between The Lakes, KY and TN. Paper presented at the annual meeting of the Association of the Southeastern Biologists, Greenville, South Carolina. Abstract: ASB Bulletin 44:129.

Glickauf, S. and J. Fralish. 1997. Herbaceous richness and cover in shelterwood cut forest stands at Land Between The Lakes, KY and TN. Paper presented at the annual meeting

of the Association of the Southeastern Biologists, Greenville, South Carolina. Abstract: ASB Bulletin 44:123.

APPENDIX F. MANUSCRIPTS IN PREPARATION

Fralish, J. S., S. B. Franklin, and S. M. Kettler. The forest communities and site relationships at Land Between The Lakes, Kentucky and Tennessee.

Franklin, S. B., P. A. Robertson, and J. S. Fralish. Effect of fire, thinning and herbicide treatments on upland *Quercus* stand composition, structure, and soil nutrients.

Franklin S. B., P. A. Robertson, J. S. Fralish, B. P. Klubek, and F. Ponder. Effect of prescribed burning on the physiological diversity of soil microbial groups and soil nutrients in upland hardwood forest stands.

Fralish, J. S., S. B. Franklin, *et al.* The Land Between The Lakes Forest Ecosystem, Kentucky and Tennessee (proposed book).

APPENDIX G. THESES IN PREPARATION

Glickauf, S. P. The effect of shelterwood cutting on the woody and herbaceous understory. Master of Science Thesis. Department of Forestry, Southern Illinois University, Carbondale, Illinois.

Ferdous, M. L. GIS modeling of landscape surface temperature patterns at Land Between The Lakes, Kentucky and Tennessee. Master of Science Thesis. Department of Forestry, Southern Illinois University, Carbondale, Illinois.

Fisher, M. J. The effect of site conditions on white oak (Lepidobalanus) wood density at Land Between The Lakes, Kentucky and Tennessee. Master of Science Thesis. Department of Forestry, Southern Illinois University, Carbondale, Illinois.

Tallman, L. R. 1997. The midcanopy component of compositionally-stable and unstable forest communities at Land Between The Lakes, KY and TN. Master of Science Thesis. Department of Forestry, Southern Illinois University, Carbondale, Illinois.

APPENDIX H. SELECTED ABSTRACTS AND METHODS

The following abstracts or summaries are taken from articles published in books, journals and proceedings, and from dissertations and theses. Some text has been eliminated or modified to reduce duplication. The abstracts-summaries are categorized under six major headings with the number under each heading indicated.

1. LAND BETWEEN THE LAKES VEGETATION HISTORY.

Franklin, S. B. 1994. Late Pleistocene and Holocene vegetation history of Land Between The Lakes, Kentucky and Tennessee. Transactions of the Kentucky Academy of Science 55:6-19.

ABSTRACT. The vegetation history of Land Between The Lakes (LBL), Kentucky and Tennessee, is summarized beginning with the Pleistocene Series. A zonation of boreal, northern deciduous/*Pinus* and southern deciduous/*Pinus* spp. similar to that in North America today was compacted below the Laurentide Ice Sheet. Boreal or northern hardwood species dominated LBL during glacial extensions and alternated with southern and prairie constituents during warmer and drier periods.

The Holocene, a warming and drying period, followed the Pleistocene and was accompanied by the onset of human occupation. During the height of this middle period, Hypsithermal, mesophytic species retreated to bottomlands and protected coves while *Quercus*, *Carya*, and herbaceous species dominated uplands. Following the Hypsithermal, the climate became cooler and more moist. Southern *Pinus* and *Quercus* spp. migrated north and invaded prairie and open forest. However, succession was delayed by aboriginal disturbance, which included annual burning and swidden agriculture.

When Europeans began exploring the LBL area, they found bottomland hardwoods of enormous size and upland park-like forests with an herbaceous understory. Europeans began settling the area in the late 1700s. Their influence on the vegetation included: farming; grazing; whiskey distilling; timber cutting for charcoal production, railroad ties, and other wood products; and damming the Cumberland and Tennessee rivers. Agrodeforestation and the control of wildland fire led to the reversal of forest dominance across the landscape. Bottomland forests were converted to agricultural land and were later inundated by Kentucky Lake and Lake Barkley. Previously open uplands succeeded to closed forest, currently dominated by *Quercus* species.

2. FOREST HEALTH.

Wellbaum, E. M. 1989. Site, stand and tree characteristics associated with oak decline and mortality at Land Between The Lakes, KY and TN. Master of Science Thesis. Department of Forestry, Southern Illinois University, Carbondale, Illinois.

ABSTRACT. Oak decline is described as a complex of disease symptoms resulting from unspecified environmental or physiological conditions. In the early 1980s, symptoms such as thin, chlorotic foliage, reduced growth, and top dieback gradually appeared in oak stands throughout the central and southern hardwood forest regions. Unprecedented levels of mortality were soon reported, as in the case of the 1986 remeasurement of permanent Continuous Forest Inventory (CFI) plots in the Land Between the Lakes (LBL) recreation area. Between 1976 and 1986, LBL timber mortality tripled over the previous ten-year period.

To study variability in oak mortality at LBL, tree characteristics (species, DBH, crown class, percent rot) were analyzed to determine common characteristics of trees dying during the decline period. Most individual tree characteristics were not correlated. Mortality was shown to be greatest in black oak (*Quercus velutina*) and lowest in white oak (*Quercus alba*). Site and stand variables (aspect, percent slope, slope position, soil complex, stocking percent, present and past live basal area, past mortality, stand age) were used to construct models to explain variability in basal area mortality. Those contributing most to the variance in 1986 mortality were 1986 live basal area, 1976 live basal area, and slope aspect, which accounted for up to 83 percent of the variance. Models most effective in explaining 1986 mortality were largely ineffective in explaining (pre-decline) 1976 mortality. Basal area mortality was shown to increase as slope aspect approached northeast.

Procedures. Data for this study were collected by TVA personnel for the continuous Forest Inventory (CFI) of Land Between the Lakes in 1966, 1976, and 1986. One hundred fifty-seven permanent plots were systematically located with four plots per 2.5-minute subdivision. Excess variability for this study was reduced by including only plots located in the upland hardwood or blackjack oak-hardwood cover types defined by TVA (1965). Stands younger than 40 years in 1986 and plots cut since 1966 were excluded. Ninety-eight plots fit these criteria and were considered in the analysis.

Plot slope position, percent slope, and aspect were determined in the 1966 inventory. For all inventories, stems were measured on nested circular plots. Sawtimber trees [stems ≥11.00 inches in diameter at breast height (DBH)] were measured on a 1/5-acre plot; pole timber trees [stems <11.00 inches and ≥5.00 inches DBH] were measured on a 1/20-acre plot. Stand basal area (BA) in square feet/acre was calculated from recorded tree diameters for each of the three surveys. In 1987, cores were taken from two dominant or codominant trees per plot to estimate stand age. Information on soil types and properties was obtained from county soil survey reports.

Aspect was transformed following the procedures of Beers *et al.* (1966) on the recorded azimuths. The value 0.00 was assigned to the southwest aspect (225 degrees azimuth), the aspect that is the warmest, retains the least moisture, and hence has the lowest productivity. The scale grades equivalently in both directions ending at 2.00, the value assigned to a northeast slope (45 degrees azimuth).

Two approaches were used to compare recent (between 1976 and 1986) mortality increases in oak/hickory with normal mortality levels (between 1966 and 1976). In the first approach, the relationship between mortality and continuous site and stand variables was studied. Variables were then incorporated into multiple regression models using the R-SQUARE and STEPWISE procedures of the Statistical Analysis System (SAS). Dependent variables were 1976 basal area (in square feet per acre) of stems that died prior to the 1986 reinventory, and 1966 basal area of stems that died prior to the 1976 reinventory (BA86MORT and BA76MORT, respectively). Independent variables tested for contribution to the variance in mortality include: percent slope; transformed aspect; two ages determined for each plot; live basal area at the beginning and end of both survey period 3; previous basal area mortality; and percent stocking levels (Gingrich 1967) at the beginning of the survey periods.

Using the best models from the preliminary tests, the regression and general linear model procedures were then used for hypothesis testing (alpha z 0.05). The hypothesis for predicting 1986 basal area mortality was: There is no difference in mortality based on slope percent, transformed aspect, plot age, 1966 live basal area, 1966 basal area mortality, 1976 live basal area, 1976 basal area mortality, 1986 live basal area, 1966 stocking percent, 1976 stocking percent, 1986 stocking percent. Correspondingly, the hypothesis for predicting 1976 basal area mortality was: There is no difference in mortality based on slope percent, transformed aspect, age, 1966 live basal area, 1966 basal area mortality, 1976 live basal area, 1966 stocking percent, or 1976 stocking percent. To examine for effects of nominal (class) variables, mean basal area and stem mortality were compared between two slope positions, three soil complexes, and eight aspect classes. Where differences appeared to exist, regression models were tested between classes. This was performed for both survey periods.

The second phase of the study examined 1976 characteristics of individual oaks and hickories that died prior to the 1986 resurvey. General differences between live and dead trees which appeared in the CFI reports suggested logical groupings by species and size classes for correlation analysis. Also examined were possible correlations between tree characteristics and site and stand characteristics for the plots on which trees died. Tree size and vigor (expressed by average tree DBH and percent of rot), sorted by species, crown class, soil complex, and aspect, were tested for significant differences by analysis of variance.

3. FOREST COMMUNITY COMPOSITION AND STRUCTURE.

Fralish, J. S. and Crooks F. B. 1988. Forest communities of the Kentucky portion of Land Between The Lakes: A preliminary assessment. Pp. 164-175 *in*: D. H. Snyder (ed.). Proceedings of the First Annual Symposium on the Natural History of Lower Tennessee and Cumberland River Valleys, Center for Field Biology, Austin Peay State University, Clarksville, Tennessee.

ABSTRACT. In the Kentucky or northern portion of LBL, two generally distinct xerophytic communities can be recognized. The first occurs on coarse- to fine-textured soil of south slopes, ridges, and north slopes, and is dominated by *Quercus prinus*. *Quercus stellata* is the major dominant of the second community which is found on medium- to fine-textured soil of southwest slopes and ridges. *Carya glabra*, *Q. falcata*, *Q. marilandica*, and *Q. coccinea* are components of both communities. Xeric-mesic and mesic sites found throughout the landscape generally support communities of *Q. alba*, but *Q. velutina* is the major species in some stands. *Acer saccharum* and other species of mesic sites were found to be a minor component of the forest, although it appears that they are becoming increasingly important and will replace many oak communities at elevations below approximately 140 m.

Methods. Refer to Franklin (1990) and Kettler (1990) for description of methods. Sixty-two upland stands were sampled during the summer of 1987.

Fralish, J. S. and Crooks, F. B. 1989. Forest composition, environment and dynamics at Land Between The Lakes in northwest middle Tennessee. Journal of the Tennessee Academy of Science 64:107-11.

ABSTRACT. In the Tennessee or southern one-third of LBL, xerophytic communities are dominated by *Pinus echinata, Quercus stellata* and *Q. prinus*. Communities of *P. echinata* and *Q. stellata* are relatively rare and occur on soil formed in loess overlying unconsolidated Coastal plain material (Brandon and Lax series). Stands of *P. echinata* are concentrated in the Devil's Backbone area where elevation exceeds 160 m. In most stands, *P. echinata* is being replaced by *Q. stellata* or *Q. alba*. Communities of *Q. prinus* are found on coarse gravel to fine-textured soil of south slopes, ridges, and north slopes. *Quercus velutina, Q. falcata, Q. marilandica, Q. coccinea*, and *Carya* are other components of the three communities.

Xeric-mesic and mesic sites generally support communities of *Quercus alba* but *Q. velutina* is the major species on some sites. However, communities dominated by *Q. alba* have a wider distribution and occur from south and southwest slopes to ridgetops, north slopes, and stream terraces; communities of *Q. velutina* seldom occur on north slopes or terraces. The presence of *Q. alba* communities on mesic north slopes and terraces is interpreted as the result of harvesting and fire that prevented development of communities dominated by mesophytes.

Where disturbance has been less a factor in determining forest composition at elevations below 140 m, *Fagus grandifolia* is the dominant species with *Acer saccharum* and *Q. alba* secondary in importance. Other mesophytic species were found to be a minor component of the forest although they are invading and along with *Acer saccharum,* will replace most oak communities except on the driest sites. *Acer saccharum* is the dominant species of communities on stream terraces, but *F. grandifolia, Q. alba, Liquidambar styraciflua,* and *Liriodendron tulipifera* also are important species.

Methods. Refer to Franklin (1990) and Kettler (1990) for description of methods.

Franklin, S. B. 1990. The effect of soil and topography on forest community composition at Land Between The Lakes, KY and TN. Master of Science Thesis. Department of Forestry, Southern Illinois University, Carbondale, Illinois.

ABSTRACT. Sixty-four compositionally-stable forest stands at Land Between The Lakes were studied for the purpose of relating species composition to soil and topographic factors. Compositional stability was determined by comparing overstory with understory composition index and similarity index.

COMPAH analysis separated stands into eight communities: (1) *Quercus prinus,* (2) *Quercus marilandica,* (3) *Quercus stellata,* (4) Mixed Oak, (5) *Quercus alba,* (6) *Fagus grandifolia,* (7) Mixed Mesophytic, and (8) *Acer saccharum. Quercus prinus* communities were found on upper slopes and ridgetops; medium to high elevations; southeast to south to northwest slopes; and shallow gravelly soils. *Quercus marilandica* communities were infrequent and found in small patches on southwest slopes and on sandy to silty soil containing a shallow fragipan. *Quercus stellata* communities occurred on upper slopes and ridgetops; medium to high elevations; south to southwest facing sites; and silty (loessial) soils with a shallow fragipan (<50 cm). *Quercus alba* communities were found on medium to upper slopes and ridgetops; west to south to east slopes; at medium elevations; and on silty soils with a deeper pan or cherty coastal plain soils. *Fagus grandifolia* communities generally occurred on lower slopes of north facing sites at medium to low elevations and on limestone derived soils. Mixed Mesophytic communities occur on north-facing lower slopes and cove terraces, medium to low elevations, and on soils formed in alluvium washed from limestone. *Acer saccharum* communities were found on alluvial stream terraces at low elevations; soil material ranged from rocky to silty alluvium.

Three ordination methods, weighted averages ordination using environmental adaptation values, weighted averages ordination using competitive adaptation values, and DECORANA ordination, yielded similar Gaussian coenoclines which accounted for nearly 70% of the variance. Rank orders of distribution modes showed strong similarities between the methods.

Models derived from regression analysis to estimate composition index using elevation, slope position, aspect, available water capacity, and effective soil depth accounted for 70% of the variation.

Stand Selection. A total of 137 stands were located by using LBL work area descriptions, maps, and visual examination. Criteria for selecting potential stands included: lack of disturbance, condition, age, and uniformity. Stands with evidence of fire, cutting, wind, disease, or insect damage within the life history of the overstory were excluded. Minimum stand age was based on the dominant overstory trees and was set at 80 years. Each stand had uniform site conditions (soil, aspect, slope steepness, etc.) and was at least 1.0 ha in size in order to enclose two .06 ha circular sampling plots and a surrounding buffer zone. Stand boundaries were delineated to facilitate random placement of plot centers. Stands were selected to sample the range of natural forest community types in the Kentucky portion of LBL: *Quercus stellata-Q. marilandica, Q. prinus, Q. velutina-Q. coccinea, Q. alba-Q. velutina, Fagus grandifolia-Acer saccharum.*

Field Procedures. Two points were randomly located at least 27 m apart and 13 m from the stand boundary so that plots would not overlap or extend outside the stand. When stand size was limited by soil and topographic variability, placement of the points was restricted to relatively specific areas of the stand.

Each point was used as the center of a 0.06 ha circular plot (radius = 13.82 m). In three stands located on steep narrow slopes, a rectangular 0.09 ha plot oriented with the contour was used. All stems larger than 9 cm diameter at breast height (DBH) were recorded by species and diameter to the nearest 0.1 cm. A clinometer was used to measure tree height. An increment core was taken from each of five healthy dominant and codominant trees in a stand for age determination. Four additional points were located in cardinal directions at a distance of 6.91 m (radius/2) from plot center. Each additional point was used as the center of nested quadrats. Stems taller than 10 cm but less than 1.0 cm DBH (seedlings) were recorded by species on a 0.003 ha plot (radius = 3.09 m). Stems between 1.0 and 9.0 cm DBH (saplings) were recorded by species on a 0.006 ha plot (radius = 4.37 m).

A soil pit was opened approximately the same distance to the plot centers. Soil samples for texture and nutrient analysis were taken from each horizon and placed in plastic bags. The soil profile description included horizon type, thickness, structure, stoniness, and depth of rooting. In 22 stands, bulk density samples were collected using the cone method (Black 1968). Pebbles and larger stones were left in the cone. Soil samples removed from the cones were placed in plastic bags.

Aspect (azimuth), percent slope, and slope position as a percentage of the distance between the ridgetop and nearest stream channel were recorded. Elevation (ELEV) was determined for each stand from topographical maps. Horizontal distance to opposing slope (m) was measured at the site or estimated from topographic maps for distances greater than 200 meters.

Laboratory Procedures. Soil samples collected for bulk density analysis were dried at 107° C for 48 hours and then weighed. Cone volume determined in the field was divided by weight to obtain an estimate of inter-stone soil bulk density. The average bulk density by horizon from all samples of a given horizon (*i.e.*, All A2, B, etc.) was applied to soil pits where bulk density samples were not estimated.

Soil samples were air dried, ground in a mortar and pestle, and sifted through a 2 x 2 mm sieve. The Bouyoucos hydrometer method was used for soil texture analysis (Wilde *et al.* 1979). Percent rock by volume was estimated using a bulk density of 2.65 g/cm^3 to attain a volume and then dividing by the total sample volume (including fines and rock) (Maden 1974):

$$\text{Equation 1: } \%\ Rock = \frac{volume\ of\ rock\ x\ 100}{total\ sample\ volume}$$

An average bulk density by horizon was obtained from estimates of 22 soil pits. These averages are A_1, 0.91; A_2, 1.13; B_1, 1.25; B_{21}, 1.28; B_{22} 1.43; and B_X, 1.55. When comparing AWC calculated with average BD and actual BD, less than 2 cm difference were seen in twenty stands and the maximum difference was 3.6 cm.

Available water capacity was calculated from percent silt, bulk density, horizon thickness, and percent stone, following the procedures of Fralish and Loucks (1975) and Fralish (1988):

Equation 2: $PAWC\ (\%) = (0.26\, x\ \%\ SILT) + 6.5$,

Equation 3: $HAWC\ (cm) = (PAWC\, x\ BD\ X\ HT)/100\ X\ (1 - \%\ Stone)$,

Equation 4: $AWC\ (cm) = E\ (HAWC)$.

PAWC is percent available water capacity; *HAWC* is horizon available water capacity (cm); *AWC* is available water capacity for the entire soil profile (cm); *BD* is the bulk density; *HT* is the horizon thickness; *% SILT* is percent silt; and *1- % Stone* is the percent of soil by volume occupied by soil particles <2.0 mm diameter (sand, silt, and clay). Effective soil depth was measured to the fragipan, root-impenetrable rock layer, or assumed to be 100 cm.

Azimuth (*A*) was transformed (Eq. 5) using the method of Beers *et al.* (1966). This procedure assigned values of 2.00 to northeast (cool and moist) facing slopes and 0.00 to southwest (hot and dry) facing slopes with other aspects assigned the corresponding intermediate values.

Equation 5: $A' = COS(45 - A) + 1$.

Increment cores were glued into wooden holders, sanded, and the number of rings counted using a binocular microscope. Tree age and height (m) were plotted on Carmean's (1971) site index curves to estimate site index for each stand.

Tree diameter (*D*) was converted to stem basal area (BA) (Eq. 6). Basal area values were converted to basal area per hectare (Eq. 7). Relative basal area (*Species BA/ Stand BA) x 100* was used as a species importance value (IV).

Equation 6: $BA\ (m^2) = 0.00007854\, x\ D^2$,

Equation 7: $SBA\ (m^2) = BA\ (m^2)\, x\ [10{,}000/(2\, x\ 600)]$.

Composition (Eq. 8) and similarity (Eq. 9) indices were calculated for each stand to separate stable stands from successional stands (Mueller-Dombois and Ellenberg 1974):

Equation 8: $CI = S\ (IV\ X\ CAV)$,

Equation 9: $IS = S\ (2w/a + b)$,

where *CI* is composition index; *IV* (importance value) is the relative basal area (overstory) or density (understory) of a species in a stand; *CAV* is the competitive adaptation value assigned to each species; *IS* is index of similarity; *a* is relative importance of a species in the understory; *b* is relative importance of a species in the overstory; and *w* is the amount of relative importance shared between the two stratum.

Data Analysis. Compositionally-stable forest stands were separated from successional stands by comparing composition indices from competitive adaptation values (Fralish 1988) and similarity indices generated from understory and overstory strata. Compositionally-stable forest stands were grouped into community types using COMPAH, an agglomerative clustering program (Hinkle 1988). Factor analysis, a principle component analysis using environmental variables (Muller 1982), was used to initially ordinate stands. Gaussian analysis, a program that fits distribution curves to basal area data (Gauch Chase, and Whittaker 1974), was applied to the factor analysis ordination to develop a preliminary coenocline. The mode of each species distribution, for species with at least five data points, was relativized on a one to ten scale to determine species environmental adaptation values (EAV). A refined direct gradient ordination was generated by weighting relativized species basal areas by respective EAVs following the procedures of Peet and Loucks (1977).

A weighted averages ordination (Peet and Loucks 1977), using competitive adaptation values (CAV) from Fralish (1988), was applied as a second ordination for Gaussian analysis. Gaussian analysis was performed on DECORANA (detrended correspondence analysis; Hill and Gauch 1980) ordination representing an indirect gradient of current community distribution. Forward stepwise multiple regression was used for developing models to predict composition index from soil and topographic variables. R^2 values and F statistics were used as an indication of the significance of the models. Seven randomly selected stands (10% of the total number of stands), were removed from the data set prior to analysis (McQuilkin 1976); these were used to validate the models.

Kettler, S. M. 1990. The effect of soil and topography on forest successional patterns at Land Between The Lakes, KY and TN. Master of Science Thesis. Department of Forestry, Southern Illinois University, Carbondale, Illinois.

ABSTRACT. Seventy-three successional forest stands were studied at Land Between The Lakes. Successional status was determined using one or more of the following three methods: (1) comparison of overstory and understory composition index; (2) similarity index between overstory and understory; and (3) identification of stands with environmental conditions similar to those of stands already displaying successional trends.

Stands dominated by *Pinus echinata* occur on high elevation ridgetops at LBL. With successional development these stands are converting to xerophytic oak species including *Quercus alba*, *Quercus prinus*, and *Quercus stellata*. *Quercus prinus* stands found on soils derived from loess and limestone and at low elevation contain moderate numbers of mesophytic species in the understory including *Acer saccharum* and *Fagus grandifolia*. These sites appear able to support more mesophytic communities and in the absence of disturbance will convert to them. *Quercus falcata-Q. stellata* stands found at low elevations at LBL contained large numbers of more mesophytic oaks (mainly *Q. alba*) in the understory. These stands appeared to be converting to more mesophytic, shade tolerant oaks, but moderate numbers of mesophytic species in the understory may indicate that these sites could eventually support mesophytic species. Stands dominated by *Quercus velutina* on north or east facing slopes on limestone derived soils had moderate numbers of mesophytic species in the understory. These sites appear capable of supporting mesophytic species, and stands on these sites may convert to *Acer saccharum* and *Fagus grandifolia* in the future.

Major successional changes are occurring in many *Quercus alba* stands. Stands at low elevations generally contain large numbers of *Acer saccharum* and *Fagus grandifolia* seedlings and saplings. Rapid successional changes are occurring on some sites while others appear to be converting slower, possibly because of the lack of a major seed source. Many sites supporting xerophytic species have environments similar to those of stable mesophytic stands. With a decrease in the disturbance, which allowed xerophytic species to expand their range onto better sites, communities dominated by mesophytic species will become more widespread in the future.

Field and Laboratory Procedures. Refer to Franklin (1990) for description of methods.

Office Procedure. Tree diameter was converted to basal area ($cm^2 = 0.00007854DBH$), and tree basal area was summed for both plots (total area = 0.12 ha) and multiplied by 8.33 to obtain stand basal area. Relative basal area (%) for each species was calculated as importance value (*IV*). For the understory, seedling and sapling densities were combined and relative density was calculated by species as an importance value. Mid-canopy species (*e.g.*, *Cornus florida*, *Cercis canadensis*, *Ostrya virginiana*, *Amelanchier arborea*, *Vaccinum arboreum*, and others) were excluded from the density values because of their limited development which restricts them from dominating the forest overstory.

A composition index (*CI*) (*sensu* Curtis and McIntosh 1951) was calculated for each stratum (overstory, understory) in the stand by multiplying species competitive adaptation value (Fralish 1988) by *IV* and summing for all species in a stand [$CI = S(AV \times IV)$]. Only major species were used in the calculations. Species that occurred at LBL but not in southern Illinois were assigned values based on ecological similarity to other species. Composition index differences between overstory and understory strata were examined to determine if compositional change (succession) was occurring. Generally, CI differences greater than 100 on moist sites where overstory *CI* exceeds 500 and greater than 50 on dry sites where overstory *CI* is less than 500 indicated more shade tolerant species were in the understory (higher *CI* values). This indicated a progression to more shade tolerant species (Fralish 1988; Peet and Loucks 1977).

Index of similarity (*IS*) between overstory and understory was also used to identify successional change using the formula $IS = 2W/(a+b)$, where *W* is the quantity common to both overstory and understory, and *a* and *b* are the total quantities for the respective strata (Mueller-Dombois and Ellenberg 1974). By using relativized (%) data, the actual similarity index reduces to *W*. Only major species with potential to eventually reach the overstory canopy were used in the calculations. Stands were generally considered stable if *IS* values were greater than 45% and successional if values were less than 45%.

In some stands, no seed source was available for more shade tolerant species even though the environmental conditions were similar to other sites that did have a seed source and were showing successional changes. These sites also were considered as "delayed successional" based on a comparison of environmental variables.

The relationship of stand composition to soil depth, available water capacity, aspect, distance to opposing slope, slope steepness, and slope position was examined. Stands were first grouped by dominant species (community type) and also soil type in the case of *Quercus alba* stands. Stepwise discriminant analysis (STEPDISC, SAS 1982) was performed to identify variables related to community composition and successional status. Equal numbers of stands were randomly selected from each group to be tested. Successional groups were compared to stable groups dominated by the same species and also to the expected potential vegetation. Significance level was set at the 0.05 level.

Franklin, S. B. and J. S. Fralish. 1994. The chestnut oak and post oak woodlands of Land Between The Lakes, Kentucky and Tennessee. Pp. 341-346 *in*: J. S. Fralish, R. C. Anderson, J. E. Ebinger, and R. Szefoni (eds.). North American Conference on Savannas and Barrens. Environmental Protection Agency, Great Lakes National Program Office, Chicago, Illinois.

ABSTRACT. Presettlement upland forests of the southern Illinois (Fralish *et al.* 1991), western Kentucky (Bryant and Martin 1988), western Tennessee (DeSelm 1988), Missouri (Ladd 1991), and specifically Land Between The Lakes (McCrain and Grubb 1988; Franklin 1994) are believed to have been more open than present forest communities. Following settlement, the suppression of fire permitted the open forests of presettlement Land Between The Lakes (LBL) to grow into a closed-canopy forest. Increased shading and deeper litter subsequently reduced the herbaceous vegetation. This paper presents part of the results of a long term study of forest communities at LBL located in Kentucky and Tennessee. The objective here is to present community and environmental relationships on woodland communities that likely were once barrens and savanna-like.

Close, D. D. 1996. Evaluation of herbaceous diversity and differential species in mature forest stands at Land Between The Lakes, Kentucky and Tennessee. Master of Science Thesis. Department of Forestry, Southern Illinois University, Carbondale, Illinois.

ABSTRACT. At Land Between the Lakes (LBL), 50 stands were sampled to study environmental influences affecting herbaceous species assemblages in a variety of forested communities. Nine herbaceous dominance types were described from COMPAH results *(Panicum dichotomum, Cunila originoides, Panicum boscii, Desmodium nudiflorum, Polystichum acrostichoides, Dioscorea quaternata, Actea pachypoda, Menispermum canadense*, and *Botrychium virginianum*). Herbaceous species exhibited trends based on distance to opposing slope, available water holding capacity, and aspect. Discriminant analysis consistently identified slope position as a significant environmental variable. Available water holding capacity was significant in the discriminant analysis based on the six operational variables.

Site/forest community types from the Shawnee Hill (southern Illinois) were paired with communities on analogous sites at LBL. The number of species recorded at LBL was low (25 to 66%) compared to similar sites of the Shawnee Hills. This finding suggested that prolonged historical disturbance from iron mining, moonshining, logging, and grazing over a 150 year period has had a severe impact on the ground flora.

Selection of Study Stands. Twenty-eight stands were randomly selected from each of seven compositionally stable community types described by Franklin (1990) and 22 stands from four successional community types described by Kettler (1990). A minimum of three stands per community type was sampled for seven types.

Field Procedure. During the initial study of each 1.0 ha stand, the centers of two 0.06 ha macroplots were permanently marked by a metal conduit pipe (Franklin 1990; Kettler 1990). One macroplot per stand was randomly selected for sampling. A total area of twenty square meters was sampled in each macroplot. Eight 2.0 m^2 quadrats were placed in cardinal directions 5.67 m and 11.35 m from plot center. Two additional quadrats were placed in northeast and

southwest directions 5.67 m from plot center. The left corner of the quadrat nearest plot center was used to position the quadrat. When a large tree obstructed the placement of a sampling quadrat, the quadrat was moved to the nearest 2.0 m^2 clear area.

Four 1.41 m long wooden strips stabilized by pins at the corners were used to delineate the quadrat boundary. All herbaceous plants within a quadrat were identified by genus and species when possible. Absolute percent cover was recorded for each species. Moss and lichens were assigned to a moss-lichen category and recorded by percent cover. Grasses and sedges were identified only to genus unless positive field identification to species was made; few were in fruit at sampling time. When unknowns were encountered, voucher specimens were collected and marked by date, number, stand, and macroplot number, and brought to the herbarium for positive identification. A survey was made of the stand to record any additional species not found within the quadrats. These species (14) were recorded as present. Absolute percent litter cover was also recorded for each 2.0 m^2 quadrat.

A spherical densiometer (convex mirror type) was used to estimate percent overstory canopy cover. The densiometer was mounted on a staff to level and stabilize the instrument. Four readings were taken at 6.9 m from plot center and averaged to determine mean percent canopy cover.

Leaf litter samples were taken from each of the ten quadrats. A 0.25 m^2 nested quadrat was randomly selected from one of the four corners of the two-meter square quadrat. Dead twigs smaller than 5.0 cm diameter were collected with leaf litter. Only the sections of twigs and small limbs enclosed by the 0.25 m^2 nested quadrat were collected. Litter samples were labeled by stand, macroplot, and quadrat number. Additional site and soil data were taken from the studies completed by Franklin (1990) and Kettler (1990).

Laboratory Procedure. Leaf litter samples were dried in an oven at 105° C for a minimum of 48 hours. The samples were removed and allowed to cool for one and two hours. When at room temperature, samples were weighed to the nearest 0.01 g on an electronic pan balance.

Data Analysis. Stands were grouped by community type according to Franklin (1990) and Kettler (1990). Mean total and mean percent cover by species were then calculated for each stand. Species richness was determined as the total number of species occurring within each stand sampled. Mean species richness was calculated for each community type. Site data from Franklin (1990) and Kettler (1990) as well as litter weight, litter cover, and canopy cover were used to examine variability in herbaceous cover. Percent canopy cover was measured following the procedure outlined by Lemmon (1956, 1957) and instructions included with the spherical densiometer. The densiometer was mounted on a staff and placed 6.9 m from plot center at cardinal directions. Readings taken from each cardinal direction were added and multiplied by a constant to obtain percent canopy opening: NE 1/4 + SE 1/4 + SW 1/4 + NW 1/4) x 1.04 = %. Subtracting percent canopy opening from 100 resulted in percent canopy cover: 100 - % Canopy Opening = % Canopy Cover.

Constancy was calculated as the number of stands in which a species occurred divided by the total number of stands sampled within a community. Differential species were used to define the herbaceous component of forest community types at LBL. Differential species are defined along similar guidelines presented by Kotar *et al.* (1990). Therefore, differential species are those that occur in a large proportion of stands or have a high percent cover within a given habitat type and simultaneously must be absent or occur in low percent cover in all other habitat types.

Frequently differential species are present in other habitat types where it has no diagnostic value (Kotar *et al.* 1990). The term differential species has meaning only when comparing herbaceous cover between habitat types, that is, all sites capable of supporting the same stable (climax) community. Each habitat type represents a relatively narrow segment of the gradient. (Kotar *et al.* 1990). Community types at LBL are delineated by dominant forest overstory and site conditions. In the case of stable community types, they are synonymous with specific site types (*Q. prinus* = Cretaceous gravel on steep slopes and ridgetops, *Q. stellata* = loess with a fragipan on southwest slopes, Mixed Mesophytes = loess over limestone on lower north slopes or stream terraces, etc.).

The mean number of herbaceous taxa at LBL was compared with mean numbers of taxa from the Shawnee Hills. Equivalent 100 m^2 samples were compared from analogous Shawnee Hills and LBL communities. Only 40 m^2 samples were available for comparison of the *Acer saccharum* alluvium sites.

COMPAH, an agglomerative, combinatorial technique was used with a Bray-Curtis resemblance function. Stands were clustered using the unweighted group averages method. No transformations were performed on the data set. Canonical correspondence analysis (CCA) was used in CANOCO (ter Braak 1987) to order community types based on five environmental factors: (1) distance to opposing slope, (2) slope position, (3) available water holding capacity, (4) elevation, and (5) aspect. Direct ordination using detrended canonical correspondence analysis (DCCA) in CANOCO was used to look for trends in herbaceous data as influenced by environmental factors.

Stepwise discriminant analysis was selected to analyze environmental variables that might influence the herbaceous cover. Ludwig and Reynolds (1988) suggest that including both operational and nonoperational variables in a discriminant analysis will likely weaken the results. Therefore, subsets of the environmental variables were categorized as operational (*e.g.*, soil moisture, litter weight, etc.) and nonoperational (*e.g.*, aspect, elevation, slope position) as characterized by Ludwig and Reynolds (1988). Nine variables were determined to be nonoperational and six variables were determined to be operational. Four individual discriminant analyses were run. One analysis included fifteen site, soil, and environmental variables: (1) litter weights, (2) percent litter cover, (3) percent canopy cover, (4) basal area per hectare, (5) percent sand, (6) percent silt, (7) percent clay, (8) percent rock, (9) effective soil depth, (10) available water holding capacity, (11) transformed aspect, (12) distance to opposing slope, (13) slope position, (14) percent slope, and (15) elevation. A second discriminant analysis was run using six operational variables: (1) litter weights, (2) percent litter cover, (3) percent canopy, (4) basal area per hectare, (5) effective soil depth, and (6) available water holding capacity. A third discriminant analysis was run using nine nonoperational variables: (1) percent sand, (2) percent silt, (3) percent clay, (4) percent rock, (5) transformed aspect, (6) distance to opposing slope, (7) slope position, (8) percent slope, and (9) elevation. A fourth discriminant analysis was run using variables selected for DCCA: (1) available water holding capacity, (2) aspect, (3) distance to opposing slope, (4) slope position, and (5) elevation. Groups derived from COMPAH clustering were used as the class variable in discriminant analysis.

Fralish, J. S. 1997. Community succession, stability and diversity in the central hardwood forest. *In* M. W. Schwartz (ed.). Conservation in Highly Fragmented Landscapes. Chapman and Hall, New York, New York. (Scheduled for release late 1997)

The following section is taken from the summary section of the chapter as there were no abstract or method sections.

Protection, Species Richness and Productivity. The elimination of natural disturbance such as fire has several distinct negative impacts on species richness and site productivity. A number of these effects result directly from the process of succession.

1. Loss of Black Oak Species. Death of "black oak" trees in post and white oak stands has been documented at LBL (Kentucky and Tennessee) and in Illinois. At LBL, data from the 1976 and 1986 remeasurement of permanent plots indicated that high mortality occurred in the black oak group (black; blackjack, *Quercus marilandica*; scarlet, southern red oak and northern red oak) while species of the "white oak" (white oak, post oak and chestnut oak) and hickory had relatively low mortality (Groton *et al.* 1988). Approximately 70% of the stems alive in 1988 were oak with only 20% of these in the black oak group, but approximately 45% of total mortality was black oak (Wellbaum 1989). On permanent plots at Kaskaskia Experimental Forest in southern Illinois, mortality of scarlet, black and northern red oak was higher than that of white oak with the mortality level of scarlet twice that of black oak (Schlesinger 1989).

A comparison of 10-12 year old clearcut oak stands at Land Between The Lakes indicates that species of the black oak group have a collective average importance of 20 to 31% (Snyder 1995); however, in many stands the density was double or triple that of the white oak group or hickory suggesting that the black oak group remains an important component of young stands. The importance of black oak in clearcut stands equals that of the overstory component (Groton *et al.* 1988).

The loss of black oak species (blackjack, southern red, black, and scarlet) from post oak dominated stands on xeric sites or from stands of mixed white oak and "black oak" on xeric-mesic sites is the beginning of a general loss of biodiversity as species richness (number) decreases concurrently with purification (reduced equitability) as post oak or white oak assumes greater dominance. The largest trees (70-100 cm DBH) of the shorter lived (150-175 years) "black oak" species are being phased out while trees of the longer lived (300-350 years) white oak remain. Individuals of "black oak" reach physiological maturity and the end of their life span at about 150-170 years. At 125-150 years or earlier for some species such as scarlet oak, trees begin to show the typical signs of old age: heart rot (center of stem decayed or hollow), presence of large dead branches, patches of dead bark, large broken branches and/or tops, reduced number of leaves (thin crown) and a weak root system (frequent wind thrown trees). The relatively high density and increased competition in the forest stands in addition to the drought and insect attacks of the 1980s may have reduced tree vigor which subsequently resulted in increased mortality due to secondary causal agents such as Hypoxylon canker.

2. Loss of White Oak and Hickory. On mesic sites, succession is a two-stage process. Subsequent to the loss of the black oak species group, white oak (specifically *Quercus alba*) and hickory (general life expectancy = 200-350 years) will be replaced by the more long lived (450-500 years) sugar maple and American beech. Depending on regional environmental conditions, the effect will be to create "islands" of the remaining white oak and post oak stands on xeric and xeric-mesic sites (Shawnee Hills; LBL) or to completely blanket the landscape with a near monoculture of sugar maple or American beech (Illinois Ozark Hills, Illinois Coastal Plain). Because of the predominance of oak at LBL, the diversity of community types across the landscape will increase with the addition of mesophytes, but succession will negatively impact the herb stratum.

3. Loss of Herbaceous Plants. The present high density of seedlings, saplings and small trees of mesophytic species invading oak-hickory forest has a major effect on the herbaceous layer. Data collected from Trail of Tears State Forest in the Ozark Hills indicates that as photosynthetically active radiation decreases and the amount of ground litter increases, there is a major decrease in the number of herbaceous species. Species richness increased 200% from an average of 10 species/10 m^2 sample in a forest composed of oak and hickory with a closed canopy of smaller sugar maple trees (DBH 10-20 cm) to an average of 31.5 species/10 m^2 in open stands dominated by black oak, white oak and hickory without maple, or in stands dominated by post oak. There appears to be little difference in species richness between the open black/white and post oak stands although post oak occurs on drier sites and has considerably higher PAR levels. Compared to stands without a seedling/sapling stratum, a mesophytic understory of intermediate density present in black/white oak stands reduces the number of species from 31.5 to 25 species/10 m^2. In dense sugar maple dominated forest of the Ozark Hills region, few seedlings or herbs can be observed. Wilhelm (1991) also reported a decrease in the number of summer and fall flowering species between 1925 and 1988 and related this decrease to the increase in sugar maple importance in the tree canopy.

The amount of PAR reaching the herbaceous layer and the amount of litter on the forest floor is a function of crown and stand density. The single canopy layer and relatively thin crowns of the shade intolerant/intermediate (light-demanding) oak hickory species permits considerable light penetration so that the mid-crown leaves obtain sunlight for photosynthesis. Leaves and branches at the lowest levels on the main stem are usually dead because of insufficient sunlight. The uppermost oak leaves in tree crowns are highly dissected so that light easily penetrates to the lowest leaves which have small sinuses and most leaf area for intercepting light. Similarly, the upper most leaflets of hickory tend to be the smallest on the tree. This adaptive geometry of trees (Horn 1971) permits light penetration through the canopy and increases photosynthesis not only in lower leaves but also in herbaceous plants on the forest floor. Furthermore, shade intolerant trees can not be closely packed because too much sunlight is intercepted and dieback occurs. As observed in nearly all white and black oak stands, the crowns in the upper canopy seldom touch, and in stands dominated by the shade intolerant post oak, the space between crowns is considerably greater.

Conversely, extremely shade tolerant species such as sugar maple and American beech have a high stem density, overlapping crowns and thick crowns of multiple leaf layers as lower branches remain alive. These characteristics produce a high leaf biomass. In autumn, the leaves create a thick (3-5 cm deep) litter layer that often remains throughout the growing season and smothers the new growth of herbaceous plants. The litter appears to be of sufficient thickness that new seedlings will not survive because the extending radical can not reach mineral soil and water before desiccation occurs. Bazzaz (1979) describes other relationships.

Although the invasion of mesophytes reduces the number of oak forest herbs, the herbaceous layer of maple/beech dominated communities has high species richness in some regions (Curtis 1959) and some mesic sites in the central hardwood forest (Jones 1974; Harty 1979).

Small stems of sugar maple, American beech and other mesophytes indicate the advance of this forest, but the gap between time of elimination of oak-hickory forest herbs and time of invasion of mesophytic forest herbs may be 50 to 100 years or longer and may not occur on more xeric sites. During this gap, insect populations are likely to be reduced and soil surface erosion increased, depending on seedling density. These aspects of herb importance should be the thrust of future research.

4. Loss of Shortleaf Pine. Shortleaf pine is a high light demanding (extremely shade intolerant) species that survives under a fire regime which maintains an open condition for light penetration and seedling establishment. When protected from fire, pine is rapidly replaced by oak on all sites and community diversity is reduced.

5. Reduced Mast/Productivity. Succession impacts stand productivity by reducing the amount of mast (nuts, acorns) produced for wildlife as oak and hickory are replaced by mesophytes. While beech is a mast producer, the soft tissues of maple seed quickly decompose if the seed does not germinate.

The rate of productivity also decreases as oak and hickory trees in a high light environment (direct sunlight on the crowns) grow faster than maple and beech. The physiological basis for the growth differental between these two groups is reviewed by Kramer and Kozlowski (1979), Hale and Orcutt (1987), and Kozlowski *et al.* (1991). However, there is an interesting paradox regarding the rate of growth and rate of succession. It would be reasonable to expect that stands of slow-growing oak and hickory on xeric and xeric-mesic sites should be easily replaced by faster growing invading species, while their high growth rate on mesic sites would permit the development of a compositionally stable community. The reverse situation actually occurs. The lack of soil moisture which results in slow growth on xeric sites also prevents succession to other species. High soil moisture on mesic sites permits a rapid growth rate but creates an environment suitable for development of a community dominated by shade tolerant mesophytes. In terms of resource management, the most productive oak and hickory stands are being replaced by slower growing mesophytic species while the least productive stands remain intact.

Concluding Remarks. In recent years, new attitudes developed jointly with new available scientific information have directed forest management away from timber production and toward other forest ecosystem values such as preservation of rare or endangered species, development of old growth characteristics, and maintenance of species diversity to the level thought to be present in presettlement communities (ca. 1800). Unfortunately, it is too often believed that total protection will permit the forest to maintain or restore these values. This belief possibly would be correct if oak and hickory were shade tolerant species, but they are not and thus their response is similar to other disturbance dependent, pioneer species and community types. Loss of these dominant keystone species through succession may result is loss of herbs, insects, and possibly birds.

Disturbance plays an important role in ecosystem development. Fire in particular reduces invasion of mesophytes in oak stands, and with a less dense overstory, white and black oak stands can be maintained to old growth with a full complement of understory herbs. Conversely, the extremely dense, multi-layered mesophytic forest is viewed by many as the epitome of old growth (primeval forest), yet according to early land survey records, it was rare to nonexistent in most areas of the central hardwood forest.

4. ORDINATION OF FOREST COMMUNITIES.

Fralish, J. S., S. B. Franklin, P. A. Robertson, S. M. Kettler, and F. B. Crooks. 1993. An ordination of compositionally stable and unstable forest communities at Land Between The Lakes, Kentucky and Tennessee. Pp. 247-267 *in*: J. S. Fralish, R. P. McIntosh, and O. L. Loucks (eds). John T. Curtis: Fifty Years of Wisconsin Plant Ecology. Wisconsin Academy of Science, Arts and Letters, Madison, Wisconsin.

ABSTRACT. A study of forest community and site relationships was conducted at Land Between The Lakes, a 69,000-ha area located in western Kentucky and Tennessee. A total of 133 undisturbed stands were sampled to obtain community as well as soil and topographic data. Species importance values were calculated separately for trees, saplings, and seedlings. Using adaptation values for species in southern Illinois, we developed a composition index for each stratum. Compositionally stable stands were separated from successional stands using a composition index differential and percent similarity between trees and the sapling/seedling layer. A coenocline from Bray-Curtis ordination and Gaussian analysis of data from compositionally stable stands compared favorably with a coenocline developed from weighted averages ordination developed from soil and topographic data.

The sequence of leading dominants across the gradient from xeric to mesic sites was *Quercus prinus*, *Q. stellata*, *Quercus alba, Fagus grandifolia*, and *Acer saccharum.* This sequence sharply contrasted with Bray-Curtis ordination of successional stands where the sequence of leading dominants along the gradient from xeric to mesic was *Pinus echinata*, *Quercus prinus*, *Q. falcata, Q. velutina*, and *Q. alba.* Discriminant analysis of soil and topographic factors indicated no significant difference between the site characteristics of successional *P. echinata* stands and those of compositionally stable *Q. prinus*, *Q. stellata*, and *Q. alba* stands of xeric sites, or between the characteristics of successional *Q. stellata* and *Q. falcata* stands and stable stands of *Q. alba* on xeric-mesic sites. In the mesic portion of the gradient, discriminant analysis indicated no difference between the site characteristics of successional *Q. velutina* or *Q. alba* stands and those of *Acer saccharum* stands. It appears that in the absence of major disturbance, the *P. echinata* community will be lost from LBL and that on mesic sites stands presently dominated by *Q. alba* and *Q. velutina* will be replaced by *Acer saccharum*-dominated stands. Stands on xeric and xeric-mesic sites will continue to be dominated by *Quercus* although the combination of species may vary over time.

Franklin, S. B., P. A. Robertson, J. S. Fralish, and S. M. Kettler. 1993. Overstory vegetation and successional trends of Land Between The Lakes, U.S.A. Journal of Vegetation Science 4:512-520.

ABSTRACT. One-hundred and thirty-three stands from the uplands of Land Between The Lakes were sampled. Stand data were ordinated to identify clinal patterns in the overstory vegetation. A coenocline, accounting for 52% of the species variance, was developed from the first ordination axis. Classification of stands identified nine dominance types: *Pinus*

echinata-Quercus spp., *Q. prinus, Q. prinus-Q. alba, Q. stellata-Q. alba, Q. velutina-Q. alba, Q. alba, Q. alba-Q. rubra, Acer saccharum-Q. alba-Fagus grandifolia*, and *F. grandifolia-A. saccharum*.

Compositionally-stable and unstable (successional) stands were analyzed separately. Trajectories of unstable stands include the succession of *P. echinata* to *Quercus*-dominated communities on xeric sites and of *Quercus* types to more mesophytic communities (*e.g.*, *A. saccharum* and *F. grandifolia*) on mesic sites. These shifts indicate the nature of the future climax overstory composition at LBL.

The first axis DCCA ordination for climax stands accounted for 45% of the vegetation variance. Factor Analysis identified two significant suites of variables related to vegetation: (1) soil chemistry/soil moisture and (2) soil texture. Specific variables related to variation in the climax vegetation include soil pH, calcium and magnesium, effective soil depth, available water capacity, percent rock in the soil, slope position, aspect, elevation and distance to the opposing slope.

Modal positions of species along the direct gradient ordination were similar in rank order to those derived from the indirect gradient ordination of all stands. The latter ordination represents the present forest vegetation pattern at LBL. Climax stands showed a shift in modes of *Quercus* spp. toward the xeric end of the gradient and increases in habitat width of mesophytic species. Following a reduction in disturbance, species appear to adjust to changes in competition and available habitat. That is, the dimensions of realized niches (*i.e.*, habitat widths) change with succession. The climax vegetation at LBL appears to show centrifugal organization.

Methods. Refer to Franklin (1990) and Kettler (1990) for description of methods.

Office Procedures. Data from 133 1.0-2.0 ha stands were used. We converted tree diameter to basal area (m^2/ha) and summed these values by species for each stand for use in the ordination and classification analyses. Stands were grouped into dominance types using COMPAH (combinatorial, polythetic, agglomerative hierarchical clustering; Boesch 1977). We used percent similarity as the resemblance function and the unweighted pair group average (UPGMA) method for clustering stands. We employed Stepwise Discriminant Analysis to identify environmental variables which distinguished dominance types (Trobaugh & Johnson 1988; Jha & Singh 1990). Species richness (S), stand diversity (H' = Shannon's Index), and evenness (E) were computed for each dominance type (Ludwig & Reynolds 1988):

$$H' = -S\ [(n_i/n)\ In\ (n_i/n)];\ E=e^{H1}/S.$$

Gaussian Analysis (Gauch & Chase 1974; Westman 1980) was performed using the first axis of a Detrended Correspondence Analysis (DCA) stand ordination (CANOCO; ter Braak 1986, 1987). We used the second order polynomial for detrending. Minimum threshold for curve fitting was at -1.0 and species with less than five occurrences were excluded from the analysis. Percent variance accounted for by the coenocline (*i.e.*, the sum of variance accounted for by all species/total variance * 100) was used to measure ordination success.

We applied Factor Analysis (FA) with a varimax prerotation followed by a promax rotation to determine which environmental variables accounted for most of the variance in the environmental data (Goodall 1954; Muller 1982). Parallel Analysis (PA) was established as the most accurate rule for determining the number of significant factors (Zwick & Velicer 1986). As with all multivariate analyses, determining the number of axes recovering actual gradients and the resulting changes in vegetation is difficult. The PA utilized regression equations (Longman *et al.*, 1989) to determine the 95th percentile point in distributions of eigenvalues using the same axis rotations from random data matrices with the same dimensionality as the actual data matrix. Eigenvalues generated from the FA greater than the 95th percentile PA were considered significant. Parallel Analysis can further determine significant loadings for variables in the FA. The 95th percentile point was determined by multiplying the number of factors by the number of variables by 0.05 (3 factors x 15 variables or 45 x 0.05 = 2.25 or 2). We considered the second highest promax structure loading from the PA (using 2 factors and 14 variables) as the approximate 95th percentile. We considered loadings greater than or equal to the approximate 95th percentile as significant.

Understanding species-environment relationships was facilitated by separating compositionally-stable stands from successional stands, thus separating confounding temporal from spatial (environmental) influences on vegetation composition. Species basal area and sapling and seedling density were relativized and used as importance values (IV_{100}) for overstory and understory species, respectively. We separated stands into successional and compositionally-stable groups by comparing composition index values (CI) and % similarity (PS) between the understory and overstory (Curtis & McIntosh 1951; Mueller-Dombois & Ellenberg 1974). High densities of *Oxydendrum arboreum, Nyssa sylvatica, Prunus serotina*, and *Sassafras albidum* seedlings resulted in low similarity values between overstory and understory suggesting a compositionally-unstable condition. However, these species seldom reach overstory or even in sapling size classes at LBL. Following Quarterman & Keever (1962), we used only species consistently appearing as an overstory component in the study stands for the separation. PS <45% between the two strata indicated a successional stand and a similarity greater than 60% was considered compositionally-stable. Stands with a PS of 45%-60% were further evaluated by comparing overstory and understory CI.

We calculated CI by multiplying species importance values by species adaptation values described by Fralish (1988) and summing for all species in a stand. A difference in overstory and understory CI of >50 for xeric stands (CI <500) and 100 for mesophytic stands (CI >500) indictated a successional stand. In a few instances, the environmental characteristics of a site matched those of other successional stands, but no vegetative change was evident. Consequently, we treated such stands as successional, possibly "delayed" due to the lack of a seed source (Kettler 1990). Concurrence of more than one method (CI and PS) adds robustness to the analysis (Tueller & Platou 1991). A density matrix of successional stands was ordinated using DCCA. Successional trajectories were identified by drawing vectors between overstory and their respective understory points in ordination space. Length of the vector reflects the magnitude of compositional change while direction characterized the type of change (*i.e.*, xeric to mesic) (Austin 1977; Enright 1992; Allen & Shugart 1983). A t-test was used to determine if significant (a = 0.05) successional change occurred by comparing the mean first axis scores for overstory and understory (Anonymous 1985).

To describe the potential vegetation of LBL, we analyzed the compositionally-stable stands using Detrended Canonical Correspondence Analysis (DCCA) (ter Braak 1986, 1987). DCCA relates community composition directly to known variation of the environment (Haase 1990). For the DCCA ordination, all successional stands were made passive (Schmalzer & Hinkle 1992). Only non-passive stands were used to extract ordination axes and passive stands were added later using transition formulae (ter Braak 1988). Gaussian Analysis (Gauch & Chase 1974; Westman

1980) was performed as above on the first axis of the DCCA stand ordination. We related the COMPAH classification of stands to the ordination by locating the centroid for each dominance type on the DCCA biplot (Haase 1990). Ordination scores of stands from Factor Analysis (FA) were correlated to those from the all-stand DCA and these results were compared to the DCCA. Convergence of two independent methods improves robustness of results (Gauch, Whittaker& Singer 1981; Tueller & Platou 1991).

The direct gradient analysis for compositionally stable stands and indirect gradient analysis of all stands were compared using rank order of species modes (Chaneton & Facelli 1991) and standard deviations of species distributions from Gaussian Analysis. Changes in modal position and standard deviations of species response curves should reflect the differences between the current vegetation pattern and the potential climax vegetation pattern at LBL.

5. EFFECT OF FIRE AND TIMBER HARVESTING.

Franklin, S. B., J. S. Fralish, and P. A. Robertson. 1995. The effect of prescribed burning on fuels and soil nutrients of upland *Quercus* communities. Pp. 191-214 *in*: S. W. Hamilton, D. S. White, E. W. Chester, and A. F. Scott (eds.). Proceedings Sixth Annual Symposium on the Natural History of the Lower Tennessee and Cumberland River Valleys. The Center For Field Biology, Austin Peay State University, Clarksville, Tennessee.

ABSTRACT. Results of a field experiment testing the effects of prescribed burning on fuels and soil nutrient levels are presented. Changes in fuels due to burning were assessed for one site. The greatest changes due to prescribed burning occurred in the forest floor fuels (22 - 61% reduction) and large (>7.62 cm diameter) dead and down material (12-30% reduction). Small dead and down material was not severely altered. Two treatments (burned once and burned twice) were applied and compared to a control to assess nutrient changes due to prescribed burning. Seven total sites were examined; four contained an overstory dominated by *Quercus* species with few mesophytic species in the understory (non-successional) and three contained an overstory dominated by *Quercus* species with a strong mesophytic component in the understory (successional). Ten soil samples were extracted from the A_1 horizon in each 0.04 ha plot and composited for soil nutrient analyses. Soils were collected 30 days prior to the first burn, 30 days following the first burn, and three summers following the first burn (one summer following the second burn). Most nutrients significantly increased from the preburn sample to the first postburn sample for both treatments and the control. We attribute this to increased precipitation between sample collections, which increases nutrient input, leaching, erosion, and decomposition rates. Soil pH, cation exchange capacity, total phosphorous, exchangeable phosphorus, and exchangeable potassium significantly increased after burning the oak/maple sites. Burning apparently increased litter vulnerability to leaching, releasing structurally bound materials. No significant nutrient level changes were attributable to the second burn.

Methods. Two forest conditions were studied: (1) a *Quercus alba*-dominated forest overstory with an understory of mesophytic seedlings (mainly *A. saccharum*) and saplings (successional: herewith called oak/maple), and 2) a *Q. alba*-dominated forest overstory with no mesophytic regeneration (nonsuccessional: herewith called oak/oak). Four sites of each forest condition were located and a replicate block design was established in each. Each plot was permanently marked with conduit pipe. Plots were 12 m wide, 66.6 m long, separated by a four meter buffer strip, and aligned perpendicular to slope contours. Plots were divided in half horizontally, creating two subplots 0.04 ha (12 m x 33.3 m) in size.

Four treatments were used to study response of *A. saccharum* regeneration on oak/maple sites: 1) a control, 2) one dormant season burn, 3) two dormant season burns, and 4) application of herbicide to *A. saccharum* stems. Response of oak regeneration was studied on two oak/oak sites which contained the first three of the following treatments and on two oak/oak sites which contained all five of the following treatments: 1) a control, 2) single dormant season burn, 3) successive dormant season burns, 4) mechanical thinning (first cut in a shelterwood management system, sensu Godman and Tubbs 1973; Sander *et al.* 1983); and 5) thinning and burning. Plots were chosen randomly *(i.e.,* drawing a plot number and treatment from a hat). Soil data were collected for the first three treatments.

Fuels. For an oak/oak site, fuel load was estimated using a planar intersect sampling technique for dead and down materials and a relative-weight estimate method for litter, herbaceous, and duff (Brown 1974; Brown *et al.* 1982). For dead and down material, two 33.3 m transects were randomly located perpendicular to the contour in each subplot (stratified randomization was by rolling a die and using that number as the number of meters toward the bottom right plot marker from the bottom left plot marker; this point was the beginning of the first transect; the beginning of the second transect was found in a similar way, except starting 6 m over from the bottom left plot marker, this insured a transect in each half of the subplot). Dead and down materials in the 0 - 0.64 cm Class 1 (0 - 0.25 in.), 0.64 - 2.54 cm Class 2 (0.25 - 1.0 in.), and 2.54 - 7.62 cm Class 3 (1 - 3 in.) intersecting the planar transect were counted and fuel load by weight (w) was calculated by the following formula for each size class:

$$W\,\text{(tons/acre)} = (11.64 \times N \times D \times 2 \times S \times A \times C)/N \times L,$$

where N = number of intersections for a size class, D = quadratic mean diameter (cm) by Class, 1 = .37, 2 = 1.25, and 3 = 4.03 (Brown and Roussopoulos 1974), S = specific gravity of materials (g/cm^3), averages for southern and southeast type fuels by Class, 1 = 0.70, 2 = 0.70, and 3 = 0.58 (Anderson 1978), A = nonhorizontal correction factor by Class, 1 = 1. 15, 2 = 1. 11, and 3 = 1. 03 (Brown and Roussopoulos (1974), C = slope correction factor = *I + [Percent Slope/100]2*, N = number of sample points = 2, L = length of sampling plane =33.3 m (84.6 ft.).

Diameter of dead and down material greater than 7.62 cm was measured and identified by species. The formula for calculating fuel load of dead and down material, by species, greater than 7.62 cm (Class 4) in diameter (sound and rotten) follows:

$$W\,\text{(m tons/acre)} = (11.64 \times Sd^2 \times S \times A \times C)/N \times L,$$

where: Sd^2 = summation of squared diameters, S = specific gravity for individual species (U.S.D.A. 1977), average specific gravity for rotten southern and southeast fuels greater than 7.62 cm in diameter = 0.30 (Anderson 1978), A = as above and C = as above. Species fuel load estimates were summed to obtain total fuel load >7.62 cm. An estimation of herbaceous, litter, and duff fuel were made visually (Brown *et al.* 1982).

Six m^2 sections were established equidistant from each other throughout the subplot. Five of the sections were estimated as a percent of the sixth section, which contained the heaviest fuel loading. The sixth section was collected, weighed in the field, brought back to the lab, oven-dried, and reweighed. The formula for calculating fuel load by weight of herbaceous, litter, and duff follows:

$$W\text{(kg/ha)} \;=\; S[W_i(1 + P_1 + P_2 + P_3 + P_4 + P_5)]/6,$$

where: W_1 = weight of standard plot section 6 (g/m^2), P = the percent fuel from section i of section 6, $i = 1$ through 5. Slope correction factor was ignored for forest floor fuel loadings as slopes were $<40\%$ (Brown *et al.* 1992).

Fuels were sampled immediately following the first burn and during the summer following all treatments. Data on dead and down fuels were not collected during the final sample period.

Nutrients. Approximately 30 days prior to and 30 days following prescribed burning, ten soil samples were taken from the top 10 cm of each subplot and combined for analyses. Samples were immediately air dried, and subsequently crushed, sifted through a 2 x 2 mm sieve, and sent to A & L Agricultural Laboratories for analysis of nutrients, pH, % organic matter, and cation exchange capacity. Nutrient data included hydrogen (H), potassium (K), magnesium (Mg), and calcium (Ca) as % saturation (exchangeable). Exchangeable phosphorus (P) and total P were recorded as ppm. Cation exchange capacity (CEC meq/100g), estimated nitrogen release from organic matter (ENR kg/ha), and % organic matter were also analyzed. Plots were resampled using identical methods in August, 1994, following treatments.

Burn Characteristics. Prescribed burns were initiated during the dormant season using a strip-headfire technique (Wright and Bailey 1982). Temperature (°C), percent cloud cover, wind speed, and wet/dry bulb temperature were taken prior to burning. Wet/dry temperatures were transformed into relative humidity (Weast 1966) and vapor pressure deficit (Cox 1980). Fuel moisture was determined using fuel moisture sticks (Finklin and Fisher 1990). Fire spread rate and flame height were visually estimated.

Data Analysis. Descriptive statistics were used to show changes in fuel patterns under prescribed burning because too few samples were collected for rigorous statistics. Nutrient % values were transformed using the arcsine function (Zar 1984); all other values were log transformed as suggested by Palmer (1993). Nutrient data were analyzed with a repeated measures analysis (Scheiner 1993). Data for each nutrient were separately subjected to the analysis, comparing the parallel hypothesis (PH) and flatness hypothesis (FH). The flatness hypothesis tests the time effect while the parallel hypothesis tests the time*treatment interaction and assesses whether treatments are significantly effecting changes in the data. An alpha level of 0.1 was used for the overall FH and PH tests. For FH and PH tests between time intervals, a Bonferonni correction was made (0. 1/3 time periods), and thus the alpha level was set at 0.33.

Franklin, S. B. 1996. Disturbance effects on upland *Quercus* community dynamics at Land Between The Lakes, Kentucky and Tennessee. Ph. D. Dissertation. Department of Plant Biology, Southern Illinois University, Carbondale, Illinois.

ABSTRACT. Fire and other natural disturbances have influenced the environment, vegetation structure and vegetation composition for millennia. It is essential to understand natural

disturbance effects on forest structure and composition and disturbance regimes for contemporary management efforts. In most cases, management applies some form of disturbance to the system assuming the system will recover. Leaving an area alone is also a management alternative, but the lack of stationarity in most ecosystems implies that these sites will also change. An example of this is the ever-changing oak-hickory forest of the eastern United States. The lack of regeneration of *Quercus* spp. has been a growing concern during the latter half of the 20th century. The disturbance history of Land Between The Lakes, spatial variability of fire, influences of fire on nutrients and vegetation, influence of herbicide and mechanical thinning on vegetation, and temporal relationship of fire and vegetation were examined in this dissertation. The collective studies were an effort to: (1) further understand disturbance effects in forest ecosystems; (2) further understand the general succession of oak-hickory forests to mesophytic species; (3) develop a better understanding of spatial and temporal scale influences in ecological studies; and 4) determine the efficacy of thinning, burning, and herbicide management alternatives on *Quercus* spp. regeneration and suppression of succession.

A rapid succession from prairie communities to oak communities in LBL uplands has occurred over the past 300 years. Following the evacuation of the Native American cultures (~1700), there were extreme changes (increases) in the density of woody species in LBL uplands. Forest invasion was likely in full swing by the time of European settlement (~1800), and forests were large enough to support eight iron furnaces in the mid- to late-1800s. Lack of disturbance on these sites has resulted in two major changes to LBL forests: (1) LBL forests regenerating from the late 1800s era of disturbance are closed and just now reaching a stage where canopy gaps are forming and (2) invasion of mesophytic species into the forests. The depauperate herbaceous understory of LBL forests may reflect this current phase of forest regrowth.

The significance of the two changes is their persistence. Fire is evidently no longer capable of controlling the vegetation composition and structure as fire did in the past. Prescribed burning still influenced the vegetation, forest floor, and soil nutrients, but the affects of light burns were not severe and were short-term. The system has crossed some threshold where the feedback mechanisms with fire have changed. Fuels of these upland forests are no longer made up of dry, loose grasses, but instead moist, sometimes highly packed, leaf litter. Fire intensity and severity have decreased due to this structural change in the forest floor. These changes have resulted in a transition from a prairie/savanna to a forest structure; *i.e.*, from one domain to another. The current domain is mainly controlled by climate and small-scale disturbances (*e.g.*, canopy gaps). Domains (*i.e.*, constrained temporary associations) and transitions between domains were evidenced through the analysis of long-term temporal data. The scale-dependent domain is in some way constrained or there is some attraction which yields a perseverance to change. The perseverance of the LBL forest system is due to the ability of most deciduous species to resprout following disturbance. Restoration efforts in areas which have savanna species may require rather intense disturbance prior to establishing a fire maintenance program.

Franklin, S. B., P. A. Robertson, and J. S. Fralish. 1997 Small-scale fire temperature patterns in upland *Quercus* communities. Journal of Applied Ecology. In press.

SUMMARY. (1) Two upland *Quercus* sites were burned during the dormant season. Fuel data were obtained prior to burning, fire temperatures at 3 heights were taken during the fire, and micro-topographic and vegetation data were collected following the burn. Spatial analysis and pattern analysis were employed to examine fire temperature patterns in relation to microtopography and fuels, and fire temperature effects on vegetation. (2) Fire temperatures at the surface, 33 cm above surface, and 75 cm above surface were light-to-moderate, ranging from 52-260°C. (3) Fire temperature heterogeneity and scale were affected by litter/duff biomass when slope steepness was low *(i.e.*, slope <20%). Steeper slopes had a stronger effect on fire temperature heterogeneity and scale, thus masking the influence of fuel biomass. (4) Slope steepness also influenced vortex fire behavior. Ground level leeward fire temperatures were significantly greater than windward fire temperatures only on the site with percent slope >20%. (5) Vegetation response heterogeneity and pattern scale tended to follow fire temperature patterns. Spatial analysis and pattern analysis results closely corresponded and were used simultaneously for interpreting small-scale fire temperature heterogeneity in two upland *Quercus alba* forest stands. (6) Different sampling designs may be required for assessing fire phenomena under different slope steepness.

Fralish, J. S. and Snyder, P. R. 1993. Forest regrowth in 10-12 year old clearcuts at Land Between The Lakes, Kentucky and Tennessee. Pp. 179-194 *in*: S. W. Hamilton, E. W. Chester, and A. F. Scott (eds.). Proceedings of the Fifth Annual Symposium on Natural History of Lower Tennessee and Cumberland River Valleys. Center for Field Biology, Austin Peay State University, Clarksville, Tennessee.

ABSTRACT. At Land Between The Lakes, six 10-12 year-old clearcuts of stands originally dominated by *Quercus* and *Carya* species were sampled for seedling, sapling, shrub, and vine composition and density. From two to eight 0.330 and 0.006 ha nested circular quadrats were sampled in each area. Density of shrubs, vines and other mid-canopy arborescent species ranged from about 18,000 to over 45,000 stems/ha. Seedlings and saplings of overstory canopy species ranged from 4,563 to 17,458 stems/ha. On two xeric sites (steep rocky slopes and fragipan soil) and four xeric-mesic sites (moderately deep soil of south slopes), the relative density (importance) of *Quercus* and *Carya* seedlings and saplings ranged from 71-94% of all stems of overstory canopy species. These values indicate that *Quercus* and *Carya* will dominate the next mature forest community. On two mesic sites (north and east slopes at moderate to low elevation), the importance of *Quercus* and *Carya* was substantially lower (13 and 48%); here, mesophytes, primarily *Acer saccharum*, *Ulmus rubra*, and *Fraxinus americana*, with importance values of 52% and 76%, will dominate the developing community.

Methods and Procedures. Refer to Snyder (1995) for description of methods.

Snyder, P. R. 1995. Forest regrowth in 10-12 year old clearcuts at Land Between The Lakes, Kentucky and Tennessee. Master of Science Thesis. Department of Forestry, Southern Illinois University, Carbondale, Illinois.

ABSTRACT. During the summers of 1992 and 1993, twenty 10-12 year old clearcut stands (recovering forest) were studied to determine forest composition and density of clearcut stands, to develop overstory species coenoclines, and to determine if the composition is similar to that of the understory of mature forest communities at Land Between The Lakes (LBL). Total density for overstory species ranged from a low of 4583 stems/ha to a high of 18333. Density of *Quercus* varied between 436 and 8373 stems/ha while *Carya* varied between 207 and 4500 stems/ha. Seventeen of the 20 stands were dominated by and *Carya* and three dominated by *Acer saccharum* or *Ulmus rubra*. Mesophytic species appeared in the majority of the stands. Five community types similar to those studied by Franklin (1990) and Kettler (1990) were identified: (1) Chestnut Oak-Scarlet Oak, (2) White Oak-Black Oak-Scarlet Oak, (3) Black Oak-Mixed Oak, (4) White Oak-Black Oak-Mesophytic, and (5) Sugar Maple-Red Elm. The Sweetgum-Mesophytic community type appeared in the study, but it did not appear in previous studies at LBL. It appears that communities which have developed after clearcutting are reasonably similar (percent similarity 51-68%) to the understory of mature stands. As further evidence of similarity, a coenocline of plot data showed the same sequence of major species in compositional stable stands as reported by Franklin (1990) and Fralish *et al.* (1993) although *Fagus grandifolia* was a minor species in recovering forest and *Quercus velutina* was less important in the compositionally stable forest.

It appears that where *Quercus* and *Carya* presently dominate the overstory, these stands will probably develop into oak-hickory types. In the case of the clearcut stands dominated by the mesophytic species, the conversion has already occurred and these sites must be managed appropriately. As conversion to mesophytic species continues, *Quercus* and *Carya* will be more isolated at the xeric end of the gradient. At LBL, clearcutting in most stands is sufficient disturbance to regenerate desirable species of *Quercus* and *Carya*; however, possibly the use of fire would prevent further encroachment of mesophytic species.

Selection of Study Stands. Twenty 10-12 year old clearcut areas were identified from work area maps. Work area maps and corresponding aerial photographs were used to locate old logging roads and accessibility into the clearcuts. Timber harvest records indicated that forest composition prior to clearcutting consisted primarily of *Quercus* and *Carya* species within the overstory stratum.

Field Procedures. Each clearcut site was examined to determine the range of soil and topographic conditions and the placement of transact lines. Because of soil and/or topographic variability, some clearcuts were divided into two sites and sampled separately. On a large site, one 160 m long transect line was established along the contour. Eight points were located at 20 m intervals on the transect. On small sites, five to seven points, depending on size, were located on two shorter transect lines totaling 160 m. Each point was permanently marked with a 60 cm long conduit pipe driven into the soil. Each point was used as the center of a nested 0.003 ha (30 m^2) plot and a 0.006 ha (60 m^2) plot for sampling stems seedlings and saplings, respectively. Because of stand age, stems originating as stump, root collar or root sprouts were indistinguishable from those originating from seed. Seedlings (stems >5 cm in height; DBH <1.0 cm) and saplings (DBH 1.0-9.0 cm) were counted and recorded by genus and species. A total of 149 nested seedling and sapling plots were sampled in twenty 10-12 year old clearcuts. Aspect (azimuth from north) was recorded for each plot.

Office Procedures. Aspect was transformed using the formula developed by Beers *et al.* (1966): $A' = \cos(A - 45) + 1$, where A' is the transformed aspect, and A is the direction of the slope measured in degrees azimuth measured clockwise from north. The procedure assigned values of 2.00 to northeast facing (cooler and more moist) slopes and 0.00 to southwest facing (hotter, drier) slopes with other aspects assigned corresponding intermediate values. Elevation for each plot was obtained from USGS topographic maps.

Data Analysis. Overstory species and midcanopy species data were separated from arborescent species data. "Overstory species" are defined as those woody stems which have a single central bole, grow to at least a height of 25 meters, and are commonly found at maturity as dominant or codominant trees in the forest overstory. "Midcanopy species" include vines, shrubs (multistemed) and trees less than 25 m in height at maturity. Following Quarterman and Keever (1962), *Diospyros virginiana*, *Nyssa sylvatica*, *Prunus serotina*, and *Sassafras albidum* were classified as "arborescent species" as they "approach the size and habit" of, but only infrequently obtain the stature of, mature forest overstory canopy trees. However, because of their large number, they often mask the importance of overstory canopy tree species within a combined data set.

For each plot, the number of seedlings by species and species group (overstory, arborescent and midcanopy) were converted to a per hectare basis (number of seedlings x 333.33). Relative density (importance value, IV) was calculated for each species within each group by plot:

$$\frac{\textit{Number of seedling stems of a species/ha x 100}}{\textit{Total number of seedlings for all species/ha}}$$

Density and relative density of saplings for overstory, arborescent and midcanopy species groups was calculated in a similar procedure using a conversion factor of 166.67. Plot densities were then used to calculate a site (stand) density for overstory, arborescent, and midcanopy species groups. A compositional index (CI) was calculated for the overstory species group (stratum) of each site (stand) by multiplying species competitive adaptation value (CAV) (Fralish 1988) by its respective (IV) and summing for all species [CI = sum (AV x IV)].

Seedling and sapling densities were categorized into xeric and mesic species groups. The densities of *Carya glabra*, *Carya pallida*, *Carya tomentosa*, *Carya cordiformis*, *Oxydendrum arboreum*, *Quercus alba*, *Quercus coccinea*, *Quercus falcata*, *Quercus marilandica*, *Quercus prinus*, *Quercus stellata*, and *Quercus velutina* were combined into a xeric seedling group and a xeric sapling group. Stem densities for *Acer rubrum*, *Acer saccharum*, *Carya laciniosa*, *Celtis occidentalis*, *Fagus grandifolia*, *Fraxinus americana*, *Fraxinus pennsylvanica*, *Juglans nigra*, *Platanus occidentalis*, *Quercus rubra*, and *Ulmus rubra* were used to determine the mesic seedling and sapling groups. Simple linear and multiple regression models of xeric and mesic seedling and sapling densities were used to examine the relationship to transformed azimuth and elevation.

Seedling and sapling densities for overstory species were combined into total density by species and plot. A square root transformation was made on the total density using ORDIFLEX (Gauch 1977). The square root overstory density data was analyzed using Detrended Correspondence Analysis (DECORANA; Hill and Gauch 1980). Ordination scores from DECORANA were put into CPI2, a Gaussian curve fitting program (Westman 1980) to develop major and minor species coenocline along an implied moisture gradient. The major and minor coenoclines were compared to the major and minor overstory species coenocline from Franklin (1990).

Plots were classified using Bray-Curtis resemblance function and clustered by group averages using COMPAH (Boesch 1977), an agglomerative clustering program. The overstory species data of these community types were compared to understory of compositionally stable and successional forest communities identified by Franklin (1990) and Kettler (1990). The clearcut and understory compositionally stable and successional community types were compared by using percent similarity: $PS = 2w/a+b$, where a is the sum of the species importance values for one community, b is the sum of the species importance values for the second community, and w is the sum of the lower importance values for each species. However, use of (relativized) importance value reduces PS to w.

6. RELATED RESEARCH.

Franklin, S. B., D. J. Gibson, P. A. Robertson, J. T. Pohlmann, and J. S. Fralish. 1995. Parallel analysis: a method for determining significant principal components. Journal of Vegetation Science 6:99-106.

Abstract. Numerous ecological studies use Principal Components Analysis (PCA) for exploratory analysis and data reduction. Determination of the number of components to retain is the most crucial problem confronting the researcher when using PCA. An incorrect choice may lead to the underextraction of components, but it commonly results in overextraction. Of several methods proposed to determine the significance of principal components, Parallel Analysis (PA) has proven consistently accurate in determining the threshold for significant components, variable loadings, and analytical statistics when decomposing a correlation matrix. In this procedure, eigenvalues from a data set prior to rotation are compared with those from a matrix of random values of the same dimensionality (p variables and n samples). PCA eigenvalues from the data greater than PA eigenvalues from the corresponding random data can be retained. All components with eigenvalues below this threshold value should be considered spurious. We illustrate Parallel Analysis on an environmental data set.

We reviewed all articles utilizing PCA or Factor Analysis (FA) from 1987 to 1993 from Ecology, Ecological Monographs, Journal of Vegetation Science, and Journal of Ecology. Analyses were first separated into those PCA which decomposed a correlation matrix and those PCA which decomposed a covariance matrix. Parallel Analysis (PA) was applied for each PCA/FA found in the literature. Of 39 analyses (in 22 articles), 29 (74.4%) considered no threshold rule, presumably retaining interpretable components. According to the PA results, 26 (66.7%) overextracted components. This overextraction may have resulted in potentially misleading interpretation of spurious components. It is suggested that the routine use of PA in multivariate ordination will increase confidence in the results and reduce the subjective interpretation of supposedly objective methods.

Methods. Example use of Parallel Analysis with ecological data. Environmental data were collected from Land Between The Lakes, a National Recreation Area in western Kentucky and Tennessee, USA. (Franklin *et al.* 1993). Data were visually tested for linearity with scattergrams. Factor Analysis was performed on 15 environmental variables (p) in 133 stands (n). Parallel Analysis was employed using the models derived by Longman *et al.* (1989). Factor Analysis was executed again using the correct number of components. Loadings were tested for significance using the Parallel Analysis program.

Yang, Z. 1993. Analysis of alternative designs for buffer zones around conservation areas with a spatial decision support system (SDSS). Ph.D. Dissertation. Department of Geography, Southern Illinois University, Carbondale, Illinois.

ABSTRACT. The design of a "buffer" habitat around conservation areas such as a core area in a biosphere reserve is a complicated problem in resource management because it involves resolving conflicting land use goals. Notably, maintenance of habitat conflicts with deriving economic benefits from land that may be included in a buffer zone. Until now, there has been little progress in dealing with this problem from the management perspective, and no sophisticated management tools have been developed to provide a broad range of alternative patterns for buffer zones for decision makers to choose among.

The purpose of this dissertation is to establish a theoretical framework to design a buffer zone that addresses the conflicting goals that managers must resolve and to design a Spatial Decision Support System (SDSS) to implement such a framework. This research was conducted in a core area in a recently established biosphere reserve area in Land Between the Lakes managed by Tennessee Valley Authority. This research focuses on the spatial-temporal relationship between a core conservation area and its surrounding buffer zone area in terms of ecological and economic value judgments, a temporal database structure which is essential to implement such a SDSS in this management problem, and the impacts of different spatial-temporal patterns of a buffer zone on the opportunity to derive economic benefits in the study area.

Three conservation goals specified as the number of mature pairs of pileated woodpecker *(Dryocopus pileatus)* in the study area (10, 15, 20 pairs) have been fulfilled by nine alternative spatial-temporal patterns for a buffer zone developed using SDSS. Three factors (carrying capacity of a forest stand for pileated woodpecker, the distance from a water source, and its distance from the boundary of the core area) were considered in the buffer zone design. Three combinations of these factors are used as buffer zone design criteria in developing different spatial-temporal patterns to meet the same conservation goal. In some designs, the buffer zone was considered static throughout the 60-year management period; in others, the buffer zone was allowed to expand or shrink to meet a particular conservation goal as the carrying capacity of the forest stands for pairs of pileated woodpeckers changed.

Significant differences in economic benefits can be achieved in the study area using alternative buffer zone design criteria to meet a given conservation goal. The greatest increase in economic benefits was gained by allowing the buffer zone to change periodically during the planning period, rather than retain its original location and size. Differences were determined by relating alternative combinations of design factors. For a given conservation goal, there was a design criterion that resulted in a maximum economic benefit, others were suboptimal. However, the optimum design criterion differed from one conservation goal to another. Therefore, the optimum buffer zone design is not predictive and requires use of SDSS.

Procedures to Establish the Data Base. The procedures to establish the spatial database are as follows: (1) determine the spatial resolution of the study; (2) classify the forest stands in vegetation community types; (3) select variables (spatial and non-spatial) for the buffer zone design; (4) create a spatial database as the result of the above analyses. These procedures are discussed in detail as follows.

(1) Base Map Digitizing and Study Resolution. The basic map scale for this research is 1:20,000 in order to coincide with the scale of the forest stands boundary maps, which are based on 1:20,000 aerial photographs. A USGS 7.5 minute topographic map (1:24,000) - Rushing Creek, KY.-TENN. with stands identified by TVA personnel was used as the base map in this research. This topographic map has a total of 660 forest stands of which the 343 in the five Working Areas in this USGS map sheet were digitized using, pc-ARC/INFO. An attribute file

for those 343 forest stands was created as the basic relational database for this research.

(2) Vegetation modeling. Most forest stands have suffered from a lack of information on mapped vegetation appropriate and sufficient to support the required modeling features. For instance, vegetation maps are at an inappropriate scale; data are recorded on different dates; data record only structure or floristic associations, or sometimes simply do not exist. Therefore, this research has relied on the extensive empirical modeling of vegetation distribution based on limited existing forest inventory data in the study area. The most common method in such vegetation modeling is the direct gradient analysis (Whittaker 1967, 1978; Kessell 1979) and indirect gradient analysis, or ordination methods (Bray and Curtis 1957; Orloci 1966, 1973; Gauch and Whittaker 1972; Whittaker and Gauch 1978; Kessell 1979, 1981). The direct gradient analysis method was used in this study (Gauch 1982).

Direct gradient analysis is used to display the distribution of organisms along gradients of important environmental factors. Those environmental factors could be elevation, soil moisture, soil texture, etc. Direct gradient analysis is a major research approach in community ecology. In this research, bedrock type and elevation were chosen as major environmental factors based on Fralish's study.

Because of the relatively small size of the study area (*i.e.*, 44 km^2), 150 field samples from forest inventory data are analyzed to produce direct gradient "models" that express each forest stand's vegetation structure and floristics as a function of other, easily obtained coverage in this research (such as elevation, topographic position, aspect, bedrock types, etc.). This gradient-modeling procedure is utilized in conjunction with the digitized maps, often to provide floristic, structural and diversity details not available from the maps alone.

In this study, a vegetation community distribution map was created according to Fralish's research in the area. A direct gradient analysis in the study is based on bedrock type which is highly related to soil type and elevation. According to Fralish's field observation, a 480-500 feet elevation line in the area has a significant ecological meaning and is highly related to different types of bedrock. All of the ridge tops are above such elevation, underlain by gravel deposits, and are covered by chestnut and post oak dominated communities. The slopes in the study area are underlain by limestone deposited in different geological eras. The slopes above 480-500 feet elevation are covered by a stable white oak communities which has a stable species composition. The slopes below that line are covered by successional white oak communities which are dominated by white oak and sugar maple. In the river valley, the soil is developed in alluvium deposits. Generally, river valleys are open fields which are covered by boxelder and other miscellaneous species.

The communities in the study area vary along gradients of bedrock and elevation. The original resolution of variable mapping in LBL forest stands are discussed. Ecological and economic values of each stand will be the focus of the investigation. However, boundaries of some forest stands are not congruent with the vegetation community boundaries resulting from the ecological study in this area (Fralish, personal communication). In order to preserve the consistency in the forest inventory data and take advantage of results of ecological studies in the area, the forest stand map was overlaid with the community map and stands that fell in one or more community types were subdivided. The new unit was used as an actual simulation unit in temporal analysis.

THE ANNUAL DORMANCY CYCLE IN BURIED SEEDS OF THE NATIVE WINTER ANNUAL GRASS *ALOPECURUS CAROLINIANUS*

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ABSTRACT. This study is a contribution to our knowledge of annual dormancy cycles in buried seeds of native North American winter annuals; most previous studies on dormancy cycles have been done on nonnatives. Germination responses in light (L) and darkness (D) over a range of thermoperiods were determined for freshly-matured caryopses (seeds) of the native winter annual grass *Alopecurus carolinianus* and for those exhumed from burial under near-natural temperatures in a nonheated greenhouse at monthly intervals for 7 mo and then at 2- or 6-mo intervals for 22 mo. Seeds were collected from plants growing on the Cumberland River flood plain in Montgomery County, TN. At the time of maturation, collection and burial in May 1994, seeds were dormant and did not germinate at 12/12h daily thermoperiods of 15/6, 20/10, 25/15, 30/15 or 35/20°C in L or D. Buried seeds came out of dormancy during summer, exhibiting an increase in the maximum germination temperature as dormancy loss progressed. Germination tests of seeds buried in moist soil in incubators at 5, 15/6, 20/10, 25/15 and 30/15°C for 12 wks showed that dormancy is broken at high (25/15 and 30/15°C) but not at low (5, 15/6°C) temperatures. Thus, in nature exposure to high summer field temperatures is required for seeds to come out of dormancy. Seeds exhumed in October, after 4 mo of burial in the greenhouse, germinated to 100% at all thermoperiods, except at 35/20°C in L and D, where none germinated. Buried seeds re-entered dormancy during winter 1994-1995 and became nondormant again in summer 1995. This annual dormancy/nondormancy cycle in buried seeds was repeated the following winter and summer. Seeds collected and buried in the nonheated greenhouse in May 1995 and exhumed at monthly intervals for 18 mo also exhibited an annual dormancy/nondormancy cycle, with seeds coming out of dormancy in summer and re-entering it in winter.

By the second (1995) and third (1996) autumns of burial, only 44 and 3%, respectively, of the 1994 seeds were viable. In October 1995, approximately 25% of the 1994 seeds germinated while buried, and the seedlings died; cause of death of the other buried seeds is unknown. By the second (1996) autumn of burial 46% of the seeds buried in 1995 were viable; this study is in progress. Thus, data indicate that *A. carolinianus* forms a small, short-term persistent seed bank.

Buried nondormant 1995 seeds were flooded in a pool of water in the nonheated greenhouse from October, November or December 1995 until May 1996. Seeds that had been flooded germinated to 43-99% at 15/6, 20/10, 25/15 and 30/15°C in L, while those in the nonflooded control germinated to only 0-3%. These data indicate that flooding of the flood plain habitat of *A. carolinianus* in late autumn-winter prevents induction of secondary dormancy in seeds that fail to germinate in early-to mid-autumn. In which case, *A. carolinianus* also has the capability of behaving as a spring ephemeral.

GREENHOUSE AND LABORATORY STUDIES ON THE ECOLOGICAL LIFE CYCLE OF THE FEDERAL-ENDANGERED SPECIES *DALEA FOLIOSA* (FABACEAE)

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ABSTRACT. *Dalea foliosa* is a short-lived, herbaceous perennial without vegetative reproduction known only from northern Alabama, middle Tennessee, and northern Illinois. Certain aspects of the seed and flowering stages of its ecological life cycle were investigated under greenhouse and laboratory conditions. Seed dormancy is due to a water-impermeable ("hard") seed coat that can be broken completely by mechanical scarification. Nondormant seeds germinated over a wide range of temperatures in both light and darkness. Soaking in concentrated sulfuric acid and dry-heating at 100°C broke dormancy in 50-60% of the seeds, whereas dipping them in boiling water was less effective in promoting germination. Fire caused breakdown of the hard seed coat of seeds on the soil surface, but killed the seeds. Neither freezing and thawing, soaking in absolute ethanol, nor exposing seeds to simulated summer followed by winter-stratifying temperatures broke dormancy. Seeds sown in a nonheated greenhouse and those in soil samples collected at a population site germinated over a several-year period, mostly in March and April. Thus, the species can form a persistent seed bank. No plants of *D. foliosa* flowered under a 10-h daily photoperiod (short day), whereas 100% of those given an 8-h photoperiod + a 2-h night interruption (long day) flowered. One-hundred percent of the plants kept in a heated greenhouse all winter and of those exposed to winter cold in a nonheated greenhouse flowered. Thus, *D. foliosa* is a obligate long-day plant that does not require exposure to low temperatures for bud break, shoot growth, or flowering.

SPECIES RESPONSE TO AN ENVIRONMENTAL GRADIENT FOR UNDISTURBED FOREST STANDS AT LAND BETWEEN THE LAKES, KENTUCKY AND TENNESSEE

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ABSTRACT. Variation in herbaceous species composition was studied in undisturbed forest stands distributed along a soil moisture gradient from xeric to mesic conditions. In each stand, one of two previously established 0.06 ha circular macroplots was randomly selected for study. Within the macroplot, percent cover was recorded for each herbaceous species in 10, 1.41 m^2 systematically located quadrats. Within each quadrat, litter was collected from a randomly located 0.25 m^2 nested microplot. Average canopy cover was determined from four spherical densiometer readings. Additional tree data and environmental data were available from previous studies. DCCA in CANOCO was used to examine herbaceous response to environmental factors. Nine herbaceous dominance types were identified using Bray-Curtis similarity index values in an agglomerative clustering technique in COMPAH; an unweighted pairgroup method was employed. DCCA environmental axis 1 correlated strongly with aspect ($r^2=0.96$), slope position ($r^2=0.84$), and available water holding capacity ($r^2=0.70$). Stepwise discriminant analysis of 15 variables indicated that herbaceous species response was related to slope position ($r^2=0.52$) and percent silt ($r^2=0.40$). When variables were categorized as operational (e.g., soil available water holding capacity, litter weight) and non-operational (e.g., aspect, elevation), soil available water capacity ($r^2=0.51$), slope position ($r^2=0.52$), and percent silt ($r^2=0.40$) were identified as major factors influencing herbaceous species distribution. A continuum appeared when presence data for 28 herbaceous species were plotted along a moisture gradient developed by sequencing forest community types (e.g., *Quercus prinus, Q. stellata, ..., Acer saccharum*).

THE EFFECTS OF PRESCRIBED BURNING ON UPLAND *QUERCUS* FOREST VEGETATION, LAND BETWEEN THE LAKES, KENTUCKY AND TENNESSEE

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ABSTRACT. Prescribed burnings significantly affected the forest structure of both nonsuccessional (an oak understory under an oak overstory) and successional (a sugar maple-understory under an oak overstory) upland oak sites. However, the effects of fire differed between the two site types. Burning influenced the vegetation density between 0.5 and 2.5 m above ground level. Thinning treatments resulted in increased density while burning without thinning resulted in decreased vegetation density. From ground level to 0.5 m, little effect on vegetation density was witnessed. This can be attributed to the quick recovery of most species, either by resprouting or by establishment. The altered forest structure, by altering the microenvironment for seedling establishment, may affect the future forest composition.

Forest composition was altered for specific strata depending on the site type and treatment. Prescribed burning decreased larger seedling and sapling density (stems approximately 2.5-4 cm dbh) while increasing small seedling density (<2.5 cm dbh). Herbicide application effectively eliminated the target species in the sapling strata. Thinning decreased overstory density while increasing herbaceous and seedling density. Light was a necessary factor for the understory strata to respond to burn treatments. Sugar maple seedlings decreased when burned, but increased when thinned and burned, indicating burn applications prior to thinning may be an effective management strategy for maintaining oak communities.

Simpson's diversity index was not significantly affected by the treatments. However, the data indicate a small increase of pioneer species in the seedling stratum and an increase in sedges and grasses in the herbaceous stratum. The herbaceous stratum appears to be highly variable. The long-term outcome of these treatments (e.g., effect of structural changes and basal wounds) will be addressed in the future with additional data collection.

PRELIMINARY STUDIES ON SEED DORMANCY AND GERMINATION IN SEVEN MEMBERS OF THE CAPRIFOLIACEAE

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ABSTRACT. Preliminary data will be presented on the ecology and physiology of seed dormancy and germination in seven species in three genera of the (primarily) north temperate zone plant family Caprifoliaceae: *Lonicera fragrantissima, L. japonica, L. maackii, Symphoricarpos albus, S. orbiculatus, Viburnum acerifolium*, and *V. rufidulum*.

Following an 8-wk warm stratification period at 25/15°C, *Lonicera fragrantissima* seeds germinated to 64-73% at 15/6, 20/10, and 25/15°C after incubation in light for 12 wk. However, 12 wk of cold stratification at 5°C did not break dormancy in seeds of this species. In contrast, 83-100% of the cold-stratified seeds of *L. japonica* germinated at 15/6, 20/10, 25/15, and 30/15°C after incubation in light for 2 wk. Cold stratification also broke dormancy in seeds of *L. maackii*. Freshly-matured seeds of this species germinated to 15-81% at 15/6, 20/10, 25/15, and 30/15°C after incubation in light for 2 wk, and those cold-stratified for 12 wk germinated to 75-91% over this range of thermoperiods. Embryos in freshly-matured seeds of *L. maackii* grew more at 25/15°C than at 5 or 1°C. During an 8-wk incubation period at 25/15°C in light, embryo length (mean ± SE) increased from 1.2 ± 0.07mm (fresh seeds) to 3.7 ± 0.12mm. Peak germination of *L. maackii* seeds sown in a nonheated greenhouse on 24 October 1995 occurred between 11 and 18 March 1996, when mean weekly maximum and minimum temperatures were 17.7 and 8°C, respectively.

Seeds of *Symphoricarpos orbiculatus* collected and sown in the nonheated greenhouse in late autumn 1977 germinated in early spring 1979, and those collected and sown in early spring 1979 germinated in early spring 1980 or in early spring 1981. Seeds collected and sown in late autumn 1995 have not germinated yet. Thus, apparently seeds of *S. orbiculatus* require warm followed by cold stratification to germinate; embryos grew very little (only 0.09 ± 0.002mm in length) during a 12-wk incubation period at 5 or 25/15°C in light. Although seeds of *S. orbiculatus* and *S. albus* previously have been reported to have water-impermeable seed coats, this clearly is not the case; after 1 wk on moist substrate, seed weight in both species had increased by about 30%.

Peak radicle emergence in seeds of *Viburnum acerifolium* and *V. rufidulum* incubated at 15/6, 20/10, 25/15, 30/15, and 35/20°C in light occurred at 25/15°C. After 30 and 42 wk of incubation of *V. acerifolium* and *V. rufidulum* seeds, respectively, roots had emerged in about 75% of them. In both species, embryos must grow before the radicles emerge, and they require a period at warm temperatures to do so. During a 16-wk incubation period at 25/15°C in light, embryos of *V. acerifolium* grew from a mean (± SE) length of 0.8 ± 0.08mm (fresh seeds) to 3.1 ± 0.14mm, whereas at 5°C they did not grow at all. Following radicle emergence, these species need a period of low temperatures for shoots to emerge. Of the four temperature regimes tested (5, 15/6, 20/10, and 25/15°C) on epicotyl dormancy-break *in V. acerifolium* and *V. rufidulum*, the shortest period of time for shoot (epicotyl) emergence was at 15/6°C (4-8 and 5-8 wk, respectively) and the longest at 25/15°C (14-24 and 17-42 wk, respectively).

These preliminary results suggest that all seven species have underdeveloped embryos with physiological dormancy, and thus seeds have morphophysiological dormancy (MPD). Types of MPD in seeds of these species are as follows: *Lonicera fragrantissima*, nondeep; *L. japonica* and *L. maackii*, deep complex (some seeds of *L. maackii* appear to have only morphological dormancy); *Symphoricarpos albus* and *S. orbiculatus*, nondeep complex; and *Viburnum acerifolium* and *V. rufidulum*, deep simple epicotyl.

DESICCATION-INDUCED LIMITS OF SPORE VIABILITY IN *EQUISETUM HYEMALE*

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ABSTRACT. *Equisetum* is the only surviving genus of the division Sphenophyta, which during the Carboniferous Period included many herbaceous and arborescent genera that were major components of low-elevation forests. The thin-walled, chloroplast-containing spores of *Equisetum* survive drying, but cannot tolerate this quiescent state for more than 2 wks. The hypothesis that the brief viability of *Equisetum hyemale* spores results from their inability to recover photosynthetic competence after 2 wks in the dry state was tested. Experimental spores were dried for varying times and following wetting, their photosynthetic capacity was evaluated using oxygen exchange and chlorophyll *a* fluorescence. Relative to spores desiccated for 24 h, recovery of photosynthetic performance of spores desiccated for 1 wk was slower as judged by significantly slower increases of (1) photochemical efficiency of photosystem (PS) II, (2) PS II quinone$_B$-reducing center concentration, (3) water-oxidation activity, and (4) rate of light-induced O_2 evolution. PS II competence of 2-wk desiccated spores was increasingly impaired and did not recover during rehydration. Dark respiration was not affected by desiccation time following rehydration. The results indicate that the inability to recover PS II competence after 2 wks in the dry state is responsible for the extremely short viability of *Equisetum* spores. The wet climates and numerous wetland habitats of the Carboniferous Period provided ideal conditions for sphenophytes, virtually all of which produced thin-walled, *Equisetum*-like spores. This study suggests that inhibition of the recovery of spore photosynthetic competence following 2 wks in the dry state may have contributed to the mass sphenophyte extinction during the arid Triassic Period and the restriction of extant species to wet habitats.

COMPARATIVE PHENOLOGY OF FRUIT AND SEED DEVELOPMENT IN *RHUS AROMATICA* AND *R. GLABRA* (ANACARDIACEAE)

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ABSTRACT. Phenology of fruit and seed development in *Rhus aromatica* and *R. glabra* was compared in 1996. Dates of major developmental events (including anthesis, endocarp and embryo becoming recognizable, color changes in embryo and fruit, and endocarp becoming impermeable to water) were determined. The following measurements were made at weekly intervals, beginning with anthesis: length and width of fruit, endocarp, seedcoat, and cotyledons; weight and moisture content of fruit and of seed + endocarp; germinability of isolated embryo; and endocarp impermeability.

Sexual reproduction of *R. aromatica* precedes that of *R. glabra* by about 2 months. For example, anthesis in *R. aromatica* and *R. glabra* peaked on 26 April and 27 June, respectively, at the study site in Fayette County, KY. However, the sequence of morphological and physiological events in fruit and seed development of the two species is very similar, although the length of time over which they take place may differ. The endocarp became distinguishable in *R. glabra* and *R. aromatica* one and four weeks, respectively, after anthesis. The embryo of both species became recognizable four weeks after anthesis. By this time, fruit and endocarp of both species had reached their maximum sizes. One week later, seedcoats had expanded fully, and after two weeks cotyledons had attained their maximum length and width. During the 5th and 6th week following anthesis in *R. aromatica* and *R. glabra*, respectively, isolated embryos gained the ability to germinate, and their color changed from green to creamy. One week later, fruits of both sumacs had turned red; however, physiological maturity was not reached until the 8th week (20 June for *R. aromatica* and 22 August for *R. glabra*. By this time, moisture content of seed + endocarp had decreased to 16.2 ± 0.5% (mean ± SE) in *R. aromatica* and to 9.3 ± 0.2% in *R. glabra*, and the endocarp in >85% of the fruits of both species had become impermeable to water. Although this pattern of seed development lagging behind that of the fruit also is reported in various other members of the Anacardiaceae, the lag times for *R. aromatica* and *R. glabra* seem to be considerably shorter than that of other taxa in the family.

PRELIMINARY STUDIES ON THE PHYSIOLOGICAL LIFE CYCLE OF THE MUDFLAT SPECIES *ERAGROSTIS HYPNOIDES* (POACEAE)

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ABSTRACT. A number of dams have been built on the Cumberland and Tennessee rivers for flood control. The flood control cycle normally involves gradual reduction of reservoir volume during late summer and early autumn, and following the period of high flood probability (mid-December through mid-April) pool levels are raised. Mudflats, flat areas of the former river floodplains that are exposed during the time of water-drawdown, are unpredictable habitats for plants, because water levels are not lowered at the same time, at the same rate, or to the same level each year. Thus, the life cycles of plants that colonize mudflats must be adapted to this year-to-year variation in length of the growing season.

One of the common plants on mudflats along Lake Barkley (Cumberland River) is the C_4 summer annual grass *Eragrostis hypnoides* (Lam.) BSP. We are studying the ecological life cycle of this species to determinate how it is adapted to mudflats. This talk will present preliminary results of studies by the senior author on factors required to break seed dormancy, germination requirements of nondormant seeds, and influence of germination date on days to flowering, relative growth rate, and reproductive effort.

Seeds of *E. hypnoides* are physiologically-dormant at maturity in late summer or autumn. They required 9 weeks of cold stratification (5°C), or burial at near-natural temperatures in a nonheated greenhouse from autumn until the following April, to germinate to >80% at 30/15 and at 35/20°C in nonboiled water and on moist sand; no seeds germinated at 25/15 or at 20/10°C. In August, seeds submerged in boiled water (low oxygen concentration) and in nonboiled water germinated to higher percentages at 30/15 and at 35/20°C than those on the surface of moist sand. Further, at 25/15°C seeds submerged in boiled water germinated to much higher percentages than those incubated in nonboiled water or on moist sand.

Seeds require light to germinate. Although at 30/15 and at 35/20°C seeds that had been flooded in a nonheated greenhouse from 9 November 1995, to 6 June 1996, germinated to about the same percentages as those that had been nonflooded, flooded seeds were more sensitive to light. Thus, flooded and nonflooded seeds given a single 8-hour exposure to white light and then incubated at 30/15°C in darkness germinated to 88% and 1.8%, respectively. The reason for this difference may be that flooded seeds were nondormant, whereas nonflooded ones were still in conditional dormancy; flooded soil is more conducive to loss of dormancy in seeds of *E. hypnoides* than is nonflooded soil. Germination of flooded seeds on moist sand was not affected by level of irradiance, but it was affected by length of the dark period between light exposures. Seeds exposed to a single 2-hour period of white light germinated to 27% after incubation in darkness at 30/15°C for 2 weeks, while those exposed to two 1-hour periods of white light separated by an 8-hour dark period germinated to 95%. Seeds flooded during 12 weeks of cold stratification did not germinate on moist sand in darkness at 30/15°C after a single 11-hour exposure to far-red, red, blue, or white light. However, seeds that had been flooded during burial for 10 months in a nonheated greenhouse germinated to 0%, 99%, 0%, and 98% in darkness after a single 11-hour exposure to far-red, red, blue, and white light, respectively.

Days to 100% flowering, relative growth rates (mg $mg^{-1}da^{-1}$), and percentage of reproductive effort [(reproductive organ dry weight/total plant dry weight) x 100] of plants grown from seeds sown on 5 June, 28 June, and 5 August were 72, 0.097, 7.74; 66, 0.088, 18.5; and 40, 0.200, 36.7, respectively. One-month-old greenhouse-grown plants (natural daylength) subjected to five 10-hour days in a plant growth chamber and then returned to the greenhouse on 10 July 1996, flowered one month earlier than controls.

The adaptive significance of these physiological characteristics of *E. hypnoides* to the unpredictable mudflat environment will be discussed.

TWENTY YEARS OF FOREST CHANGE AT RADNOR LAKE NATURAL AREA, DAVIDSON COUNTY, MIDDLE TENNESSEE

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ABSTRACT. A 1994 analysis of five mature forest communities at Radnor Lake Natural Area near Nashville, Tennessee, was compared with a similar 1974 study to ascertain successional trends in this protected area. The importance value [(IV = % density + % basal area + % frequency)/3] of *Acer saccharum* increased in all community types and its overall IV (average of IVs for all communities) increased from 10.0 in 1974 to 15.3 in 1994. The overall IV of *Celtis occidentalis* rose from 3.4 to 7.6 and showed increases in four of the five communities. The IV of *Acer saccharinum* in the lakeshore community rose from 10.8 to 30.3. Taxa that decreased in IV included *Carya cordiformis* (10.5 to 2.7, mesic slope community), *Juglans nigra* (4.0 to 2.6, mesic slope community; 8.3 to 5.1, ravine community), *Populus deltoides* (12.1 to 3.1, lakeshore community), *Quercus marilandica* (1.2 to 0.0, ridge community), *Quercus rubra* (8.9 to 0.0, dry slope community; 12.0 to 10.3, mesic slope community; 4.0 to 1.6, ravine community), *Salix nigra* (14.0 to 0.9, lakeshore community), and *Ulmus* spp. (6.5 to 2.5, mesic slope community; 25.1 to 0.9, ravine community; 24.7 to 15.7, lakeshore community).

The other 36 sampled tree taxa exhibited relatively minor changes in IV over the 20 year period. Total densities of tree stems decreased in all communities. In 1994, the dominant tree taxa ranked by IV were *Quercus montana*, *Fraxinus quadrangulata*, and *Carya ovata* on the ridges; *Acer saccharum*, *Celtis occidentalis*, and *Quercus montana* on the dry slopes; *Acer saccharum*, *Fraximus americana*, and *Quercus rubra* on the mesic slopes; *Acer saccharum*, *Carya cordiformis*, and *Celtis occidentalis* in the ravines; and *Acer saccharinum*, *Celtis laevigata*, and *Ulmus americana* on the lakeshore. A total of 64 species of trees and 24 taxa of shrubs and woody vines was sampled or observed at Radnor Lake Natural Area. Species rare to Middle Tennessee included *Cladrastis kentuckea*, *Gymnocladus dioicus*, and *Kalmia latifolia*.

THE ROLE OF LIGHT AND NUTRIENTS IN THE AUTECOLOGY OF THE FEDERAL-ENDANGERED *SOLIDAGO SHORTII* (ASTERACEAE). I. LIGHT

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ABSTRACT. The conceptual model of the successional relationships of the narrow-endemic *S. shortii* proposed by Buchele et al. (*Bull. Torrey Bot. Club 116, 1989, pp. 344-355*) predicts that this species will lose vigor and be shaded out as woody plant cover increases at a population site. However: (1) neither number of flowering ramets nor number of vegetative ramets of *S. shortii* increased during a 4-yr period after opening the shrub canopy above plants growing in a powerline right-of-way in Blue Licks Battlefield State Park (BLBSP); (2) a high percentage of the plants growing in full sun in the powerline right-of-way and in a glade-like area in BLBSP, where soil nutrient levels are low, do not flower; and (3) plants from seeds planted in pots and kept in a nonheated greenhouse flower their first year and for a few years thereafter, but then stop flowering. Thus, we speculated that nutrients as well as light may be important in maintaining the vigor of *S. shortii*. This first of two talks is on the effects of light on growth, flowering, and survival of *S. shortii* plants.

Twenty adult plants each were transplanted into a young redcedar thicket and into a grassy opening on 19 March 1989. Mean ($\pm$SE) photosynthetically active radiation measured at noon on 21 May 1989, a clear day, was 121 ± 32 and 1625 ± 109 μmol m^{-2} s^{-1} in the thicket and opening, respectively. Compared to plants in the opening, those in the thicket had an equal number of vegetative ramets, but significantly fewer flowering ramets in 1989 and 1990 (PLSD, $P=0.05$). In addition, capitula (flowering ramet)$^{-1}$ were much lower in shaded (mean$\pm$SE = 41 ± 5 in 1989, 34 ± 3 in 1990)- than in nonshaded (mean$\pm$SE = 97 ± 9 in 1989, 145 ± 12 in 1990) plants in 1989 and 1990. During 1991-1995, none of the plants in the thicket flowered, whereas 9-20 (mean$\pm$SE = 15 ± 2) plants flowered in the opening; plants in the thicket also produced significantly fewer vegetative ramets than those in the opening (PLSD, $P=0.05$). After 7 yr, 17 of the plants in the opening were still alive, but only 1 in the thicket.

In 1993 and in 1994, adult plants were grown under shaded [*ca.* 5 mol m^{-2} (clear-day)$^{-1}$] and nonshaded [*ca.* 30 mol m^{-2} (clear-day)$^{-1}$] conditions in a nonheated greenhouse. At the end of both growing seasons, shaded plants had significantly fewer flowering ramets, less biomass and leaf area, and a significantly higher specific leaf area [leaf area (leaf wt.)$^{-1}$] than nonshaded plants (t-test, $P\leq0.0494$). Number of vegetative ramets did not differ significantly between the two treatments (t-test, $P\geq0.3629$).

Classical growth analysis was performed on seedlings/juveniles grown in the greenhouse under the shaded and nonshaded conditions described above. Plants were harvested weekly for 7 wk between 24 April 1993 and 12 June 1993. Shaded plants produced significantly less dry biomass, and they had a significantly lower relative growth rate [plant wt. (plant wt.)$^{-1}$ day^{-1}], net assimilation rate [plant wt. (leaf area)$^{-1}$ day^{-1}], leaf area, and root/shoot ratio than nonshaded plants (t-test, $P\leq0.0074$). On the other hand, leaf area ratio [leaf area (plant wt.)$^{-1}$], specific leaf area, and leaf weight ratio [leaf wt. (plant wt.)$^{-1}$] were significantly higher in shaded than in nonshaded plants (t-test, $P\leq0.0003$).

These morphological, physiological, and growth (biomass reduction) responses of *S. shortii* to shading are typical of shade-intolerant plants. Thus, this study confirms that increased shading associated with succession is a major factor contributing to loss of vigor and eventual death of *S. shortii* plants in shaded situations.

THE ROLE OF LIGHT AND NUTRIENTS IN THE AUTECOLOGY OF THE FEDERAL-ENDANGERED *SOLIDAGO SHORTII* (ASTERACEAE). II. NUTRIENTS

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ABSTRACT. Results of the previous talk showed that plants of *S. shortii* grow better in high- than in low light. However, long-established plants do not flower in nonshaded situations in the field or in a nonheated greenhouse, and release from shading by woody plant canopy removal did not increase flowering of this species in the field. These observations led to the speculation that nutrients may be an important factor limiting flowering of nonshaded plants. Thus, we tested the effect of fertilization with N, P, and K on growth and flowering of plants in the field and in the greenhouse. In addition, plants of *S. shortii* were grown on five soil types representing a gradient of soil fertility.

In 1994, 22 plots (0.25 m^2) each containing ramets of *S. shortii* in the powerline right-of-way and in a glade-like area in Blue Licks Battlefield State Park were chosen randomly for treatment (addition of N, P, and K) in 1995 or for control (not fertilized). Data on number of flowering and vegetative ramets and capitula (flowering ramet)$^{-1}$ were collected from plants in the treatment and control plots in 1994, 1995, and 1996. In the control plots, number of flowering ramets and capitula (flowering ramet)$^{-1}$ remained nearly constant from 1994-1996, whereas in the treatment plots both variables were significantly higher in 1995 than in 1994 or 1996 (PLSD, $P=0.05$). Further, number of flowering ramets and capitula (flowering ramet)$^{-1}$ were significantly higher for plants in treatment than in control plots in 1995 and 1996 (t-test, $P \leq 0.03$), but not in 1994 (t-test, $P \geq 0.733$). Although the number of vegetative ramets in treatment and control plots remained about constant from 1994-1996, it was significantly higher in control than in treatment plots in 1994 and 1995 (t-test, $P \leq 0.0430$), but not in 1996 (t-test, $P=0.175$).

Potted adult plants in the greenhouse that did not flower in 1992 were chosen for treatment or control (as above); treatment pots were fertilized in spring and in summer 1993 and 1995. Fertilized 1993- and 1995 plants produced a significantly higher number of flowering ramets and capitula (flowering ramet)$^{-1}$ than nonfertilized ones (t-test and PLSD, $P \leq 0.05$). Number of vegetative ramets was about equal for fertilized and nonfertilized pots in 1993, but it was significantly higher in nonfertilized than in fertilized pots in 1995 (PLSD, $P=0.05$). In contrast, none of the 1993-fertilized or 1993-nonfertilized plants flowered in 1994 (year no fertilizer was added). However, number of vegetative ramets in 1994 was significantly higher in the 1993-fertilized than in the 1993-nonfertilized pots (t-test, $P=0.0001$).

Seedlings planted in soils derived from five types of bedrock (phosphatic limestone, calcareous shale, dolomite, sandstone, black shale) were grown for 78 d in the greenhouse in both 1995 and 1996. At the end of the growth period, hierarchy of dry weight of *S. shortii* among the five soil types was phosphatic limestone > calcareous shale > sandstone > black shale = dolomite. This hierarchy was associated closely with levels of phosphorus in the soils, but not with levels of nitrogen, potassium, calcium, magnesium, zinc, organic matter, or pH.

Altogether, results of field and greenhouse studies strongly suggest that both light and nutrients are limiting factors for growth and reproduction of *S. shortii* in the field. A conceptual model will be presented that incorporates the role of light and soil nutrients, succession, and intensity of disturbance on population vigor of *S. shortii*, and management implications of these studies will be summarized briefly.

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