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

HELD AT BRANDON SPRING GROUP CAMP
LAND BETWEEN THE LAKES
MARCH 3 AND 4, 1995

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 Sixth 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 3 and 4 March 1995. 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 representative of the three sponsoring institutions. Representing Austin Peay State University and The Center for Field Biology was its Director, Dr. Benjamin P. Stone. Dr. David White, Director of the Hancock Biological Station, spoke on behalf of Dr. Gary Bogess, Dean of the College of Arts and Sciences at Murray State University. Mr. Richard Lowe, Specialist and Team Leader, represented LBL General Manager Ms. Ann Wright. Three invited presentations related to the theme "Water Quality and the Exotic Biota" followed. The first speaker, Dr. John Barko, U.S. Army Corps of Engineers, Waterways Experiment Station, Vicksburg, Mississippi, treated the importance of nutrients to growth of submersed aquatic vegetation and the impact of that vegetation on nutrient transport from sediments to the water column. Besides effects of submersed vegetation on nutrient dynamics, Dr. Barko also spoke about the importance of these plants on the hydrology of aquatic ecosystems and their effect on sediment transport. Invasion of *Daphnia lumholtzi* into Norris Reservoir in east Tennessee was the topic of the second report, presented by Dr. Clyde Goulden. Dr. Goulden, Philadelphia Academy of Sciences, described the rapid invasion of this exotic cladoceran in reservoirs across the southern United States and the concern over its potential impact on the rest of the zooplankton community and other aquatic communities dependent on zooplankton. According to Dr. Goulden, success of *D. lumholtzi* as an invader appears to be related to its ability at predator avoidance. This exotic daphniid does not appear to be affecting other daphniids adversely. The final presentation Friday afternoon, given by Dr. Gerald Mackie of the University of Guelph, Ontario, was an evaluation of the 23 species of exotic mollusks introduced to North American. This review included a comprehensive overview of the biological, chemical, and physical requirements of these species and the potential impact they have on the ecology and distribution of native species. Dr. Mackie evaluated adaptive features of the exotic species that might influence their success in regulated streams which have physical, chemical, and biological characteristics that are markedly different from unregulated streams and natural lakes. Written reports of all three presentations are included in these proceedings.

Friday evening Dr. George Folkerts, Auburn University, gave an excellent lecture entitled "Aquatic and Wetland Habitats of the World: Fate and Future." While most were enthralled with the lecture content, the beautiful photographs illustrating it, and the style and charisma of Dr. Folkerts, most admitted to a sense of sadness and foreboding at seeing the precarious nature of these habitats. Dr. Folkerts illustrated this precarious situation with numerous species of plants and animals from around the world that are at the very brink of extinction due to habitat destruction. That it will take only a single disturbance event such as a toxic spill, a drainage canal or a dam to destroy some of these special ecosystems is deeply disturbing to most people. Dr. Folkerts left us with a powerful message, to be ever vigilant of political, economic and personal agendas that can lead rapidly to further losses of these habitats. It only takes one time to destroy forever what has required millions of years to evolve.

Contributed papers were read Saturday morning. The large number of contributions necessitated holding three sessions. Session I, entitled "Aquatic Biology and Water Quality" had 11 presentations and was moderated by Dr. Steven Hamilton, Austin Peay State University. Session II, "Aquatic Biology and Zoology," with 12 talks, was moderated by Dr. James Sickle, Murray State University. Moderating the 14 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 these proceedings. While most opted to publish only an abstract, nine full length papers are presented in these proceedings, two from Session I and seven from Session III.

The style and format of these proceedings follow that established in previous proceedings of these symposia. Drs. White and Hamilton organized and edited the Invited Papers; Dr. Hamilton edited abstracts and papers from Session I; Dr. Scott, The Center for Field Biology, edited abstracts in session II; and Dr. Chester edited abstracts and papers from Session III. Dr. Hamilton brought all these papers together into the final format.

## 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 biennial 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. The help of these individuals and others forgotten was critical to the success of this symposium and completion of these proceedings. All complete manuscripts were reviewed fully. We appreciate the comments of all reviewers as this process greatly enhances the quality of these proceedings. While we (the editors) would wish this publication to be error free, most likely it is not and for this we assume responsibility.

# SYMPOSIUM REGISTRANTS

Following, in alphabetical order, is a list of those individuals who registered at the 1995 symposium. Institutional affiliation (when available), city (of the person's institution or home), and state are also given.

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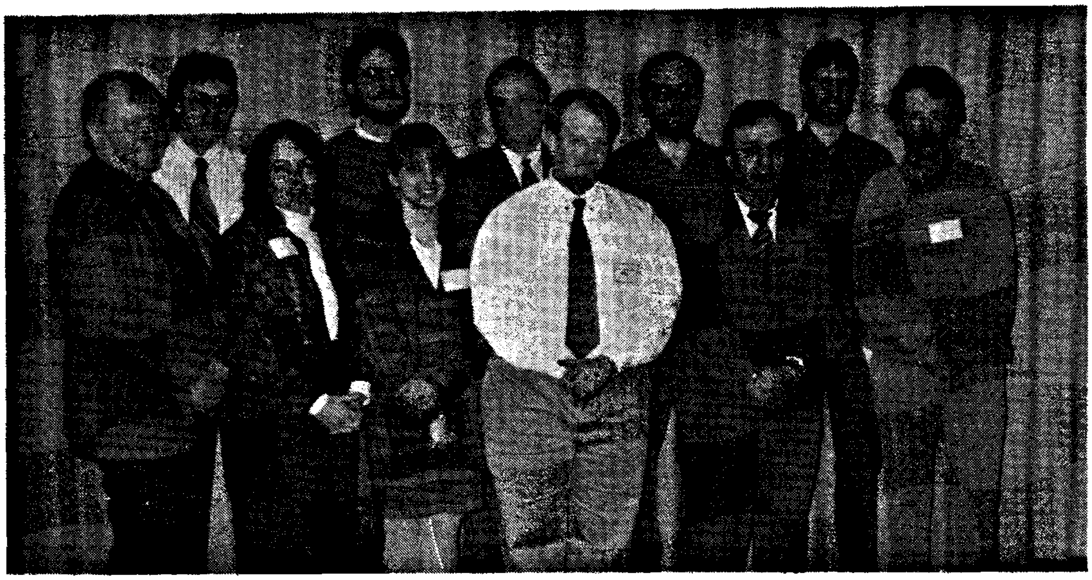
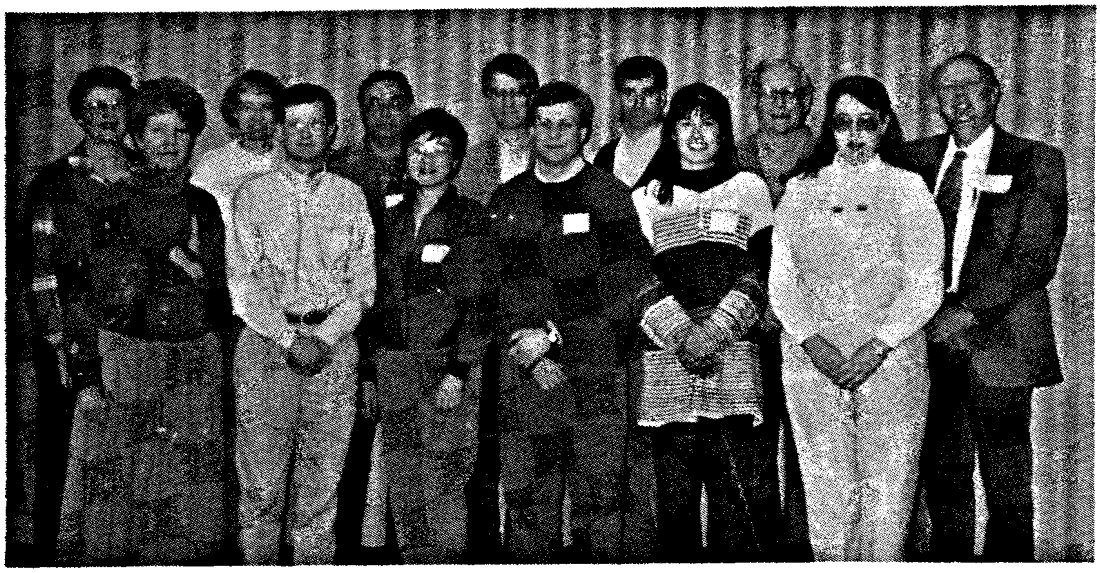


**Session I: Aquatic Biology and Water Quality** - (from left to right) D. Owen, J.R. Smith, D. Lingle-Hamilton, T. Johnston, J. Kaswell, G. Maddox, T. Neville, B. Naugle, H. Kobraei, S. Hamilton, D. White.

**Session II: Aquatic Biology and Zoology:** - (from left to right) B.T. Miller, M. Varner, E.A. Bababunmi, C. Rozelle, D. Dailey, J.B. Sickel, D.A. Leek, P.V. Lindeman, B. Sharp, H.N. Blalock, A.F. Casper, B.D. Moyer, M.L. McReynolds.



**Session III: Botany** - (from left to right) M.L. McReynolds, S. Noel, C.C. Baskin, J.L. Walck, J.M. Baskin, X. Li, R.L. Jensen, J. Lebkuecher, S.B. Franklin, B. Lee, H.R. DeSelm, P. Snyder, E.W. Chester.

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# INVITED PAPERS

# WATER QUALITY AND THE EXOTIC BIOTA

Friday, March 3, 1995

Moderated by:

David White
Murray State University

# EFFECTS OF SUBMERSED AQUATIC MACROPHYTES ON SEDIMENT AND WATER QUALITY

JOHN W. BARKO

USACE Waterways Experiment Station, Environmental Laboratory, Vicksburg, MS 39180

**SUMMARY. Submersed aquatic macrophytes rely primarily on sediment as a direct source of nitrogen (N), phosphorus (P), and micronutrients for their nutrition. The availability of these elements in sediments is affected markedly by sediment type but also can be influenced by macrophyte growth. Results of a variety of studies have indicated that macrophyte species, even with relatively diminutive root systems, can significantly deplete sediment N and P pools. From fertilization experiments involving sediments from a variety of locations, macrophyte growth on nutritionally-depleted sediments has been shown to be limited by the availability of sediment N but not P.**

**Through uptake from the sediment, aquatic plants transport nutrients directly to the overlying water column. Elevated pH, associated with plant photosynthesis, further enhances nutrient (phosphorus) flux from sediments. Water circulation induced by diel heating and cooling of surface water in aquatic plant beds facilitates nutrient exchanges with the adjacent open water of aquatic systems. These processes can result in enhanced phytoplankton (chlorophyll) production and deteriorated water quality conditions. However, in shallow-high energy environments, these potential negative effects on water quality may be overshadowed by the ability of aquatic macrophytes to moderate current and wave energies, thereby reducing sediment resuspension, turbidity, and concentrations of suspended particulate materials.**

**The vigor of submersed macrophyte beds is likely maintained by nominal inputs of sediment providing a nutritional subsidy. However, excessive inputs of sediment can result in macrophyte declines due to burial or to unfavorable irradiance conditions. Hydrologic factors and watershed activities that influence seasonal dynamics and magnitudes of sediment transport in aquatic systems need to be evaluated within the context of their effects on submersed macrophyte growth. The effects of aquatic plants on water quality conditions in aquatic systems need to be considered within the context of basin morphometry, hydrology, and local climate.**

## INTRODUCTION

Submersed macrophytes are unique among rooted aquatic vegetation because they link the sediment with overlying water. This linkage is responsible for great complexities in nutrition and has potentially important implications for nutrient cycling. It has become clear that, in addition to serving as a base for physical attachment, sediments also provide a source of nutrient supply to submersed macrophytes. Sediment composition exerts an important influence on macrophyte productivity and species composition. Recent attention among aquatic macrophyte ecologists has focused on interactions between aquatic macrophyte growth and sediment nutrient status. Attention is presently being focused also on specific processes in the littoral zone affecting sediment nutrient dynamics.

During the 1970's, accelerated eutrophication of freshwater systems due to excessive phosphorus loadings in both North America and Europe lead to interest in the role of rooted submersed macrophytes in the nutritional economy of aquatic systems. At that time it was unclear whether submersed macrophytes functioned as sources or sinks for phosphorus. Given potential access by these plants to nutrients in both the water column (foliar uptake) and sediments (root uptake), it has been necessary to quantitatively evaluate nutrient source-sink relationships involving both soluble and particulate nutrient fractions. Evaluations have necessitated combinations of laboratory and field studies. Results of these studies conducted by the USACE Waterways Experiment Station (WES) are highlighted here, as reported during the Sixth Symposium on the Natural History of Lower Tennessee and Cumberland River Valleys, "Water Quality and Exotic Biota".

## Macrophyte Nutrition and Growth

For many years, controversy has persisted regarding the role of roots versus shoots and sediment versus open water in the nutrition of submersed aquatic macrophytes (reviewed by Sculthorpe 1967; Denny 1980; Smart and Barko 1985; Agami and Waisel 1986; Barko *et al.* 1986, 1991). Quantification of the relative contribution of sediment and water to nutrient uptake by submersed macrophytes remains critical to improved understanding of littoral nutrient cycling and littoral-pelagic nutrient exchanges. Based on a variety of information sources (references above and personal knowledge), a generalized synthesis of sources of nutrient uptake by rooted submersed macrophytes is provided here.

Phosphorus and nitrogen have been studied most extensively, and for these nutrients sediment is the primary source for uptake (Barko *et al.* 1991). Sediment appears to be the principal site for uptake of iron, manganese, and micronutrients as well. These latter elements tend to coprecipitate and usually are present in extremely low concentrations in oxygenated surface waters. Dissolution products of relatively abundant salts are taken up principally from the open water. Among these ions, potassium and calcium are potentially most important in affecting submersed macrophyte growth. Potassium can be obtained from the sediment but is taken up by submersed macrophytes most abundantly from the open water (Barko 1982, Huebert and Gorham 1983, Barko *et al.* 1988). Under some conditions this element may be exchanged by submersed macrophyte roots for ammonium ions in sediment (Barko *et al.* 1988). Calcium is a component of the carbonate system and plays an important role in photosynthetic bicarbonate utilization (Lowenhaupt 1956, Smart and Barko 1986).

Given the significance of sediment in supplying N and P to submersed macrophytes, it has been important to evaluate the effects of macrophyte growth on sediment nutrient availability. Evidence indicates that rooted submersed macrophytes, even with relatively diminutive root systems, are capable of significantly depleting pools of N and P in sediments (Prentki 1979, Trisal and Kaul 1983, Short 1983, Carignan 1985, Barko *et al.* 1988, Chen and Barko 1988). Under some circumstances, depletion of sediment nutrient pools by aquatic macrophytes can be expected to influence macrophyte growth. From fertilization experiments involving sediments from a variety of locations, macrophyte growth on nutritionally-depleted sediments has been shown to be limited by the availability of sediment N, but not P (Barko *et al.* 1991).

Sedimentation provides an important means of nutrient renewal to the littoral zone and, in large part, may balance nutrient losses due to macrophyte uptake. Factors affecting sedimentation have been studied extensively in the open water (e.g., Hakanson 1977, Kamp-Nielson and Hargrave 1978) but to a much lesser extent in the littoral zone of lakes. Aquatic macrophyte beds serve as effective traps for inflowing dissolved and particulate materials (Wetzel 1979, Patterson and Brown 1979, Carpenter 1981, see also below). Moeller and Wetzel (1988) have suggested that sedimentation of algae from macrophyte leaf surfaces may provide an important link for transfer of nutrients absorbed from the water (by algae) to the sediment surface. Similarly, it has been reported that, under conditions of nutrient enrichment, decomposing filamentous algae can provide major inputs of N and P to sediment (Howard-Williams 1981). The vigor of submersed macrophyte beds is likely maintained by nominal inputs of sediment providing a nutritional subsidy. However, excessive inputs of sediment may result in macrophyte declines due to burial or to unfavorable irradiance conditions.

## Macrophytes on Sediment P Release

Great attention to the P economy of submersed aquatic macrophytes reflects the unparalleled importance of this nutrient in the eutrophication of lacustrine systems (Schindler 1974, 1977). Given the demonstrated capacity of submersed macrophytes to take up P directly from sediments, vegetation of the littoral zone needs to be viewed as a direct source of this nutrient to the water column (Barko and Smart 1980, Carignan and Kalff 1980, Smith and Adams 1986, Barko *et al.* 1991). In addition, submersed macrophytes can influence P dynamics in aquatic systems by altering the pH of the water column (James and Barko 1991).

The process of photosynthesis in submersed macrophytes results in oftentimes dramatic increases in the pH of the surrounding water column. For example, studies conducted with the U.S. Geological Survey in *Hydrilla* beds in the Potomac River revealed diel changes in pH between values of about 7.0 and 10.0 (Carter *et al.* 1988). Because pH values are logarithmic, the changes indicate large (nearly one thousand-fold) variations daily in hydroxyl and hydrogen ion concentrations. From concurrent studies conducted at Eau Galle Reservoir in Wisconsin, it has been demonstrated that elevated pH beyond about 9.0 can result in significant increases in rates of phosphorus release from surficial sediments (James and Barko 1991). In simple terms, the mechanism for release appears to involve chemical exchange of hydroxyl ions for phosphate ions in sediment.

Phosphorus released from sediments under conditions of elevated pH can account for a significant portion of the total mass of this element loaded internally in aquatic systems. For example, James and Barko (1994a) demonstrated that about 25 percent of the total seasonal internal phosphorus load into Eau Galle Reservoir was derived from littoral sediments. Phosphorus released from littoral sediments (*i.e.*, within macrophyte beds) tends to be transported directly into the upper mixed layer of lakes and reservoirs (see below). Thus, contributions to the phosphorus economy of algal communities in surface waters can be significant. The seasonal periodicity of internal phosphorus loadings into the upper mixed layer of Eau Galle Reservoir appears to influence not only the nutrient budget but phytoplankton productivity and the vertical migratory behavior of phytoplankton populations as well (James *et al.* 1992).

## Macrophytes on Hydraulic Circulation

On a daily basis, shallow near-shore regions of aquatic systems typically heat and cool more rapidly than deep open-water regions due primarily to differences in mixed volume (Stefan *et al.* 1988). The presence of submersed macrophytes in shallow regions contributes to the development of thermal gradients in both the vertical and lateral planes, as foliage near the water surface converts solar irradiance to heat. Thermal gradients give rise to density gradients that promote hydraulic circulation.

In Eau Galle Reservoir in Wisconsin and in Guntersville Reservoir in Alabama, dye studies have been conducted for several years in combination with close-interval thermal monitoring in an attempt to evaluate the seasonal dynamics of convective transport phenomena (James and Barko 1991, 1994b). Implications of these studies directed at P flux are far-reaching, because hydraulic circulation driven by convection can affect many kinds of dissolved constituents in water. Dissolved constituents may include contaminants or herbicides in addition to nutrients. As emphasized above, hydraulic transport from the littoral zone in combination with nutrient (P) release from sediments can contribute significantly to nutrient cycling in aquatic systems.

## Macrophytes on Sediment Resuspension

In addition to effects on soluble constituents of the water column in aquatic systems, submersed macrophytes also play an important role in mediating the resuspension and transport of sediment and associated particulate constituents. Sediment resuspension and discharge of sediment downstream in Marsh Lake (Minnesota) were examined during 1991 and 1992 under a variety of wind conditions (James and Barko 1994c). Based on a theoretical wave model, nearly the entire sediment surface area of this reservoir (81-100%) can be disturbed by wave activity at wind velocities as low as 15 km/h blowing from any direction. However, as an apparent result of dense submersed macrophyte beds that in 1991 covered nearly the entire lake, measured sediment resuspension was much less frequent than expected from wave theory.

Critical thresholds of wind velocity required to resuspend sediment in Marsh Lake were much higher in 1991 than in 1992 when plants were essentially absent. The presence of dense submersed macrophyte populations in 1991 resulted in a much lower frequency of resuspension events than in 1992. In addition, discharge of resuspended sediment downstream was much less in 1991 when submersed macrophytes were abundant than in 1992 when macrophytes were absent. In Marsh Lake submersed macrophytes appear to significantly influence water quality conditions (e.g., chlorophyll concentrations and turbidity) by mediating sediment resuspension. Reduced discharge of sediment from this system results in water quality improvements downstream as well.

## MANAGEMENT CONSIDERATIONS

It is apparent that submersed aquatic macrophytes, through a variety of mechanisms, can have important influences on sediment and water quality in aquatic systems. The significance of these influences can be expected to vary with climate, basin geomorphology, macrophyte density and species composition. In systems where sediment and water quality are of concern, resource management practices should be devised and implemented with consideration for the influence of submersed macrophyte beds.

Nitrogen is a key element in the growth of rooted aquatic macrophytes. Thus, attention to this particular element needs to be elevated to the same level as for P. Advances in our understanding of factors regulating sediment N availability may be prerequisite to the development of innovative aquatic plant management approaches via ecological means. Towards this end, the role of submersed macrophytes in the N economy of aquatic systems needs to be investigated more thoroughly. A variety of physical, chemical, and biological processes (e.g., sedimentation, mineralization, and particulate movement by benthic invertebrates) that potentially contribute to sediment N availability needs to be evaluated within the context of macrophyte nutrition (Barko *et al.* 1991). In addition, hydrologic factors and watershed activities that influence seasonal dynamics and magnitudes of sediment (and nutrient) transport in aquatic systems need to be evaluated within the context of their effects on submersed macrophyte growth.

Studies of nutrient cycling and hydraulic transport in macrophyte beds are of great value in providing information on rates and volumes of nutrients being exchanged with the open water of aquatic systems. Information on littoral-pelagic nutrient fluxes needs to be expanded in assessing direct effects (*i.e.*, through uptake) and indirect effects (*i.e.*, through reconfigured thermal structure) of macrophyte stands on water quality. Interactions between macrophytes and phytoplankton in aquatic systems need to be examined more fully through consideration of littoral-pelagic hydraulic interactions.

The goal of aquatic plant management in many cases may be an increase, rather than a decrease, in the distribution of submersed aquatic macrophytes. For example, results of studies conducted in Marsh Lake (see above) suggest that the development and maintenance of stands of submersed aquatic macrophytes may be an effective management tool for limiting wind-driven sediment resuspension and sediment discharge in shallow impoundments and lakes. Thus, macrophyte growth in some lakes (particularly shallow wind-swept basins) perhaps should be encouraged, rather than discouraged.

## ACKNOWLEDGMENTS

The information summarized herein derives from the efforts of a large number of investigators who have over the years contributed substantially to progress in the Ecological Technology Area of the Aquatic Plant Control Research Program, managed and administered by the USACE Waterways Experiment Station.

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# THE INVASION OF *DAPHNIA LUMHOLTZI* SARS (CLADOCERA, DAPHNIIDAE) INTO A NORTH AMERICAN RESERVOIR

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**ABSTRACT. During a one year period from late 1990 through 1991, *Daphnia lumholtzi* Sars, a sub-tropical/tropical cladoceran invaded reservoirs throughout the southeastern part of the United States. This species was previously known to occur only in Africa, southeastern Asia, and Australia. The species is characterized by having a long head spine and smaller lateral spines that are generally thought to be defenses against predators. We studied the seasonal pattern of its occurrence during a two year period following its invasion into Norris Reservoir, a Tennessee Valley Authority reservoir located in north-central Tennnessee. *Daphnia lumholtzi* was first encountered in the reservoir in late 1991 in the Clinch River arm near the dam. In 1992, an extensive bi-weekly sampling program determined that it was found in abundance in the upper part of the Clinch River arm during August. In 1993, it occurred in the same areas of the reservoir but was most abundant in late fall (October and November). Collections from 1994 suggest that it again occurred in greatest abundance in the same area during the late autumn. It was never found in the stomach contents of fishes from the Reservoir. It does not appear to have replaced other daphniid populations in the reservoir. Based on our study, we conclude that the primary characteristics that have made *D. lumholtzi* a successful invader into the Reservoir are its defenses against predation.**

## INTRODUCTION

*Daphnia lumholtzi* is a tropical and subtropical cladoceran that is an important component of the zooplankton of many lakes of Africa, Australia, and Asia. It occurs primarily in large lakes although in Australia it also can be found in temporary ponds and reservoirs (Benzie 1988). In 1990 and 1991, in the very short time period of 13 months, *D. lumholtzi* appeared in several North American reservoirs distributed from eastern Texas, Missouri, Kentucky and Tennessee, eastward to the Carolinas, Florida and the Gulf states. Sorensen and Sterner (1992) first recorded it in plankton samples from Fairfield Reservoir (area = 953 ha; mean depth= 6.5 m) located near Arlington, Texas in January 1991, and subsequently found it in two other reservoirs, Joe Pool Lake and Lake Murvaul. Havel and Hebert (1994) reported finding it in samples from five reservoirs in Missouri and one in Florida in the fall of 1991. Work and Gophen (1995) describe its occurrence in Oklahoma, and Havel *et al.* 1995 reported on its widespread simultaneous occurrence in reservoirs in several other states in the southeast. Unfortunately there are few prior collections from these reservoirs that enable us to determine when *D. lumholtzi* first appeared. In one of the few exceptions, Sharpe and White (in preparation) determined that the first major occurrence of *D. lumholtzi* in Kentucky Lake, KY was as early as August 1990. Kentucky Lake is a long reservoir that is the last of a chain of reservoirs constructed on the Tennessee River by the Tennessee Valley Authority (TVA). By late 1991 this species was reported from several other TVA reservoirs.

Several important ecological and biogeographical questions are immediately asked when exotic terrestrial or freshwater species are encountered as immigrants. From where did the immigrant forms come? How did they move to a new continent? How were they able to successfully invade new environments? More specifically for *D. lumholtzi*, how could it invade reservoirs located throughout the entire southeastern U.S. during such a brief time (13 months)? What impact has it had, or will it have, on local reservoir ecosystems; will it persist; and what will its future impact be on fisheries?

Interest in the colonization of *D. lumholtzi* is enhanced by its unique morphology (Sorensen and Sterner 1992). It is a moderate-sized species of the dapniid subfamily Ctenodaphniinae characterized by a long head spine and lateral shell spines, as well as by the usual daphniid tail spine (Sars 1885). The head spine can be as long as the body but is variable in length (Sorensen and Sterner 1992). Similar head spines or helmets in other daphniids and Cladocera are regarded to be defenses against predation by invertebrates or young fishes (*e.g.*, Barnhisel 1991a, b). In the "monacha" form the head spine is missing. Green (1967) reported circumstantial evidence that the morphs with long head spines were less susceptible to fish predation than morphs lacking the head spine.

The purpose of this study was to determine how this immigrant could be so successful in invading a relatively typical southeastern reservoir, specifically Norris Reservoir located in north-central Tennessee. The specific questions we address are (1) what habitats does *D. lumholtzi* now occupy in the reservoir and does its distribution coincide with the populations of other abundant taxa in the reservoir; (2) what are the morphological, physiological and ecological characteristics of *D. lumholtzi* that may have made it a successful invader in these habitats; and (3) what will be its impact on reservoir ecosystems?

## Norris Reservoir

The Norris Reservoir dam is below the confluence of the Clinch and Powell rivers in north-central Tennessee and was constructed in the mid-1930s, the first dam built by the TVA. The reservoir covers an area of about 13,850 hectares (34,200 acres). The Clinch River arm is more than 115 kilometers long and the Powell River arm is 90 kilometers long. Near the dam the reservoir water depth is greater than 40 meters but becomes much more shallow in the head waters.

Water chemistry varies throughout the reservoir and during different seasons, as is typical in deep, productive lakes. At Norris Dam in 1993, the reservoir was thermally stratified with surface water temperature about 22°C and temperatures of the hypolimnion about 7°C in May. In Big Sycamore Creek, an important location for *D. lumholtzi* in the upper part of the reservoir, the water was not as distinctly stratified with a surface water temperature of 23°C and bottom water temperature of 14°C in May. Dissolved oxygen varied between 8 and 9 mg $L^{-1}$ at the dam site. At Big Sycamore Creek, oxygen of water near the bottom declined to between 3-6 mg $L^{-1}$.

Later in early August, the epilimnion temperature at the Norris Dam was 29°C, and the hypolimnion remained at 7°C and dissolved oxygen concentration of 8-9 mg $L^{-1}$. At this time in Big Sycamore Creek, water temperature at the surface was 28°C and bottom water about 24°C, with dissolved oxygen 6.3 mg $L^{-1}$ at the surface and almost 0 mg $L^{-1}$ near the bottom. Later in early November, the reservoir was not thermally stratified at the dam site; it was about 17°C throughout most of the water column, with a small decline near the bottom. Dissolved oxygen did vary, however, from about 6.5 mg $L^{-1}$ down to 35 m, and then it dropped to less than 1 mg $L^{-1}$ below 40 m. Water temperature in Big Sycamore Creek was 8°C, and dissolved oxygen was near 10 mg $L^{-1}$ throughout the water column.

**Reservoir Fisheries.** Norris Reservoir is stocked with fishes and has angling seasons for the following fish species: walleye, sauger, white bass, crappie, striped bass, catfish, bluegill, largemouth and smallmouth bass, and spotted bass. Zooplanktivorous forage fish consist primarily of threadfin shad (*Dorosoma petenense* (Günther)), gizzard shad (*Dorosoma cepedianum* (Lesueur)), and alewives (*Alosa pseudoharengus* (Wilson)), although the latter is not as abundant as the two smaller species.

## METHODS

In 1992, an ambitious sampling program was initiated by TVA under the direction of Mr. David Tomljanovich. Samples were collected every two weeks from May until December at several locations along the Clinch River arm of the reservoir. The sampling program was continued in 1993 with the addition of larval fish sampling.

### Station Locations.

Zooplankton samples were collected from 15 stations along the length of Norris Reservoir (Figure 1, Table 1) from November 1991 to December 1993. Sample stations were selected with a major focus on the Clinch River arm of the reservoir where *D. lumholtzi* was first encountered. Larval fish were collected only in the middle and upper Clinch River arm of the Reservoir.

For purposes of data analysis, the reservoir collection locations were divided into three zones (Table 1; Fig. 1). Zone 1 extends from the dam, located at Clinch River Mile 80 (CRM 80), to below CRM 98. The mean water depth of this zone is 41 m (S.D. = 8.7 m). Zone 2 includes the middle part of the reservoir from above CRM 98 to below CRM 129 and has a mean water depth of 27 m (S.D. = 10 m). Zone 3 extends from CRM 129 to the head waters of the reservoir (the last sampling location is CRM 141) with a mean water depth of 12 m (S.D. = 7.8 m) and includes Big Sycamore Creek (BSC).

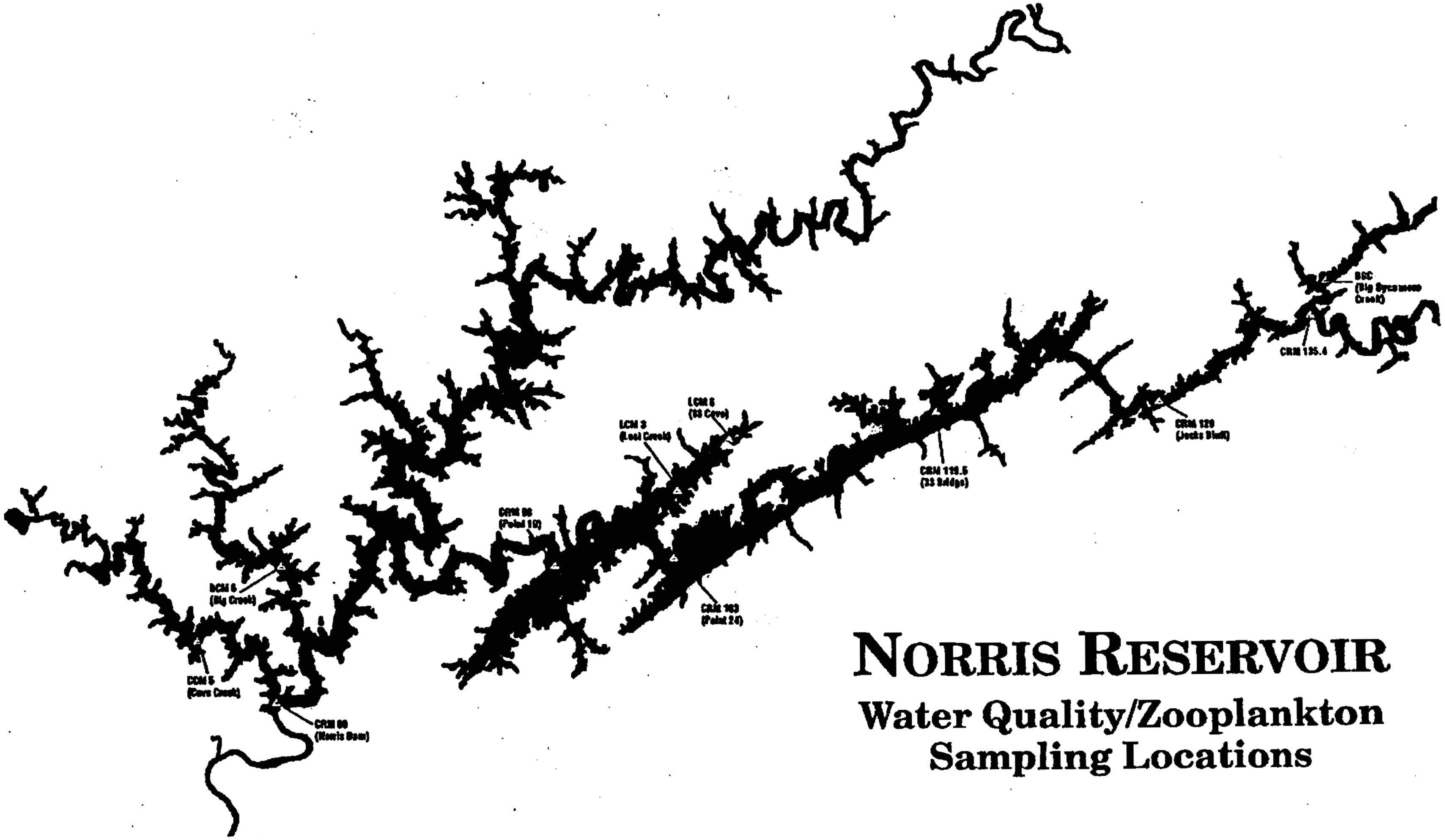

Figure 1. Map of Norris Reservoir, TN with numbered collection stations on the Clinch River arm (see Table 1 for location names). Stations are labeled as CR (Clinch River) and the river mile.

Table 1. Collection locations, station numbers, and years sampled for study of the distribution and abundance of *D. lumholtzi* in Norris Reservoir, Tennessee.

| **Sampling Location** | **Zone** | **Station** | **91** | **92** | **93** |
|---|---|---|---|---|---|
| C80 | 1 | 1 | X | X | X |
| C86 | 1 | 4 | | | X |
| C87 | 1 | 2 | X | X | X |
| CCM5 (Cove Creek) | 1 | 6 | | | X |
| CCM3 (Cove Creek) | 1 | 7 | | | X |
| C98 | 2 | 3 | X | X | X |
| MCM3 (Mill Creek) | 2 | 8 | | X | X |
| TBC (Too Big Cove) | 2 | 10 | | | X |
| C110 | 2 | 11 | | X | X |
| C116 | 2 | 17 | | | X |
| C119 | 2 | 12 | | X | X |
| C121 | 2 | 13 | | X | X |
| LSTC (Lost Creek) | 2 | 16 | | | X |
| C129 | 3 | 14 | | X | X |
| C133 | 3 | 20 | | | X |
| C135 | 3 | 21 | X | X | X |
| C140 | 3 | 22 | | X | X |
| C145 | 3 | 25 | | | X |
| BSC (Big Sycamore Creek) | 3 | 24 | X | X | X |

**Sample Collection.**

The zooplankton were sampled from a vertical column of water using a 30.5 cm diameter x 91 cm long conical net made of 153 micron mesh opening Nitex netting cloth. All samples were collected during daylight hours from an anchored boat. Two vertical tows were taken by lowering the net each time to just above the lake bottom and raising the net at approximately 1 m sec$^{-1}$. The zooplankton were washed into the cod-end bucket, and the net contents were rinsed from the bucket into a sample jar. Zooplankton were preserved with 5% formalin.

Larval fish were collected at night using a 0.5 m diameter net attached to a metal frame which was suspended from a winch assembly. The net consisted of Nitex netting with 750 micron mesh opening and was tapered with a removable cod-end bucket. Ten-minute surface tows were made at each sample site with the net submerged approximately one meter below the surface of the water. After each individual tow was completed, the contents were rinsed into the cod-end bucket and transferred to jars and preserved with 10% formalin.

## Sample Transfer and Handling.

Samples were transferred to the Academy of Natural Sciences of Philadelphia for analysis. All CRM 80, 87, 98, 119.5, and Big Sycamore Creek (BSC) samples, were analyzed in 1992 and 1993. Several additional sites also were analyzed (Table 1). Samples were assigned catalogue numbers during processing and data analyses. Sample information recorded on data sheets for each sample included the sample location, depth, date as well as species composition and number.

Daphniids were identified following keys and descriptions in Brooks (1957). *Daphnia pulicaria* Forbes was identified from the description by Forbes (1893). *Daphnia lumholtzi* was identified by reference to Sars (1885). Copepods and rotifers were not identified or counted in zooplankton samples. Although copepods were not common in the samples, we found them in abundance in fish guts. The abundance of rotifers and copepod nauplii could not be quantified because the collection net (150 $\mu$m mesh) would allow small rotifers and nauplii to escape.

The zooplankton in most samples were too numerous to be counted without sub-sampling. Each sample was first either concentrated or diluted to a 160-ml volume in a graduated cylinder. If samples needed to be concentrated, an inverted 10 ml pipet with a fine mesh netting was used to withdraw water from the sample. If dilution was required, clean water with formalin was added to the cylinder. The sample was then poured into a two-chambered Folsom-type zooplankton sample splitter and divided several times to reduce the number of individuals for counting; generally a 1/16 or 1/32 sub-sample was counted. Sub-samples were concentrated as described above, and transferred to a Bogorov cell for counting. For samples that did not require splitting, the volume was concentrated to 20 ml (to fill the Bogorov cell), and the entire sample was counted.

A minimum of 200 Cladocera was identified and counted for each sample. The abundance of the zooplankton sampled in a vertical net tow was calculated by dividing the number of counted organisms by the volume of the sampled water column. The volume of the sampled water column was calculated by multiplying the cross-sectional area of the sample net by the sampled water depth. Because the sample was typically diluted for counting purposes, a relevant dilution factor (split) also was applied.

### Larval Fish Stomach Analysis.

Larval fish samples were rinsed with de-ionized water to remove excess formaldehyde. The sample was then poured into a sieve to rinse off zooplankton from the fish. Larvae were identified to species using Lippon and Moran (1974). The abundance of fish in the sample was then determined. If a sample contained fewer than 25 fish, the sample was not used for diet analysis. Samples containing fish less than 15 to 20 mm in length also were not analyzed because zooplankton were seldom found in their stomachs.

Twenty-five individuals from each suitable sample were selected randomly for stomach analysis. Dissection of fish consisted of making three cuts, below the gill, along the ventral side, and above the anal opening. The skin of the dissected area was folded back exposing the body cavity. The esophagus was located and followed down to the stomach. The stomach, extending from below the esophagus to the intestine, was transferred to a small dish. The stomach was then cut open and its contents flushed out with water. Cladocera in the stomach were identified to species, copepods to order, and then enumerated.

### Data Analysis.

Data were entered into a spreadsheet program and formatted for analysis. Calender dates were changed to Julian dates for data analysis (Table 2). Because samples had to be collected during four to seven days, a mean Julian date was calculated for each collection period. Mean population estimates for each species were estimated for each modified Julian date (= one sampling period) as the statistical mean and standard error of the mean for individuals in all samples belonging to each reservoir zone.

Table 2. Julian dates for seasons of the year as used in the present study.

| Season | Dates | Julian Dates |
|---|---|---|
| Winter | 12/21 - 3/20 | 355 - 79 |
| Spring | 3/21 - 6/20 | 80 - 171 |
| Summer | 6/21 - 9/20 | 172 - 263 |
| Fall | 9/21 - 12/20 | 264 - 354 |

Mean numbers for populations (either as number $m^{-3}$ or $L^{-1}$) for each zone were used for further data analysis using either SYSTAT (Ver. 5.0 for Windows) or SAS (Ver. for Windows). Zooplankton abundance data were log-transformed before statistical analysis.

# RESULTS

## Distribution of *Daphnia lumholtzi*: 1991-1993.

*Daphnia lumholtzi* was first found in zooplankton samples collected from Zones 1 and 2 on November 17 and December 8, 1991 (Fig. 2). No other samples were collected at the time nor do prior samples exist for the reservoir. Its abundance was low (0.04 - 0.4 ind. $L^{-1}$), but subsequent collections in 1992 and 1993 indicated that it was seldom abundant at that time and at those stations (Fig. 2-4). There was no method by which to determine when this immigrant first appeared in detectable numbers in Norris Reservoir.

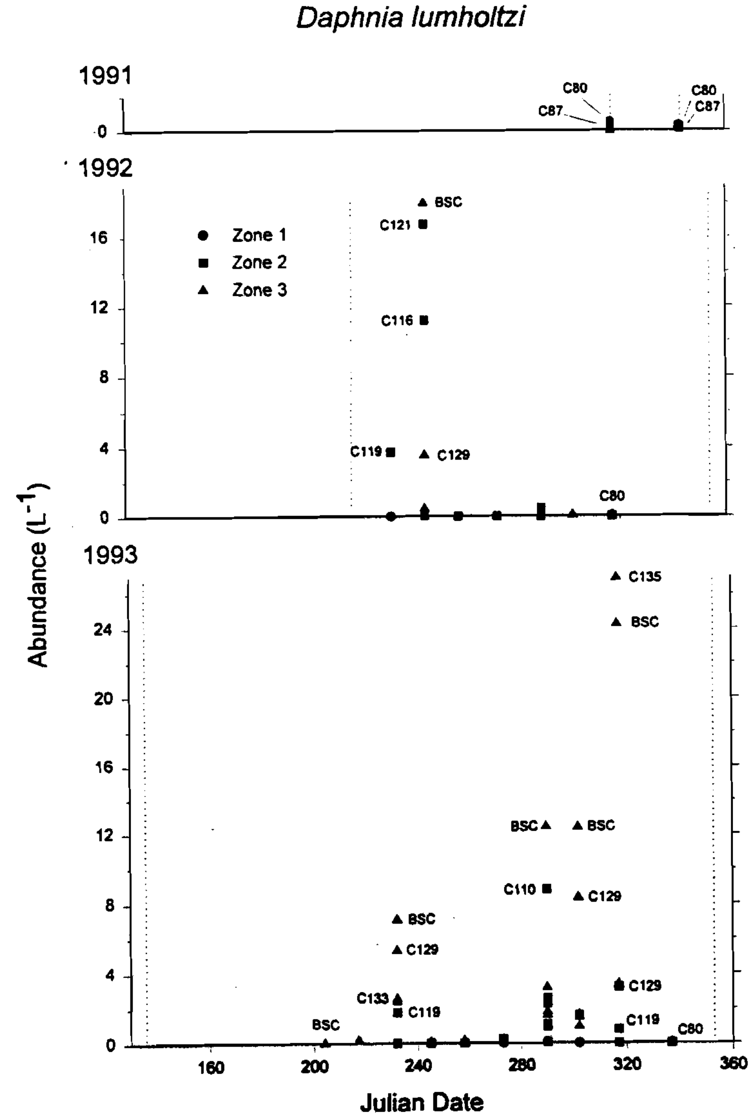

Figure 2. Occurrence and distribution (station location) of *Daphnia lumholtzi* in Norris Reservoir, TN during 1991-1993. Station locations as given in Table 1.

In 1992, *D. lumholtzi* was found in almost equal abundance in Zones 2 and 3 with average peak densities of more than 7 individuals $L^{-1}$ (ind. $L^{-1}$). Highest densities of 17 to18 ind. L occured in late August (Fig. 3; Big Sycamore Creek, and at CRM 129 to 116; Fig. 1). The population quickly disappeared in early September and was not abundant for the remaining part of the year.

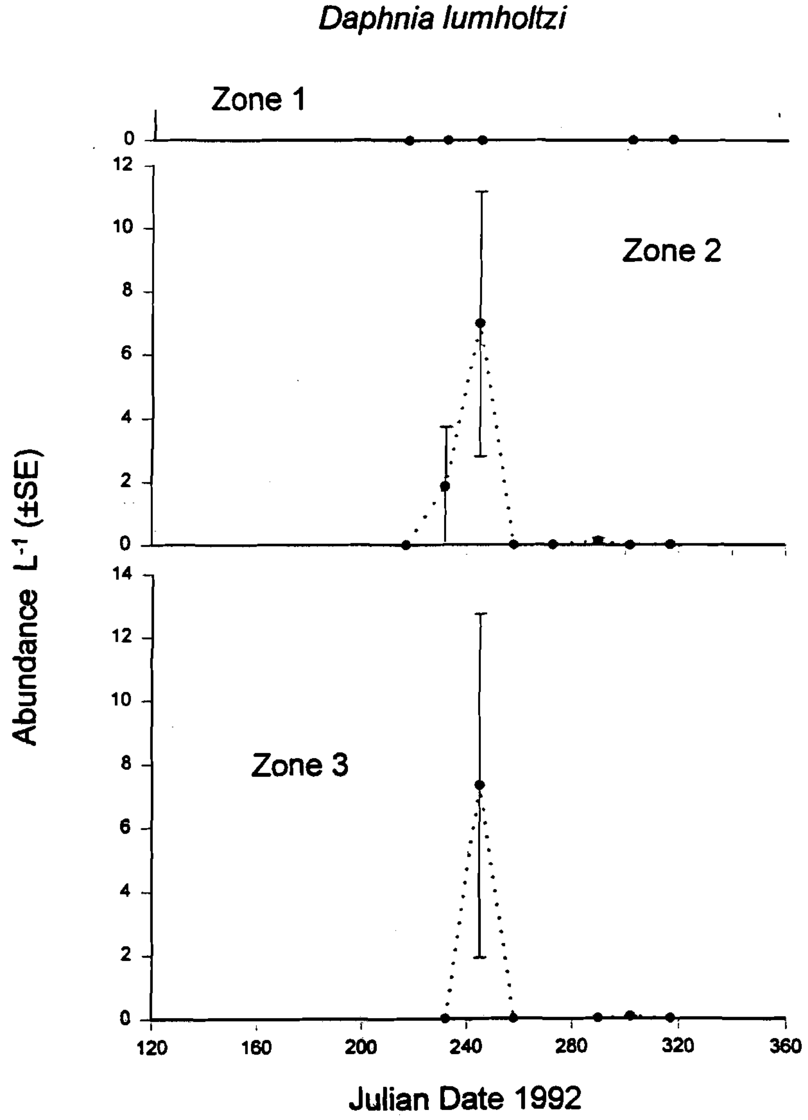

Figure 3. Mean abundance ($L^{-1}$) and and zonal distribution of *Daphnia lumholtzi* in Norris Reservoir during 1992.

In 1993, *D. lumholtzi* appeared in late July and early August, with an average peak density of *ca.* 4 ind. $L^{-1}$ in Zone 3 (Fig. 4; Big Sycamore Creek and CRM 133 to 119), substantially less abundant than in 1992, and then declined by mid-August. Its most downstream location was CRM 121. It rebounded, however, in early October and in Zone 2 reached a peak abundance in late October of ca. 3 ind. $L^{-1}$. In Zone 3, again primarily in Big Sycamore Creek and in the Clinch

River (between CRM 133 and 110), it attained densities from 9 ind. $L^{-1}$ to as many as 24 to 26 ind. $L^{-1}$, a very high density for such a large species. It disappeared by early December. Although it was present in Zones 1 and 2 in November, it was represented by only one or fewer individuals $L^{-1}$. It did occur at the dam site (CRM80) suggesting that it was found throughout the reservoir. Several samples collected during late October and throughout November of both 1992 and 1993 contained males and resting eggs.

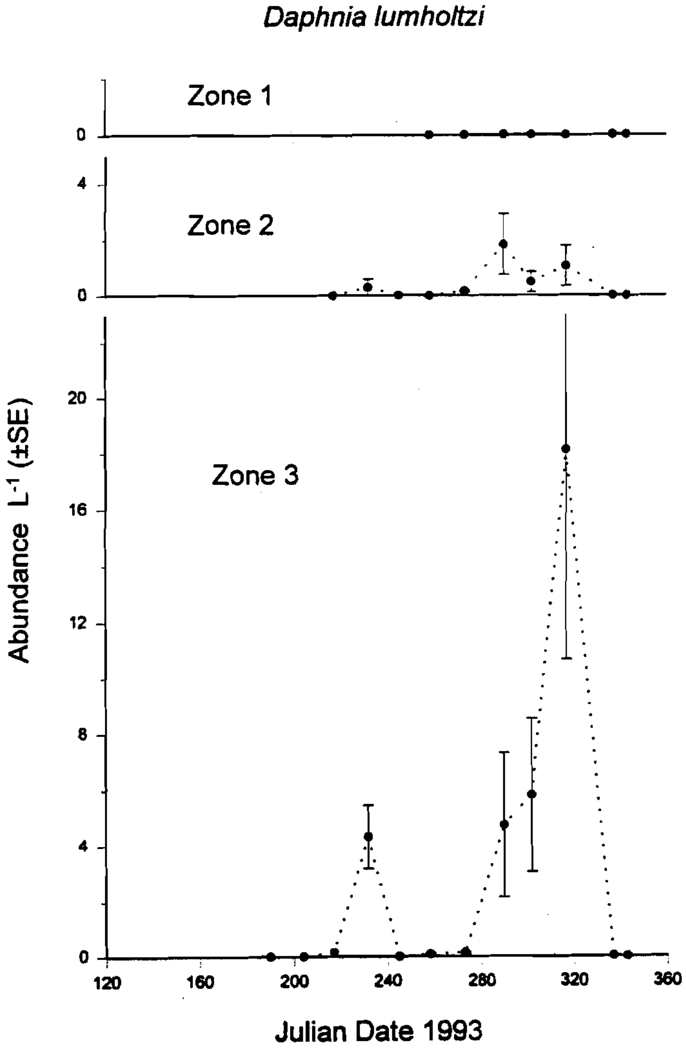

Figure 4. Mean abundance ($L^{-1}$) and zonal distribution of *Daphnia lumholtzi* during 1993.

## Distribution of Other Zooplankton: 1992.

In 1992, sampling began after Julian date 215 (August 2), Cladocera were the most abundant zooplankton group encountered in these collections. Copepods were rare and were not counted. The mesh size of the plankton net was too large to quantitatively collect rotifers and copepod nauplii.

Two species of *Daphnia* were very abundant in Norris Reservoir during the time of this study, *D. pulicaria* Forbes and *D. retrocurva* Forbes. Both of these species were most abundant in the late spring and early summer (Figs. 5 and 6); the samples we analyzed did not include the early spring period when they first began to increase so we do not know when either species is most abundant in Norris. In 1992, *D. pulicaria* was primarily distributed in Zones 1 and 2 with its greatest average abundance of 3.5 ind. $L^{-1}$ (Fig. 5; range from 0.9 to 5.9 ind. $L^{-1}$) in Zone 2. Its abundance remained low throughout the remainder of 1992. *Daphnia retrocurva* also declined from its highest density in the earliest collected samples to a low by September 11 (Fig. 6). But its abundance increased again to 6.3 ind. $L^{-1}$ in late September, followed by a sharp decline in October, and then was not a significant part of the plankton in late 1992.

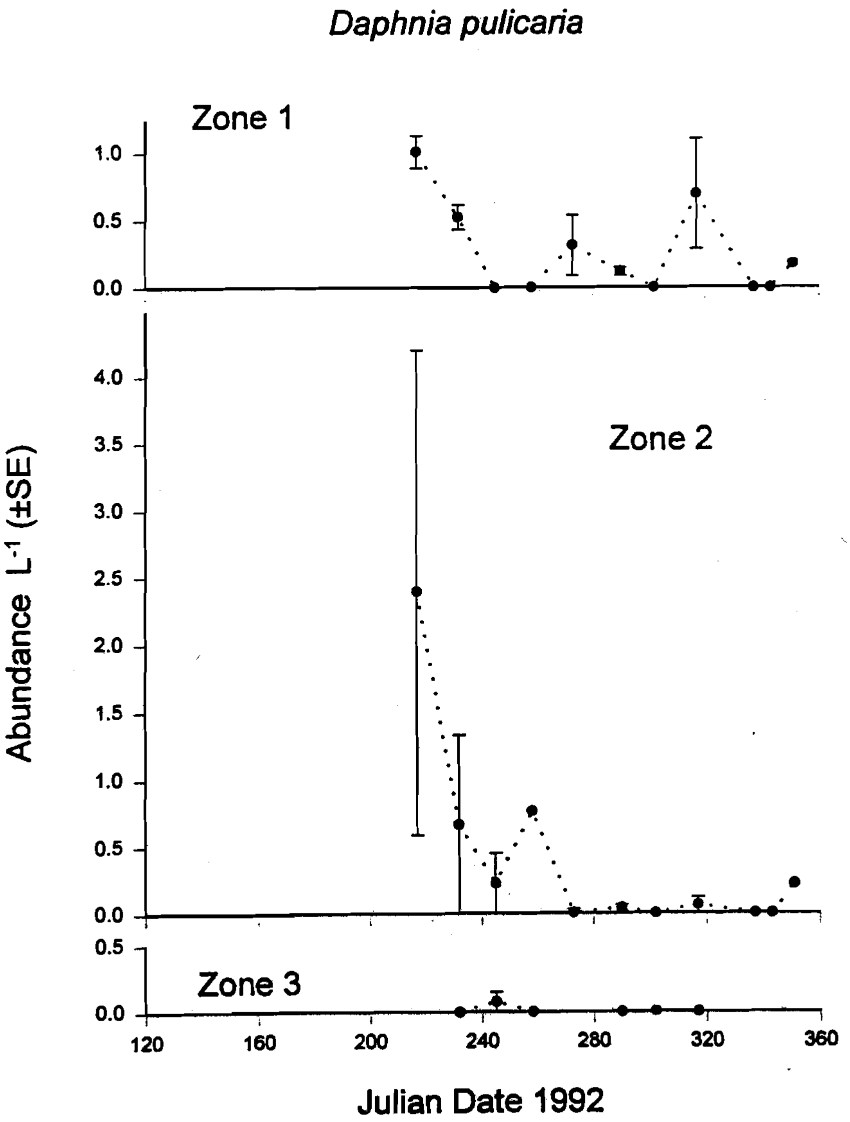

Figure 5. Mean abundance ($L^{-1}$) and zonal distribution of *Daphnia pulicaria* during 1992.

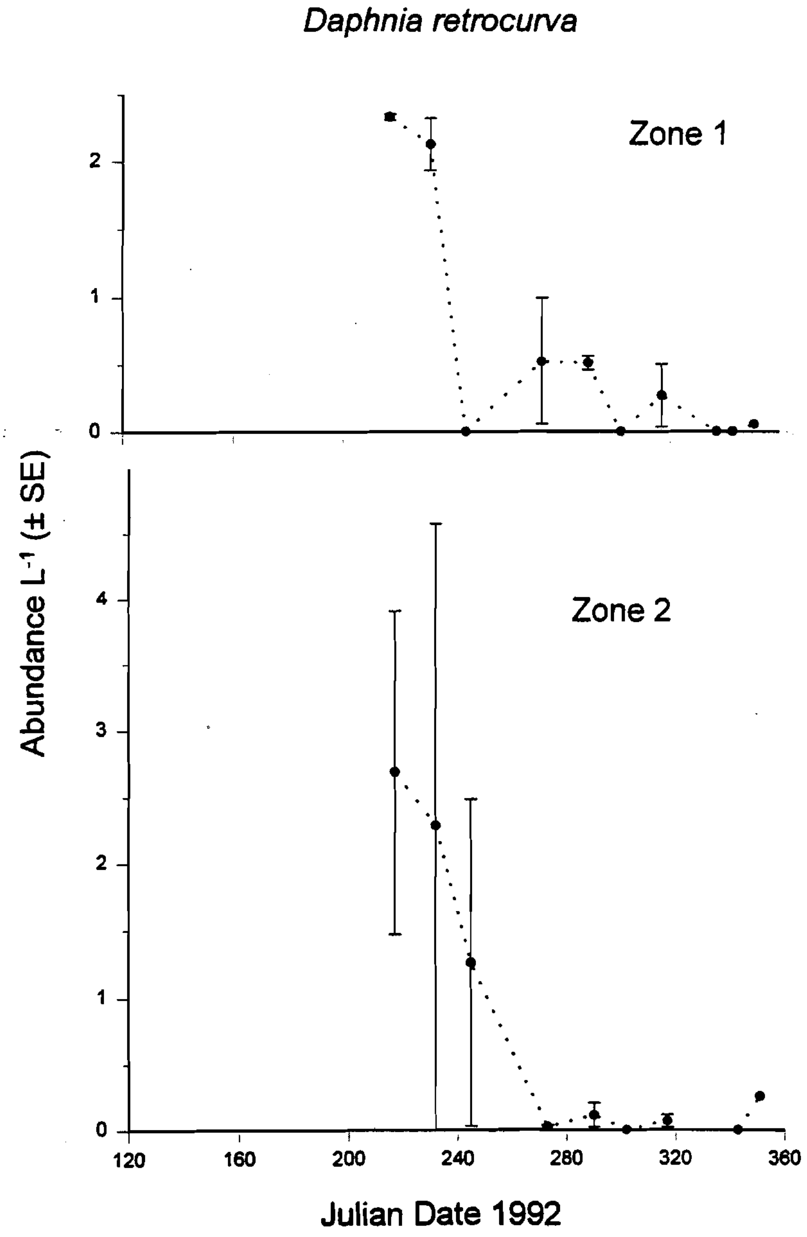

Figure 6. Mean abundance (L$^{-1}$) and zonal distribution of *Daphnia retrocurva* during 1992.

The other dominant cladoceran present in Norris Reservoir is *Bosmina longirostris* (O.F.M.). It was at a low density in late July and began increasing in early August to an average maximum density of 4 ind. L$^{-1}$ at the end of August (Fig. 7; range 0.1 to 12.2 ind. L$^{-1}$) and afterwards declined throughout autumn. *Bosmina* was most abundant in Zone 2, less common in Zone 1, and rare in Zone 3. *Diaphanosoma* sp. had a low abundance (< 1 ind. L$^{-1}$) in all zones but was most abundant in Zone 3 in late August (Fig. 8). *Simocephalus* sp., which is normally found on littoral weeds, was encountered in the zooplankton but was never abundant ( Fig. 9).

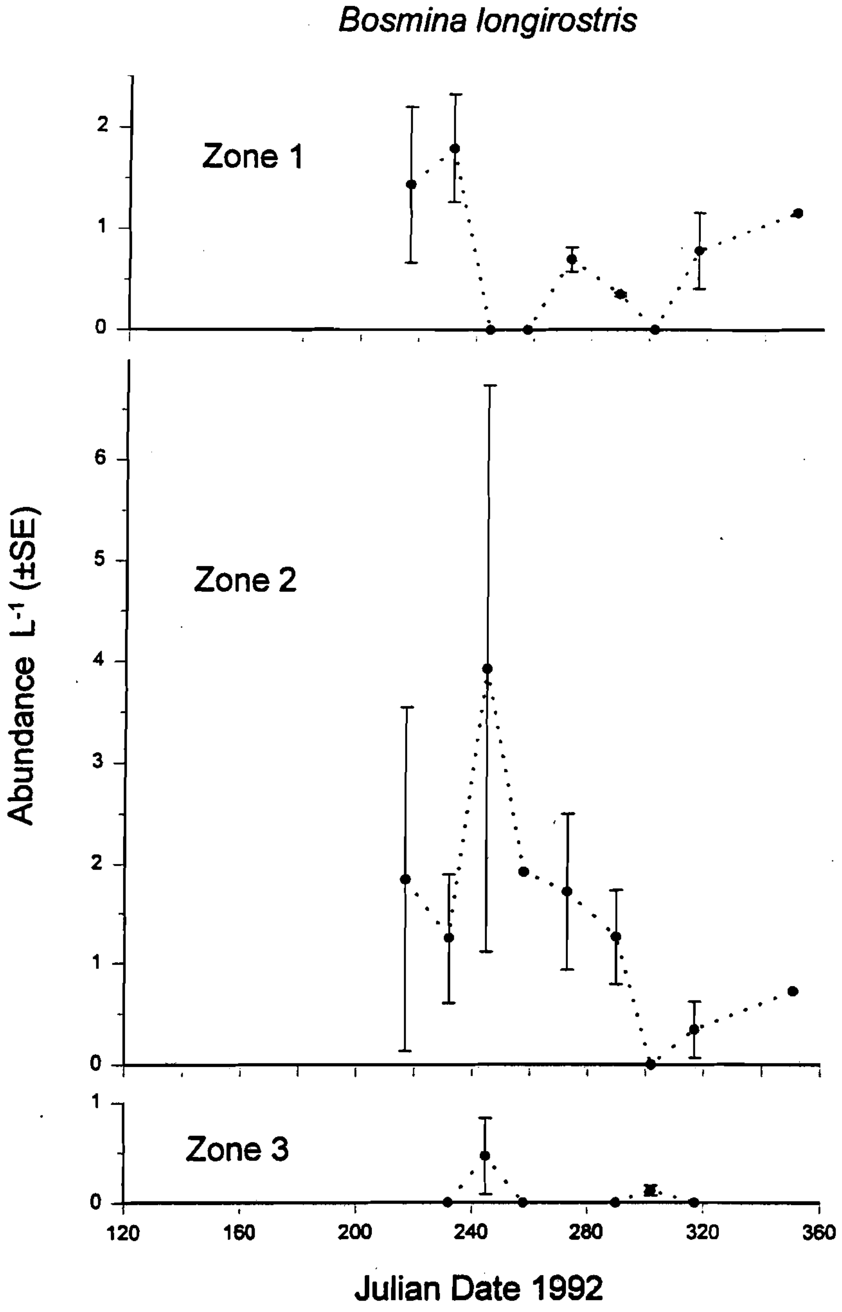

Figure 7. Mean abundance ($L^{-1}$) and zonal distribution of *Bosmina longirostris* during 1992.

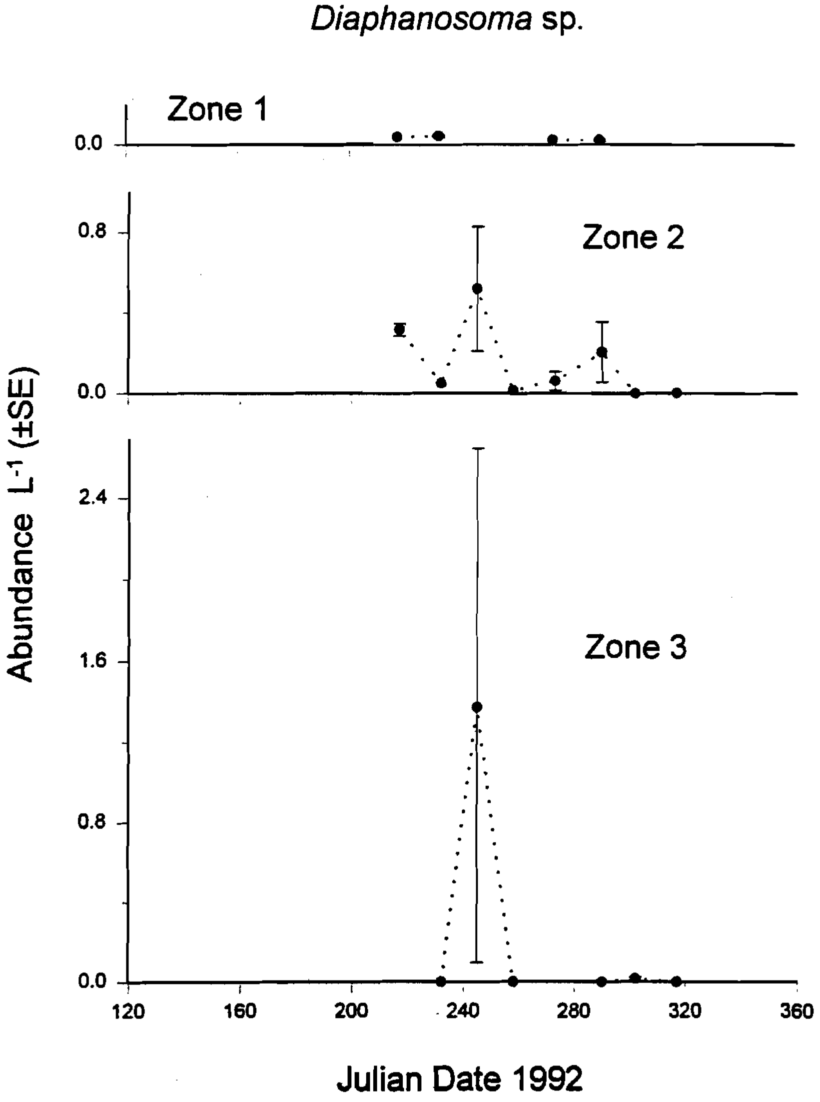

Figure 8. Mean abundance ($L^{-1}$) and zonal distribution of *Diaphanosoma* sp. during 1992.

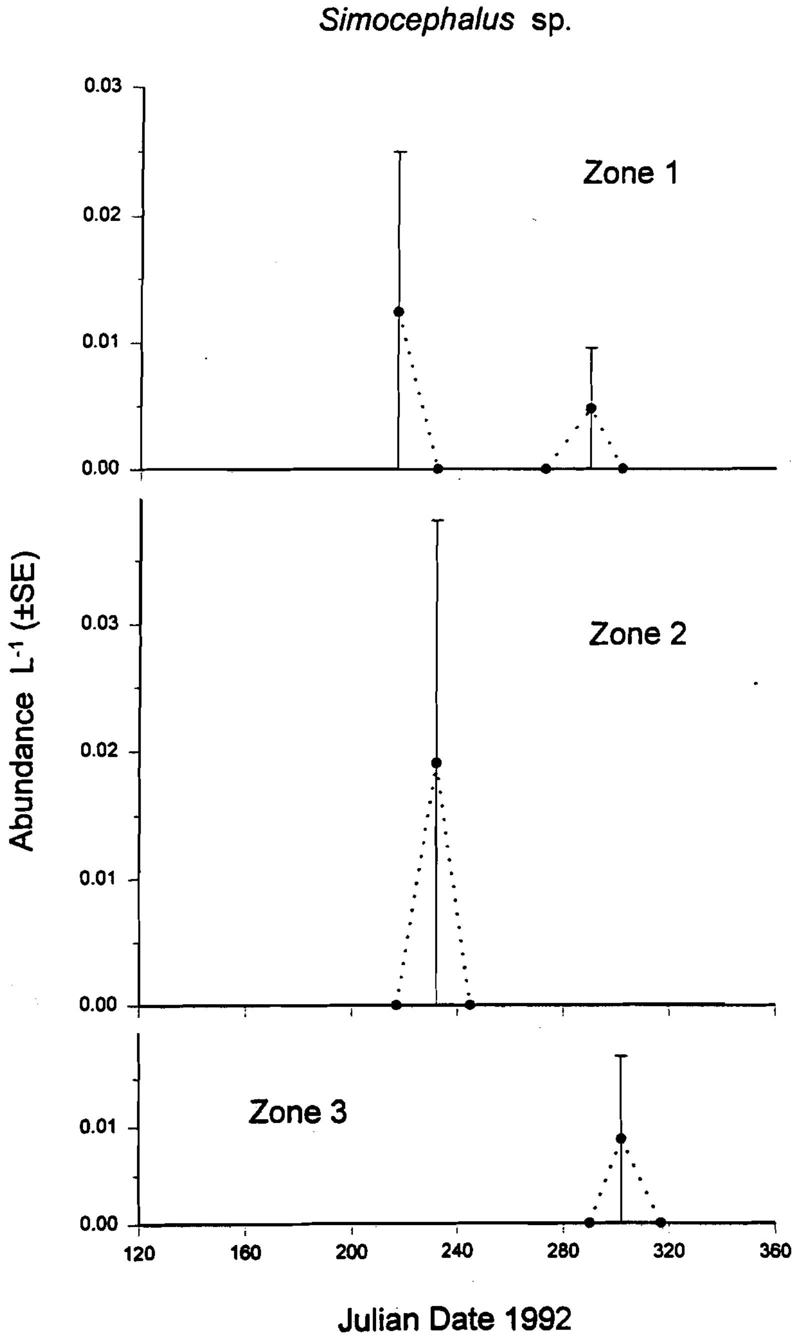

Figure 9. Mean abundance ($L^{-1}$) and zonal distribution of *Simocephalus* sp. during 1992.

Two invertebrate predators were encountered. *Leptodora kindtii* (Focke) was most abundant in October in Zones 1 and 2 during 1992 (Fig. 10). *Chaoborus* sp. (Insecta, Diptera) was found during the late summer and early autumn only in Zone 2 (Fig. 11).

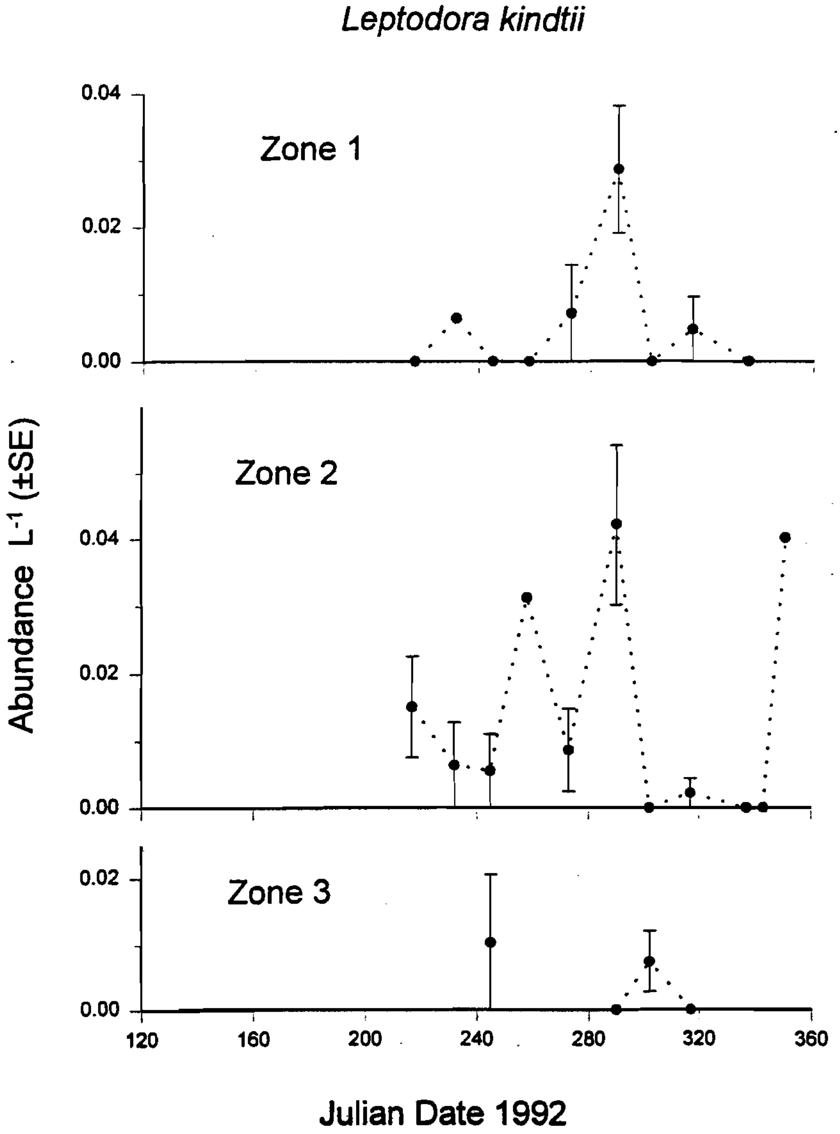

Figure 10. Mean abundance ($L^{-1}$) and zonal distribution of *Leptodora kindtii* during 1992.

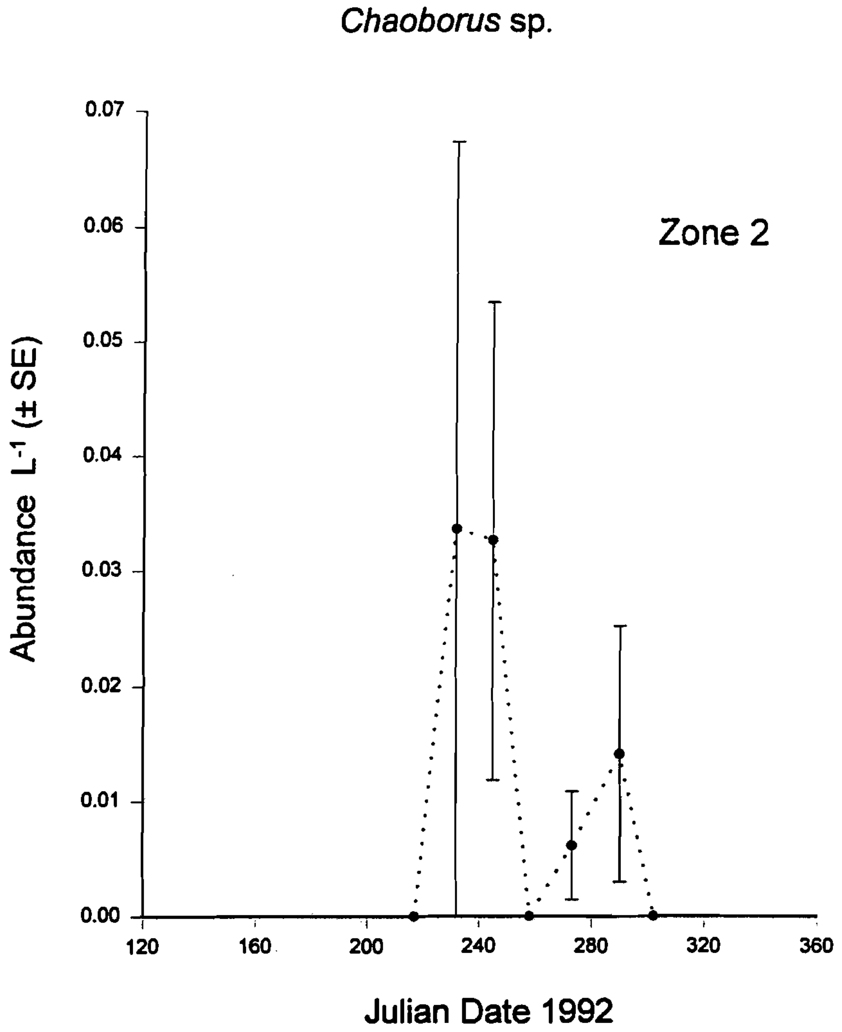

Figure 11. Mean abundance ($L^{-1}$) and zonal distribution of *Chaoborus* sp. during 1992.

## Distribution of Other Zooplankton: 1993.

*Daphnia pulicaria* had its maximum density in Zones 1 and 2 in May 1993, when zooplankton sampling began that year, and except for a peak in Zone 2 in early July, it remained scarce throughout the rest of the year (Fig. 12). It was never a significant part of the zooplankton in Zone 3 in 1993. This was the same pattern as seen in 1992. *Daphnia retrocurva* had its greatest abundance in Zone 3 in May and declined thereafter (Fig. 13). Lower in the Reservoir (Zones 1 and 2), however, it increased in abundance to maximum densities in mid-July (Julian date 205) and then declined for the remainder of the year. This differed from its abundance pattern in 1992 by the absence of an autumn peak in October.

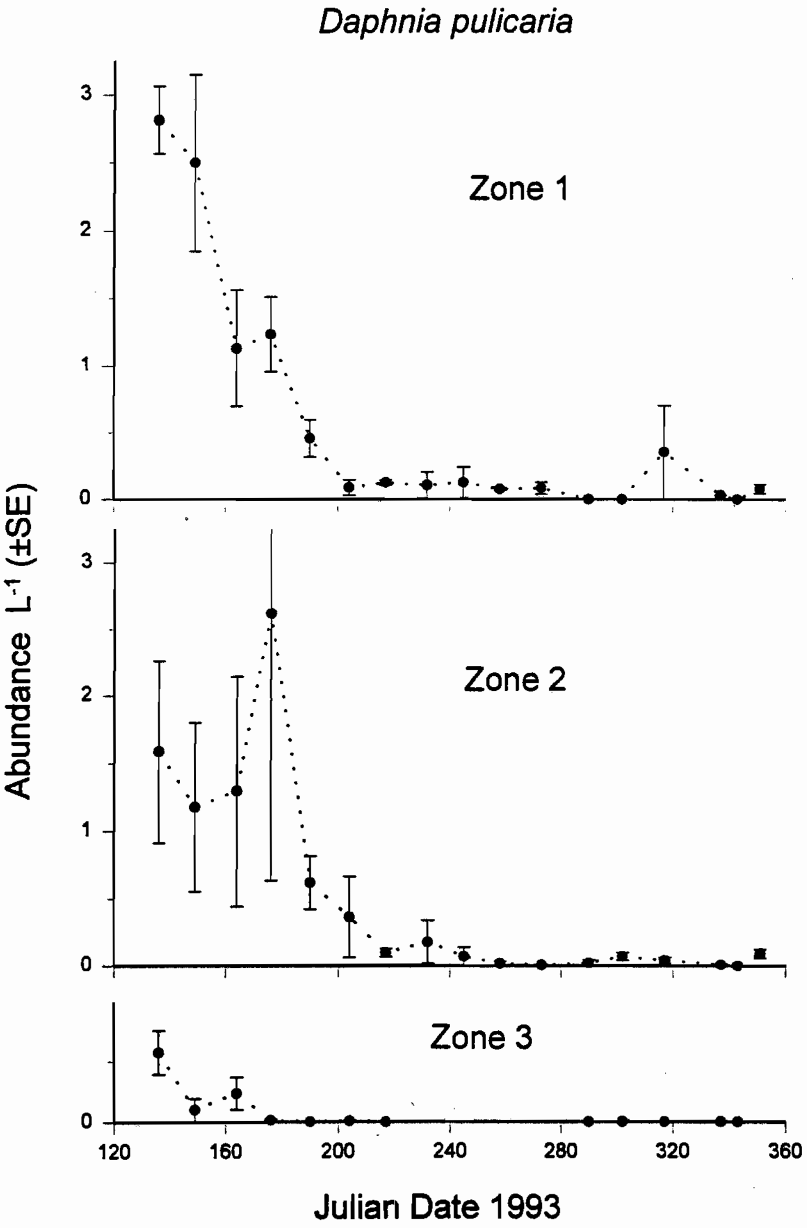

Figure 12. Mean abundance ($L^{-1}$ ) and zonal distribution of *Daphnia pulicaria* during 1993.

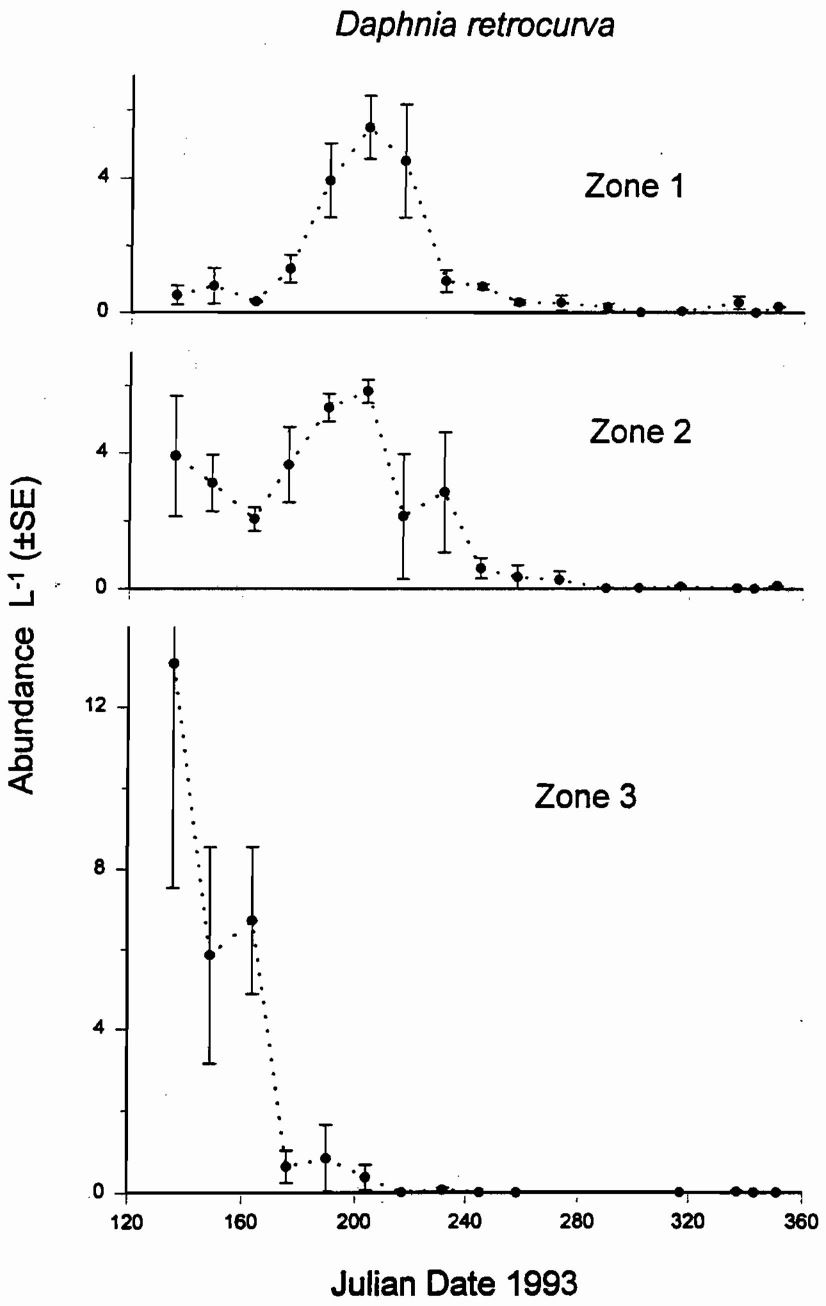

Figure 13. Mean abundance ($L^{-1}$) and zonal distribution of *Daphnia retrocurva* during 1993.

In 1993, *Bosmina longirostris* were again uncommon during June and July in Zones 1 and 2 but increased in abundance from early August through early October (Fig. 14) Its greatest abundance was only 6 ind. $L^{-1}$ in Zone 1, but its numbers were quite variable as indicated by the broad standard error. In the upper Clinch River arm of the reservoir in Zone 3, *Bosmina* was most abundant in late May through early June. Neither *Diaphanosoma* nor *Simocephalus* (Figs. 15 and 16) composed significant populations in our samples from the reservoir during 1993 and both appeared to be more abundant in the Zones 2 and 3 than near the dam. In contrast, *Leptodora kindtii* were more widespread seasonally in Zones 1 and 2 than in Zone 3, except in the late spring when it was initially common in Zone 3 (Fig. 17). However, the insect predator, *Chaoborus*, had a distribution similar to *Diaphanosoma* and *Simocephalus*, primarily occurring in the more shallow areas of the reservoir (Fig. 18).

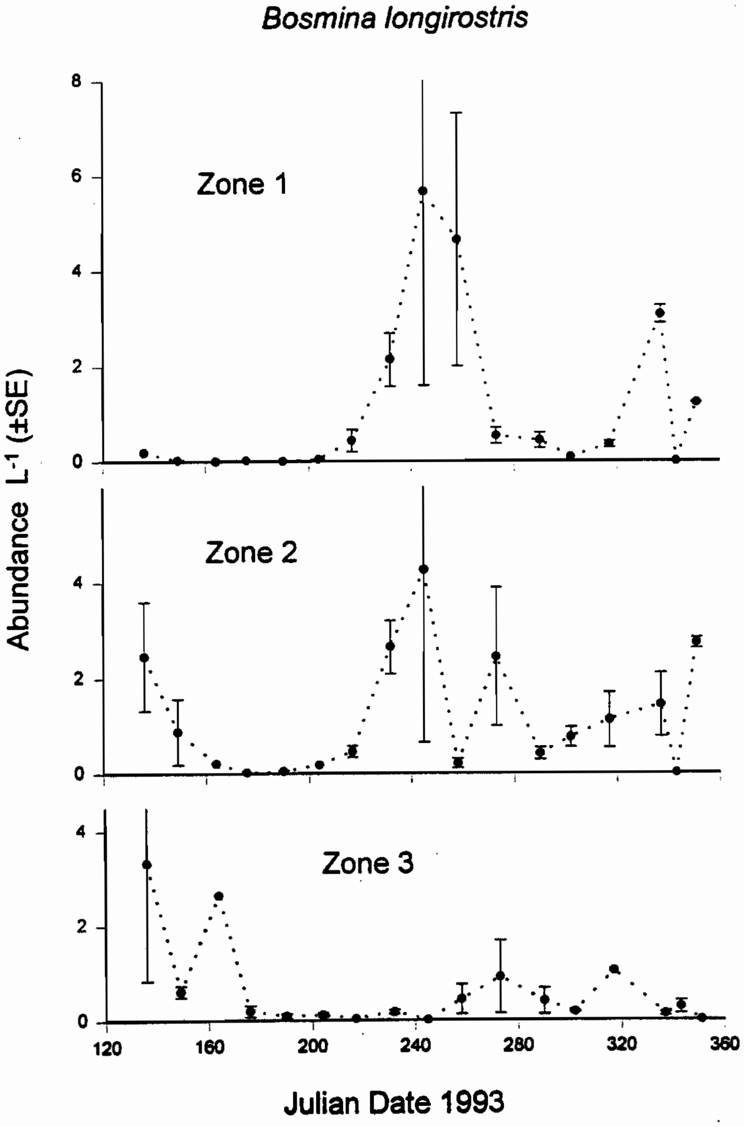

Figure 14. Mean abundance ($L^{-1}$) and zonal distribution of *Bosmina longirostris* during 1993.

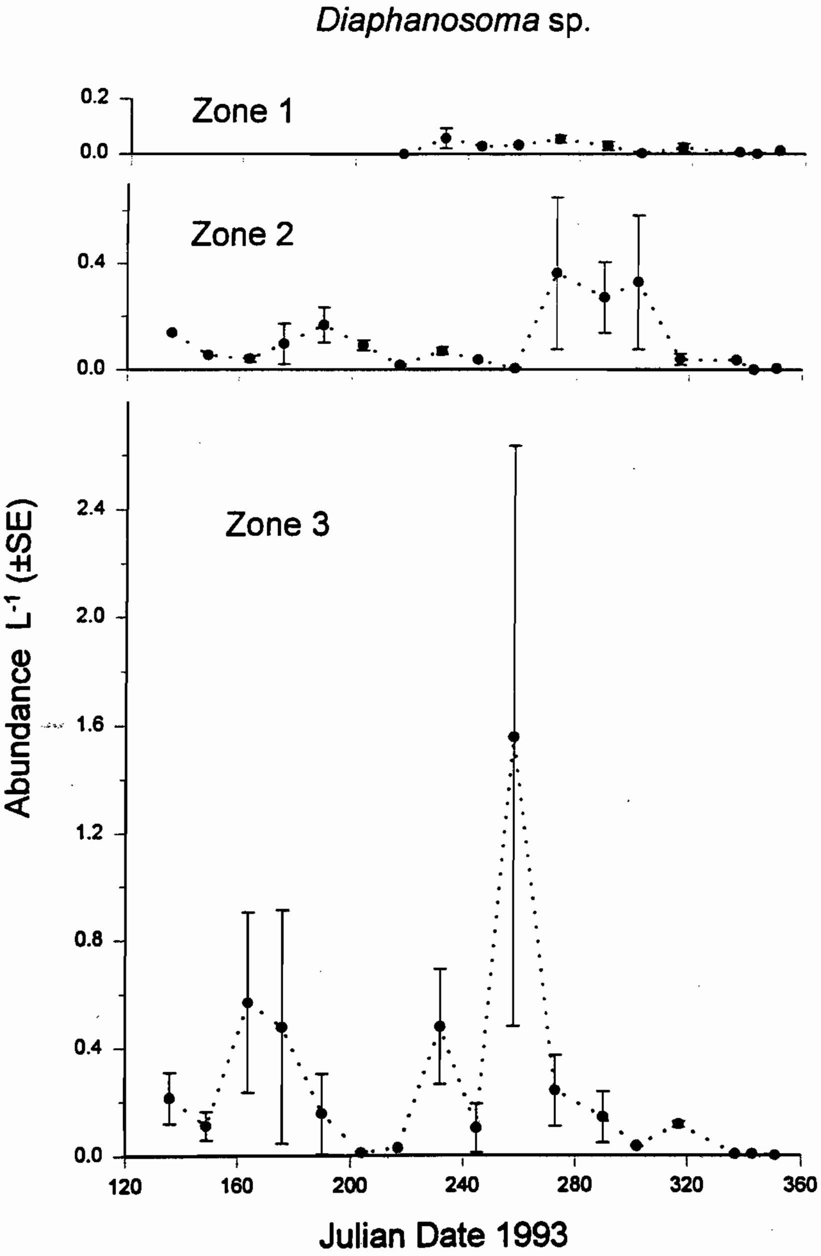

**Figure 15.** Mean abundance ($L^{-1}$ ) and zonal distribution of *Diaphanosoma* sp. during 1993.

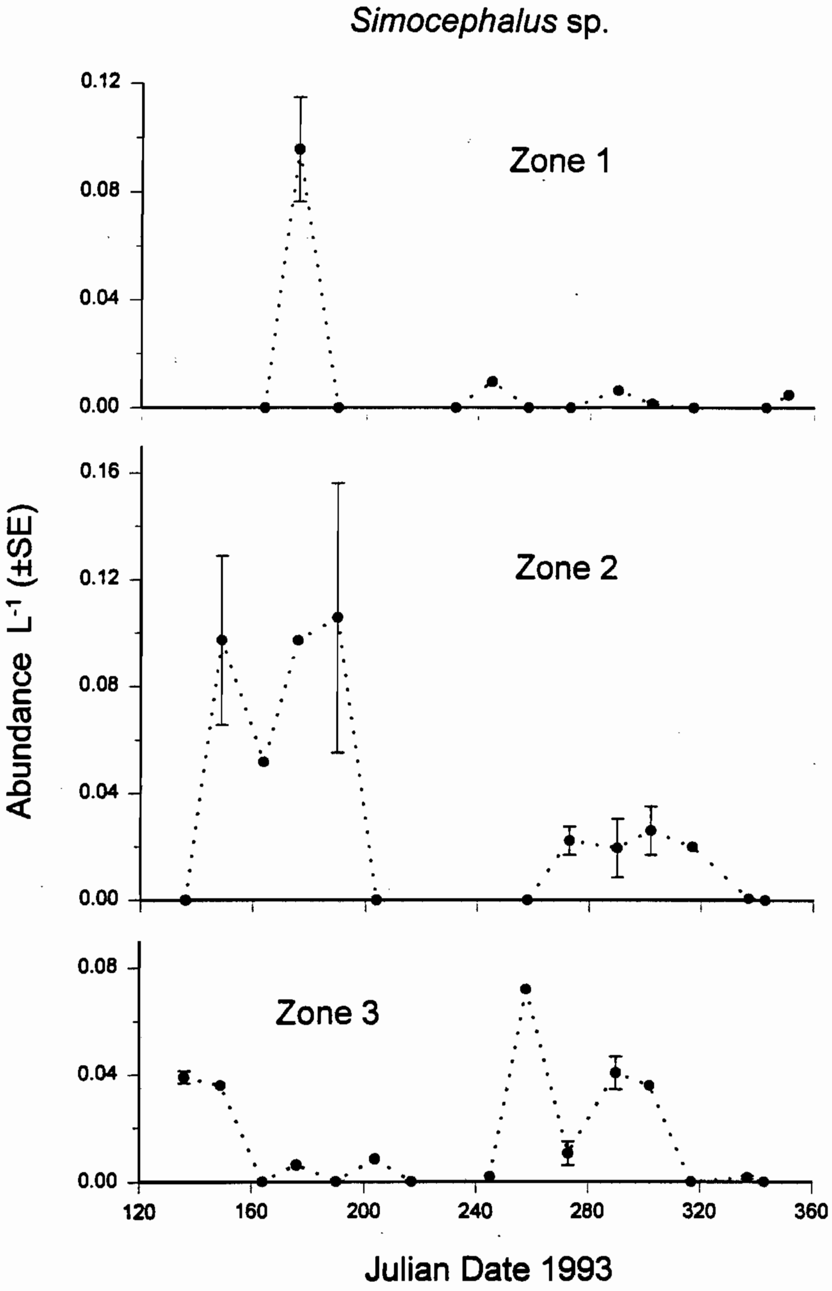

Figure 16. Mean abundance ($L^{-1}$) and zonal distribution of *Simocephalus* sp. during 1993.

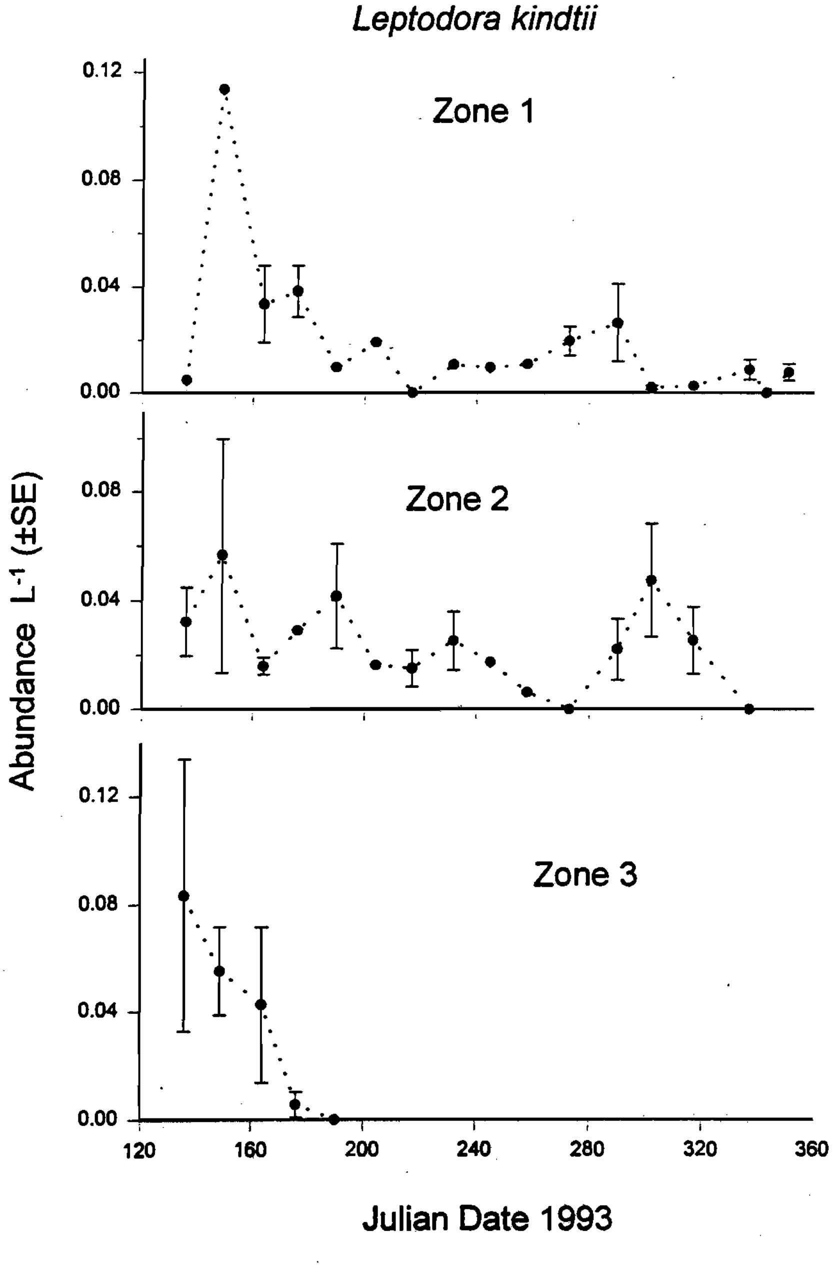

Figure 17. Mean abundance ($L^{-1}$ ) and zonal distribution of *Leptodora kindtii* during 1993.

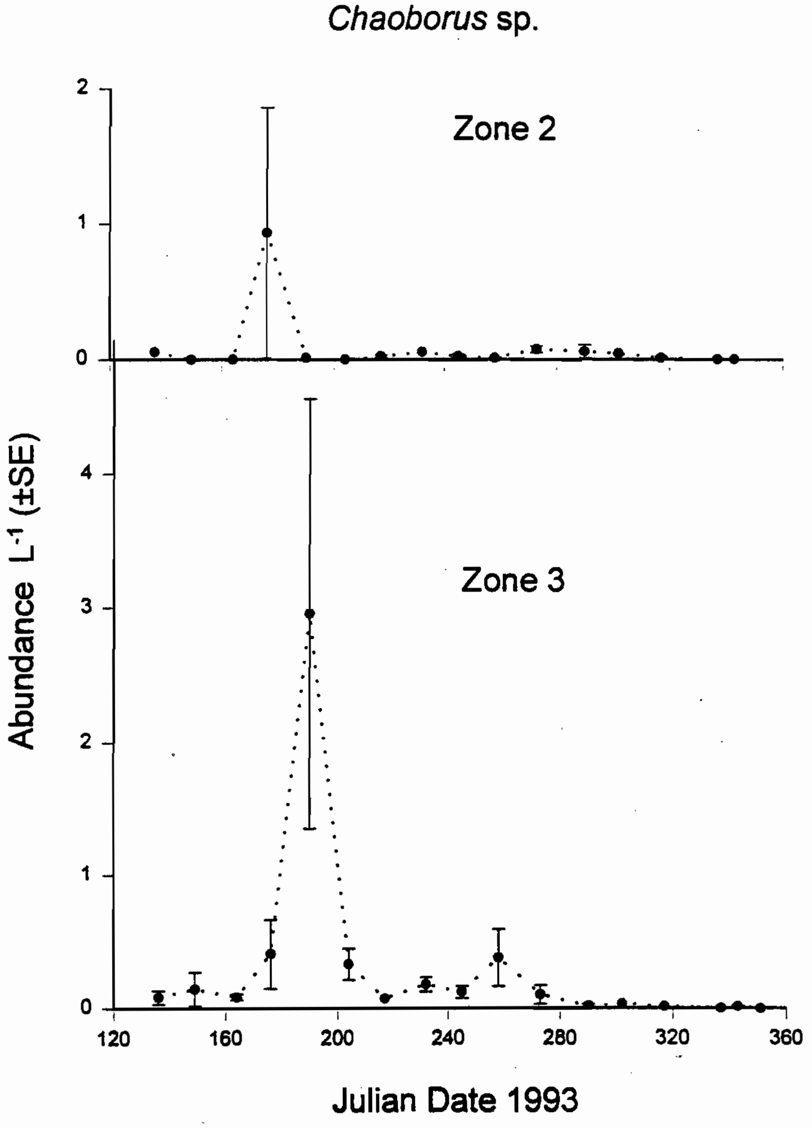

Figure 18. Mean abundance ($L^{-1}$) and zonal distribution of *Chaoborus* sp. during 1993.

## Zooplankton Abundance in Fish Stomachs.

Stomach contents of fishes caught in the summer of 1993 from June to September were analyzed (Fig. 19). Data here only include results from thread-fin shads. Gizzard shad and alewives were present in the collections, but their numbers were not sufficient to be useful for analysis. At the beginning of the collection period, copepods were by far the most numerous components of the diet, but they declined in importance in late June and were never again important in the diet of thread-fin shad. By July, Cladocera composed a large part of the diet, and were again important in November. The summer peak of Cladocera in the diet primarily consisted of *D. retrocurva* but later in the year *B. longirostris* were abundant in the stomachs. No individuals of *D. lumholtzi* were found in the stomachs of any of the fishes. However, we did not examine stomach contents of large fish.

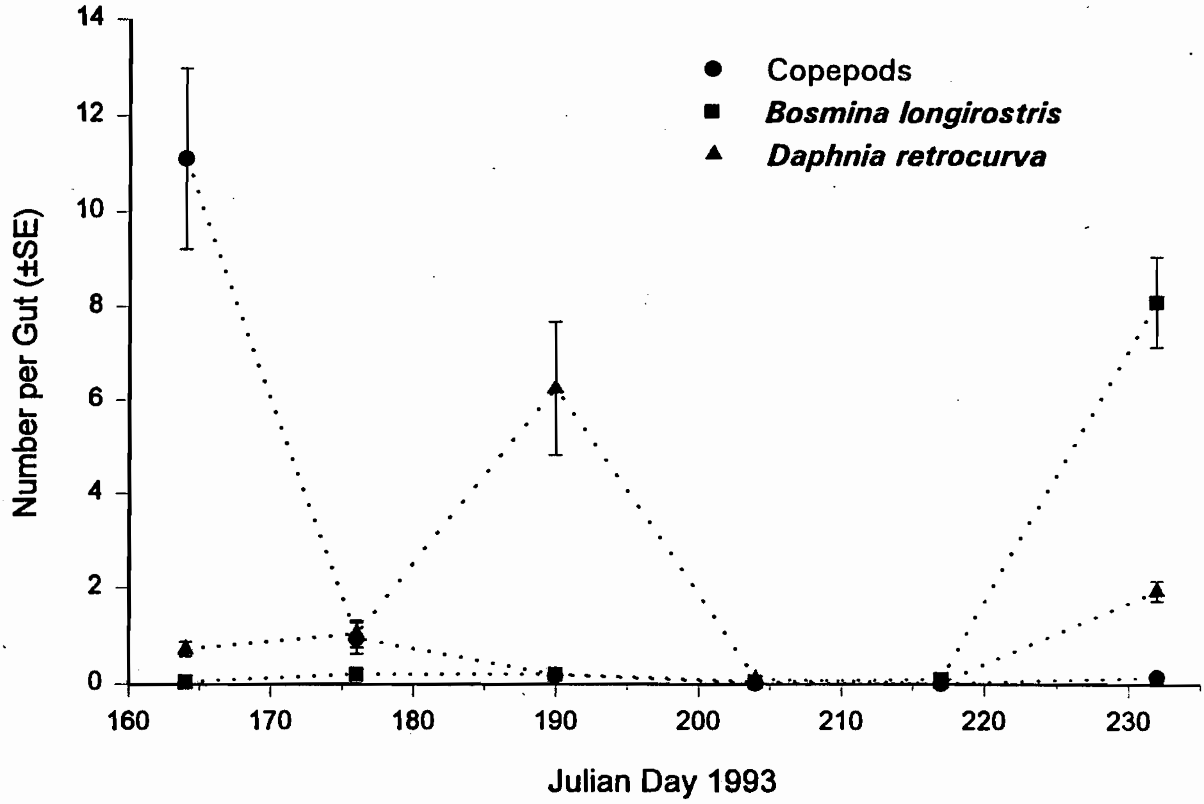

Figure 19. Relative composition of zooplankton taxa present in stomachs of threadfin shad in Norris Reservoir during 1993.

## Data analysis.

To determine if there were significant seasonal, zonal and depth effects on the distribution of *D. lumholtzi*, relative to the habitat distribution of other zooplankton taxa in Norris Reservoir, we examined main effects of season, zone, and depth nested within zones on log-transformed abundance data with a nested ANOVA (SAS 1994, Ver. for Windows). Significance was based on the Type III sum of squares (Shaw and Mitchell-Olds 1993) (Table 3 for both 1992 and 1993).

In 1992, there was a significant effect of zones on *D. lumholtzi*. The species was virtually restricted to Zones 2 and 3, and very rare in Zone 1 (Table 3, Fig. 3). Seasonal effects were not significant although the species was present in substantial numbers only in August. *Daphnia pulicaria* and *D. retrocurva* both had significant zonal effects, and significant depth effects within each zone. Seasonal effects were significant only for *D. retrocurva*.

Table 3. Nested ANOVA of main effects on zooplankton taxon abundance of season, reservoir zone, and depth nested in zones for both 1992 and 1993 in Norris Reservoir.

| **TAXA** | **YEAR** | **ANOVA** | **SEASON (4)** | **ZONE (3)** | **SEASON*ZONE** | **ZONE (DEPTH=5)** |
|---|---|---|---|---|---|---|
| ***Bosmina*** | 1992 | **0.0154*** | 0.9695 | **0.0171*** | 0.7716 | 0.1576 |
| | 1993 | **0.0022*** | 0.2361 | **0.0148*** | 0.1082 | 0.1149 |
| ***D. pulicaria*** | 1992 | **0.0003*** | 0.0701 | **0.0009*** | 0.4996 | **0.0117*** |
| | 1993 | **0.0001*** | **0.0001*** | **0.0007*** | 0.2279 | **0.0001*** |
| ***D. retrocurva*** | 1992 | **0.0001*** | **0.0124*** | **0.0001*** | 0.1333 | **0.0001*** |
| | 1993 | **0.0001*** | **0.0001*** | 0.1414 | **0.0001*** | **0.0001*** |
| ***Diaphanosoma*** | 1992 | 0.6407 | 0.1106 | 0.4822 | 0.4862 | 0.5380 |
| | 1993 | **0.0001*** | 0.1313 | 0.2129 | **0.0079*** | **0.0347*** |
| ***Leptodora*** | 1992 | 0.9248 | 0.2744 | 0.8456 | 0.7018 | 0.8999 |
| | 1993 | **0.0001*** | **0.0016*** | 0.3378 | 0.3176 | 0.8440 |
| ***Chaborus*** | 1992 | 0.4116 | 0.8560 | 0.0744 | 0.9545 | 0.5452 |
| | 1993 | **0.0001*** | **0.0017*** | **0.0001*** | **0.0035*** | 0.5766 |
| ***D. lumholtzi*** | 1992 | **0.0070*** | 0.0726 | **0.0014*** | 0.3692 | 0.2485 |
| | 1993 | **0.0001*** | **0.0001*** | **0.0202*** | 0.2566 | 0.0634 |

In 1993, *D. lumholtzi* had significant seasonal and zonal effects but again had no depth within zone effect. It was concentrated in Zone 3 but was primarily abundant during the late fall and early winter. It tends to be found more in shallow depths, and a linear regression of log-abundance on depth for all zones combined was significant (P = <0.001, adjusted $r^2$ = 0.159; b = 0.085; N = 153) and indicated a negative relationship with depth. This may be an artifact of zones because it was primarily found in the headwaters area of the reservoir that are more shallow; when depth was nested within zones in the ANOVA there was no depth effect. Both *D. pulicaria* and *D. retrocurva* had significant seasonal patterns and *D. pulicaria* also had a significant zonal pattern. *Daphnia retrocurva* was more broadly distributed in the reservoir in all zones in 1993 than had been observed in 1992. Both taxa had significant depth effects within zones in 1993. A linear regression of the log of species abundance regressed on water depth for all zones combined indicated a highly significant positive relationship with depth for both species for 1993 (*D. pulicaria*: P <0.001; b = 0.118; adjusted $r^2$ = 0.353 and for *D. retrocurva:* P < 0.001; b = 0.32; adjusted $r^2$ = 0.303; N for both = 153). *Bosmina* showed only an effect of zone, primarily occurring in zones 1 and 2 in 1992 and 1993, and there was no effect of depth. None of the other zooplankton taxa were sufficiently abundant to have an effect on the distribution of *D. lumholtzi*. *Diaphanosoma* had no season, zone, or depth within zone effects in 1992, but in 1993, it did show a significant season*zone interaction or depth within zones effects. *Leptodora* had a significant season effect found only in the summer of 1993. *Chaoborus* had both season and zone and season*zone interaction effects in 1993.

To test for associations among taxa we looked for presence or absence associations of *D. lumholtzi* with the presence or absence of other zooplankton species. We performed a contingency table analysis contrasting the presence or absence of all species paired against each other, with a two-way contingency table using Yule's coefficient of association (Q) to determine significance and direction (positive or negative) for the association (Bishop *et al.* 1975) (Table 4 for 1992, Table 5 for 1993). For both 1992 and 1993, *D. lumholtzi* had a significant negative association with *D. pulicaria* and *D. retrocurva* and a negative or absence of association with the other taxa. *Daphnia pulicaria* and *D. retrocurva* were highly positively associated with each other, although the maximum abundance of *D. retrocurva* occured somewhat later than for the former species. In 1993, *D. lumholtzi* had a significant negative association with *Leptodora* but a positive association with *Diaphanosoma* sp. and with *Chaoborus* sp. All three forms primarily are found in the upper portion of the reservoir. *Daphnia pulicaria* and *D. retrocurva* were highly positively associated with each other in 1993. *Bosmina longirostris* showed no positive or negative association with any of the other zooplankton taxa in either 1992 or 1993.

Table 4. Results of two-way contingency table analysis, using Yule's "Q" for determination of significance and its sign, for presence or absence of pairs of enumerated zooplankton taxa in Norris Reservoir during 1992.

| | | | | | | |
|---|---|---|---|---|---|---|
| *D. pulicaria.* | P= 0.110<br>Q=1.00 | | | | | |
| *D. retrocurva* | P=0.152<br>Q=1.00 | **P=<0.004**<br>* Q=0.778 | | | | |
| *Diaph.* | P=0.498<br>Q=-1.00 | P=0.833<br>Q=0.077 | P=0.813<br>Q=-0.084 | | | |
| *Chaoborus* | P=1.000<br>Q=0.000 | **P=<0.018**<br>* Q=-0.731 | P=-0.781<br>Q=-0.113 | P=0.686<br>Q=0.179 | | |
| *Leptodora* | P=0.311<br>Q=1.000 | P=0.118<br>Q=0.500 | P=0.432<br>Q=-0.304 | **P=0.019***<br>Q=0.690 | P=0.422<br>Q=-0.304 | |
| *D. lumholtzi* | P=0.341<br>Q=-1.000 | **P=<0.019**<br>* Q=-0.735 | **P=<0.001***<br>Q=-0.918 | P=0.335<br>Q=0.077 | P=0.054<br>Q=0.750 | P=0.976<br>Q=-0.009 |
| | *Bosmina* | *D. pulicaria* | *D. retrocurva* | *Diaph.* | *Chaoborus* | *Leptodora* |

Table 5. Results of two-way contingency table analysis, using Yule's "Q" for determination of significance and its sign, for presence or absence of pairs of enumerated zooplnkton taxa present in Norris Reservoir during 1993.

| | | | | | | |
|---|---|---|---|---|---|---|
| *D. pulicaria.* | P= 0.852<br>Q=-0.039 | | | | | |
| *D. retrocurva* | P=0.584<br>Q=0.119 | **P=<0.001**<br>* Q=0.947 | | | | |
| *Diaph.* | P=0.104<br>Q=0.329 | **P=0.008***<br>Q=-0.444 | P=0.065<br>Q=-0.348 | | | |
| *Chaoborus* | P=0.169<br>Q=0.292 | **P=<0.001**<br>* Q=-0.550 | **P=<0.001***<br>Q=-0.642 | **P=0.001***<br>Q=0.534 | | |
| *Leptodora* | P=0.842<br>Q=-0.042 | **P=<0.001**<br>* Q=0.680 | **P=<0.001***<br>Q=0.740 | P=0.163<br>Q=0.243 | **P=0.002***<br>Q=-0.498 | |
| *D. lumholtzi* | P=0.675<br>Q=0.091 | **P=<0.001**<br>* Q=-0.828 | **P=<0.000***<br>Q=-0.891 | **P=0.014***<br>Q=0.428 | **P=<0.001**<br>* Q=0.623 | **P=0.001***<br>Q=-0.524 |
| | *Bosmina* | *D. pulicaria* | *D. retrocurva* | *Diaph.* | *Chaoborus* | *Leptodora* |

## DISCUSSION

*Daphnia lumholtzi* has rapidly colonized numerous reservoirs in the southeastern United States. In this study, we have examined the habitats within one reservoir that it has been able to invade and become established. We first wanted to determine if the distribution of *D. lumholtzi* were distinct from other zooplankton populations?

*Daphnia pulicaria* and *D. retrocurva* have strong seasonal and zonal effects and positive depth effects within zones. They primarily are found during the spring and early summer and are concentrated in Zones 1 and 2 of the reservoir. The major difference among these two species is that *D. retrocurva* is abundant after a decline in abundance of *D. pulicaria*, suggesting the possibility that *D. retrocurva* replaced *D. pulicaria* as the dominant pelagic zooplankton taxon. This pattern could be due to competitive interactions, but it is more likely the expected result of a size-selective predation by fishes, which appears to be important in the reservoir; *D. retrocurva* is smaller than *D. pulicaria*. *Daphnia lumholtzi* had a highly significant negative association with the other two daphniids (Tables 4 and 5). It was primarily encountered in August of both years after the seasonal decline of the other daphniids but was most abundant in 1993 in late October, November and early December when the other daphniids were very rare.

Fish diet studies suggested that, when *D. retrocurva* was abundant during midsummer, it was strongly selected by thread-fin shad. *Daphnia pulicaria* also is highly vulnerable to predation by larger fishes although we seldom encountered it in the small fish which composed most of our observations. In contrast, *D. lumholtzi* was never encountered in the stomachs of larval or juvenile fishes. Gophen (1979) suggests, however, that it is ingested by large fish.

*Bosmina longirostris* appears to occupy a unique feeding habitat in the reservoir, independent of other taxa. Although it was widely distributed throughout the reservoir in all zones and during all seasons, it showed no positive or negative association with the three daphniid species. It did compose a large part of the diet of thread-fin shad during the fall, such as during late September 1993 just prior to the increases in *D. lumholtzi*.

Has *D. lumholtzi* replaced other populations previously abundant in the reservoir? There is no evidence in our results to support an argument that this invader has replaced other populations. Indeed, in 1992 we found very few zooplankton present in samples at the collection sites where *D. lumholtzi* was most abundant during 1993. If species diversity of this reservoir were in an equilibrium condition, the basic predictions would be that there should have been a replacement of some other population(s) (Petraitis *et al.* 1989). Can reservoir systems attain equilibria in species number? This is an old reservoir; there is no reason to believe that an equilibrium could not be attained. Alternatively, it is possible that fish predation is so intense that very few zooplankton taxa can survive when fish are feeding, except *D. lumholtzi*.

What are the morphological, physiological and ecological characteristics of this species that may have made it a successful invader in these habitats? In a review of ecological characteristics of invading species, Crawley (1987) argued that the most fundamental characteristic of a successful establisher, including those introduced for biological control purposes, appeared to be a high intrinsic rate of natural increase. The population growth rate (r) of *D. lumholtzi* is low, much lower than the other daphniid species present in the reservoir. Crawley also listed other traits important for an invading species, such as ability to find space or resources, and defenses against resident predators, parasites, or disease causing organisms. The presence of spines, as are found in *D. lumholtzi*, appears to be a strong deterrent against fish predation (Barnhisel 1991a, 1991b). Indeed, the population growth rate of *D. lumholtzi* might be low due to its investment of resources into development of its defensive spines. The shallow areas of lakes and reservoirs where *D. lumholtzi* is mostly found tend to have more predator pressure than deeper, open water areas. All indications are that *D. lumholtzi* has been a successful invader in these areas because of its ability to minimize predator pressure.

We conclude that the success of *D. lumholtzi* as a colonizer is due to its defenses against the major invertebrate and fish predators in Norris Reservoir and not to its competitive superiority over other daphniids for food resources. Its primary seasonal occurrence during late autumn, suggests that despite its ability to survive intense predator pressure, the higher reproductive rates of *D. pulicaria* and diurnal migration are able to compensate sufficiently for fish predation that *D. lumholtzi* populations cannot replace it in the main part of the reservoir. However, if predator pressure on *D. pulicaria* were to significantly increase, it is possible that *D. lumholtzi* could become more widespread in the reservoir. Because of the inability of young fish to feed on this species, probably it would have a strong negative effect on the reservoir fisheries, at that time.

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# ADAPTATIONS OF NORTH AMERICAN EXOTIC MOLLUSCA FOR LIFE IN REGULATED RIVERS AND THEIR POTENTIAL IMPACTS

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**ABSTRACT. There are at least 755 species of freshwater mollusks in North America. Fifteen of the 485 species of gastropods are introduced while 7 of the 270 bivalves species are introduced. The biology and ecology of all the introduced species are examined for possible adaptive features for life in regulated streams in relation to common physical, chemical, and biological characteristics of reservoirs (*e.g.*, fluctuating water levels, depositional substrates, paucity of submerged macrophyte biomass and diversity, etc.).**

**The exotic species of mollusks with the greatest potential for reservoir ecosystem impacts are those with life cycles that have planktonic larvae. Main stream impoundments will act as breeding reservoirs that throughout the year will "seed" and replenish downstream habitats and populations that, like upstream populations, would not otherwise be able to sustain themselves. Upstream populations cannot be self sustaining because currents continually erode adult populations and carry larvae downstream for distances approximately equal to velocity (km/day) x duration of larvae in plankton. Dreissenid populations extending 100 m in streams cannot maintain their positions in the streams unless the water velocity is less than 0.00006 m/sec, a velocity exceeded in most streams, and possibly many reservoirs. The duration of impacts will be equal to the life span of the population (< 2 years).**

**The degree of biofouling downstream will be mostly a function of the reproductive and growth potential of the breeding colony in the upstream reservoir(s). This in turn is a function of the quality of the habitat(s) in the reservoir(s). Firm substrates (*e.g.*, rocks, concrete dam structure, etc.) will promote the development of epifaunal, byssate exotic species (*i.e.*, dreissenids) while soft substrates will promote the development of infaunal bivalves (and quagga mussels). Because most exotic species themselves will provide substrate for byssate forms, the probability of colonization of reservoirs by dreissenids is greatly enhanced.**

**Possession of a planktonic larval phase is an adaptation for life in lentic habitats, including reservoirs. Oviparous and ovoviviparous habits are adaptations for life in lotic habitats. Biofouling mollusks are all exotic species characterized by possession of a planktonic larval phase which provides recruitment that exceeds by three to four orders of magnitude that of native species and other exotic species with oviparous or ovoviviparous habits. Exotic mollusks which are either ovoviviparous or are ovipositors are not biofouling. Impacts of exotic species will include little or no impact (most gastropods), beneficial uses (*e.g.*, as escargot), and negative impacts, including human health concerns (some gastropods are intermediate hosts of dangerous human parasites) and numerous ecological and socio-economic impacts.**

## INTRODUCTION

There has been no thorough review of exotic freshwater Mollusca in North America. With the notoriety of zebra mussels and Asian clams in recent years, it is perhaps timely to examine the impacts, or potential impacts, of all exotic freshwater mollusks in North America. Table 1 lists all the species of gastropods and bivalves that have been introduced. Although the taxonomy of freshwater gastropods and bivalves is still somewhat in disarray, on the basis of species described in Burch (1975a,b; 1989) and Rosenburg and Ludyanskiy (1994) there are 755 species of freshwater Mollusca in North America. Of these, 485 species are gastropods and 270 species are bivalves. About 3% (15) of the gastropods and 3% (7) of the bivalves are exotic (Table 1). Of the 22 species of exotic mollusks, only three (*Corbicula fluminea, Dreissena polymorpha, Dreissena bugensis*) have caused enormous ecological and/or socio-economic impacts. Most of the remaining 18 exotic species are relatively benign (*i.e.*, compared to the three above) and in most cases serve to increase the diversity of benthic macroinvertebrates in aquatic habitats where they are found. Some, such as the apple snail, *Pomacea canaliculata*, have the potential to cause severe crop damages; others, such as *Biomphalaria*, *Marisa cornuarietis*, *Pomacea canaliculata*, and *Melanoides tuberculata* are intermediate hosts of infectious bacteria or trematode and nematode parasites. The distribution in North America, the method of introduction (if known), and the impacts or potential impacts of exotic Mollusca are described and then their biological and ecological characteristics (Table 2) are examined with reference to their potential adaptability to life in impoundments.

In order to predict potential impacts of an exotic organism, a mollusk in this case, on the ecology of an ecosystem we must first know the adaptability of the mollusk to the chemical, physical, and biological attributes of the system being invaded. This can be an enormous task for regulated stream ecosystems because of their vast differences in morphometry, limnological conditions, release depth, flow dynamics, geographical location, and uses of the impounded water (Neel 1963, Hall 1971, Ackerman *et al.* 1973, Baxter 1977, Hannan 1979, Ward and Stanford 1979a). Nevertheless, there are some common features that can be of predictive value in assessing the adaptability of an invading mollusk and its potential impact on the impounded ecosystem and downstream. The task is made somewhat easier if we confine our discussions to **on-stream**, or open, reservoirs, that is reservoirs located on streams so that the discharge of the stream passes through the impoundment (Hannan 1979). The only other type of reservoir is **off-stream**, or closed, which have no natural inflow or outflow (Hannan 1979). The closed impoundments are not discussed here because they tend to be isolated, are rather rare, and have few case history studies to make an appraisal.

The open reservoirs can be classified as **main-stream** (run-of-the-river), **transitional**, or **deep storage** (Hannan 1979). Most of the discussion herein relates to the deep storage reservoirs because depth has a profound effect on the distribution of mollusks and hence their potential impact. Ward and Stanford (1979b) summarize some of the common features of impoundments, and they are discussed first in order to develop a scenario that will permit an assessment of the adaptability of exotic mollusks and their potential impact(s) on the impounded stream. Then the biological and ecological attributes of the exotic species are examined in relation to the common features of impoundments. The biological and ecological attributes fall under eight headings: (i) mode of life and habitat, (ii) dispersal mechanisms, (iii) physiological adaptations to seasonal variations in common reservoir attributes, (iv) predators, (v) parasites, (vi) reproductive potential and productivity, (vii) life cycle, and (viii) food and feeding habits. The attributes of reservoirs and each exotic species are then integrated to predict potential impacts in the impoundment and downstream. Finally, potential impacts of exotic mollusks on the ecology of the reservoir and socio-economic impacts on users of the reservoir are examined.

Table 1. List of species of gastropods and bivalves introduced (one questionable - ?) into lakes and streams in North America. The ratio of the introduced species to the total native species in the same genus to the total native species in the family are shown in parentheses. The significance of these ratios are discussed in the text.

- GASTROPODA
  - Subclass Prosobranchia
    - Family Neritinidae (0:3)
      - None
    - Family Valvatidae (1:10:10)
      - *Valvata piscinalis*
    - Family Viviparidae (2:0:18)
      - *Cipangopaludina chinensis malleatus*
      - *Cipangopaludina japonicus*
    - Family Ampulariidae (2:1:3)
      - *Marisa cornuarietis*
      - *Pomacea bridgesi*
      - *Pomacea canaliculata?*
    - Family Bithyniidae (1:0:0)
      - *Bithynia tentaculata tentaculata*
    - Family Micromelaniidae (0:1)
      - None
    - Family Hydrobiidae (1:0:152)
      - *Potamopyrgus antipodarum*
    - Family Thiaridae (2:0:0)
      - *Melanoides tuberculata*
      - *Thiara granifera*
    - Family Pleuroceridae (0:153)
      - None
  - Subclass Pulmonata
    - Family Acroloxidae (0:1)
      - None
    - Family Lymnaeidae (1:0:46)
      - *Radix auricularia*
    - Family Physidae (3:31:34)
      - *Physella acuta*
      - *Stenophysa marmorata*
      - *Stenophysa maugeriae*
    - Family Planorbidae (1:1:42)
      - *Biomphalaria glabrata*
    - Family Ancylidae (0:11)
      - None

- BIVALVIA
  - Subclass Heterodonta
    - Family Margaritiferidae (0:3)
      - None
    - Family Unionidae (0:224)
      - None
    - Family Sphaeriidae (4:23:34)
      - *Sphaerium corneum*
      - *Pisidium amnicum*
      - *Pisidium henslowanum*
      - *Pisidium punctiferum*
    - Family Corbiculidae (1:0:0)
      - *Corbicula fluminea*
    - Family Dreissenidae (2:0:1)
      - *Dreissena polymorpha*
      - *Dreissena bugensis*

Table 2. Biological and ecological characteristics of mollusks introduced (one questionable - ?) into North America. Habitat: Le = lentic or large, slow rivers, Lo = lotic, Ind = found in either lotic or lentic habitats; Me = can tolerate mesotrophy, Eu = can tolerate eutrophy; Li = usually in littoral zone, Be = usually benthic, Epi = usually epibenthic, Inf = infaunal. Feeding Habits: Al = feeds mainly on algae, De = feeds mainly as epipsammic browser on detritus , Fi = filter feeder, Ga = gatherer of bacteria, algae, detritus using cilia on foot, Pr = predaceous on eggs of other snails, Ve feeds on vegetation. Reproduction: Mo = monoecious, Di = dioeceious, Pa = parthenogenetic, In = internal fertilization, Ex = external fertilization, Ov = oviparous, Ovo = ovoviviparous, Ov-Te = lays calcium coated eggs terrestrially, Pl = planktonic larvae. Life Cycle: Dr = direct development, La = larval stages present, numbers indicate longevity in years. Physiology: AI = anoxia intolerant, Fa = facultative air breathers and can avoid anoxia, Ey = eurythermous, Wst = warm stenotherm, Wey = warm eurytherm (cannot tolerate freezing) but occurs throughout a wide temperature range.

| | Habitat | Feed. Habit | Reprod. | Life Cycle | Physiology |
|---|---|---|---|---|---|
| **GASTROPODA** | | | | | |
| **Subclass Prosobranchia** | | | | | |
| Family Valvatidae | | | | | |
| *Valvata piscinalis* | Le, Me, Li | Al | Mo, In, Ov | Dr, 1 | AI, Ey |
| Family Viviparidae | | | | | |
| *Cipangopaludina chinensis* | Le, Me, Be | De, Fi? | Di, In, Ovo | Dr, 2-4 | AI, Ey |
| *Cipangopaludina japonicus* | Le, Me, Be | De, Fi? | Di, In, Ovo | Dr, 2-4 | AI, Ey |
| Family Ampulariidae | | | | | |
| *Marisa cornuarietis* | Ind, Me, Be | Al, De | Di, In, Ov | Dr, 2-3? | AI, Ey |
| *Pomacea bridgesi* | Ind, Eu, Be | Al, De | Di, In, Ov-Te | Dr, 2-3? | Fa, Wst |
| *Pomacea canaliculata*? | Ind, Eu, Be | Al, De | Di, In, Ov-Te | Dr, 2-3? | Fa, Wst |
| Family Bithyniidae | | | | | |
| *Bithynia tentaculata* | Le, Eu, Be | Al, De | Di, In, Ov | Dr, 2-3 | AI, Ey |
| Family Hydrobiidae | | | | | |
| *Potamopyrgus antipodarum* | Ind, Me?, Be | Al, De | Pa, In, Ov | Dr, 1-2? | AI, Ey |
| Family Thiaridae | | | | | |
| *Melanoides tuberculata*[1] | Tropical | Al? | Di, In, Ovo | Dr,2-3 | AI, Wst |
| *Thiara granifera*[1] | Tropical | Al? | Di, In, Ov | Dr, ? | ?, Wst |
| **Subclass Pulmonata** | | | | | |
| Family Lymnaeidae | | | | | |
| *Radix auricularia* | Le, Eu, Li | Al, De | Mo, In, Ov | Dr, 1 | Fa, Ey |
| Family Physidae | | | | | |
| *Physella acuta* | Le, Eu, Li | Om | Mo, In, Ov | Dr, 1 | Fa, Ey |
| *Stenophysa marmorata*[2] | (Le, Eu, Li)? | Om? | Mo, In, Ov | Dr, 1? | Fa, Wst |
| *Stenophysa maugeriae*[2] | (Le, Eu, Li)? | Om? | Mo, In, Ov | Dr, 1? | Fa, Wst |
| Family Planorbidae | | | | | |
| *Biomphalaria glabrata*[3] | Ind, Eu, Li | Pr, Ve | Mo, In, Ov | Dr, 1 | Fa, Wst |
| **BIVALVIA** | | | | | |
| **Subclass Heterodonta** | | | | | |
| Family Sphaeriidae | | | | | |
| *Sphaerium corneum* | Le, Eu, Inf | Fi, Ga | Mo, In, Ovo | La, 1-2 | AI, Ey |
| *Pisidium amnicum* | Le, Eu, Inf | Fi, Ga | Mo, In, Ovo | La, 1-2 | AI, Ey |
| *Pisidium henslowanum* | Le, Eu, Inf | Fi, Ga | Mo, In, Ovo | La, 1 | AI, Ey |
| *Pisidium punctiferum* | Le, Me, Inf | Fi, Ga | Mo, In, Ovo | La, 1 | AI, Ey |
| Family Corbiculidae | | | | | |
| *Corbicula fluminea* | Ind, Me, Inf | Fi, Ga | Di, In, Ovo/Pl | La, 2-4 | AI, Wey |
| Family Dreissenidae | | | | | |
| *Dreissena polymorpha* | Le, Eu, Epi | Fi, Ga | Di, Ex, Pl | La, 1-2 | AI, Ey |
| *Dreissena bugensis* | Le, Eu, Ep-In | Fi, Ga | Di, Ex, Pl | La, 2-3 | AI, Ey |

# DISTRIBUTION AND IMPACTS OF MOLLUSCA INTRODUCED INTO NORTH AMERICA

Table 1 lists all species of freshwater Mollusca that have been introduced into North America. The following descriptions provide summaries of their countries of origin, current distribution in North America, and reported ecological and/or socio-economic impacts to date.

## GASTROPODA

### Subclass Prosobranchia

Family Valvatidae

*Valvata piscinalis* (Fig. 1d) - Introduced from Europe into the lower Great Lakes where it is abundant. The species was first recorded from Lake Ontario in 1913 (Clarke 1980) and has since spread to lakes and large rivers in all states and provinces (Mackie *et al.* 1980) bordering the Great Lakes. The species appears to be relatively benign in its impact potential, and competition with native gastropods probably is its most serious threat.

Family Viviparidae

*Cipangopaludina chinensis malleatus* (Fig. 1b) is more widely introduced than *Cipangopaludina japonicus*, the former occurring in western (California, Arizona, Colorado), eastern (Florida north to Ontario, Quebec, and Nova Scotia, Canada), and most central states while the latter has been recorded only from Massachusetts, Michigan, and Oklahoma (Burch 1989). Both species are used as food by the Chinese. *Cipangopaludina c. malleatus* was probably introduced by the Chinese about 1892 when they were first found in a Chinese vegetable store in San Francisco (Hanna 1966). Both species occur sporadically but are abundant when they do occur. Nothing is known about the ecological impact of either species, but competition with other common viviparids, such as *Campeloma* and *Viviparus* species, is possible. Both species have a positive socio-economic value, *C. c. malleatus* still being sold as food in Chinese markets in San Francisco (Hanna 1966). The biological and ecological attributes of both species summarized in Table 2 are based on descriptions in Jokinen (1983) and Clarke (1980).

Family Ampulariidae (Fig. 1a, native *Pomacea paludosa*)

*Marisa cornuarietis* - Originally from northern South America and southern Central America, the species was introduced into Florida, probably in the mid 1950's (Hunt 1958). Its ecological impact is unknown, but it is thought to be an efficient competitor of food resources (Cedeno-Leon and Thomas 1982). The species has potential to be of beneficial socio-economic value because it acts as a predator on the eggs and juveniles of snails, such as *Biomphalaria glabrata* (see description below), that are intermediate hosts of trematodes causing schistosomiasis (Cedeno-Leno and Thomas 1982).

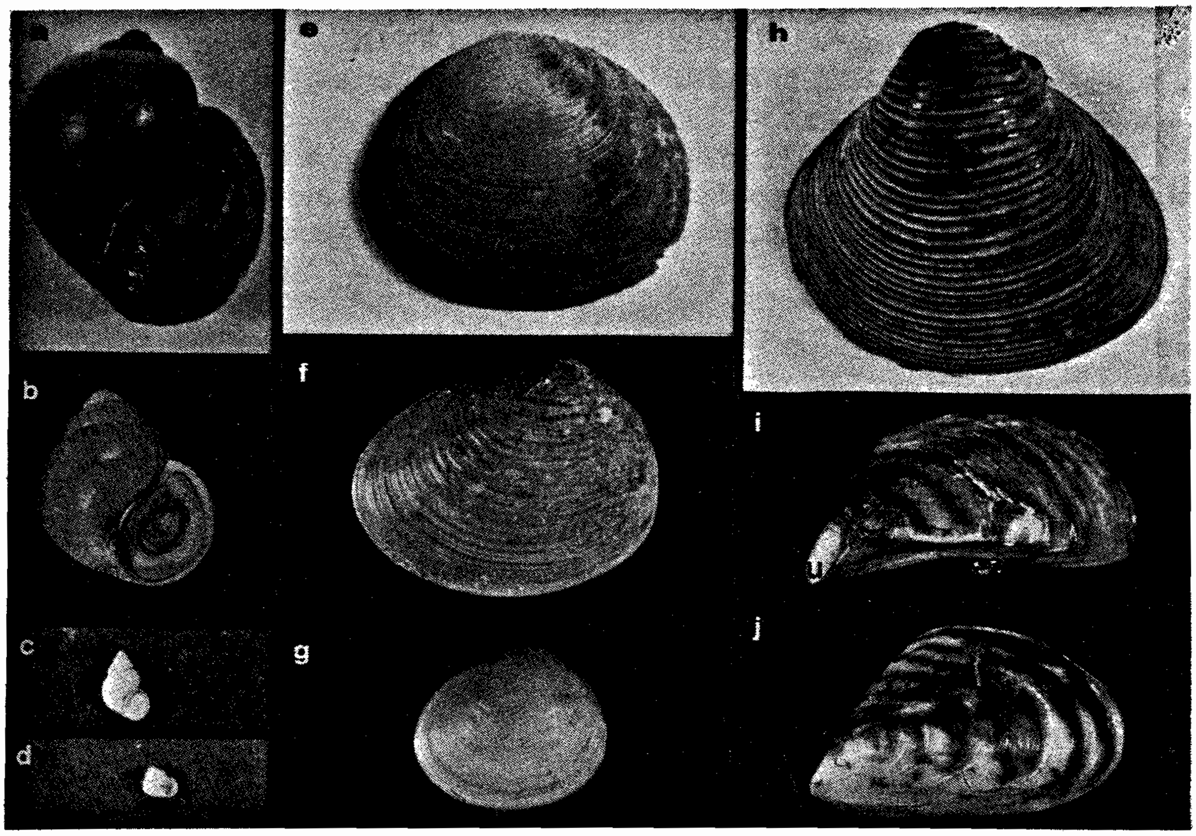

Figure 1. Some mollusks introduced into North America. Gastropoda: Prosobranchia; (a) *Pomacea paludosa* (native to North America), ht = 4.5 cm; (b) *Cipangopaludina chinensis malleatus*, ht = 3.5 cm; (c) *Bythinia tentaculata tentaculata*, ht = 8.9 mm; (d) *Valvata piscinalis*, diam = 3.2 mm. Bivalvia: Sphaeriidae; (e) *Sphaerium corneum*, lgth = 7.5 mm; (f) *Pisidium amnicum*, lgth = 5.8 mm; (g) *Pisidium punctiferum*,lgth = 3.4 mm; (h) *Corbicula fluminea*, lgth = 3.6 cm; (i) *Dreissena polymorpha*, lgth = 2.8 cm; (j) *Dreissena bugensis*, lgth = 2.4 cm.

*Pomacea bridgesi* - Introduced into Florida from Brazil, apparently in the early 1960s (Clench 1966). Little is known about its ecology, but it probably is similar to other pomaceans, such as *P. urceus* (Burky 1974). Pomaceans are well known for their amphibious nature, having one part of their mantle cavity containing a ctenidium and another part modified as a gas-filled lung (Burky 1974). Nothing is known about the ecological impact of the *Pomacea bridgesi* in North America, but any impacts would probably include competition with other amphibious snails living in warm waters.

*Pomacea canaliculata* - Introduced into Hawaii in the late 1980s, it is a voracious feeder on rice plants and taro leaves and threatens to destroy a $2 million taro industry state wide; it also puts people at risk of contacting Leptospirosis, a bacterial disease, and is a potential carrier of the rat lungworm, *Angiostrongylus cantonensis*, a nematode parasite that causes meningo-encephalitis in humans (Wayne Kobayashi, pers. comm. and brochure, "Apple Snail (*Pomacea canaliculata*)" Department of Agriculture, State of Hawaii). The species was introduced either by the aquarium trade or as a food; it is currently being sold in Hawaii as escargot (Wayne Kobayashi, Department of Agriculture, State of Hawaii, pers. comm.). The species lays bright pink egg clusters on taro and other objects on land. Apparently the species has been reported since in Florida but appears not to have caused the same concerns as in Hawaii (Terry Bills, National Biological Service, National Fisheries Research Center, La Crosse, WI, pers. comm.). The species has the same amphibious adaptations of other pomaceans and lives in tropical climates in rivers, streams and ponds (Table 2). The snail can burrow into the mud and survive for several months without water.

### Family Bithyniidae

*Bithynia tentaculata tentaculata* (Fig. 1c) - Introduced into the Great Lakes via ballast in ships. The species was first recorded in Lake Michigan in 1871 (Robertson and Blakeslee 1948) and has since spread throughout most states and provinces bordering the Great Lakes. It is an opportunistic species and is thought to be responsible for the eradication of pleurocerids in the Erie Canal (Baker 1916) and Oneida Lake (New York) (Harman 1968). The species forms large populations in richly eutrophic and moderately polluted waters (Table 2) (Harman 1968). It is one of the most abundant mollusks in the Great Lakes (Berry 1943) but apparently cannot live in streams with turbulent water (Harman 1968).

### Family Thiaridae

*Melanoides tuberculata* - Native to much of Africa and the eastern Mediterranean countries, throughout India, southeast Asia, Malaysia and southern China, northern Japan, northern Australia and the New Hebrides, the species was introduced in the early 1970s into Florida, Texas and Arizona (Dundee 1974). The ecology (Table 2) is described by Dundee and Paine (1977). Its greatest impact probably will be in relation to its role as intermediate host of the human liver fluke (*Opisthorchis sinensis*) (Dundee and Paine 1977). *Melanoides tuberculata* has a tropical distribution and apparently will not succeed in temperate climates.

*Thiara granifera* - Native to Malaysia and the Phillippines, this species was introduced to Florida in the early 1950s (Abbott 1952) and Texas in the early 1960s (Murray 1964). Apparently it has an ecology (Table 2) (Murray and Wopschall 1965) and potential impact similar to *M. tuberculata*, but it is the intermediate host of the Oriental lung fluke, *Paragonimus westermani* (Abbott 1952).

## Subclass Pulmonata

### Family Lymnaeidae

*Radix auricularia* - "Widely introduced but of spotty occurrence in North America" (Burch 1989). The species is native to Europe and Asia and was first recorded from Montana by Baker (1913). Clarke (1980) suggests that it is especially common in muddy substrates of lakes, ponds, and slow-moving rivers (Table 2) near major cities. Its ecological and socio-economic significance is unknown, but it is probably an efficient competitor with some native lymnaeids.

Family Physidae

*Physella acuta* - Native to Europe, Mediterranean regions, and Africa, the species has been introduced into Australia, Hawaii and perhaps parts of continental United States (Burch 1989). Its current distribution is unknown, as are its biology and ecology. There is no information on its ecological or socio-economic significance in North America.

*Stenophysa marmorata* - Introduced into Texas and native to Brazil, Guatemala, Uraguay, Venezuela, and the West Indies (Te 1978), but its biology, ecology and ecological and socio-economic significance have not been determined, although it appears to be prefer warm water in ponds and slow-moving rivers (Table 2).

*Stenophysa maugeriae* - The species is native to Mexico and is recorded only from Texas (Te 1978). Like *S. marmorata* it appears to prefer warm water in ponds or slow-moving rivers (Table 2). Its biology and ecological and socio-economic significance in North America is unknown.

Family Planorbidae

*Biomphalaria glabrata* - Introduced to Florida, the species is of quarantine significance because it is the intermediate host of *Schistosoma mansoni*. It is native to West Indies, Venezuela, Surinam, French Guiana and Brazil (Burch 1989). Much of the research has been oriented toward methods to control its spread, such as developing attractants and arrestants (Thomas 1982, Thomas *et al.* 1975, Thomas *et al.* 1983). It appears to prefer warm, slow-moving waters.

## BIVALVIA

### Subclass Heterodonta

Family Sphaeriidae

All species of exotic sphaeriids appear to have been introduced from Europe via discharge of freshwater ballast into the Great Lakes. All four exotic species (Table 1, 2) are common in the Great Lakes and/or its drainages (Mackie *et al.* 1980). The ecological and socio-economic impacts have not been determined for any of the introduced species. Most exotic species are common intermediate hosts of trematode parasites but so are the native species (Mackie 1976).

*Pisidium supinum* has also been considered an introduced species (Burch 1975b), but several fossil records from Idaho and Alberta (Herrington 1962) suggest that it is indigenous to North America.

*Sphaerium corneum* (Fig. 1e) - Apparently introduced from Europe into the Great Lakes (it is most common in Lake Erie and Lake Ontario) (Herrington 1962) in the early 1900s, the species has dispersed slowly into lakes and large rivers of states bordering the Great Lakes. It is the most common *Sphaerium* in Britain (Ellis 1978) and adapts well to almost any kind of habitat (*e.g.*, ponds, ditches, swamps) (Table 2). However, in North America it is relatively uncommon. If the species occurs in reservoirs it will not be in the drawdown zone because it does "... not like .... drying ponds and streams" (Boycott 1936). Its slow rate of dispersal may be an indication of its poor ability to compete with native species of *Sphaerium*, although it is very abundant in Lake Erie (Mackie *et al.* 1980). There are no apparent negative ecological or socio-economic impacts of its introduction.

*Pisidium amnicum* (Fig. 1f) - Found in the drainage systems of St. Lawrence River and the Great Lakes (Burch 1975b), the species occurs throughout Europe as far north as Naples, eastward through Siberia to Lake Baikal, and in Algiers (Woodward 1913). Both *P. amnicum* and *S. corneum* probably were introduced in the mid to late 1800s, the earliest record being 1899 in Hamilton Bay of Lake Ontario (Sterki 1899). In Europe the species lives in rather clean waters, large and small rivers, brooks, ditches and lakes among vegetation (Table 2) (Ellis 1978). It has been found as deep as 30 m in Europe. Its ecological and socio-economic impacts are unknown, but its low densities in most populations suggest it is not a good competitor with most native sphaeriids.

*Pisidium henslowanum* - This species is common and generally distributed in Scandinavia, France, Germany, Belgium, former U.S.S.R., and Britain (Woodward 1913, Ellis 1978). It is relatively uncommon in North America but is generally distributed in the Laurentian Great Lakes where it was probably introduced. Most records are of its occurrence are in rivers and lakes in states bordering the Great Lakes. Harris (1973) gives an anomalous record of this species in western Canada, but it is probably *Pisidium supinum* because he based the identification on Herrington's (1962) description for *Pisidium henslowanum* form *supinum*. In Europe, the species inhabits streams, rivers, canals, lakes and ponds, usually on fine sediments (Ellis 1978). It appears to have little ecological significance other than competing with other sphaeriids and increasing the diversity of the macroinvertebrate community.

*Pisidium punctiferum* (Fig. 1g) - This rare species has been recorded only from Florida and Texas (Burch 1975b). Native to Mexico, Central America and the Caribbean Islands, it appears to have advanced northward from Mexico into Texas and then into Florida. The date of its introduction is unknown. Burch (1975b) suggests that standing or slow-moving water, aquatic vegetation, and muddy substrates are probably typical habitat features for the species. It appears to be a tropical species, but its ecological and socio-economic impacts are unknown.

### Family Corbiculidae

*Corbicula fluminea* (Fig. 1h) - Introduced from east Asia and first recorded from Washington State in 1938. It since has spread south to California and across the United States to Florida, and in the Mississippi River system from Louisiana north to the upper Ohio River (Burch

1975b). This is a very prolific, opportunistic species that has imposed a serious problem in competition with endemic species of bivalve fauna, clogs pipelines, and is a serious pest of dredged sands destined to be used in the manufacture of concrete (Morton 1979). The species probably was introduced with the arrival to the U.S.A. of Chinese immigrants who in their native land cultivate the species for food (Morton 1979). See Britton (1979) for details of the species' biology and ecology summarized in Table 2.

### Family Dreissenidae

*Dreissena polymorpha* (Fig. 1i) - The species was found and described for the first time in the northern part of the Caspian Sea and in the Ural River by Pallas in 1769 (Mackie *et al.* 1989). In the early 19th century the geographical range of *D. polymorpha* was dramatically extended: To Hungary in 1794; then a rapid invasion of Britain, first in Cambridgeshire in the 1820's, London in 1824, Yorkshire 1831-33, Forth and Clyde Canals in 1833, and in the Union Canal near Edinburgh in 1834, with numerous other records from 1835 onwards (Morton 1993); the invasion was just as rapid in Germany, to Rotterdam in 1827, Hamburg in 1830 and Copenhagen in 1840 (Morton 1979). The invasion of the zebra mussel throughout the former USSR was just as startling; from the Davina River Basin in 1845, through the Mariinsk Canal system to western Europe, and more recently (1960's) through the Oginski and Moscow Canals (Mackie *et al.* 1989). Extension of its range in the former USSR is still occurring at a rapid rate. The species appeared in the Scandinavias in the 1940's and since has appeared in numerous Swiss lakes (Mackie *et al.* 1989). It is now in Italy, Finland, Ireland, and the Iranian coast of the Caspian Sea (Mackie *et al.* 1989).

The zebra mussel was first introduced into Lake St. Clair in 1985 or 1986 via freshwater ballast from an oceangoing vessel (Hebert *et al.* 1989) and spread to all the Great lakes within two years. By 1991 it had spread outside the Great Lakes drainage systems to the Mississippi River and within two years the species had migrated downstream to its current southern limit at New Orleans. The species now occupies most of the major river systems, such as the Mississippi, Missouri, Ohio, Illinois, Tennessee, Cumberland, and Hudson rivers. Carlton (1993) describes twenty-three different potential mechanisms by which the species has been or can be dispersed in the larval and adult stages. See Nalepa and Schloesser (1993) for details of the species' biological and ecological attributes summarized in Table 2.

The ecological and socio-economic impacts are the severest of all species introductions to date. Mackie *et al.* (1989) describe nine different categories of impacts:

(1) **Industrial and Domestic Pipelines:** Accumulations cause (i) reductions in the bore of pipes; (ii) reduced flow through the pipe due to friction loss (turbulent flow instead of laminar); (iii) electro-corrosion of steel or cast iron pipes; (iv) deposition of empty mussel shells at the pipe outlet; and (v) tainting and possible contamination of the water upon death (especially when killed as part of a massive control program).

(2) **Underground irrigation systems.**

(3) **Encrusting the hulls of boating and sailing vessels.**

(4) **Loss of endemic species of Unionidae.** Gillis and Mackie (1994) have since shown that all native unionids on the Ontario shores of Lake St. Clair, where the mussel was first introduced, have been eliminated by the zebra mussel.

(5) **Increased their potential as vectors of parasites whose definitive hosts are commercially important species of fish and/or waterfowl.**

(6) **Fouling of fishing gear**, especially trap nets and pound nets that are left in the water for extended periods of time.

(7) **Encrusting of navigation buoys to the point that the buoys sink deeper in the water than normal.**

(8) **Formation of shoals of shell debris on beaches that will detract from the beach's recreational and aesthetic value.**

(9) **Loss of commercial fisheries**, especially fish species that feed on plankton that zebra mussels will quickly deplete through their filtering feeding activities.

*Dreissena bugensis* (Fig. 1j) - The species was first found in Lake Ontario in 1989 and may have been introduced at the same time as the zebra mussel, but because it can live in deeper water the species may not have been discovered until later. Its ecological and socio-economic impacts are similar to the zebra mussel. However, because it can live as an infaunal species in profundal sediments (Claxton and Mackie 1995) its ecological impacts will be extended to deeper water. The biological and ecological characteristics summarized in Table 2 are based on descriptions in Dermott (1993).

## GENERAL CHARACTERISTICS OF RESERVOIRS

A thorough description of the general characteristics of regulated rivers is beyond the scope of this paper and readers are referred to Neel (1963), Hall (1971), Ackerman *et al.* (1973), Baxter (1977), Hannan (1979), and Ward and Stanford (1979a). These authors give excellent descriptions of the morphological, physical, chemical, and biological characteristics of impoundments and are liberally utilized below. However, only aspects of each of those characteristics which might affect the successful invasion of exotic species of mollusks in regulated rivers is discussed below.

## MORPHOLOGICAL CHARACTERISTICS

The shoreline development of impoundments is usually much greater than that of natural lakes and typically has a dendritic shape. The creation of bays offers increased opportunities for exotic species to inhabit compared with the original stream bed. The dendritic arms of the new impoundment represent the mouths of parent streams and generally contain a composite of riverine and lentic species. Although the development of the shoreline is ultimately reduced through waves, currents and ice, the species assemblage is different than in the lake proper. Only the truly lentic forms are found in the deepest part of the impoundment which is typically near the dam. The diversity of species in the impoundment itself will depend on the physics and chemistry of the water, especially with respect to thermal stratification and the development of anoxia in hypolimnial, or at least deeper, water.

If the impoundment has annual drawdowns, shallow areas of bays and inlets and margins of the main impoundment will be dominated by species that can survive desiccation for extended periods (months) of time. These species must not only be able to tolerate drying conditions but freezing conditions in temperate climates as well. In tropical climates the species (*e.g.*, pomaceans) must be able to burrow into the mud to avoid desiccation.

The maximum depth, normally near the dam structure, will determine whether thermal stratification will occur. Very few mollusks occur in the hypolimnia of lakes, the most common being a few species of sphaeriids, such *Pisidium conventus* and *Sphaerium nitidum*. However, none of the introduced sphaeriids are typical inhabitants of profundal sediments. The only species that exhibits several adaptations to a profundal existence is *D. bugensis*, as discussed below. Otherwise, most of the introduced species are common in the shallow epilimnial (below the drawdown level) regions of lakes (Figs. 2 and 3), assuming that their tropical or temperate requirements are present.

## PHYSICAL CHARACTERISTICS

Temperature and turbidity are probably the two most important physical variables to affect the distribution and abundance of introduced mollusks. Temporal and spatial variations in molluscan communities will occur because each species has its own thermal thresholds for growth and reproduction. The main parent stream and the upper reaches of the impoundment receiving these waters generally will have cooler temperatures than the main impoundment. Also, the daily variations in temperature will be greater than in the main impoundment. Hence, euthermous forms will be especially common in these areas. Below the impoundment, where water temperatures will be cold if there is hypolimnial discharge, cold stenotherms may occur, but generally water temperatures fluctuate widely enough that euthermous forms are present here as well. Stenothermous forms are characteristic of impoundments in climatic regions that show only small seasonal variations in temperature. For example, cold stenotherms will be common in arctic climates and warm stenotherms in tropical climates.

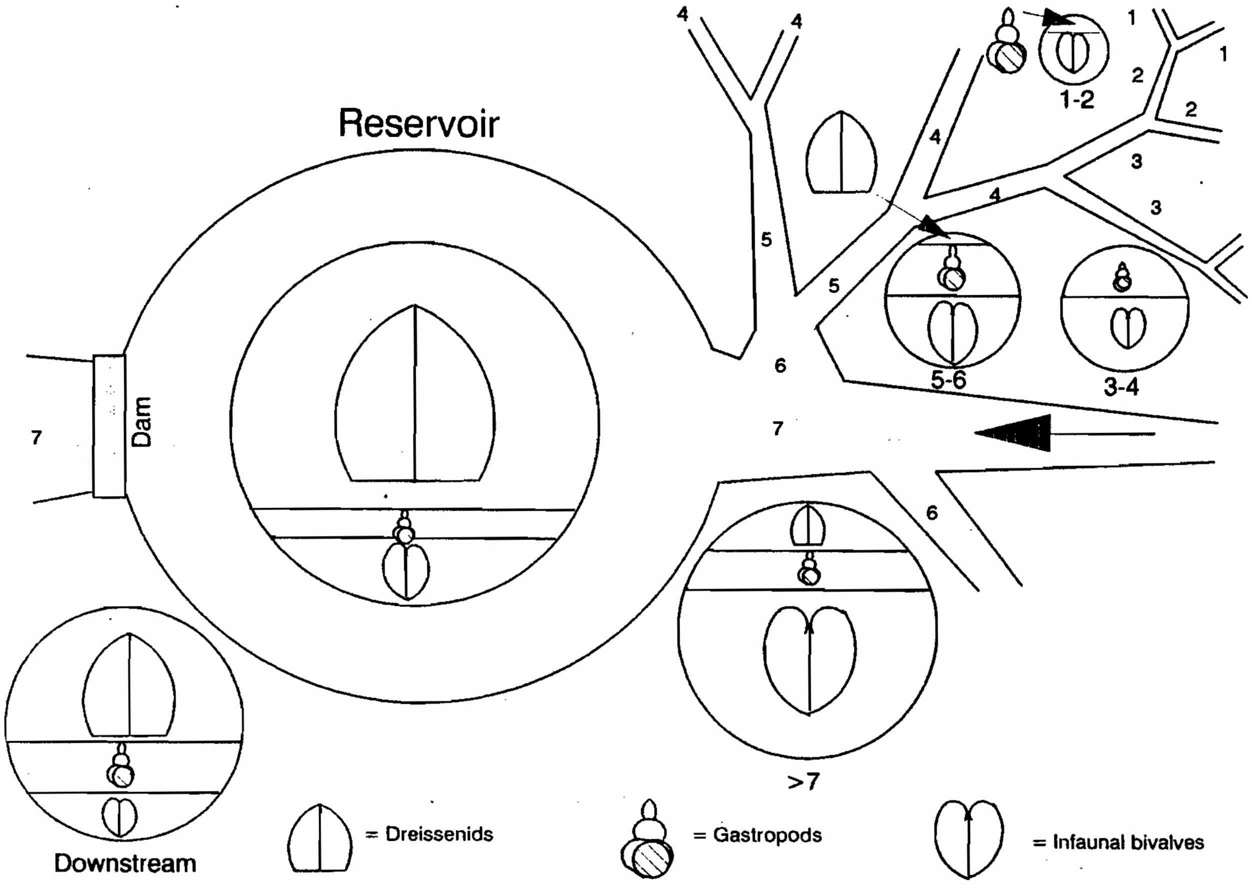

Figure 2. Schematic representation of changes in functional feeding habits of mollusks and modes of life upstream and downstream of an impoundment as predicted by the River Continuum Concept. The relative size of each circle and the segments within depict the dominance of each molluscan habit and habitat within the stream orders (numbers) shown.

Vertical variations in temperature also are present in most impoundments, but only those deep enough will form hypolimnia where temperatures will be close to 4°C throughout the year. Many impoundments do not form a distinct hypolimnion, but temperatures in the lower strata may still be about 7 to 10°C lower than in the upper strata. Because most temperate species of mollusks have thermal thresholds for growth around 10°C and for reproduction around 15°C, the temperature difference is sufficient to prevent the formation of large biomasses in deeper water strata. Of the exotic mollusks, the exception might be *D. bugensis* (Figs. 2 and 3), as discussed below.

Turbidity has direct and indirect effects on mollusks. Turbidity directly affects the respiration and filtration rates of bivalves, the rates declining with increasing turbidity (Burky 1983). Turbidity indirectly affects mollusks in impoundments because high silt loads eventually cover their preferred substrates. Infaunal forms (*e.g.*, most bivalves) will be favored over epifaunal forms (especially gastropods) and byssate bivalves, although it appears that *D. bugensis* may be an exception (Figs. 2 and 3), as discussed below. In general, substrates become softer and siltier with increasing distance from the inflow. This would suggest that epifaunal forms will dominate the upper reaches (nearest the inflow) while infaunal forms will prevail in the lower reaches (Figs. 2 and 3). However, some infaunal species have a preference for (or can tolerate) erosional substrates which are firm (Figs. 2 and 3).

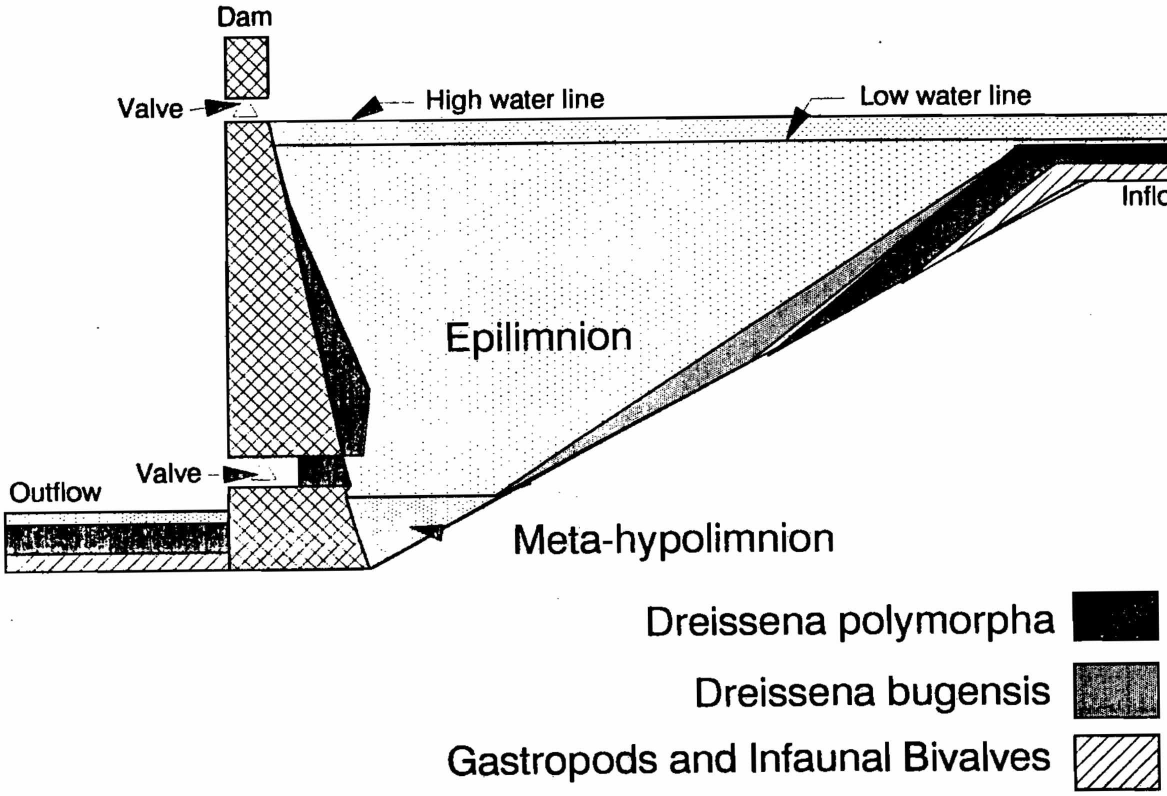

**Figure 3. Schematic longitudinal profile through the inflow, reservoir, and discharge showing relative abundance and location of dominant exotic mollusk groups. Thickness of areas indicate relative abundance.**

## CHEMICAL CHARACTERISTICS

All mollusks have a requirement for calcium but the threshold levels for growth and reproduction differs for each species. Assuming that these levels are present, the next most important chemical variable is probably dissolved oxygen content. Very few species, including exotics, can tolerate anoxia for extended periods of time. Impoundments which are eutrophic to mesotrophic will have lower oxygen concentrations in the deeper strata than in the upper stata. This, with cooler temperatures, probably limits the vertical distribution of most mollusks to the epilimnial depths.

Other chemicals are of indirect importance. For example, nutrient levels, such as phosphorous content, is important in that it limits algal productivity which grazing gastropods and filter feeding bivalves depend upon for food. Alkalinity, pH and hardness usually are related to calcium levels, so if calcium content is suitable these variables probably will not affect variations in abundance of the species within the impoundment. The cycling of nitrogenous compounds (*e.g.*, nitrate, nitrite, ammonia) is mainly a microbial process and large accumulations of ammonia and/or nitrite are lethal to mollusks, but the occurrence and abundance of mollusks are not directly affected by either compound until such conditions arise.

## BIOLOGICAL CHARACTERISTICS

Baxter (1977) gives some general principles which help to predict the course of development of a new ecosystem and provides a general conceptual framework for interpreting observed events. Among these are Thienemann's Rules of diversity, the concept of succession, the concept of pulse stability, the concept of the ecotone, and the theory of island biogeography. All will help to predict the success of each of the exotic species during the maturation of the impoundment. Some species may be more successful during the early stages of impoundment, before the floor is covered with fine silt. The most opportunistic species will move in first and some probably will prevail. Others will be more successful after conditions have stabilized.

Dreissenids and corbiculids probably are the most opportunistic species of all the molluscan species that have been introduced. Their numbers and distribution throughout the impoundment may change over time, but they will persist. Some even will be found in the drawdown zone but if they do not withdraw with the falling water level they will perish. This is supported by events that occured in some of the first reservoirs to be constructed on the River Volga in the former USSR; chironomids colonized in huge numbers first, along with motile aquatic arthropods and *Dreissena* (Baxter 1977). Other mollusks, and tubificid oligochaetes remained confined to the old river bed. Tubificid oligochaetes invaded the reservoir later. Dreissenids will not dominate until the plankton community develops. If the parent streams have low primary production, it will take two to three years to develop a large phytoplankton biomass. Often during the initial stages, filamentous forms of blue-green algae dominate, but dreissenids will not succeed because they utilize diatoms or single-celled green algae.

The development of an eulittoral zone (zone between high water and low water marks) is dominated by the practice of drawdown (Baxter 1977). In natural lakes this zone is subjected to a short period of flooding (usually spring) followed by a long period of exposure (summer, fall, and winter). In reservoirs the situation is commonly reversed, with a long period of submergence (spring, summer, and part of the fall) and a short period of exposure (late fall and winter). Drawdowns reduce the diversity of benthic species because those caught in the drawdown zone without some adaptation to survive exposure will perish. The most successful macrophytes are emergent species because they do not collapse when the water level recedes; submerged species rely on the buoyancy of water to keep them afloat and will collapse and die during drawdowns. Hence, littoral fauna, such as many species of gastropods, including most exotic species, are poorly represented in reservoirs with extensive drawdowns.

It is conceivable that dreissenids could alter the concepts in reservoir ecology, particularly pulse stability and successional changes. Dreissenids are very productive and their enormous numbers may alter the duration and/or the magnitude of pulse stability of the reservoir because dreissenids exhibit their own pulse stabilities. For example, the filtering activities of enormous numbers of dreissenids is well known to accelerate the sedimentation rate of suspended particles, including algae, which will affect primary and secondary productivity in the water column. This is bound to affect the pulse stability, trophic relationships, and hence successional changes within the reservoir.

## ADAPTABILITY OF EXOTIC MOLLUSKS TO REGULATED RIVERS

Ward and Stanford (1979b) examined the effects of stream regulation on changes in the diversity and abundance of benthic invertebrates in 23 different reservoirs (relative to unregulated streams or stations further downstream). Of 14 that reported effects on Mollusca, 8 reported increases in abundance, 4 reported decreases in abundance, 1 reported no change in abundance, and 1 reported an increase in gastropod abundance but a decrease in bivalve abundance. Although diversity was calculated for all benthic invertebrates, only 1 reported an increase in diversity, the rest reported decreases in diversity in the reservoir. It is difficult, if not impossible, to make a general conclusion regarding the success of exotic species in reservoirs. Some species will succeed in upstream locations only, others within the impoundment, and still others in downstream locations only. There will be other species that will succeed only in specialized habitats, such as *Pomacea* within drawdown zones. Table 2 summarizes the main biological and ecological features of each of the exotic species. These are examined and discussed below in order to predict the success of species according to their adaptability to reservoirs with specific reference to their (1) mode of life and habitat; (2) dispersal mechanisms; (3) physiological adaptations to desiccation, turbidity tolerance, thermal tolerance, and hypoxia tolerance; (4) predators; (5) parasites; (6) reproductive potential and productivity; (7) life cycle; and (8) food and feeding habits.

### MODE OF LIFE AND HABITAT

Prosobranchia

Exotic viviparids and ampullariids are so large that vegetation will not support them. Usually they are found living on the sediment feeding on epipsammic algae and detritus. Pomaceans are amphibious and have a lung for respiring while in the atmosphere and a ctenidium for respiring while submerged. They also oviposit their shelled eggs on land, the newly hatched snails seeking water when born or, like the adults, burrowing into the mud for several months until water reappears. The pomaceans prefer slow-moving, warm water and are common in the eulittoral zones of lakes, ponds, and rivers. *Bythinia* also is benthic and occurs on the sediments. The remaining prosobranchs tend to live in littoral and sublittoral zones grazing on attached algae, but becaue these zones are poorly developed in reservoirs with fluctuating water levels, they will not become dominant members of the reservoir molluscan community. Exotic species tend to be most common on depositional type substrates and, therefore, become most abundant in streams with low velocities, such as those entering many lakes (Figs. 2 and 3), or on sandy bottoms of lakes.

## Pulmonata

As with native pulmonates, their exotic counterparts are most abundant in the littoral and sublittoral regions of lakes. Most have very thin, fragile shells and cannot maintain themselves in strong currents characteristic of low order streams. Moreover, as the river continuum concept predicts, grazers, like gastropods, are not abundant until epiphytic algae begins to accumulate in stream orders above 3 (Figs. 2 and 3).

## Sphaeriidae

Native sphaeriids occur in a wide variety of aquatic habitats and conditions. However, the exotic species, while tolerant of a wide variety of water quality including some organic enrichment (*e.g.*, mesotrophy to eutrophy), are more common in lentic waters than in lotic ones, except large rivers (*e.g,,* St. Lawrence River). The exotic species will occur in reservoirs and will migrate to deeper waters to avoid fluctuating water levels. Unlike native species of *Musculium* and one species of *Sphaerium* (*occidentale*) which have adaptations for life in ephemeral habitats (McKee and Mackie 1980, 1981, 1983), the exotic species will occur mainly in areas that are permanently below the drawdown zone (Figs. 2 and 3). None of the exotic species are known to occur in small streams, but large densities are common in rivers with depositional substrates (Mackie and Qadri 1973). Like all bivalves, sphaeriids are filter feeders but are capable of a form of deposit feeding where cilia on the foot direct food particles through the pedal gape to the labial palps where initial food sorting occurs.

## Corbiculidae

*Corbicula* is an opportunist and will quickly invade a wide variety of habitats (*e.g.*, streams, rivers and lakes in silt, firm sand with emergent vegetation, stable gravel, rip rap, or even concrete channels) under a variety of aquatic conditions (Ingram 1959, Sinclair and Isom 1961, Bickel 1966, White and White 1977, Britton 1979). *Corbicula* populations can be markedly affected by fluctuating water levels, but even after a population has been seriously depleted, total repopulation can occur within one to two years (White 1979). Densities of Asian clams in reservoirs can be greater in the hypolimnion (*e.g.*, 12 m) than in the epilimnion (8 m), although dissolved oxygen levels must be near saturation (Abbott 1979). Because of colder temperatures in the hypolimnion (maximum 20°C) than in the epilimnion (maximum 27°C), the allometry of shell growth is depressed in deeper water (Abbott 1979). For these reasons, and others discussed later, corbiculids will successfully adapt to a variety of reservoirs ranging widely in morphology and limnology and become one of the dominant filter feeders in the benthic communities upstream, within the reservoir, and downstream (Figs. 2 and 3).

### Dreissenidae

Large freshwater lakes and rivers are the favorite habitats of dreissenids (Strayer, 1991). However, zebra mussels also do well in cooling ponds, quarries, and irrigation ponds of golf courses (Mackie and Schloesser 1995) and are capable of living in brackish water or estuaries where the salinity does not exceed 8 to 12 ppt (Strayer and Smith 1993, Kilgour *et al.* 1994). The incipient lethal salinity for zebra mussel post-veligers is near 2 ppt and for adults (5-15 mm) it is between 2 and 4 ppt (Kilgour *et al.* 1994). Quagga mussels are less tolerant of higher salinities than are zebra mussels (Mills *et al.* 1995).

*Dreissena polymorpha* has an exclusively epifaunal habit, but *D. bugensis* has an ability for an infaunal habit in deeper waters and epifaunal habit in shallower waters (Mackie 1995). In the Great Lakes the ratio of quagga to zebra mussels increases with increasing depth down to about 50 m (Mackie 1995). The greatest densities of both species in Lake Erie occur at about 12 m. Only quagga mussels occur in Ekman grab samples taken at these depths (Dermott 1993). It appears that quagga mussels are able to alter their shell allometry for an infaunal existence; they are thinner and lighter in weight in soft profundal sediments than on firm inshore substrates, whereas zebra mussels exhibit little or no changes in shell allometry on firm or soft substrates.

With the adaptability of quagga mussels to life in soft sediments at great depths, provided oxygen is near saturation, dreissenids have the potential to invade all types of reservoirs (Figs. 2 and 3). Densities will be low to negligible in the drawdown zone but will increase down to about 12 m (Figs. 2 and 3). Hypolimnial discharges deeper than this and which maintain high oxygen levels (Mackie *et al.* 1983) will encourage growth on the concrete structure, especially in the region of the discharge port, and may even foul the port itself (Figs. 2 and 3). Also, dreissenids tend to develop greater biomasses in flowing waters (*e.g.*, pipelines) of moderate velocities (< 1.5 m/sec) where their filter feeding efficiency can be enhanced by a constant delivery of food to the siphons. Dreissenids also will be a dominant part of the downstream benthic communities (Figs. 2 and 3).

## DISPERSAL MECHANISMS

Most authors (Kew 1893, Boycott 1936, Baker 1945, Malone 1965, 1966; Rees 1965) agree that waterfowl and shorebirds are primarily responsible for dispersing mollusks overland to isolated bodies of water. Gastropods attach to feet and feathers of birds and once removed from water, retain their viability for a sufficient period of time to effect overland dispersal for great distances (Malone 1965a). Large insects are effective dispersal agents for small snails and clams over short distances (Rees 1965). In general, external transport (*e.g.*, feet and feathers) is a more effective dispersal mechanism than internal transport via the digestive tract (Mackie 1979). Hanna (1966) ascribes the introduction of most western North American mollusks to ports of entry in baggage and mail, although most are marine and terrestrial mollusks. A very common dispersal mechanism is transport of snails by immigrants, from their native countries, for food, some (e.g *Pomacea* spp.) of which is sold as escargot. Other introductions have been attributed to the aquarium trade.

These dispersal mechanisms probably apply to most exotic species of mollusks, including Corbiculidae, but the dreissenids have a variety of other potential dispersal mechanisms. The diversity of potential dispersal mechanisms of byssate biofoulers, in particular, has impressed upon us the near impossibility of preventing their spread once introduced. There are at least twenty-three different means by which larval and adult dreissenids can be dispersed, only three of which are naturally mediated: water currents, birds, and other animals (Carlton 1993). "It is not a question of IF it will get here, it is a question of WHEN it will get here" is now a common cliche for describing the dispersal powers of these two families of biofouling bivalves.

While currents are an effective mechanism for dispersing planktonic larval stages, it is not effective for sustaining populations in streams. The byssal apparatus will help to maintain the position of the adults in the streams, but the flow of water will carry the larvae well downstream of the parent population which ultimately will disappear, unless an upstream population can rejuvenate the colony. This is discussed further under "Life Cycle." Hence, the planktonic larval stage is seen as an adaptation for life in lentic systems, including reservoirs.

## PHYSIOLOGY

The physiological ecology of mollusks has received considerable attention and a thorough treatment of the gastropods and bivalves is beyond the scope of this paper. Burky (1983), McMahon (1983) and Aldridge (1983) give detailed accounts, including feeding, respiration, reproduction, life cycles, etc. in bivalves, pulmonates and prosobranchs, respectively. Although few references are made to exotic species, the descriptions for native species probably apply (with some exceptions) to exotic species.

Of the physical and chemical stresses that characterize many impoundments, desiccation, siltation or high turbidity, variable temperatures, and anoxia will favor the development of species that physiologically have requirements for these features, or else have the tolerances or abilities to adapt to these features. Organisms that live in impoundments must be able to (1) either avoid desiccation in the drawdown zone or be adapted to survive prolonged periods of exposure; (2) live an infaunal existence in the soft sediments that settle out in the impoundments, adapt to an infaunal existence if they are epifaunal, live only on substrates (*e.g.*, concrete wall of dam) that support an epifaunal existence, and/or tolerate the high turbidities characteristic of impounded streams; (3) be eurythermous over all temperature ranges or at least in their normal temperature range (*e.g.*, tropical eurytherms and temperate eurytherms); and (4) have the physiological adaptations to deal with short periods of anoxia or low oxygen tensions or else live only in the epilimnion which may at times be supersaturated with oxygen.

### Desiccation

Of all the exotic species of mollusks, only a few appear to have adaptations for surviving prolonged periods of desiccation or exposure. Most species of *Pomacea* can burrow into the mud and survive several months without water. Other species of introduced gastropods cannot tolerate even short periods of desiccation. Although some native sphaeriids (*e.g.*, *Sphaerium occidentale,* *Musculium securis*) have physiological and life history adaptations for life in ephemeral habitats (McKee and Mackie 1980, 1981, 1983), the exotic species of sphaeriids have been reported only from permanent bodies of water, in fact mostly large lakes or rivers.

Asian clams can survive short periods of exposure, but will succumb after about two weeks in low humidities and four weeks in high humidities (McMahon 1979b). In fact, McMahon (1979b) recommends periodic drawdowns in reservoirs to control Asian clam populations. Zebra and quagga mussels are even less tolerant of desiccation, surviving only 5 days in low humidities to 13 (quagga mussels) or 22 days (zebra mussels) at high humidities (Ussery and McMahon 1994). However, unlike Asian clams which desiccate, the mussels succumb to accumulations of toxic anaeorobic end-products during desiccation (Ussery and McMahon 1994). The time to death of zebra mussels is even more rapid at freezing temperatures, occurring in less than 24 h at -3°C (= 27°F) (Clarke *et al.* 1993).

Apparently, the only species of exotic mollusk that will adapt to and dominate in the drawdown zone are the ampullariids. All other mollusks must either withdraw with the receding water level, or else perish.

### Turbidity Tolerance

Of all the physiological parameters of importance to exotic mollusks, tolerances to turbidity are the least understood. Associated with increasing loads of suspended particles is increasing sedimentation rates, especially in lakes or streams with depositional current velocities. Also, increased turbidities reduce light penetration resulting in lower primary production. Therefore, non-grazing and infaunal forms of exotic mollusks will be favored over grazing and epifaunal forms. As a result, gastropods will be replaced by filter-feeding bivalves. Although filter-feeding rates are depressed in waters with high silt loads (Sprung and Rose 1988), much of the inorganic material (*i.e.*, silt) is captured by gill cilia and mucous and is rejected as pseudofaeces. Studies in European lakes and canals indicate that *Dreissena* plays a significant role in processes of biological self-purification and improvement in water quality in aquatic systems (Mackie *et al.* 1989). This is not a consequence of a high individual filtration capacity, but rather to the enormous numbers of mussels that usually prevail in aquatic systems. As bivalves, the zebra mussel's filtration rate (10-100 ml/ind./hr) is intermediate between Unionidae (60-490 ml/ind./hr) and Sphaeriidae (0.6-8.3 ml/ind./hr) (Hinz and Schiel 1972, Stanczykowska *et al.* 1976).

However, large biomasses of pseudofaeces accumulate on the bottom, often causing a shift in energy from the pelagic zone to the benthic zone (Griffiths 1983). This has implications on altering concepts in reservoir ecology, especially pulse stability and successional changes. Dreissenids may add to the duration and/or the magnitude of pulse stability because their population densities exhibit their own pulse stabilities; the filtering activities of enormous numbers of dreissenids is bound to affect the pulse stability of the reservoir. Similarly with succession, dreissenids dramatically accelerate the sedimentation rate of suspended particles, and the rates of trophic changes that normally occur in new impoundments could be dramatically altered.

## Thermal Tolerance

Tolerance of gastropods to temperature extremes is an intra- and interspecific variable (Aldridge 1983). Some pomaceans can cool themselves 5-10°C below ambient by evaporation when heat stressed, but this mechanism is available only to snails adapted to a terrestrial life (Aldridge 1983). Aquatic snails must either tolerate or acclimate to changing temperatures.

The thermal tolerances of biofouling bivalves (dreissenids and corbiculids) are well described but virtually unknown for most other exotic Mollusca. The upper thermal limits of *Corbicula* are higher than for *Dreissena*. The instantaneous upper lethal temperature of *Corbicula* is 44°C for clams acclimated to 32°C and the lowest lethal temperature is 33°C for clams acclimated to 5°C (Mattice 1979); 36°C is the minimum long-term chronic upper lethal temperature (McMahon and Williams 1986). For zebra mussels the chronic lethal temperature is 34-37°C (McMahon *et al.* 1993) while the acute lethal temperature ranges from about 33°C (Jenner and Janssen-Mommen 1993) to 42.3°C (Neuhauser *et al.* 1993). However, previous acclimation temperature greatly affects both the acute and chronic lethal temperatures (Iwanyzki and McCauley 1993, McMahon *et al.* 1993). The tolerance times at different temperatures increases with increasing acclimation temperature and decreasing shell size and decreases with increasing exposure temperature (McMahon *et al.* 1993).

Nearly all the thermal tolerance studies were conducted to determine the feasibility of using thermal stress to control biofoulers. Epilimnial temperatures in reservoirs usually are higher than temperatures in the parent streams, but the hypolimnial temperatures are colder than parent stream temperatures. In general, mollusks, like all other aquatic organisms in impoundments, adjust their upper thermal tolerance limits by acclimating to increasing summer temperatures as the summer progresses. Most mollusks have the ability to seek a preferred temperature and can usually find it in thermally stratified reservoirs. This includes even the byssate forms because they can translocate by releasing themselves from their byssal attachment and resettle in a more suitable thermal regime. Although their new position will depend on current patterns in the reservoir, most will resettle in a more downstream position.

## Hypoxia Tolerance

Of the exotic gastropods, only the pulmonates and ampullariids have the abilities to avoid anoxia by rising to the surface and respiring atmospheric oxygen. However, even they, as with all other exotic species, are obligated to utilize dissolved oxygen in the water when submerged and are essentially hypoxia intolerant. Ampullariids have a part of their mantle adapted into a gas-filled lung and can avoid anoxic conditions, but when submerged their ctenidial gill requires oxygenated water in order to survive.

There are distinct differences in the abilities of exotic species of mollusks to tolerate anoxia (McMahon 1979a, Aldridge 1983, Burky 1983, McMahon 1983, Holopainen 1987, Matthews and McMahon 1994), but none can survive prolonged anoxic conditions. The relatively poor tolerance of all exotic species to prolonged anoxia will restrict most species to the shallow, well oxygenated surface waters of reservoirs.

## PREDATORS

Fish and waterfowl, and occasionally aquatic mammals (muskrat, otters), are the main predators of all mollusks, including exotic species. Many waterfowl seek invertebrates high in protein and calcium contents, such as Mollusca, particularly during egg production periods (Rogers and Korschgen 1966, Krapu and Swanson 1975). Some turtles (*e.g.*, *Graptemys pseudographica kohnii*) also feed on Asian clams and small gastropods (Lindeman 1995).

The dreissenids, and to some extent the corbiculids, have planktonic larval stages which are preyed upon mainly by crustacean zooplankton (*e.g.*, *Cyclops*) and larval fish, but the relative importance of these prey groups to the total mortality of larval stages is unknown (Mackie *et al.* 1989). Conn and Conn (1993) reported predation of larval stages also by the cnidarian, *Hydra americana*. Hydrozoans often are present in large numbers attached to mussels and capture food in currents generated by the siphons of the mussels.

Adult zebra mussels have a very high nutritional value of the tissues, with 60.7% protein, 12.0% lipid, 19.0% carbohydrate, and 5.9% ash (Cleven and Frenzel 1992) and are consumed in large quantities by crayfish, fish, and waterfowl (Mackie *et al.* 1989). The nutritional value changes seasonally (Walz 1978). Perry *et al.* (1995) suggest that streams containing *Orconectes* crayfish either will be less susceptible to invasion by dreissenids or at least the mussels will be maintained at lower densities than streams without crayfish. However, as discussed below, the success and densities of dreissenids in streams will be more a function of the ability of upstream colonies being able to replace senescent populations downstream via settlement of veliger produced upstream.

Zebra mussels have been found in the stomachs of walleye, yellow perch, freshwater drum, white suckers, and a few others. The relative contribution of the fish species to predation of zebra mussels is unknown. The freshwater drum, *Aplodinotus grunniens*, has been investigated in detail by French and Bur (1993) who reported that predation on zebra mussels increases as drum size increases, with large drum feeding almost exclusively on zebra mussels. The freshwater drum has molariform pharyngeal teeth for crushing shells of the dreissenids (French and Bur, 1993), but the species is most common in large lakes and rivers.

The impact of waterfowl on zebra mussel densities is variable, from little or no effect to significant decreases, up to 97% in zebra mussel biomass in some lakes in the Netherlands, especially in the winter months (Mackie *et al.* 1989). In North America, dreissenids form a major part of the diet of greater (*Aythya marila*) and lesser (*A. affinis*) scaup, buffleheads (*Bucephala albeola*), oldsquaws (*Clangula hyemalis*), and white-winged scoters (*Melanitta deglandi*) (Knapton Long Point Bird Observatory, pers. comm.); the distribution of greater and lesser scaup at Long Point, Lake Erie appears to be influenced by the distribution of dreissenid beds.

There is a high probability that crayfish, fish, reptiles, waterfowl, and mammals will be important predators contributing to mortality of exotic mollusks in reservoirs. While some predators may limit the population sizes of some species of exotic gastropods, it is unlikely that any will limit the population sizes of the byssate biofoulers, or *Corbicula*.

## PARASITES

The parasites of some exotic species of gastropods are very harmful to humans. Paragonimiasis in man, caused by the Oriental lung fluke, *Paragonimus westermani,* uses *Thiara granifera* as its intermediate host (Abbott 1952). The deadly blood fluke, *Schistosoma mansoni*, has as its intermediate host, *Biomphalaria glabrata*. *Melanoides tuberculata* is the intermediate host of the human liver fluke, *Opisthorchis sinensis* (Dundee and Paine 1977). These parasites could become a major problem in reservoirs harboring their intermediate hosts.

Freshwater bivalves are common intermediate hosts of trematode parasites whose definitive hosts are fish, waterfowl, and sometimes man (Olsen 1967). Mackie (1976) has reviewed trematode parasitism of sphaeriids. Dreissenids are not common vectors of parasites (Stanczykowska 1977). Protists and digeans are the most common parasites, with Nematoda observed sporadically in zebra mussels. Many protists are common parasites, but they do not seem to "affect the numbers" of the zebra mussel (Stanczykowska 1977). Trematodes are less common parasites of zebra mussels than are protists, the greatest infestation rate observed being 10%. The most dangerous protists are ciliates of the family Ophryoglenidae which parasitize the digestive gland and may kill the mussel (Stanczykowska 1977). The only other parasitic ciliate reported in dreissenids is *Concophthirus*, but adverse effects on the bivalve host are unknown (Molloy *et al.* 1995).

Species of *Phyllodistomum* and *Bucephalus* are important parasites of dreissenids in lakes of the Netherlands (Davids and Kraak 1993); the infestation prevalence is usually about 1% and may go as high as 10%. The effects of parasites on *D. polymorpha* appear to be minimal, at least until high emissions of cercariae of *B. polymorphus* occur (Mackie *et al.* 1989). Intensity of parasitism by *P. folium* is directly correlated to shell size of *D. polymorpha*, the maximum number recorded being 200 at a shell size of 24-28 mm.

Toews *et al.* (1993) reported a 2.9% prevalence of plagiorchiid metacercariae in mussels and 2.7% prevalence of adults and juvenile aspidogastrids in mussels from two sites in Lake Erie. The ciliate, *Ophryoglena*, occurred with 1.3% prevalence at a site in Lake St. Clair and 2.7 to 4.3% prevalence at two sites in Lake Erie. Toews *et al.* (1993) concluded that mass development of zebra mussels may increase the infection rate in definitive hosts, especially fish and waterfowl. The oligochaete, *Chaetogaster limnaei*, and the chironomid *Paratanytarsus*, also have been reported as commensals in zebra and quagga mussels (Conn *et al.* 1994, Ricciardi 1994).

The only other "parasitic group" reported is sponges. Ricciardi *et al.* (1995) recently reported lethal overgrowths of three sponge species, *Eunapius fragilis*, *Ephydatia muelleri*, and *Spongilla lacustris*, on zebra mussels. The sponge colonies spread over the entire shell of the zebra mussel and smother their siphons. The sponges also inhibit settlement of dreissenids and outcompete them for hard substrate (Miner *et al.* 1995).

The parasites of reservoirs will include the extant and rheophilous parasites of the parent streams and those that are introduced by various vectors. The rheophilous parasites will tend to disappear and the parasitic fauna of lakes and slow rivers eventually will dominate. Fish parasitism is well documented for reservoirs (see Hoffman and Bauer 1971 for review), and Mackie *et al.* (1983) describe changes in fish parasitism in a new impoundment and differences upstream and downstream. It is anticipated that parasites introduced by exotic species of mollusks will exhibit similar patterns, with rheophilous assemblages dominating upstream, lacustrine assemblages dominating the reservoir, and the incidence of parasitism being reduced downstream.

## REPRODUCTIVE POTENTIAL AND PRODUCTIVITY

In general, ovoviviparous forms are less fecund than oviparous forms because brooding space for the developing larvae within parents is limiting. In sphaeriids, for example, the internal shell volume remains relatively constant so that the reproductive output cannot be significantly altered and always will be relatively low (Kilgour and Mackie 1990). Although the numbers are highly variable, ovoviviparous forms are about an order of magnitude less fecund than oviparous forms (*e.g.*, 10:100). Even though many ovoviviparous forms are parthenogenetic, reducing the risk of having to find a mate, the fecundities still are relatively low. Even ovipositing, oviparous forms have low natalities relative to planktonic oviparous forms. Ovipositing oviparous forms are about three to four orders of magnitude less fecund than planktonic oviparous forms (*e.g.*, 100:100,000 to 100:1,000,000).

The reproductive potential and productivity of dreissenids is the greatest of any mollusks that have ever been introduced into North America. Densities of veligers and adults in the Great Lakes are among the highest reported to date in the world. Mean monthly densities of veligers in the western basin of Lake Erie and its island region are 126-268/L in July and August, whereas European waters averaged about 10-100/L in the same period (Nalepa and Schloesser 1993). Mean densities (#/m$^2$) of adults range from about 54,000 - 779,000 in Lake Erie to 43,000 - 200,000 in Lake St. Clair (Pathy 1994). Average densities of adult mussels in European lakes range from about 5,000 to about 115,000/m$^2$ (Mackie *et al.* 1989).

The abundance of *D. polymorpha* appears to be related to trophic type, the largest populations occurring in mesotrophic to eutrophic waters (Mackie *et al.* 1989), although Stanczykowska (1964) found no relationship between abundance of *D. polymorpha* and trophic status of lakes. Dreissenids typically have a contagious distribution, often occurring independently of other molluscan species (Bishop and DeGaris 1976), although this may be because dreissenids have displaced other mollusks, as recent reports by Gillis and Mackie (1994) have shown.

*Dreissena* exhibits a tremendous development in numbers directly after invasion into a new habitat. Mackie *et al.* (1989) describe a period of intensive development usually lasting for about 5-10 years after which population density decreases and becomes more-or-less stable at a much lower level (Mackie 1993). Typically, two- to three-fold fluctuations (decreases and increases) in abundances occur, but population crashes, such as those that have occurred in some Mazurian lakes, are rare (Mackie *et al.* 1989). In Lake St. Clair, where the zebra mussel was first found in North America, populations increased for five years (1986 to 1991) and then decreased in 1992 and 1993 to about 50% of the peak value (Mackie 1993).

The biomass of *Dreissena* in a given body of water usually is related to the density (Stanczykowska 1976), but the average biomass of populations is highly variable among lakes (*e.g.*, 0.13 to 20 kg/m$^2$) and within lakes (*e.g.*, 0.05-10.5 kg/m$^2$) (Mackie *et al.* 1989). Some of this variation is due to variations in body condition of mussels and in length-weight relationships (Stanczykowska, 1964). The slenderness, flatness, and ratio of wet to dry weight show little variation within and among lakes, average size and weight tends to vary considerably among lakes but only slightly within lakes; body (tissue) weight and shell weight vary in the same manner among lakes (*i.e.*, lakes with high shell weights also have high body weights) (Mackie *et al.* 1989).

Estimates of annual production of *D. polymorpha* in European waters, including reservoirs, vary between 0.1 and 29.8 g/m$^2$/yr dry body weight and 3.3 and 525.9 g/m$^2$/yr total dry weight (Mackie *et al.* 1989). In the Great Lakes annual production of zebra mussels appears to be higher than most European populations, about 150 g/m$^2$/yr dry body weight (Dermott *et al.* 1993). In European waters the P/B ratio usually varies between 0.42 and 0.65 for dry body weight and 0.47 and 0.81 for total dry weight, but occasionally up to 6.8 (*e.g.*, Lake Constance) (Mackie *et al.* 1989). Dermott *et al.* (1993) reported a P/B ratio of 4.7 for a population in Lake Erie. There are no production data for dreissenids in North American reservoirs.

## LIFE CYCLE

Most gastropods are oviparous, laying eggs in masses on firm substrates such as macrophytes, rocks, and logs. Development is direct and tiny snails emerge from the eggs. The exceptions to this are the Viviparidae, which are ovoviviparous, and the Ampullariidae, which oviposit calcareous-shelled eggs under fairly dry conditions (Aldridge 1983). The numbers of eggs oviposited by oviparous forms varies considerably within and among species (Aldridge 1983), but rarely are more than 100 produced by one female (ampullariids may produce several hundred per female). The ovoviviparous forms are less fecund and usually produce less than 10 per parent.

The Corbiculacea are monoecious, the Sphaeriidae being simultaneous hermaphrodites (Mackie 1984) and *C. fluminea* apparently being dioecious or monoecious in lentic waters (Morton 1983) and female or monoecious in lotic waters (Morton 1986). Internal fertilization is used in all native species of bivalves and in *Corbicula*. However, in *Corbicula* the fertilized eggs are brooded in gill chambers of the parent where they develop through the trochophore, veliger, pediveliger, and straight-hinge stages before being released as umbonal juveniles to the plankton (Fig. 4b). The umbonal juveniles may swim for one to three days before they settle on the substrate to begin their benthic existence.

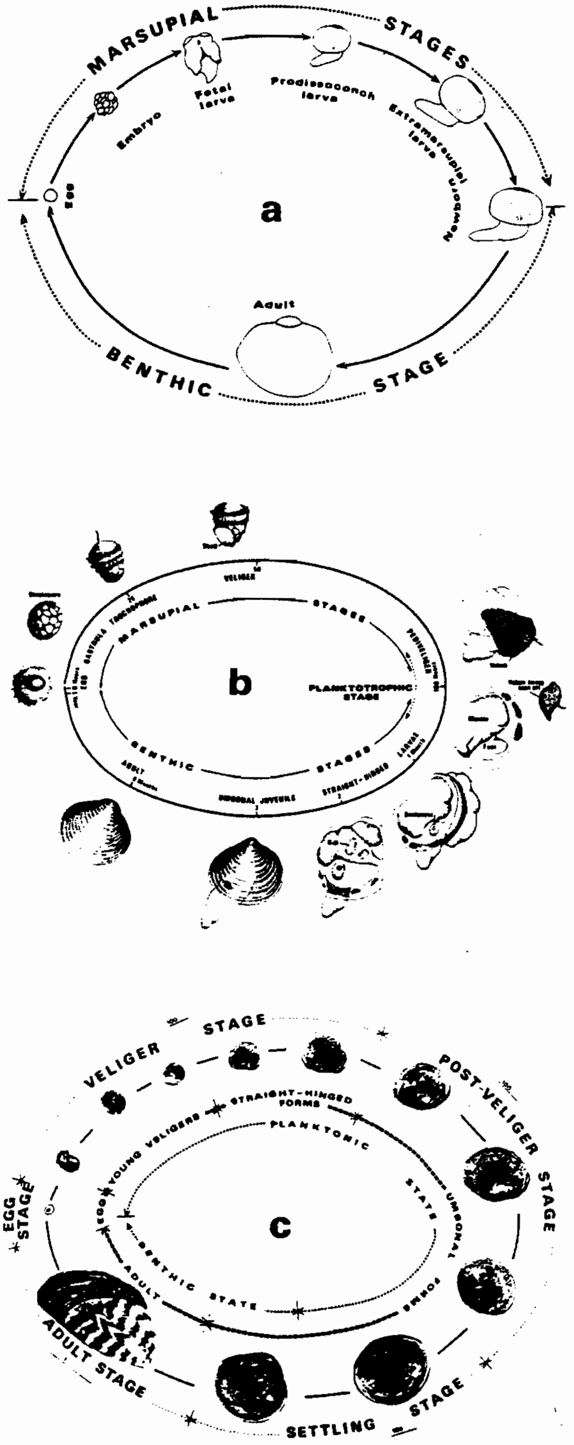

Figure 4. Life cycles of exotic groups of bivalves. (a) Sphaeriidae, (b) Corbiculidae, (c) Dreissenidae where text references to trochophore stages are shown as young veligers, D-form is shown as straight-hinge forms, velichoncha and pediveliger stages are shown as umbonal forms, and plantigrades are shown as the last settling stage.

The Sphaeriidae are ovoviviparous (Mackie 1978) and brood their young in brood sacs on the inner gills of the parent (Fig. 5). Four marsupial stages are recognized (Fig. 4a): (i) embryos first appear as gastrula in single-walled primary sacs, (ii) embryos develop most of the organ systems and mature through the fetal larvae stage to the shelled prodissoconch stage within brood sacs, (iii) prodissoconch larvae grow in size to become extra-marsupial larvae which outgrow their brood sacs and tear the sac wall to eventually lie free in the inner gill space, and (iv) extra-marsupial larvae are born through the excurrent siphon and begin a benthic existence as newborn. Complete larval development requires 1 to 3 months, depending on species.

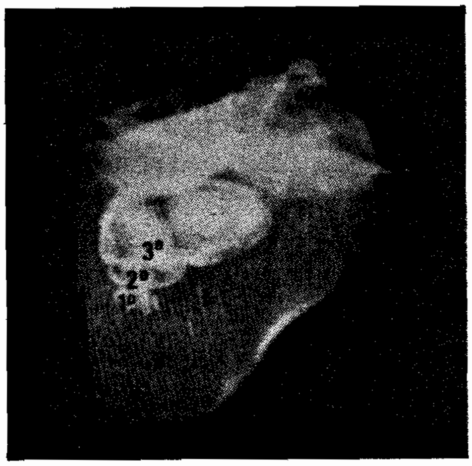

Figure 5. Photograph of inner gill of a sphaeriid showing a primary brood sac (1°) with embryos, a secondary brood sac (2°) with fetal larvae, and a tertiary brood sac (3°) with prodissoconch larvae (about 0.8 mm shell length).

*Corbicula* displays a lower fecundity than *Dreissena*, with 25,000 to 75,000 veligers produced in the lifetime of a single clam (Aldridge and McMahon 1978), compared with 100,000 to more than one million eggs produced annually by a single female zebra mussel (Nalepa and Schloesser 1993). Native species of Sphaeriidae, on the other hand, have very low fecundities (*e.g.*, 1 - 40 eggs per adult) because they are brooders (Mackie 1984). Because only a small number of larvae can be brooded by any one parent, the number of larvae that are produced is rather small. Hence, external fertilization and development partly explains why *Dreissena* will be much more prolific than native species of bivalves in North American surface waters.

The most prolific mollusk species in freshwater are the introduced dreissenids, with over one million eggs per female each year in its two to three year life span (Nalepa and Schloesser 1993). The larvae pass through several developmental stages, including trochophore, D-shape, veliconcha, pediveliger, and plantigrade (Fig. 4c), as described by Ackerman *et al.* (1994). However, up to 99% mortality of the larval stages may occur before settlement occurs (Nalepa and Schloesser 1993). Most of the mortality may occur during the settling event if the plantigrade form does not find a suitable substrate on which to attach. In spite of this high mortality, the dreissenids are the most productive of all the exotic mollusks (see Reproductive Potential and Productivity).

The best reproductive adaptations for life in streams are an ovoviviparous habit, where the young are brooded inside the parent, or an oviparous one where the eggs are attached to the substrate. These adaptations allow the animals to maintain position in the streams. Many can migrate further upstream by crawling against the current, especially during low-flow periods.

Possession of a planktonic larval stage may be a great dispersal mechanism, but it is not a good adaptive feature for sustaining adult populations in streams because the young cannot maintain their positions upstream. The distance that the larvae are carried depends upon the velocity and the duration of the planktonic stage. Because the planktonic stage of most dreissenids lasts 10 to 30 days (average 21 days) (Baldwin 1995), the larvae will be carried long distances before they are able to settle and attach to the substrate. Even in streams with low velocities (0.1 m/sec) larvae are not able to swim against the current and will be carried downstream. As an example, and selecting a stream with a low current velocity (0.1 m/sec) and larvae that develop and settle quickly in 10 days, the larvae will be carried 86.4 km downstream! (0.1 m/sec x 1 km/1000 m x 10 days x 60 sec/min x 60 min/hr x 24 hr/day = 86.4 km or 8.64 km/day). Hence, dreissenids introduced to a stream will survive one life span at best, unless they are dispersed again to the same site, which is not likely if there are no adults upstream, or there is an impoundment to retain the planktonic larvae. Indeed, reservoirs will serve to provide breeding habitats for establishing and maintaining populations downstream. Once rivers become slow enough and currents are such that the position of the developing larvae can be maintained up to and including settlement, the populations can be self sustained by the adults attached to the bottom. Indeed, without mainstream reservoirs, dreissenids would not succeed, or at least would not be as great a pest, in most rivers in North America. For example, streams with an average velocity of 0.1 m/sec (= 8.64 km/day) would carry larvae with development times of 20 to 30 days, about 173 to 260 km downstream before settlement would occur. For a population to maintain its position within 100 m of itself, the average water velocity must be less than 0.00006 m/sec, a velocity exceeded in most streams, and possibly many reservoirs (based on Drift distance = Average Development Time x Water Velocity; therefore, velocity = 100 m/21 days = 100 m/(21 days x 24 hrs/day x 60 min/hr x 60 sec/min) = 0.00006 m/sec). Only back eddies in pools of rivers, mainstream impoundments or reservoirs would provide such currents for the complete development of the larvae.

Fig. 6 shows the predicted changes in relative abundance of exotic species of mollusks in an unregulated river (Fig. 6a) relative to a regulated river (Fig. 6b). Populations of dreissenids can be greatly enhanced by regulating the stream because the reservoir acts as a breeding ground for downstream populations. Any increase in abundance of dreissenids probably will be accompanied by a decrease in abundance of other mollusks, due either to competition with other filter feeders or to settlement and attachment upon their shells which ultimately leads to their death.

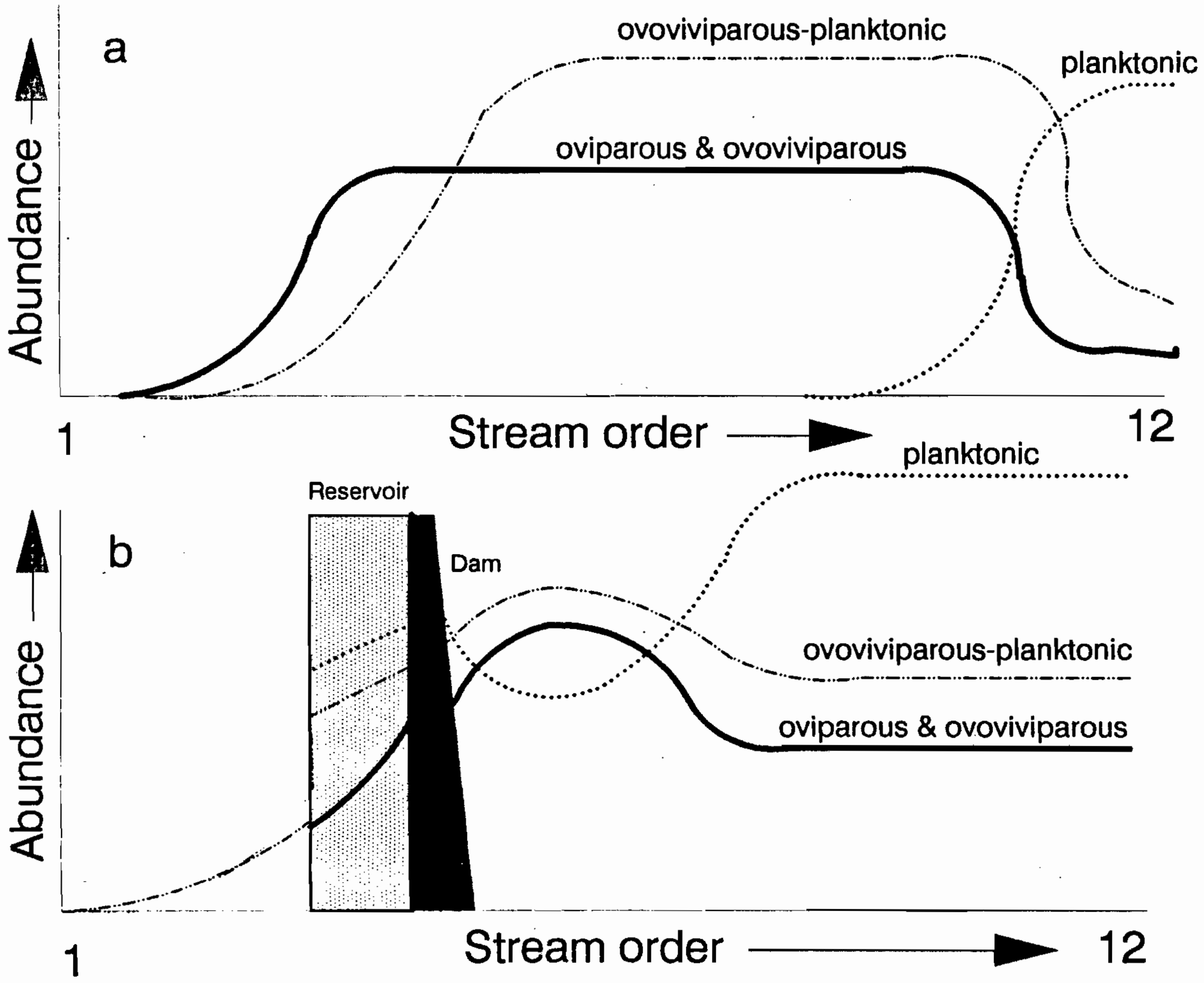

Figure 6. Schematic representation of the relative abundance of exotic groups of mollusks according to their types of reproduction in: (a) an unregulated stream and (b) a regulated stream. Planktonic group includes dreissenids; ovoviviparous-planktonic includes the corbiculids; oviparous and ovoviviparous includes all the gastropods and sphaeriid clams.

## FOOD AND FEEDING HABITS

All gastropods, including the introduced species, are grazers. They have a radula that is used like a rasp to grind attached bacteria, protists and/or algae from hard surfaces. Some feed on algae attached to sand or mixed in with sand (epipsammic feeders). Some feed on detritus and take in sand particles as triturating agents to grind the detritus (Aldridge 1983, McMahon 1983). Epipsammic feeding involves taking in one or a few large sediment particles into the buccal cavity, where organic material is ingested and sand particles are regurgitated (Aldridge 1983).

Other gastropods are deposit feeders, usually on sediments that are fine-grained, relative to the body size of the animal. Many viviparids are adapted for filter-feeding using cilia on their ctenidial gill (Aldridge 1983), although not as efficiently as occurs in bivalves.

In bivalves, food selection is performed by a variety of cilia, including those in the mantle cavity (gills, labial palps and foot) and in the stomach and midgut. In dreissenids, cilia in the mantle cavity and stomach select particles of 15-40 μm for food but can filter out particles as small as 0.7-1.0 μm in diameter from the water (Mackie *et al.* 1989).

The filtration rate of dreissenids is affected by shell size, turbidity, temperature, and concentrations of certain sizes and kinds of algal cells (*e.g.*, *Chlamydomonas*) and bacterial cells (Mackie *et al.* 1989). The filtration capability of *D. polymorpha* in relation to its role as a clarifier of water in an entire lake, epilimnion or littoral zone, has been reviewed by Neumann and Jenner (1992); they describe applications of zebra mussels in water quality management, particularly as water clarifiers. Although mussels are efficient clarifiers, the suspended materials accumulate on the bottom as faeces and pseudofaeces. The size of faecal and pseudofaecal pellets varies with mussel size and the settling velocities, and the rate of accumulation greatly exceeds normal sedimentation processes (Dean 1994).

## POTENTIAL IMPACTS OF EXOTIC MOLLUSCA IN RESERVOIRS

The potential impacts can be divided into three general categories: (i) Little or no potential ecological impact; (ii) potential beneficial socio-economic uses; (iii) potential ecological and/or socio-economic harm. The extent of the impacts will depend not only on the species that invade the reservoir but also the uses of the reservoir.

### SPECIES WITH LITTLE OR NO OBVIOUS ECOLOGICAL IMPACT

Most introduced species will have little or no obvious impacts on the ecology of the ecosystem. Although most freshwater mollusks are intermediate hosts of numerous species of trematodes whose definitive hosts are fish or waterfowl, there are few studies that have assessed the added impact of introduced mollusks with their trematodes on definitive hosts. It is not anticipated that the exotic species of mollusks will add significantly to the infestation of definitive hosts that are already infected by trematodes of native species of mollusks. All exotic species will have to compete with their native counterparts for food and space, but very few (*Bythinia tentaculata* may be an exception) are known to have replaced native species; rather they seem to have added to the diversity of molluscan fauna. Included in this group are

*Valvata piscinalis*
*Cipangopaludina chinensis malleatus*
*Cipangopaludina japonicus*
*Bythinia tentaculata tentaculata* (with some exceptions)
*Potamopyrgus antipodarum* (see addendum)
*Radix auricularia*

*Physella acuta*
*Stenophysa marmorata?* (little known about its ecology)
*Stenophysa maugeriae?* (little known about its ecology)
*Sphaerium corneum*
*Pisidium amnicum*
*Pisidium henslowanum*
*Pisidium punctiferum*

In summary, 13 of the 22 species of introduced mollusks appear to be of little or no potential ecological risk to most reservoirs.

## SPECIES OF POTENTIAL SOCIO-ECONOMIC BENEFIT

Species which are known to have some beneficial uses (given in parentheses) include

*Cipangopaludina chinensis malleatus* (as food, especially for immigrants)
*Cipangopaludina japonicus* (as food, especially for immigrants)
*Marisa cornarietis* (as predator of eggs and young of *Biomphalaria glabrata*)
*Pomacea bridgesi* (as food, especially for immigrants, and escargot)
*Pomacea canaliculata* (as food, especially for immigrants, and escargot)
*Corbicula fluminea* (as food, especially for immigrants)

In summary, 6 of the 22 species of introduced mollusks have been demonstrated to have some beneficial uses to man. Because many of the species also have potential negative impacts (see below), it is not anticipated that most of the species listed will be introduced to the reservoir specifically for their potential beneficial uses.

## SPECIES OF POTENTIAL ECOLOGICAL AND/OR SOCIO-ECONOMIC HARM

There are several types of potentially harmful socio-economic impacts. These include (i) Vectors of Human Parasites; (ii) Agricultural Impacts; (iii) Industrial and/or Utility Impacts; (iv) Navigational Impacts; and (v) Recreational Impacts. The ecological impacts can be divided into: (i) Biological Impacts, and (ii) Limnological Impacts.

## SOCIO-ECONOMIC IMPACTS

### (i) Vectors of Human Parasites:

Species which are known to act as intermediate hosts of parasites harmful to man include (parasites given in parentheses):

*Pomacea canaliculata* (rat lung worm, *Angiostrongylus cantonensis*, causes a form of meningitis in man)
*Melanoides tuberculata* (human liver fluke, *Opisthorchis sinensis*)

*Thiara granifera* (Oriental lung fluke, *Paragonimus westermani*)
*Biomphalaria glabrata* (human blood fluke, *Schistosoma mansoni*)

These mollusk species, in particular, should be actively searched for and eliminated before they spread.

(ii) Agricultural Impacts:

*Pomacea canaliculata* is known to cause crop damage and should be eliminated if the reservoir is to be used for irrigating agricultural crops of Taro or rice. Also, *Dreissena* and *Corbicula* are known to clog irrigational pipes.

(iii) Industrial and Utility Impacts:

If the reservoir is to be used by industries and utilities for cooling water or drinking water, accumulations of *Corbicula* and *Dreissena* will cause (i) reductions in the bore of pipes, (ii) reduced flow through the pipe due to friction loss (turbulent flow instead of laminar), (iii) electro-corrosion of steel or cast iron pipes, (iv) deposition of empty mussel shells at the pipe outlet, and (v) tainting and possible contamination of the water upon death (especially when killed as part of a massive control program).

(iv) Navigational Impacts:

If the reservoir is on a major shipping route, or is used by barges, *Dreissena* can encrust the hulls of boats and sailing vessels and encrust navigation buoys to the point that the buoys will sink deeper in the water than normal.

(v) Recreational Impacts:

Most reservoirs have some recreational value, including swimming, sailing, and fishing. *Dreissena* is known to cause formations of shoals of shell debris on beaches that will detract from the beach's recreational and aesthetic value. For example, broken shells are sharp and cut the feet of swimmers. Many beaches on Lake Erie have signs posted recommending the use of sandals to avoid cuts on feet. The impacts of dreissenids on sailing and fishing are described above under Navigational Impacts and below under Biological Impacts.

## ECOLOGICAL IMPACTS

(i) Biological Impacts:

The Mississippi River and Illinois River, with their impoundments, are valuable resources for Unionidae which are harvested for the Pacific cultured pearl industry. Dreissenids have been shown to cause losses of endemic species of Unionidae through a variety of mechanisms (Mackie 1991, Gillis and Mackie 1994). *Dreissena*, occurring in enormous numbers, also increases the potential of parasites finding an intermediate host, thus increasing the risk for parasitizing commercially important species of fish and/or waterfowl. Losses of commercial fisheries, especially fish species that feed on plankton removed by the filtering feeding activities of zebra mussels, also can be anticipated. These losses can occur through fouling of fishing gear, especially trap nets and pound nets that are left in the water for extended periods of time. Increases in dreissenid biomasses may be accompanied by decreases in biomasses of sphaeriids and some gastropods and chironomids (Dermott *et al.* 1993, Dermott and Klerc 1995) and increases in biomasses of amphipods, flatworms, oligochaetes, and some gastropods and chironomids (Griffiths 1993). However, recent studies by Dermott and Klerc (1995) show that increases in abundance of *D. bugensis* have been followed by decreases in the abundance of the burrowing amphipod, *Diporeia*, which in turn has been accompanied by declines of smelt which feed on the profundal amphipod. The increases in light transmission (see below) has been accompanied by increases in biomasses of sublittoral macrophytes.

(ii) Limnological Impacts:

Because of their efficient filtering activities, large numbers of *Dreissena* and *Corbicula* can cause rapid changes in the limnological features of impoundments. This includes (i) increases in water clarity, where Secchi depths doubled within three or four years of invasion, with a concomitant lowering of phosphorous and chlorophyll *a* levels (Leach 1993); (ii) increases in levels of soluble reactive phosphorous, silica, nitrate-nitrogen and ammonia-nitrogen (Beeton 1995); and (iii) accelerated sedimentation rates of inorganic and organic contaminants bound to particulates (Dobson 1994, Dean 1994).

## CONCLUSIONS

The mollusks with the greatest potential for reservoir ecosystem impacts are those with life cycles that have planktonic larvae (Fig. 6). Main stream impoundments will act as breeding reservoirs that throughout the year will "seed" and replenish downstream habitats and populations that, as with upstream populations, would not otherwise be able to sustain themselves. Upstream populations cannot be self sustaining because currents continually erode adult populations and carry larvae downstream for distances approximately equal to velocity (km/day) x duration of larvae in plankton (average 21 days). For a population to maintain its position within 100 m of itself in the stream, the average water velocity must be less than 0.00006 m/sec, a velocity exceeded in most streams and possibly many reservoirs.

The degree of biofouling downstream would be mostly a function of the reproductive and growth potential of the breeding colony in the upstream reservoir(s). This in turn is a function of the quality of the habitat(s) in the reservoir(s). Substrates that promote an epifaunal existence favor the development of byssate biofoulers while substrates that promote an infaunal existence will promote non-byssate biofoulers. Because non-byssate biofoulers themselves provide substrate for byssate biofoulers, the probability of colonization of reservoirs by biofoulers is greatly enhanced (once they have been introduced).

Possession of a planktonic larval phase is an adaptation for life in lentic habitats, including reservoirs (Fig. 6). Oviparous and ovoviviparous habits are adaptations for life in lotic habitats. Biofouling mollusk species are all exotic species characterized by possession of a planktonic larval phase which provides recruitment that exceeds by four to five orders of magnitude that of native species and other exotic species with oviparous or ovoviviparous habits. Exotic mollusks which are either ovoviviparous or oviparous egg layers are not biofouling, but competition for food and space may affect the diversity of native Mollusca either upstream or downstream of impoundments. Impacts of exotic species will include little or no impact (most gastropods), beneficial uses (*e.g.*, as escargot), and negative impacts, including human health concerns (some gastropods are intermediate hosts of dangerous human parasites) and numerous ecological and socio-economic impacts.

## ADDENDUM

Since the preparation of this manuscript, another exotic species of gastropod was reported from the Great Lakes by Zarenko *et al.* (1995). This newest introduction is *Pomatopyrgus antipodarum* of the family Hydrobiidae (Fig. 7). It is native to New Zealand. The species was first discovered in Britain in brackish water in 1859 and then in 1893 in freshwater (McMillan 1968). McMillan (1968) described the species as *P. jenkinsii*, but Winterbourne (1970) considered the name to be a synonym of *P. antipodarum*. The species was discovered first in 1991 in Lake Ontario offshore Wilson, New York, at a depth of 15-20 m; it since has been found in numerous other sites in 4-20 m depths of water in Lake Ontario and the Welland Canal (Zaranko *et al.* 1995). It appears to be most abundant in sand and fine sand (silt). The species is mostly parthenogenetic with males rarely occurring (McMillan 1968, Winterbourne 1970). Keeled forms with and without spines also are common in the Great Lakes. As far as is known, the species is not a nuisance in its native habitats, but in Lake Ontario it occurs in large densities, exceeding those of other hydrobiids, suggesting that it may be outcompeting other hydrobiids in the Great Lakes (Zaranko *et al.* 1995). Other features of the species are summarized in Table 2.

Figure 7. *Potamopyrgus antipodarum*, ht = 5.1 mm, collected from Lake Ontario near Wilson, New York, left is dorsal view, right is aperature view showing paucispiral operculum.

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# CONTRIBUTED PAPERS

## SESSION I: AQUATIC BIOLOGY AND WATER QUALITY

**Saturday, March 4, 1995**

**Moderated by:**

**Steven Hamilton**
**Austin Peay State University**

# ASSESSMENT OF BIOTIC INTEGRITY IN TWO SECOND ORDER STREAMS IMPACTED BY GOLF COURSE CONSTRUCTION

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**ABSTRACT. Earth moving, timber removal and other activities associated with construction of a golf course near Pickwick Dam, Hardin County, Tennessee, exposed two second order streams to intense sedimentation and channel alteration. In order to formulate a stream rehabilitation plan, the biological integrity of the impacted streams were assessed and compared with the integrity of two unimpacted reference streams. Simple qualitative multiple habitat sampling methods were used to assess these streams. Macroinvertebrate samples were collected with a benthic dip net and hand collected from rocks and other course materials in the streams. Macroinvertebrates were collected in approximate proportion to their abundances. In the laboratory specimens were and identified to the lowest practical taxon, usually genus or species. Because specimens were picked in only approximate proportion to their abundances, it was necessary to assign them to relative abundance categories before biological metrics could be calculated. To assess the biotic integrity of these streams based on these samples the following biological metrics were used: taxa richness; biotic index (B.I.); the ratio of Ephemeroptera, Plecoptera and Trichoptera to Chironomidae (EPT:Chiro); and functional feeding group (FFG) analysis. Taxa richness was low in the impacted streams compared to richness in the reference streams. Calculation of EPT:Chiro shows that the impacted streams were dominated by generally more pollution tolerant chironomids, while the reference stream communities were dominated by the generally pollution intolerant EPT (mayflies, stoneflies, and caddisflies). High biotic indices for the impacted sites further demonstrated the presence of a pollution tolerant community compared to that found in the reference streams. A functional feeding group analyses revealed a more sediment tolerant community dominated by collector-gatherers and shredders while the more sensitive collector-filterers and scrappers (grazers) were absent or under represented. In contrast, the reference streams had a nearly balanced representation from each of these four FFGs. This simple biological assessment of the aquatic macroinvertebrate communities demonstrates the degradation of the biological condition of the impacted streams due to heavy sediment loading.**

# ASSESSMENT OF WATER QUALITY IN MIDDLE TENNESSEE USING MACROINVERTEBRATE COMMUNITY ANALYSIS: METHODS AND RESULTS

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**ABSTRACT. Water pollution abatement, prevention and regulation is the mandate of the Tennessee Division of Water Pollution Control (WPC). Six field offices are located throughout the state to monitor and enforce State water quality laws. WPC is the lead agency defining and biologically assessing ecoregion reference streams in Tennessee. Forty counties in middle Tennessee are under the jurisdiction of the Division's Nashville Field Office (NFO). NFO biological surveys focus on benthic macroinvertebrates (BMI) as indicators of overall stream health. Biological integrity of the BMI community is assessed primarily through quantitative sampling of the highly productive riffle habitat using traveling kick methodology (TKM), and qualitative sampling of other available habitats. The quantitative TKM sample is subsampled by randomly removing 200-300 macroinvertebrates from the sample using a gridded pan, as described by the U.S.E.P.A. Rapid Bioassessment Protocol manual (Plafkin et. al. 1989). Some researchers believe subsampling methods provide an insufficient representation of the full sample. However, we believe subsampling of the TKM sample provides sufficient biological data to allow a thorough analysis of water quality. To test this, TKM samples were collected at six sites in Rock Creek, Coffee County, and three sites in Trace Creek, Humphreys County. For each site, a comparison of biological metrics from subsamples (total of 200-300 organisms) versus a completely picked sample (all organisms removed), provided the same overall water quality assessment. Comparisons of replicated 100-organism subsamples show high similarity implying that each subsample is representative of the community within the full sample. The subsample adequately represents the relative abundance of the taxa within the stream community as long as a large representative sample has been taken. The data demonstrates that, when compared with more conventional methods, subsampling coupled with the TKM decreases sample processing time, while providing the same overall water quality assessment.**

## INTRODUCTION

There are 19,124 miles of streams in Tennessee, ranging from slow-moving sandy-bottom streams in the west to cascading mountain streams in the east. Unfortunately, human activities have had a detrimental effect on most stream ecosystems. The protection of Tennessee waterbodies began with the creation of a Stream Pollution Control Board in 1945, followed by the comprehensive state Water Quality Control Act of 1971. The prevention and regulation of water pollution in Tennessee is the mandate of the Department of Environment and Conservation, Division of Water Pollution Control.

The state is divided into 6 regions of varying size, each served by a field office located in the major cities (Figure 1). Regional enforcement of state laws and monitoring of water quality within the 40 counties of Middle Tennessee is handled by the Nashville Field Office (NFO).

Responsibilities of the NFO include ensuring compliance of state-permitted wastewater dischargers (also known as point source dischargers) through on-site inspections and monitoring of the facilities' operational reports. These permitted dischargers are primarily industries and municipal sewage treatment plants (STP). In addition, all types of nonpoint pollution sources are monitored and regulated, except for agriculture and silviculture activities which are generally exempt from water quality laws. Industrial stormwater runoff and stormwater from major cities (populations >100,000) must now be monitored and meet certain requirements and limitations. Runoff from construction activities is also regulated with strict erosion control measures now required. Tennessee is one of the few states with a program regulating stream alteration activities such as channelization, gravel dredging, and bridge and road construction.

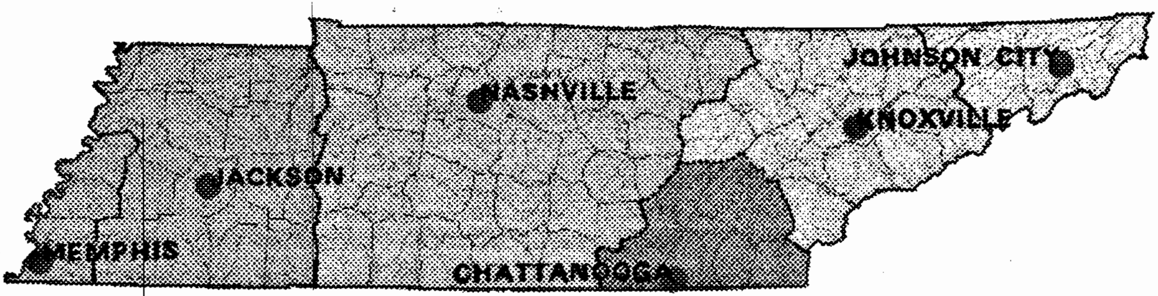

**Figure 1.** Locations of Tennessee Division of Water Pollution Control regional field offices and the areas these serve.

A constant effort is made, especially by Division biologists, to assess all of the waterbodies in the region to determine the degree to which they support their designated uses which include: (1) propagation of fish and aquatic life, (2) recreation, (3) irrigation, and (4) livestock watering and wildlife. The health of streams and lakes is assessed through chemical and biological surveys. Permit compliance is often determined by surveying the receiving stream upstream and downstream of a point source discharge. Also, WPC is the lead agency defining and biologically assessing ecoregion reference streams within Tennessee.

NFO stream surveys focus on benthic macroinvertebrates as indicators of overall stream health. Other characteristics of the study site are investigated as well. Habitat assessment is performed, evaluating the upstream watershed, geologic formation, substrate composition, canopy cover, and bank stability. Velocities, depths, width, and total flow of the stream reach are measured. Physical parameters such as temperature, pH, conductivity and dissolved oxygen are recorded, and a wide range of chemical parameters are evaluated.

Evaluation of aquatic organisms to determine water quality is advantageous because stream biota respond both to chronic pollutants present in low amounts and to large doses of a pollutant infrequently released into a waterway, both of which chemical sampling usually miss. Benthic macroinvertebrates (BMI) are particularly good indicators of pollution because they are naturally present in high numbers and are very diverse. Unlike fish, BMI cannot swim away from a pollution "slug" traveling downstream, and most species complete at least one life cycle every year, so the effect of a contaminant on any stage of the life cycle will be evident within a shorter period of time (Klemm *et al.* 1990). The biological integrity of the BMI community is assessed by sampling all available stream habitats.

Many agencies shy away from using BMIs to determine water quality and permit compliance because past methods of sampling have been very time consuming, requiring many days in sample processing. Regulators have always been in short supply, so it has been difficult to justify spending days to weeks at a microscope on one "wildfire" while hundreds "burn out of control." The U.S. Environmental Protection Agency published a 1989 manual (Plafkin *et al.* 1989) suggesting the use of a subsampling method which substantially decreases the processing time required for the hundreds to thousands of macroinvertebrates taken in a typical sample. This method allows samples to be processed much faster allowing the regulator to use the results for enforcement in a more timely manner and freeing the biologist to monitor more streams.

Some researchers have questioned the effectiveness of subsampling and are concerned that subsamples are not representative of the entire sample. However, this subsampling technique has been used typically in conjunction with two fixed-position 1 $m^2$ kick net samples that may not be representative of the entire riffle community. Therefore, subsampling of this small and possibly unrepresentative sample may not be appropriate. The traveling kick method sample, which is used by NFO, covers all microhabitats within the riffle, providing a more representative sample. This larger sample is then subsampled. The resulting subsample should represent the same relative abundances of taxa within the riffle community sampled, as that which would be found in the entire sample.

## METHODS

### Study Sites

Figure 2 plots 23 of the 62 biological surveys performed by the NFO within the last two years and graphically presents the 16,892 $mi^2$ region regulated by NFO. Much of the data within this paper concerns two of these surveys conducted in 1993. In Humphreys County, Trace Creek was surveyed and compared with a watershed reference site on nearby Hurricane Creek. A second biological survey was conducted on Rock Creek in Coffee County with a site on a different Hurricane Creek in adjacent Moore County used as a reference site.

Trace Creek is the receiving stream of the Waverly sewage treatment plant (STP). This is an extended aeration lagoon facility designed to treat and discharge 2 million gallons/day (MG/D). Relatively frequent violations of permitted effluent limitations have occurred in the past, especially for ammonia nitrogen. Two sites on Trace Creek were surveyed, one located just upstream and the other 0.62 miles downstream of the discharge point. A comparable site on nearby Hurricane Creek served as a watershed reference. Because most receiving streams flow through urban areas and may already be stressed, a watershed reference stream provides a comparison to the receiving stream upstream of the discharge. This allows for a determination of baseline degradation in the receiving stream above the discharge point.

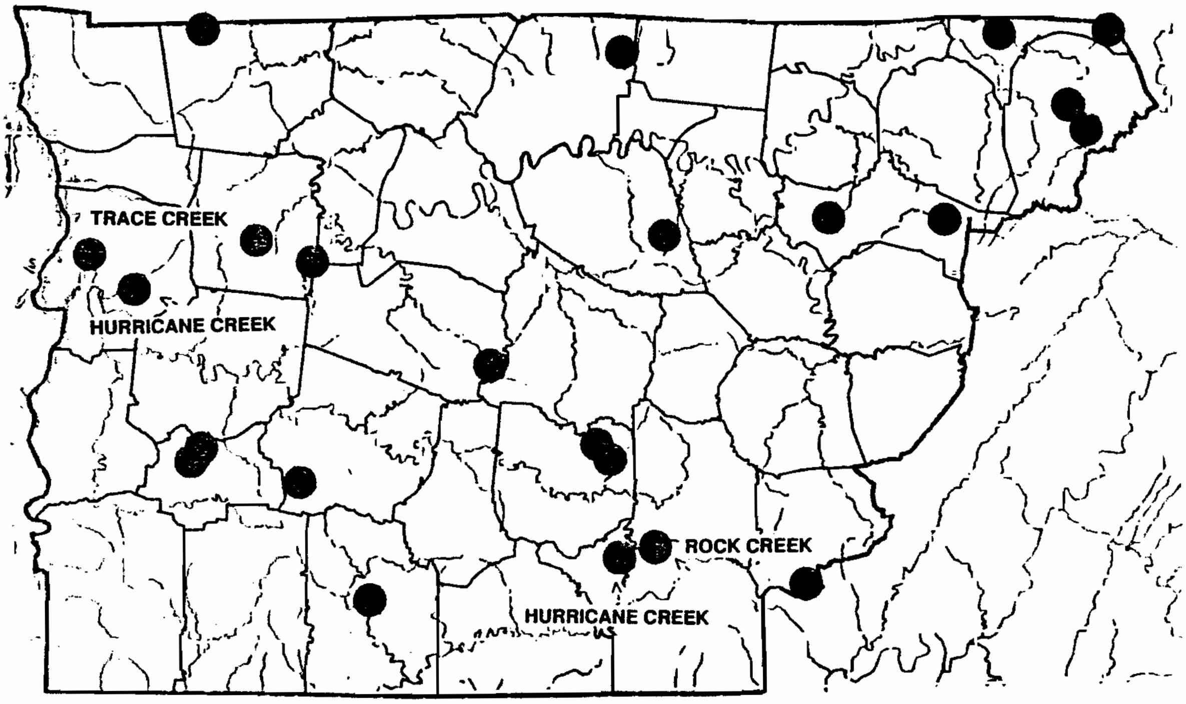

Figure 2. Locations of selected biological surveys conducted by NFO within Middle Tennessee (1993-1994). Area shown = 16,892 $mi^2$

Rock Creek receives wastewater from the Tullahoma STP. This facility is designed to treat and discharge 5 MG/D, but has historically been overtaxed, with peaks of up to 15 MG/D. The treatment facility is a sequential batch reactor, which discharges effluent periodically (usually every two hours) rather than continuously. This results in unnaturally rapid and massive changes in flow and chemical nature on a regular basis. Variations occur in all measurable physical parameters for at least 1.5 miles downstream of the discharge point. These variations usually occur 12 times per day. Measurements at a site located 0.5 mile downstream showed a cyclical increase of 567% in the flow rate of Rock Creek during the batch discharge at this STP.

Five sites on Rock Creek were surveyed. One site upstream of the discharge was used as the reference comparison for the sites downstream of the discharge and four sites were selected below the discharge with three in the areas of established low dissolved oxygen and one site in an area of recovery. A site on nearby Hurricane Creek (Moore County) was used as a watershed reference for comparison to all sites on Rock Creek.

## Sampling Method

The BMI community was assessed through sampling of all available stream habitats. Riffle habitats were sampled semi-quantitatively using a traveling kick method (TKM). A kicknet was placed on the substrate and moved in an upstream and diagonal direction while the substrate was agitated in front of the net by the feet or hands of the sampler. Macroinvertebrates disturbed from the substrate are carried into the net by the current. The riffle was sampled over a set length of time and area, the movements taking the sampler to all areas of the riffle. The collected material was then placed in a sieve bucket. Larger debris was rinsed clean in the bucket and discarded. The sample was then placed in a mason jar, labeled, preserved, and returned to the NFO laboratory for subsampling. A second riffle TKM sample was collected at each site from which all of the organisms were picked at the site, preserved, and returned to the field office for identification. Other available habitats in the stream were sampled qualitatively. These habitats may include root masses along the banks, selective picks of substrate too large to be kick sampled (i.e., large rocks, logs), organic debris within the stream (i.e., leaf packs, small twigs), or aquatic macrophyte beds. Therefore, survey collection resulted in two complete riffle samples from each site, a riffle kick sample which was brought back for subsampling, and another riffle kick sample which was completely picked in the field.

## Subsampling

Subsampling of the TKM sample was performed using an 18 in. x 12.5 in. white plastic tray which had been divided into 28 two in. x two in. grids. The sample, with debris, was placed into the tray and evenly distributed among the grids. Excess water was carefully removed with an aspirator until the sample settled into the grids. A grid was then randomly selected and all organisms within the selected grid were removed and counted.

Random selection of grids and removal of organisms within those grids was repeated until a minimum of 100 organisms had been removed. It may be necessary to select more than one grid to achieve the minimum of 100 organisms. Once a grid is selected, all organisms were removed from it, even if the total number of organisms exceeds 100. In order to insure that the subsamples were representative of the entire sample, two or three replicate 100-organism subsamples were removed from the tray without redistribution of the sample within the gridded pan. For most of the stream surveys which were conducted during the last two years, replicate 100-organism subsamples were taken from each sample. In Trace Creek two replicate subsamples were taken from each tray; for Rock Creek, three subsamples were taken.

## Statistics and metrics

All organisms were identified to the lowest practical taxon whether from TKM subsamples or completely field-picked TKM samples. Morisita's coefficient of similarity was used to compare the replicate subsamples. This statistic measures similarity based on the shared taxa present and the abundances within those taxa. The index range is from 0.0 (complete dissimilar) to 1.0 (complete similarity).

From the BMI sample data, comparisons were made between reference conditions (upstream of the discharge and at the watershed reference site) and the impacted conditions (downstream of the discharge). Comparisons are based on metrics (Table 1) generated by the BMI data following procedures in EPA's Rapid Bioassessment Protocol (Plafkin *et al.* 1989) and the Arkansas RBP (Shackelford 1988).

TABLE 1. Bioassessment metrics used for analyses of benthic macroinvertebrate samples.

| Metric | Description |
|---|---|
| Taxa richness [a] | total number of taxa (species or species group) identified in the sample or community |
| Biotic Index [b] | a measure of the community tolerance to pollution based on assigned tolerance values of taxa collected in samples (see formula and description in text below) |
| Ratio of EPT and chironomid abundances [a] | compares abundances of the generally pollution intolerant Ephemeroptera (mayflies), Plecoptera (stoneflies) and Trichoptera (caddisflies) to abundances of the generally pollution tolerant Chironomidae (midge flies) |
| Dominant taxa (Shackelford, 1988) [c] | number of the five most abundant taxa common to both impacted and reference sites |
| EPT Index [a] | the number of EPT (mayflies, stoneflies, caddisflies) taxa (*i.e.*, richness of EPT) |
| Community Similarity [c] | Percent Similarity; similarity based on shared taxa and numbers within those taxa |
| Ratio of Shredders to Total # of indiv. [a] | ratio of the abundance of the shredder feeding group to the total abundance of the sample |

[a] - Score is a ratio of study site to reference site x 100
[b] - Score is a ratio of reference site to study site x 100
[c] - A comparison of the reference station is incorporated

Following the EPA RBP procedures, a score representing the sum of the metric scores is obtained for each site and compared to the reference site score to obtain the percent comparability to reference conditions. The percent comparability obtained for each site will fall within one of the designated condition categories: severely impaired, substantially impaired, slightly impaired, or nonimpaired (Table 2). The degree of impairment within a study site was determined using results from both the subsampled TKM sample and the completely-picked TKM sample.

TABLE 2. Condition categories based on the percent comparability of the study site to the reference conditions (Plafkin *et al.* 1989).

| % comparability of study site to reference conditions | Condition category |
|---|---|
| >83% | Nonimpaired |
| 54-79% | Slightly impaired |
| 21-50% | Substantially impaired |
| <17% | Severely impaired |

The biotic index is a commonly used metric used to assess the overall pollution tolerance of the BMI community. The biotic index is calculated by assigning each taxon a predetermined value according to its known or presumed tolerance to pollution (Klemm *et al.* 1990, Lenat 1993). The biotic index is calculated as follows:

$$BI=\frac{\Sigma n_i a_i}{N}$$

where $n_i$ is the number of individuals in taxon i, $a_i$ is the assigned tolerance value of taxon i, and N is the total number of individuals in the sample. Individual tolerance values ($a_i$) range from 0 - 10 and the final biotic index (BI) is a mean tolerance (0 - 10) for the entire community providing a measure by which the pollution status of the site can be determined. When used as part of the EPA RBP metrics, a comparison is made to a reference site. In this study, BI scores were calculated using data from both the subsamples and completely picked samples.

## RESULTS AND DISCUSSION

Within many of the NFO stream surveys, each subsample was replicated for quality assurance. Morisita's coefficient of similarity revealed near perfect similarity of taxa and number within these replicated subsamples, implying that the subsamples accurately and repeatedly represent the BMI community present within the full TKM sample. The similarity ranged from a low of 0.873 to 1.00 (completely similarity) and average 0.98.

Taxa richness was determined for the two replicated 100-organism subsamples from TKM samples collected at the two sites on Trace Creek and the single reference site. The replicate subsamples were very similar in number of taxa present (Figure 3). At the site upstream of the STP, there were 19 taxa in the subsample and 22 in the second subsample. There were 20 taxa in one subsample and 19 taxa in the other subsample downstream of the STP. From the watershed reference site there were 13 and 15 taxa, respectively, in the first and second subsamples.

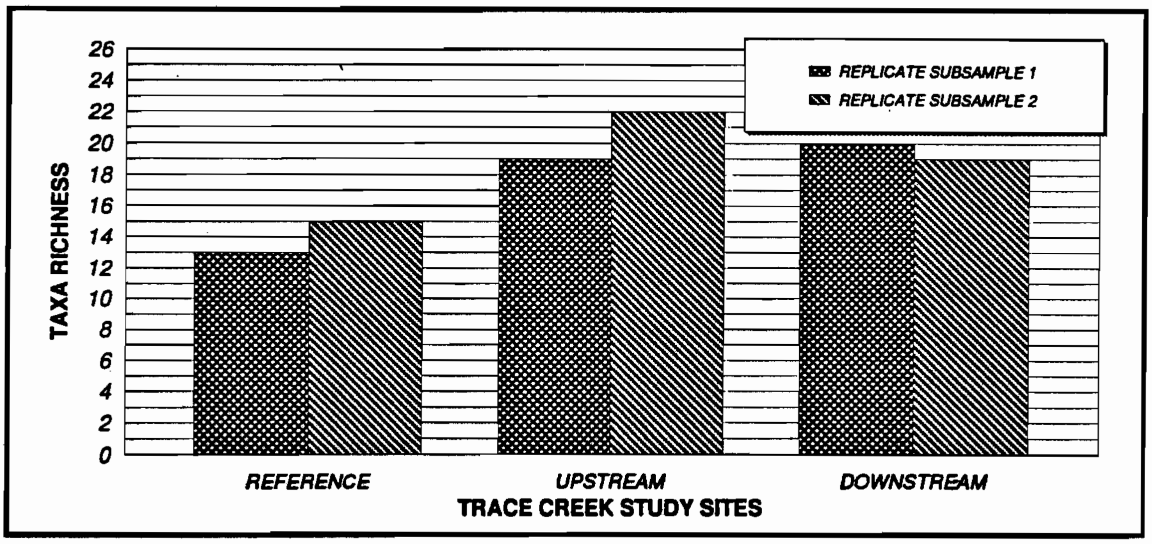

Figure 3. Taxa richness within replicate subsamples for Trace Creek study sites; "UPSTREAM" of Waverly STP, "DOWNSTREAM" of STP, "REFERENCE" = watershed reference site on Hurricane Creek (Humphreys County).

Replicate subsamples from Trace Creek study sites were also very similar in relative abundances within taxa. Morisita's coefficient of similarity revealed near perfect similarity between the replicate subsamples from Trace 01 (0.930), Trace 02 (0.996) and Trace 03 (0.982).

Within the Rock Creek survey, three replicate subsamples from the TKM samples were taken for each of the five sites along Rock Creek and for the reference stream site. As with the Trace Creek study, the numbers of taxa found at each site were very similar, with differences between each of the three replicate subsamples ranging from 0 to 3 taxa at each site (Figure 4).

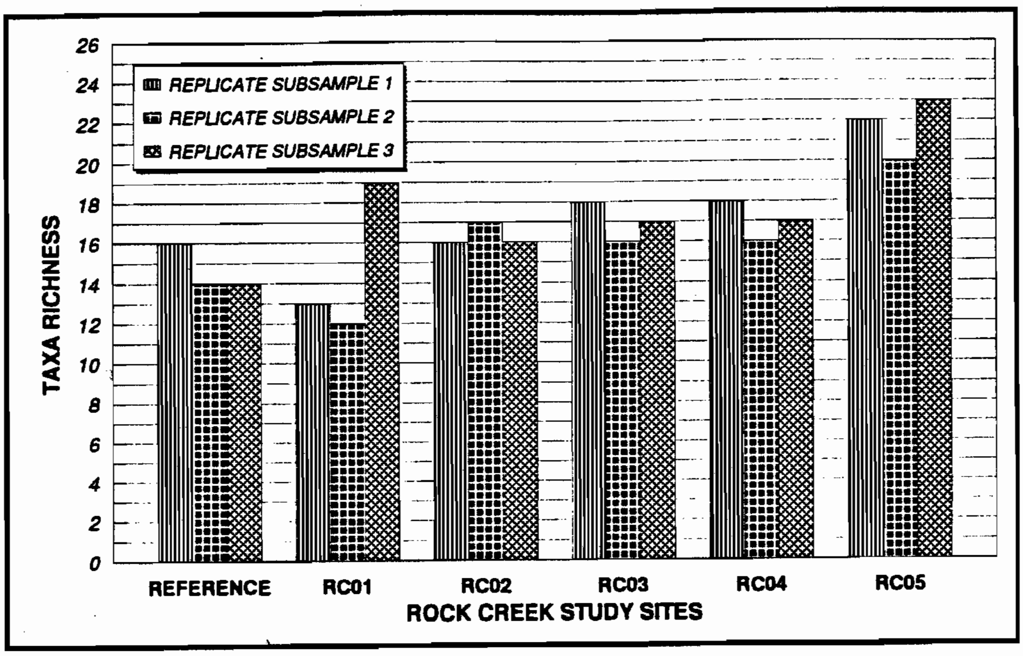

**Figure 4. Taxa richness of each of three replicate subsamples per site within Rock Creek study. RC01 = upstream of Tullahoma STP, RC02 - RC05 = sites sequentially downstream of STP, "REFERENCE" = watershed reference site on Hurricane Creek (Moore County).**

An exception is Site 01; here the number of taxa found ranged from 12-19 taxa between the three replicate subsamples. However, when Morisita's coefficient of similarity is applied (incorporating relative abundances among taxa) these replicate subsamples appear very similar (Table 3). Apparently several rare taxa were picked in one of the replicate subsamples taken from the Site 01 TKM sample.

TABLE 3. Morisita's Coefficient of Similarity for subsamples of the sample collected at each site in the Rock Creek survey. Subsamples are compared as pairs (e.g., subsample 1 to subsample 2, 1 to 3, and 2 to 3) for each sample. RC01 = site upstream of STP, RC02-RC05 = sites downstream of STP, REF = watershed reference site on Hurricane Creek.

| Morisita's Coefficient of Similarity for: | RC01 | RC02 | RC03 | RC04 | RC05 | REFER |
|---|---|---|---|---|---|---|
| **Replicate subsample 1 compared to replicate subsample 2** | 1.000 | 0.995 | 0.990 | 0.951 | 1.000 | 0.964 |
| **Replicate subsample 2 compared to replicate subsample 3** | 0.873 | 0.967 | 1.000 | 0.995 | 1.000 | 0.971 |
| **Replicate subsample 1 compared to replicate subsample 3** | 0.940 | 0.987 | 1.000 | 0.955 | 1.000 | 1.000 |

Evaluation of the replicate subsample data shows that a subsample is random and representative of the original full sample. The major question is whether or not picking and identifying a 100-organism subsample will provide the same water quality assessment results as would removing and identifying all organisms within the sample. At each Trace Creek site, Biotic Index values calculated for completely picked TKM samples and for subsampled TKM samples follow the same trends (Fig. 5). The relationships revealed by the subsample data is sufficient for constructing conclusions with regard to impacts of point source discharges.

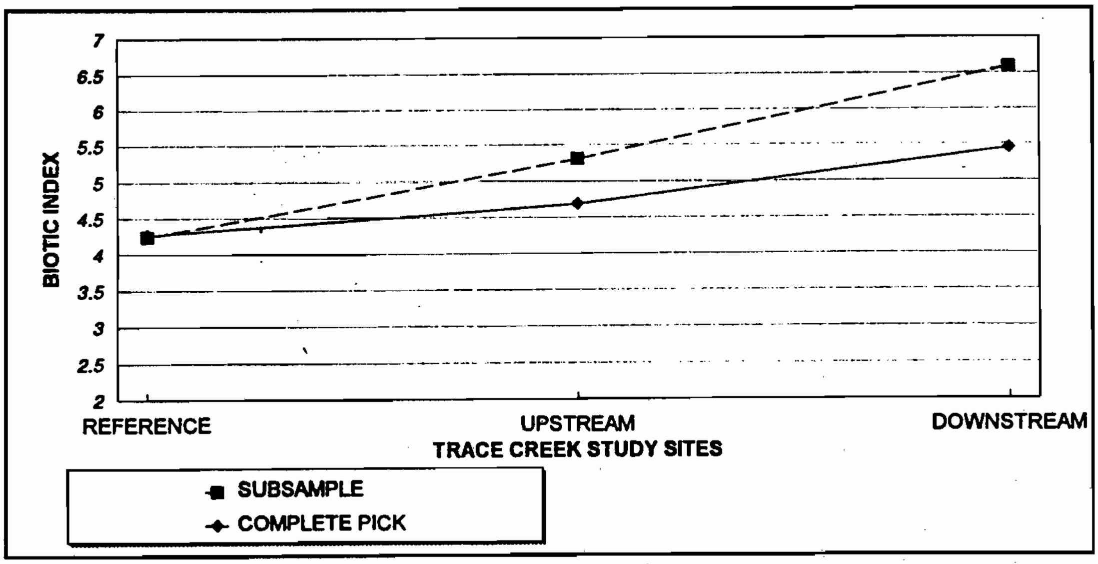

Figure 5. Biotic indices from Trace Creek survey. "UPSTREAM" of Waverly STP, "DOWNSTREAM" of STP, "REFERENCE" = watershed reference site on Hurricane Creek (Humphreys County).

Similar results were found among biotic indices for the six sampling sites on Rock Creek, where the same relationships were demonstrated with both subsamples and complete samples (Fig. 6). Comparing relative Biotic Index values among the sites, it appears the time-consuming process of removing and identifying all organisms from a sample does not produce substantially different results from those derived applying the subsampling method.

The RBP metrics were calculated for both subsample and complete pick data. At Trace Creek (Fig. 7), the downstream site was compared to the upstream site (DS/US), and the upstream site and the downstream site were each compared to the watershed reference stream (US/REF and DS/REF), Hurricane Creek in Humphreys County. The downstream site falls in the "substantially impaired" category with 46% comparability (DS/US) using both the subsample and complete pick data. Comparison of the upstream site to the reference stream (US/REF) yielded different percentages of impairment, however, the overall condition category was the same, "slightly impaired". Similarly, comparing the downstream site of Trace Creek to the watershed reference (DS/REF), the percent impairment was numerically different, however, the overall condition category was the same, "substantially impaired".

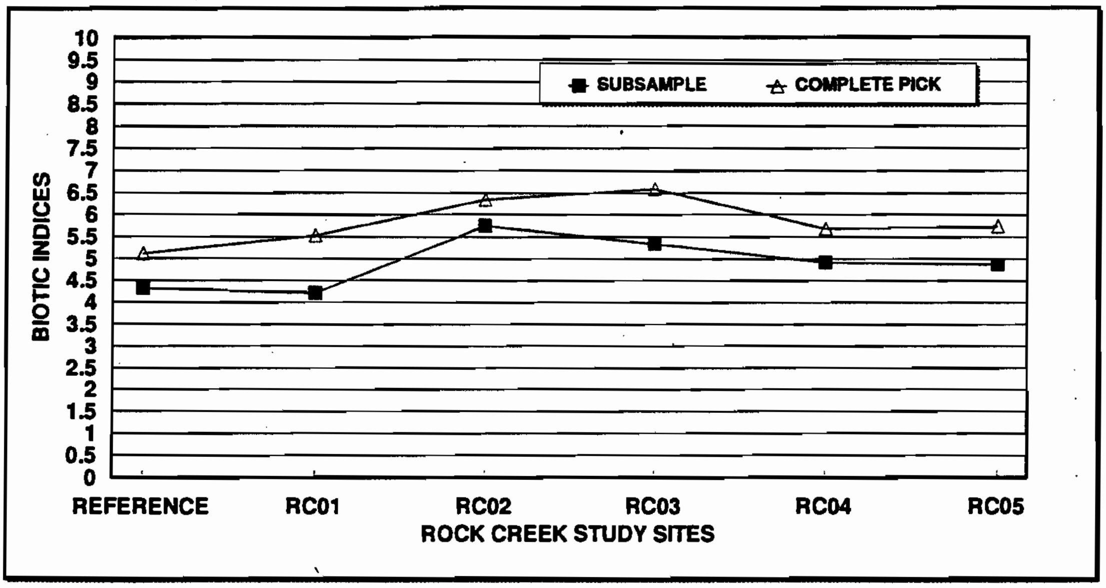

Figure 6. Biotic indices from Rock Creek survey. RC01 = uspstream of Tullahoma STP, RC02 - RC05 = sites sequentially downstream of STP, "REFERENCE" =watershed reference site on Hurricane Creek (Moore County).

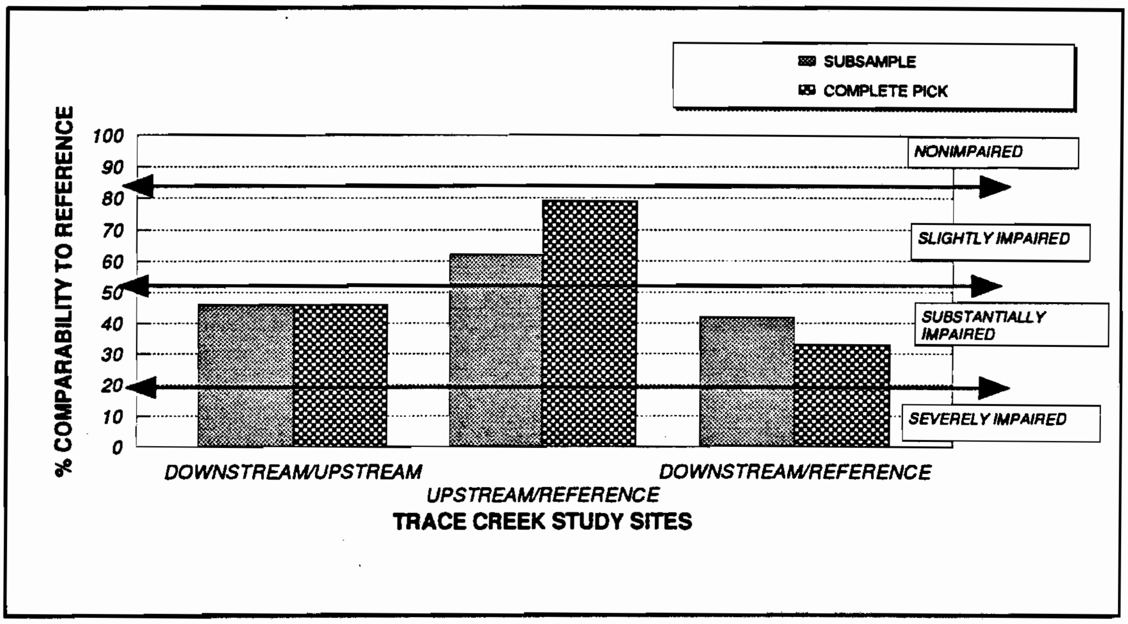

Figure 7. Percent comparability among Trace Creek survey sites. "UPSTREAM" of Waverly STP, "DOWNSTREAM" of STP, "REFERENCE" = watershed reference site on Hurricane Creek (Humphreys County).

Similarly for the Rock Creek survey, metric scores and percent comparability calculated and compared using both complete pick and subsample data (Fig. 8). The downstream sites RC02-RC05 were each compared to the upstream site (RC01) and the upstream site was compared to the watershed reference stream, Hurricane Creek in Moore County. Comparing the upstream site to the reference condition (RC01/REFERENCE), the same degree of impairment, "slightly impaired," was found using both the complete pick and subsample. When downstream sites RC02, RC03 and RC04 were each compared to the upstream site, the resulting degree of impairment was the same in each case for both the completely picked and subsampled TKM samples. RC02, the site immediately below the outfall, was "substantially impaired" (50% comparability) and RC03, RC04 and RC05 were all "slightly impaired." Therefore, subsampling of the Rock Creek TKM samples ultimately provided the same water quality information as picking and identifying all of the organisms.

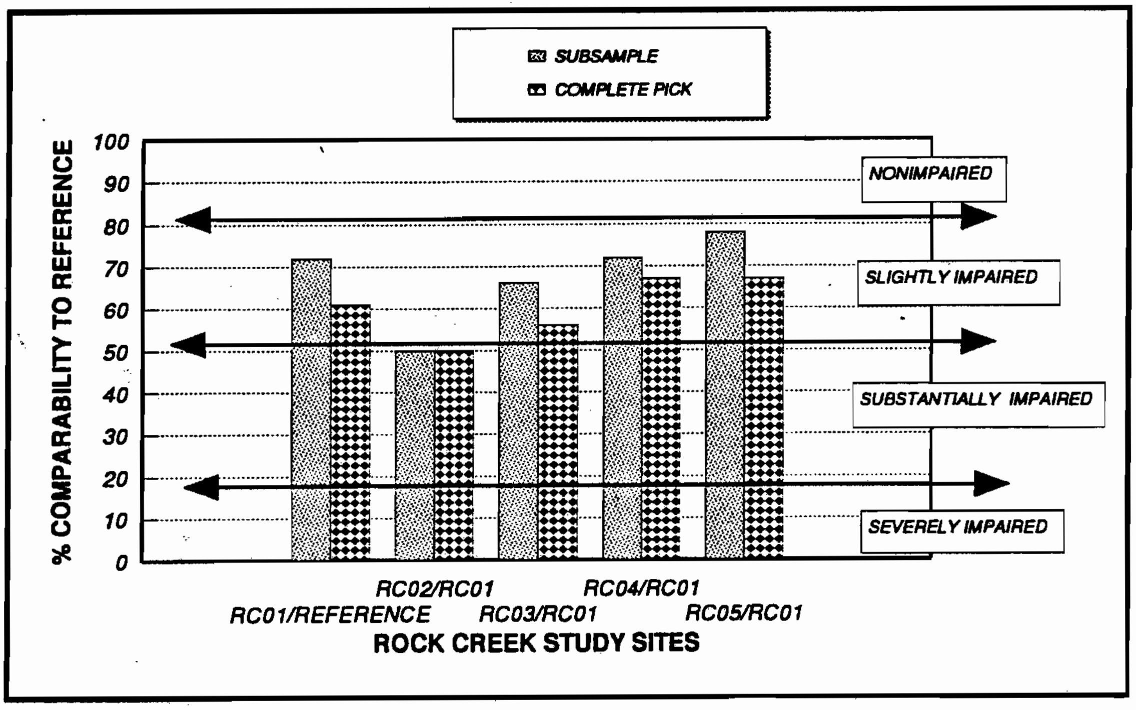

**Figure 8.** **Percent comparability among Rock Creek survey sites. RC01 = upstream of Tullahoma STP, RC02 - RC05 = sites sequentially downstream of STP, "REFERENCE" = watershed reference site on Hurricane Creek (Moore County).**

The success we have had using the subsampling method, as opposed to the experience of other researchers, apparently stems from the use of the traveling kick method of sampling. This sampling procedure covers a much larger area and variety of microhabitats within a stream riffle than does other techniques such as 1 $m^2$ kick screen, Surber samplers, or other fixed position samplers. While subsampling from these latter sampling procedures has been questioned, the NFO method of subsampling from an initially large and diverse sample seems to provide data representative of the BMI community from a site. Comparisons between replicate subsamples within each site finds that a subsample represents the BMI community found within the entire sample. Subsampling saves manpower in collecting and sample processing while providing the same water quality assessment as the time-consuming process of picking and identifying all of the organisms in the sample. The relative abundances, biotic index, and degree of impairment within a BMI community were similar within a subsample as within a complete sample in our investigations.

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# POPULATION DYNAMICS AND HISTOPATHOLOGY OF PARASITES FROM FRESHWATER MUSSELS IN KENTUCKY LAKE

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**ABSTRACT. A total of 165 specimens of a freshwater mussel, *Quadrula quadrula*, was collected, 8-10 per month, from March 1993 through October 1994 and examined for parasites. All mussel specimens were collected from a single embayment of Kentucky Lake. Two species of parasites were found. They were *Unionicola vikitra*, an aquatic mite, and a trematode, *Aspidogaster conchicola*. The prevalence of *U. vikitra* on hosts was 98% during the study period. Abundance, mean intensity, and ranges were 7.4, 7.5, and 0-5.7, respectively. The prevalence of *A. conchicola* was less than *U. vikitra*; 69% versus 98%. Abundance, mean intensity, and range values for *A. conchicola* were 2.2, 3.2, and 0-17, respectively. Seasonal data indicated that the abundance of *U. vikitra* increased with rising water temperatures. However, the abundance of *A. conchicola* remained fairly constant during the entire study period, regardless of temperature. Previous studies of aspidogastrid diets have indicated ingestion of circulatory cells and/or kidney epithelial cells by examination of parasite gut contents. The act of ingestion of host kidney tissue by *A. conchicola* was observed during this study by utilizing standard histological techniques.**

# USING FLUORESCENT OLIGONUCLEOTIDE PROBES TO STUDY MICROBIAL POPULATIONS IN KENTUCKY LAKE SEDIMENTS

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**ABSTRACT. Because the microflora of the sediments is responsible for most of the chemical flux between the sediment and the water, an understanding of the activities of the bacteria in the sediments is critical to our understanding of the chemical cycles in the sediments and the water of Kentucky Lake. The first step in our efforts to study the microflora has been to determine the succession of prokaryotes in the sediment under various chemical and physical conditions. To that end we have adapted a method, developed to identify bacteria in water samples and in culture, to identify groups of bacteria present in sediment samples. The method employs fluorescent oligonucleotide probes, specific to the 16S rRNA of groups of Eubacteria and Archea, to stain bacteria freed from the sediments.**

**Ten grams of sediment is blended in 0.1% sodium pyrophosphate for 1 minute and the sediment pelleted in a microcentrifuge tube at the slowest speed possible (approximately 1,000 rpm). Recently we have found that the bacteria can be floated off the blended sediment with polyvinylpyrrolidone. Following the centrifugation, 10 ml of sample is placed on a slide, allowed to dry, and treated with ethanol:formaldehyde (9:1). The slide is then rinsed briefly and allowed to dry. The stain containing the probe is applied with a coverslip and incubated overnight at 37°C. The coverslip is removed and the slide rinsed in three changes of buffer. The slide is then dried and the bacteria counted using a fluorescence microscope.**

# GC/MS SIM ANALYSIS OF CHLORPYRIFOS MOSQUITO CONTROL AGENT IN SEDIMENTS AND WATER OF BLOOD RIVER EMBAYMENT, KENTUCKY RESERVOIR

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**ABSTRACT. Chlorpyrifos, or Dursban, is a systemic pesticide effective against a wide range of arthropods. Although very effective against newly-hatched mosquitoes, its more general environmental effects do not make it a reagent of choice for widespread control of these pests. However, under selected conditions of water level and small-scale use, it is a reasonable candidate for mosquito control. In May 1993, collaborating with research biologists from TVA's Muscle Shoals, Alabama facility, our MSU-CSL team studied the dynamics of Chlorpyrifos interactions in the sediments, waters, and certain fish of Wildcat Creek inlet in Blood River embayment of Kentucky Reservoir. In addition to almost 300 analyses of water and sediment samples, multiple analyses were performed on fathead minnows held in traps in the aerially-dusted study location, but, most likely due to too short time of the study, no insecticide buildup was noted in these fish.**

**Sediment and water samples were collected from twelve sites along three transects in the study area, and brought back to MSU-CSL for storage and analysis. The protocol employed followed existing or recently approved EPA methods for water, sediment, and tissue analyses. The method employed Soxlet and/or liquid/liquid extraction, preconcentration and solvent exchange, separation by capillary-column gas chromatography, and detection and quantitation using a mass spectrometric detector operating in selected ion monitoring (SIM) mode. An external calibration method of quantitation was used, and data analysis was expedited through use of the software available within the Hewlett-Packard GC/MS instrument array DataStation, along with QuattroPro software available in other systems of the laboratory.**

**Analyses were carried out on over 300 samples of sediment, water and fish, with multiple "runs" routinely done for maintenance of quality control and quality assurance. Large differences were noted in the levels of Chlorpyrifos found in each of the matrices studied. Levels in water ranged from below the 0.20 ppb detection limit (BDL) upwards to 50 ppb (micrograms/L). Many of the sites showed a delayed release of Chlorpyrifos to the water, with maximization in the 4.5 to 6 hour period after application, followed by an irregular decrease (up to 48 hours after application) later. The insecticide was not detected in any of the fish samples; where the detection limit was also 0.20 ppb. The sediments contained the greatest fraction of the pesticide. Here, Chlorpyrifos values ranged from under 0.20 ppm (mg/Kg) to over 50 ppm, and there also appeared to be an initial delayed release followed by a much slower (if at all) decrease in Chlorpyrifos with increase in time after application. This is not surprising, since the anoxic condition of the sediments under the reservoir regime in force would be expected to slow breakdown of Chlorpyrifos by an oxidative pathway. Mosquito extirpation data, coupled with the Chlorpyrifos level/time data, suggests that the pesticide can be used in selected situations with extended water turnaround time, enlarged shallow water regimes, in carefully-selected embayment locations, without a significant short-term antagonistic effect on the endemic fish, as a mosquito control agent.**

# SEDIMENT TRACE ELEMENTS IN THE LEDBETTER CREEK EMBAYMENT

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**ABSTRACT. For the past year, work has been underway on quantifying trace elements in the bottom sediment of the Ledbetter Creek Embayment of Kentucky Lake. Using x-ray fluorescence (XRF) spectroscopy, ten elements ranging from potassium to zirconium have been identified in the top 35 cm of the sediment. Patterns have emerged for these elemental distributions which indicate concentrations near the mouth of the embayment are highest with those in the back of the embayment being the lowest. In an effort to understand these distribution patterns, work is underway to measure particle-size distributions in the sediment and to identify correlations that might exist between particle size and elemental concentrations for each of the ten elements under investigation. Preliminary results clearly show an inverse relationship between elemental concentrations and particle size for eight of the ten elements. Two of the ten elements show increased concentrations with increasing particle sizes. Work is continuing on sites from the mouth to the back of the Ledbetter Creek Embayment in an attempt to determine if the differences in elemental concentrations can be explained mainly by the differences in particle size distributions.**

# A STUDY OF PRIMARY PRODUCTION IN HOLLY FORK AND BAILEY FORK CREEKS IN HENRY COUNTY, TENNESSEE

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**ABSTRACT. Holly Fork, a channelized stream, and Bailey Fork, a relatively undisturbed stream, were studied during the summer of 1993 utilizing photosynthetic-biomass, chlorophyll-content, and diurnal oxygen-curve techniques to evaluate primary production. In both of these sandy-bottom streams, 20 transects were utilized to sample macrophytes, wood- and sand-associated periphyton, and phytoplankton. Stream morphological characteristics including submerged wood surface area, flow, depth, and light regimes were also determined. The combination of these methods permitted importance value comparisons of macrophytes and algae to primary production as well as the contributions of submerged wood and sand as primary-producer substrates. The results demonstrate that relatively undisturbed Bailey Fork has 10 times the submerged wood surface area, a corresponding 10-fold increase in wood associated-periphyton biomass, and three times the productivity as determined by the diurnal oxygen-curve technique relative to channelized Holly Fork. Phytoplankton and sand associated-periphyton biomass did not differ significantly between the two streams and are very minor contributors to primary production relative to wood-associated periphyton. These results indicate that submerged wood is a very important substrate for primary producers in sandy-bottom streams and that wood removal during channelization of sandy-bottom streams significantly reduces primary productivity.**

# THE PRIMARY PRODUCTION OF KENTUCKY LAKE

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**ABSTRACT. The experimental data of this study, which yields primary productivity, was collected by the monitoring group of the Center for Reservoir Research at Murray State University. This paper focuses on theoretical modeling of primary production in Kentucky Lake reservoir for the years of 1991, 1992, and 1993. The various physical, chemical, and biological parameters show extreme differences for these three years and present a severe test for theoretical modeling of primary production for Kentucky Lake reservoir. Theoretical models for primary production, which were developed for natural lakes and coastal waters, were found not to apply to a small body of water such as a reservoir unless they were modified. In addition to the parameters in the earlier mentioned models, we have studied the effects of parameters such as available nutrients, retention time, and temperature on primary production in Kentucky Lake reservoir. The temperature of the reservoir has a very stable pattern for all three years. In general as the temperature increases, so does the primary production. However, because of the reservoir size, the effects of retention time and available nutrients cannot be ignored. Direct comparison of theoretical and experimental primary production values shows readily that retention time and nutrients must be included in any successful working model to predict primary production for the Kentucky Lake reservoir. Although the modified theoretical model which we present is specific to Kentucky Lake reservoir, the prediction of the model is relevant to any system with similar characteristics.**

## INTRODUCTION

Primary production is the basic building block in an ecological system. There are many biological, physical, and chemical factors which will affect the production rate. In a large system, these factors have been studied in detail and incorporated into mathematical models that can reasonably predict primary production. However, in a smaller system such as a reservoir, these models are not accurate predictors for primary production. This is due in part to differing characteristics that exist between the two types of systems. A factor such as retention time has a great effect on primary production in a reservoir, whereas in a large system, it may be negligible. In most large impoundments, the dominant primary producer is phytoplankton. The two primary factors that control phytoplankton productivity in reservoirs are light and nutrient availability (Kimmel *et al.* 1990, Bannister 1992). However, because of the size, the residence time of water in reservoirs highly influences phytoplankton production levels and biomass (Soballe and Kimmel 1987).

There are three major aims of this study. The first is the analysis of Kentucky Lake's primary production. The environmental factors and primary production rates were gathered for the years 1991 through 1993. During this three-year period, data was calculated and evaluated to discover different trends and correlations. Each of the environmental factors, such as temperature and turbidity, was compared to primary production over the same period. We have a large amount of data available to us. It is important to organize it into a usable form. By doing this, some probable correlations have been discovered and are being studied in detail.

The second objective of this study is to analyze existing mathematical models that may be able to predict theoretical primary production in Kentucky Lake. To accomplish this task, the experimentally derived parameters are inserted into the existing models in order to calculate the theoretical primary production. The results from these models are then compared to the experimental primary production values. These models allow us to see the functionality and the importance of the data. Once the similarities and the differences are noted, we will begin to employ our third and final objective.

The final objective is concentrated on creating a more accurate and reliable working model for the theoretical calculation of primary production in Kentucky Lake. As stated earlier, an important difference between a natural lake and a reservoir is the effect of retention time on the system. In a small reservoir system, even a little movement in the flow of water can make a difference in the primary production. This difference will affect the nutrients, turbidity, and the amount of carbon dioxide present. Therefore, these variables must be incorporated into any mathematical model to determine experimental primary production in a reservoir system. Trying to create a more accurate and reliable theoretical model will enable us to make conclusions concerning the importance of different variables involved in primary production. With this knowledge and understanding, not only can an improved model be formulated, but predictions of future primary production rates can possibly be forecasted.

Our study site is on the manmade Kentucky Lake. It is located in Western Kentucky and Northwestern Tennessee. There are two hydroelectric dams located on the lake, Kentucky Dam at the northern end and Pickwick Dam at southern end of the lake. The Tennessee Valley Authority (TVA) is responsible for the operation of these dams to produce hydroelectric power and to maintain the water levels of the lake system. The study area for this research is concentrated within the central region of Kentucky Lake. Data is collected from various sites within this area. These sites include locations at the mouths of creeks on both the eastern and western sides of the lake, as well as sites within the channel, which flows through the center of the lake (Fig. 1).

## EXPERIMENTAL DATA AND METHODS

Various data from different sources are obtained to study Kentucky Lake. The Center for Reservoir Research's Long Term Monitoring Group takes a research cruise on Kentucky Lake every sixteen days, in accordance with the Landsat satellite. However, due to hazardous winter weather conditions, this may vary. The order of the sites is randomly picked by a computer, which ensures an unbiased collection of data. On-site testing and sampling are carried out at each of the primary production sites. Table 1 provides a list of important terms and notes to use as a reference.

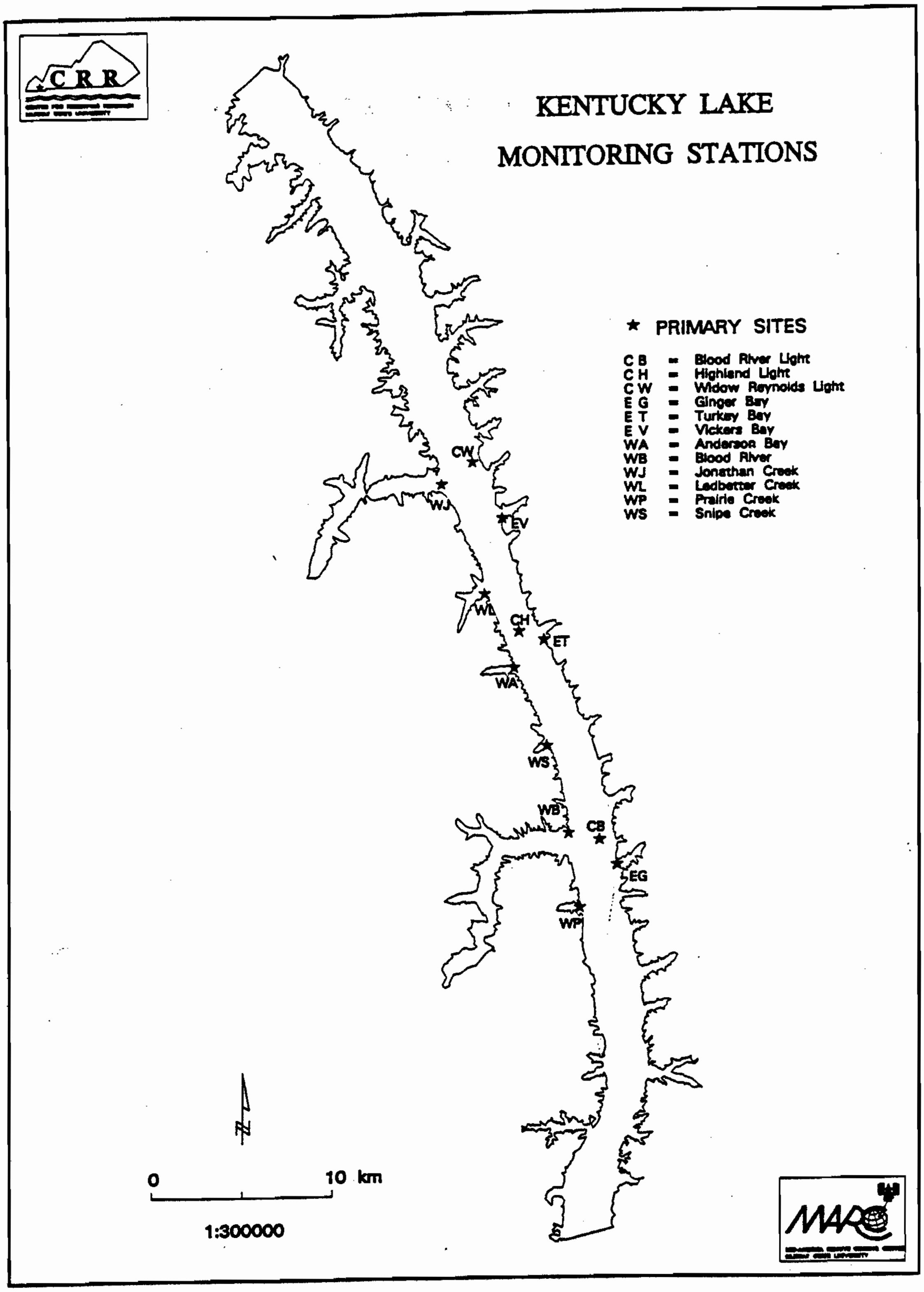

Figure 1. The monitoring group of the Center for Reservoir Research collects data from the primary data collection sites on Kentucky Lake Reservoir every sixteen days.

**Table 1. Important terms and notes.**

Photosynthetically Available Radiation (PAR): In this study, utilized to relate the rate of photosynthesis of aquatic plants to ambient light. PAR is supplied to us in mol/m$^2$, but we convert it to W/m$^2$.

$\Delta T$: The time of sunset minus sunrise. With the help of a sine curve, $\Delta T$ is put into comparable units with PAR.

KD: Assessed in m$^{-1}$, KD is the light attenuation coefficient and a measure of the decrease of light intensity as depth increases. Though we are presently measuring light attenuation of different wavelengths (red, green, blue), in this work only the KD for natural light (white) is used.

Temperature and Turbidity: Temperature and turbidity are measured at the water's surface and a one-meter intervals below the surface. Temperature is measured in degrees Celsius where as turbidity is measured in nephelometric turbidity units. Both temperature an turbidity are averaged by station for a given cruise.

Nutrients: Water samples collected from each site are taken to the laboratory where the nutrients assessed. Nutrient data that we are concerned with are nitrate/nitrite ($NO_3$/$NO_2$), soluble reactive phosphorus (SRP), and silicon dioxide ($SiO_2$). The units are mg/L.

Hydrology: Data provided by the TVA provided hydrological aspects into this study. This data revealed that the water retention times and flushing rates had an impact on nutrient availability and hence on phytoplankton production. The retention time, measured in days, is determined by the lakes flushing rates, measured in ft$^3$/s.

Carbon Assimilation (CAS): Water samples are collected at each station and are allowed to incubate for two hours on the boat. Using the $^{14}C_6$ method, potential productivity can be determined. We only involve primary sites in the calculation of CAS. CAS is averaged by station, then by cruise date and is measured in units of milligrams of carbon per liter per hour.

Biomass: Chlorophyll-a and phaeophytin-a readings are taken from raw water samples. Biomass is calculated by adding chlorophyll-a and phaeophytin-a readings together. Biomass is measured in units of micrograms per liter, however, for our calculations, we have converted it into milligrams per liter.

Experimental Primary Production: To calculate primary production carbon assimilation and biomass values are used. Primary production is measured in units of milligrams of carbon per milligrams of chlorophyll-a per hour. Experimental primary production is calculated by dividing the averaged carbon assimilation by the averaged biomass. This calculated experimental primary production represents the station average for a given cruise date.

Temperature and turbidity measurements are taken at the surface and at one-meter intervals for the depth of each site. Secchi disk results, pH of the water, as well as light intensity readings at 1 m and 5 m and other related data are gathered. It should be noted that light intensity readings at 5 m are not always possible, due to shallow depths. When this occurs, readings at 2 or 3 m are used and accounted for in analysis. Water samples are collected at each primary site for two purposes. The first is for the 2-hour on board incubations needed for $^{14}C$ method of finding potential productivity. The second is collected for various laboratory analysis such as ***chlorophyll-a***, phaeophytin-*a*, nitrate/nitrite, phosphorus, and silicon dioxide.

In order to calculate all of our data, we must receive information from other sources. Hancock Biological Station, the monitoring facility on Kentucky Lake, has a sensor that monitors PAR (photosynthetically available radiation) daily with regular interval readings. The Tennessee Valley Authority (TVA) is the source for information pertaining to the retention time and the flushing rate of the reservoir system. This information is then carefully examined to determine the significance of various components affecting the primary production. These variables then can be incorporated into a better working model for Kentucky Lake and other reservoirs like it.

There are several steps in calculating the experimental data for primary production. After receiving the raw data, we first must calculate each component. Since several factors such as PAR and retention time are taken daily, the values for each must be averaged together so that one generalized data point may be had for each cruise date. Since the factors which effect primary production occur either during or before each cruise date, we begin averaging the values from the first day of the year to the first cruise day. This same standard is repeated for each successive cruise, always beginning with the first day after a cruise and ending with the successive cruise.

Others factors, such as temperature and turbidity, are taken as a depth profile at each station. Therefore, to find the data point for each station, the readings from each depth must be averaged together. Next, these individual station points are averaged together to obtain a value for the entire lake for each cruise day. After we have carried out all the possible calculations, we then examine possible correlations between various factors such as light intensity and primary production.

The monitoring group at Hancock Biological Station provides the raw data to us so we can calculate the experimental primary production rate. To calculate the primary production rate, carbon assimilation and biomass values are used. Primary production is calculated by dividing the average carbon assimilation (CAS) by the average biomass. This is given by the equation:

$$\frac{CAS}{biomass} = Primary\ Production\ Rate\ per\ Station$$

where *CAS* is the carbon assimilation average per station for each cruise date, and ***biomass*** is the added values of chlorophyll-*a* and phaeophytin-*a* per station for each cruise date. Primary production is measured in units of milligrams of carbon per milligrams of chlorophyll-*a* per hour. This calculated experimental primary production represents the station average for a given cruise date. These values are then averaged together to obtain the single primary production rate for Kentucky Lake per cruise date. The primary production averages for 1991, 1992, and 1993 are then plotted against Julian dates (Fig.2).

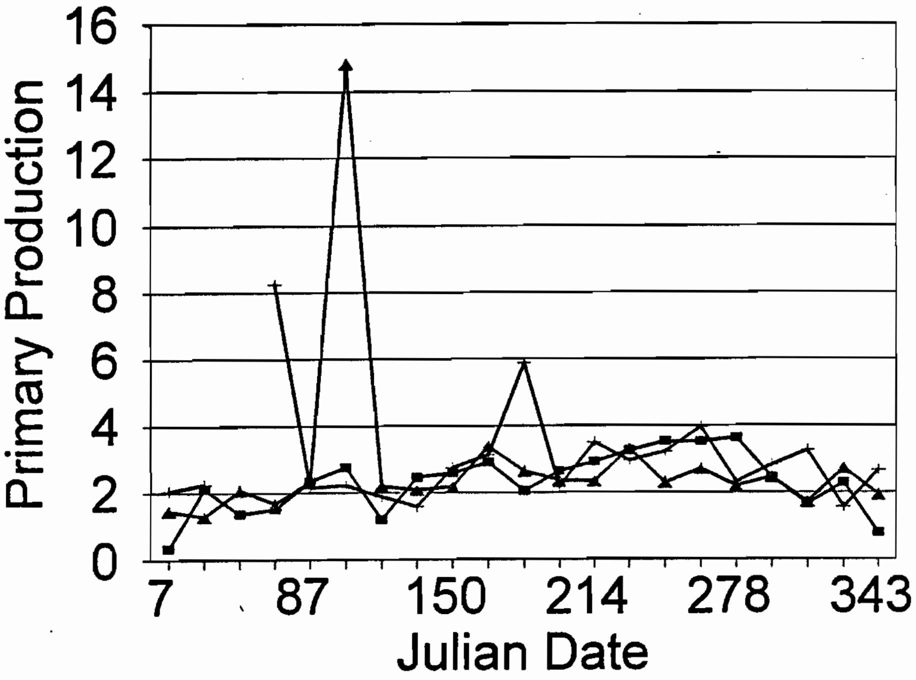

**Figure 2.** Experimental Primary Production (mg C/mg Chl *a*/Hr.) which is the average value of carbon assimilation (mg C/Hour) over all data collection sites normalized to the Biomass (mg Chl *a*) as a function of Julian Date is calculated (1991 ■, 1992▲, 1993 ✚).

In 1991, primary production does not have a large peak as compared to 1992 and 1993. However, in 1992 and 1993 there is a tremendous increase in primary production during the first of the year. In 1992, one large peak occurs sometime in April. As for 1993, there are two peaks showing up, one is in March and another in June. One of the objectives of this study is to determine what causes these drastic increases in the primary production rates. Several environmental factors have been studied in order to determine correlations between them and the primary production.

We seek the importance of various physical, chemical, and biological factors in the primary production of Kentucky Lake. Some factors are affected by still other variables. We have examined the temperature of the lake for 1991, 1992, and 1993. The average temperatures for all three years are very similar (Fig.3). Primary production shows a linear relationship with temperature. It appears that the peaks of primary production are not due to temperature, but are due to other factors, since the peaks are observed at different times in the three years.

Other possible correlations can be made concerning primary production. When CAS and biomass are plotted against primary production, they represent a linear relationship between one another ( Fig. 4). An increase in CAS is usually accompanied with an increase in biomass.

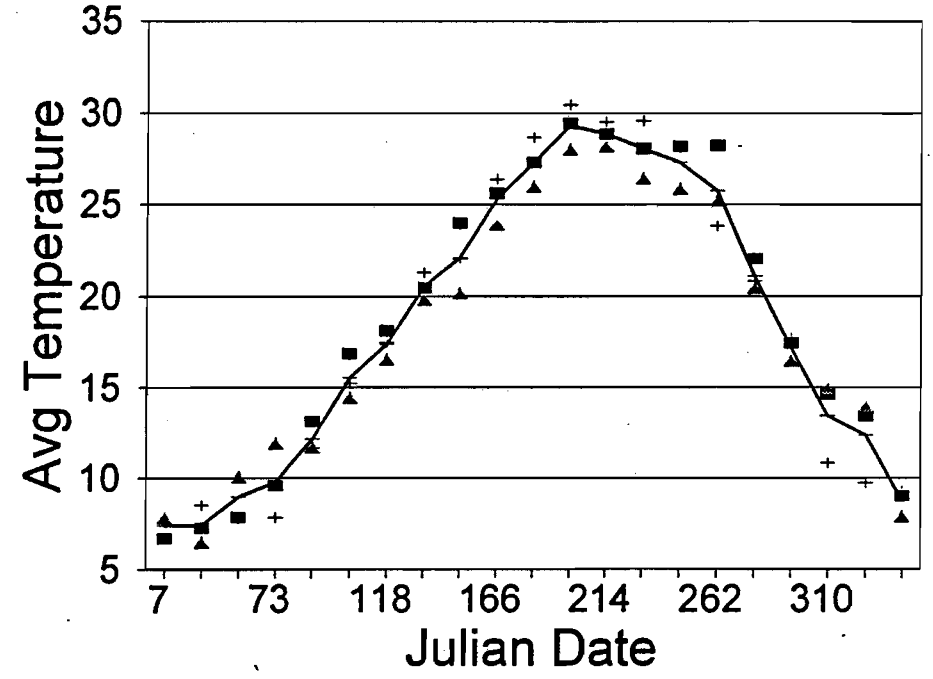

Figure 3. Temperature (°C) is averaged over water column and then averaged over data collection sites. for 1991(■), 1992 (▲), and 1993 (+) as a function of Julian Date. Here the solid line indicates the average value of Temperature over three years (1991-3)

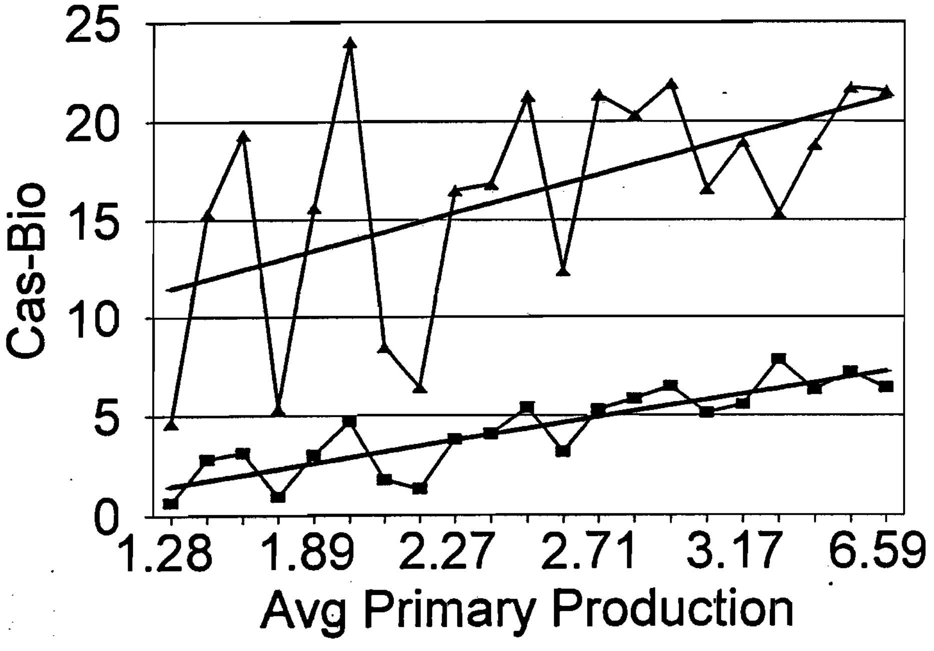

Figure 4. Relationship between Average Carbon Assimilation for 1991, 1992, and 1993 (mg C/Hr) and Normalized Primary Production (mg C/mg Chl a/Hr) is the upper curve. Lower curve is the relationship between Average Biomass (mg Chl *a*) for 1991, 1992, and 1993 and Normalized Primary Production (mg C/mg Chl *a*/Hr). The best liner fit to each curve is also computed and shown respectively

We have also considered possible correlations between primary production and nitrate/nitrite. The average nitrate/nitrite is inversely proportional to the average primary production for 1991, 1992, and 1993 (Fig.5). It seems as the extra nutrients are consumed by the photosynthetic organisms, the primary production rate increases. Conversely, as primary production tapers off, the nutrients began to build up. A possible explanation for the huge peaks in primary production at the first of the year (spring bloom) may be due to the fact that Kentucky Lake does not freeze over, however, it does cool enough too slow primary production. This creates a back up of nutrients that can be consumed by the phytoplankton when sufficient light is available and the water becomes warmer. As a result in spring, primary production will increase due to high concentrations of nutrients available to photosynthetic organisms.

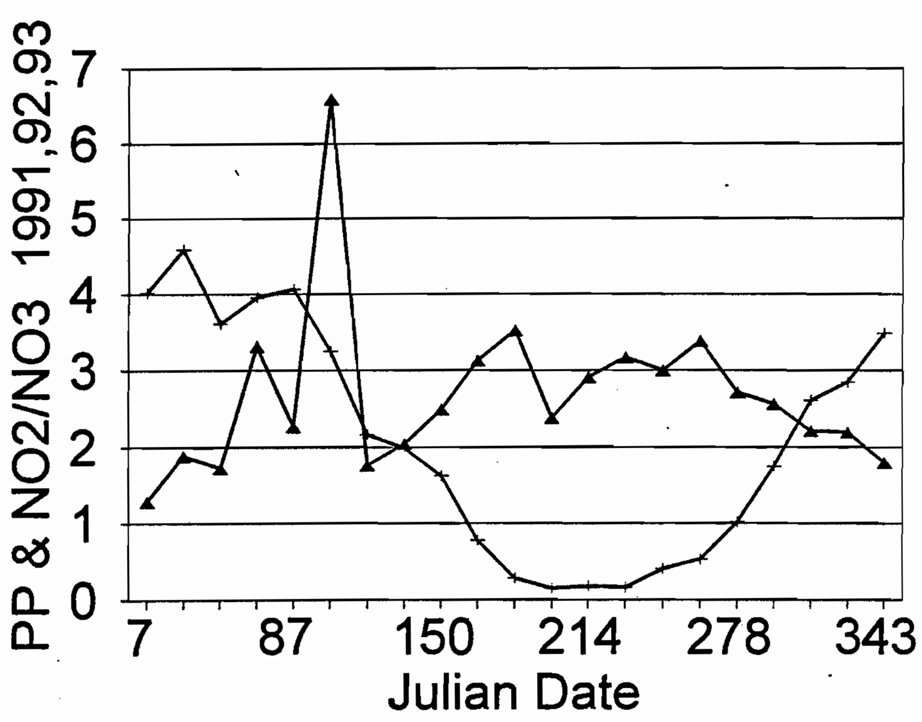

Figure 5. Three years (1991-3) values of Nitrate/Nitrite (NO$_3$/NO$_2$) is average over all data collection sites (mg, ✚) along with Experimental Primary Production (mg C/mg Chl *a*/Hr, ▲) are computed for Julian Date.

Another correlation under study is between primary production and retention time. There is a strong relationship between the two. The smaller the body of water, the greater the affect of retention time. Kentucky Lake is not a large system. Therefore, the amount of rainfall and/or the opening and closing of the gates at either dam will have an effect on the primary production. Primary production and retention time are proportional to one another (Fig. 6). As the retention time increases so does primary production, likewise as the retention time decreases so does the primary production. As water is added to the system, nutrients are added as well. Decreased retention time does not allow for these nutrients to be utilized. Increased retention time will give photosynthesizers the chance to uptake the nutrients. However, extended retention time can possibly have a decreasing effect on primary production because once the nutrients are depleted, there are no new nutrients being added to the system.

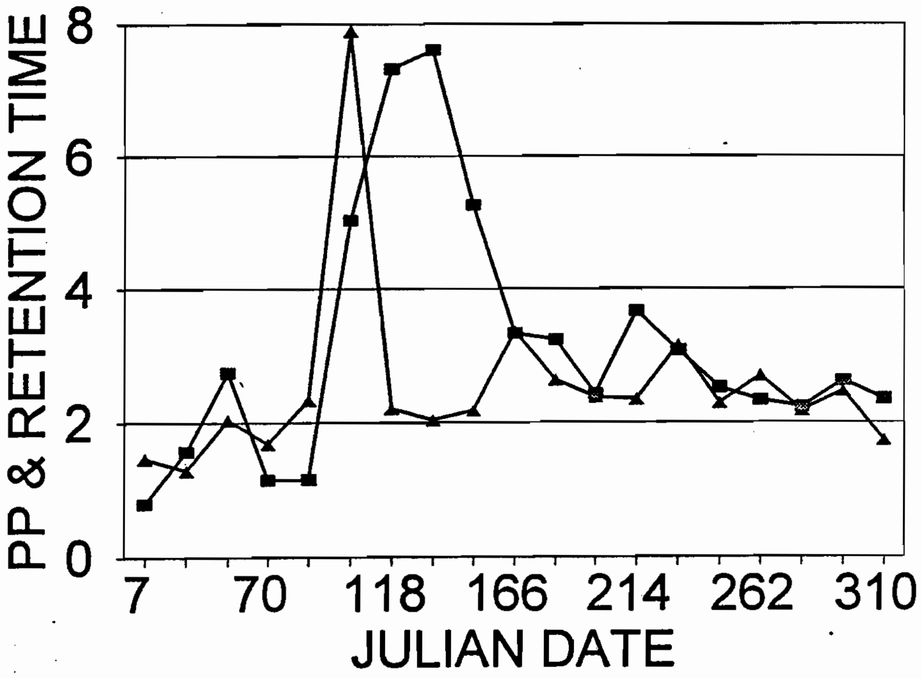

Figure 6. Strong relationship exist between the resident time of water (Day) with Experimental Primary Production (mg C/mg Chl *a*/Hr,▲). Here the values of resident time for 1992 (■) are multiplied by 0.1 in order to show them with their corresponding values of Primary Production.

## Theoretical Models

The second objective of this study deals with the analysis of existing mathematical models for the prediction of primary production in an aquatic system. Most of the theoretical models for calculating the primary production are developed for natural lakes (McBride 1992, Morel 1991, Platt 1989). Some of these models developed for marine systems can make moderately correct predictions (Platt and Sathyendranath 1988, Jassby and Platt 1976, Keller 1989). These models were compared with our experimental primary production to determine the accuracy of their predictions. The experimental data reflecting the environmental parameters from the years 1991, 1992, and 1993 were used in six of these working models. The calculation of the primary production is carried out by integrating the momentary primary production of these models over possible values of depth and time.

The light attenuation coefficient is needed to find the light intensity at any depth (Chambers 1988). We calculated the attenuation coefficient using the light readings at 1 and 5 m which are obtained from the monitoring group. The light intensity at any time and at any depth is provided by:

$$I(z,t)=I_{\max}Sin(\pi t)e^{-K_d z}$$

where $I(z,t)$ is the light intensity, $t$ is the time, and $k_d$ is the attenuation coefficient (McBride 1992). A typical relation for the instantaneous primary production provided by Baly (1935) is shown below:

$$P^{B}(I,z,t)=\frac{P^{B_M}\alpha I}{P^{B_M}+\alpha I}$$

The instantaneous primary production rate needs to be integrated over time and depth,

$$<p>=\int_{0}^{depth}\int_{sunrise}^{sunset}P^{B}(I,z,t)dzdt$$

where $<P>$ is the averaged primary production, $P^B(I,z,t)$ is the instantaneous primary production which is a function of light intensity ($I$), depth ($z$), and time ($t$). The explicit relation for the production rate then takes the following form

$$<p>=\int_{0}^{depth}\int_{sunset}^{sunrise}P_{m}^{B}\frac{[I_{0,\max}\exp(-kz)Sin(\pi T)]}{[\surd(I_{0,\max}\exp(-kz)(Sin(\pi T))^{2}+Ik^{2}]}dzdt$$

In the theoretical models, $k_d$ or the light attenuation coefficient, temperature of the lake, and retention time, which is calculated by the inflow subtracted by the outflow, is used to compute the theoretical primary production of Kentucky Lake. Comparison of these theoretical values of primary production with that of the experimental values of primary production, which is calculated from the $^{14}C$ method, reveals that the two are not congruent. The theoretical models did not predict the fluctuations in primary production which were seen experimentally.

Another typical instantaneous primary production is given by

$$P^B = P_m^B \tanh\left(\frac{\alpha I}{P_m^B}\right)$$

where $P_M^B$ is the maximum possible production under the given condition and $\alpha$ is the slope of light saturation curve (Platt 1989). The predictions of the primary production in the beginning and at the end of the year are reasonable. However, in the middle of the year the model has an inaccurate prediction for the primary production.

The final objective of this study focuses on creating a more accurate and reliable working model for determining primary production in Kentucky Lake. The parameters, such as retention time and nutrients, appear to be important factors in predicting the primary production of a system like this. We have modified the theoretical equation for instantaneous primary production to include the effect of retention time, nutrients, and temperature of the reservoir system. Thus any instantaneous primary production, $P^B(I,z,t)$ is modified by the following factors,

$$P_{new}^B = 0.05T[0.07 * Ret + P_M^B(I,z,t) * SiO2]/2$$

where $Ret$ is the retention time, and $T$ is the temperature. Another relation which also seems to provide reasonable results is given by

$$P_{new}^B = [0.1 * Ret + P_M^B(I,z,t)]/2$$

This modified model yields peaks which were absent in the previous marine models. However, the locations of the peaks do not correspond with the peaks observed for the experimental primary production's peaks. Of the three years, 1991 experimental data matches the best with the new model (Fig. 7). In 1992 and 1993, the peaks are not matching up with the experimental data (Fig.8 & Fig.9). One reason for this may be due to the way we average the given data. We average portions of the data over a period of sixteen days. As a result of this averaging, some of the peaks were not as pronounced as they should be, and sometimes the timing of the peak could be off by as much as 16 days. When the data is plotted daily, it has different characteristics than when plotted by its average values.

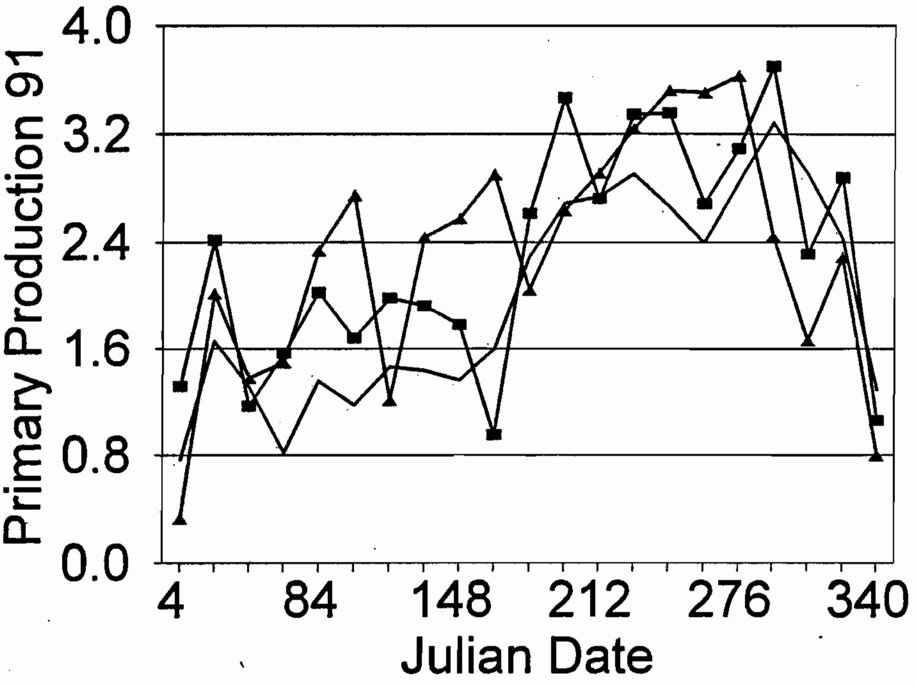

Figure 7. Comparison of Theoretical Primary Production (■) and Experimental Primary Production (▲) along with the Improved Theoretical Primary Production (X) are calculated. In these calculation the values of PAR, Light attenuation coefficient, Temperature and resident time of waters are used for 1991.

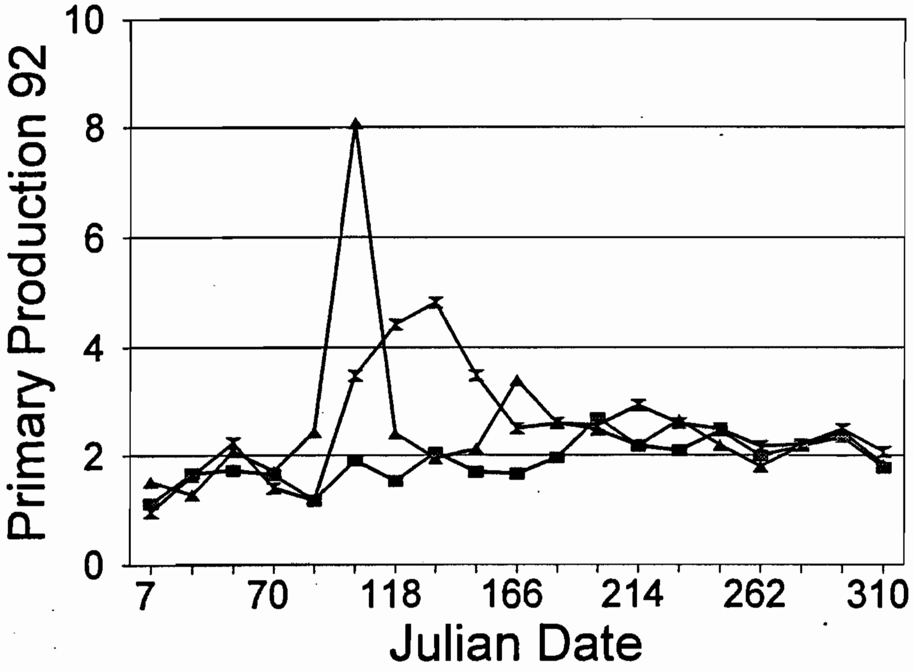

Figure 8. Comparison of Theoretical Primary Production (■) and Experimental Primary Production (▲) along with the Improved Theoretical Primary Production (X) are calculated. In these calculation the values of PAR, Light attenuation coefficient, Temperature and resident time of waters are used for 1992.

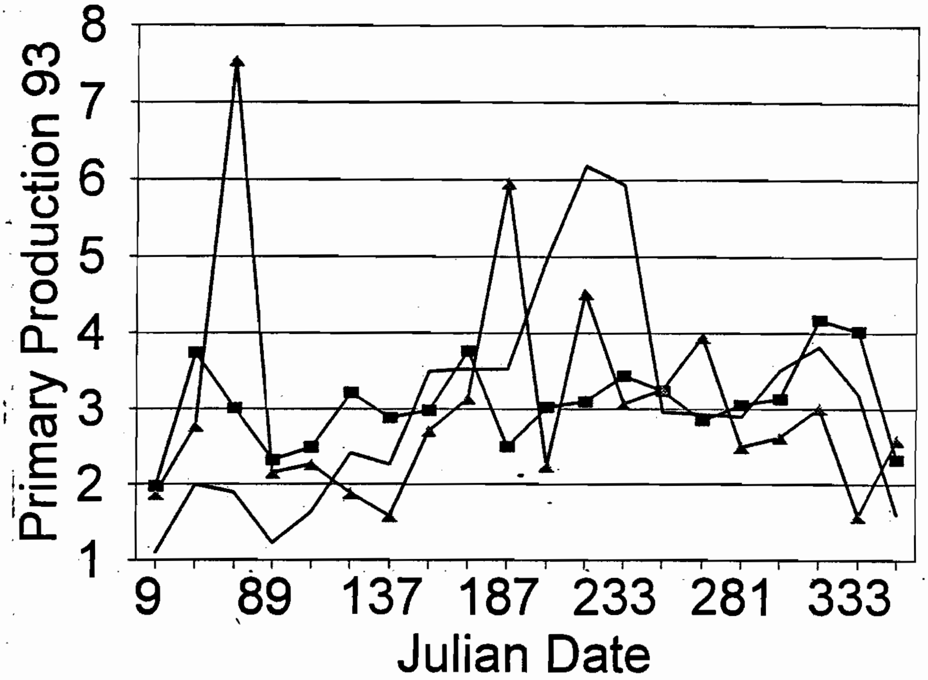

Figure 9. Comparison of Theoretical Primary Production (■) and Experimental Primary Production (▲) along with the Improved Theoretical Primary Production (X) are calculated. In these calculation the values of PAR, Light attenuation coefficient, Temperature and resident time of waters are used for 1993.

It seems likely that other parameters such as retention time, nutrient fluctuations, etc. have to be taken into account in the theoretical model of primary production. Because of the size, these parameters did not play a critical role in the primary production of a big natural lake. However, our calculations show that parameters such as retention time and nutrients are important in predicting the primary production rate.

## ACKNOWLEDGMENT

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# A CALIBRATION OF TWO NON-POINT SOURCE POLLUTION MODELS FOR A PORTION OF THE BLOOD RIVER DRAINAGE BASIN, WESTERN KENTUCKY AND TENNESSEE

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**ABSTRACT. This study describes the development of a water quality sampling program and the utilization of the acquired data to test the reliability of two non-point source pollution models. Blood River is the largest tributary of Kentucky Lake in the portion of the lake covered by Murray State University's KLGIS (Kentucky Lake Geographic Information System). Previous studies have suggested that Blood River is a major source of nutrients and turbidity to Kentucky Lake. The first objective is to determine the actual yield of both nutrients and sediment from the Blood River catchment. Secondly, predicted values from AGNPS (Agricultural Non-point Source Pollution Model) will be compared to the measured values of nutrient and sediment yields. Next, the measured values will be compared to predicted values from a new model SWAT (Soil and Water Assessment Tool). The input for both models will be extracted from GIS layers contained in the KLGIS. Finally, the models will be compared to each other to determine which model predicts the best. This study will be the first attempt to compare measured values of nutrient and sediment yields to those predicted by non-point source pollution models for the catchment. Because SWAT is so new, this study will provide a unique opportunity to be one of the first people to test the model.**

# SOME EFFECTS OF THE 1993 MISSISSIPPI RIVER FLOOD ON KENTUCKY LAKE

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**ABSTRACT. The entire Mississippi River System, including the Ohio, Missouri, Red, Tennessee and Cumberland Rivers, can be manipulated through series of locks and dams to manage for flood control. Record rainfall in the Midwestern United States in 1993 produced devastating floods along the upper Mississippi River, particularly in July and August, that required unusual management strategies for several of the major tributaries. Kentucky Lake is the furthest downstream of more than 40 reservoirs in the Tennessee/Cumberland River drainage basin. Even though near drought conditions existed in the Tennessee/Cumberland Basin, required water quality releases from the upstream reservoirs maintained a nearly normal flow to Kentucky Lake. To prevent additional flooding on the Mississippi, water had to be retained in Kentucky Lake and then released rapidly in coordination with release from other systems. Two such controlled retention-releases periods produced unusually rapid fluctuations in hydraulic retention time (HRT) from 309 - 20 days. High HRT resulted in temporary $O_2$ stratification, release of N and P from bottom sediments, and rapid responses (2-4 days) in primary productivity (from 40 to 80 mg C/m$^3$/hr). Periods of rapid drawdown (low HRT) resuspended bottom sediments not only in the mainstem of the reservoir but also in a number of tributary embayments. When HRT in Kentucky Lake returned to previous years' levels once the Mississippi River flood receded, primary productivity, $O_2$ profiles, and turbidity returned to normal patterns, and no long-term effects of the events were observed on either the benthic or water column environment.**

# CONTRIBUTED PAPERS

## SESSION II: AQUATIC BIOLOGY AND ZOOLOGY

Saturday, March 4, 1995

Moderated by:

**James B. Sickel**
**Murray State University**

# FRESHWATER MUSSEL FAUNA OF THE LOWER CUMBERLAND RIVER, KENTUCKY

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**ABSTRACT. A survey of unionid mussels was conducted on the Kentucky portion of Lake Barkley to evaluate the commercial mussel resource and establish sites for a long-term monitoring program. Scuba divers collected samples from 74 sites within four different habitat types that represented the major lake habitats, excluding the main channel where few mussels occur because of summertime anaerobic conditions. The habitats selected were the old river levees, floodplain, shoreline and embayments. Only nine species of mussels were found. Their percent abundance was as follows: *Amblema plicata* (17.76), *Anodonta grandis* (2.32), *A. imbecillis* (0.21), *A. suborbiculata* (1.9), *Fusconaia flava* (0.21), *Megalonaias nervosa* (2.53), *Obliquaria reflexa* (3.8), *Quadrula nodulata* (6.55), and *Q. quadrula* (64.67). The same three species, *Q. quadrula, A. plicata,* and *Q. nodulata*, were most abundant in three of the four habitats, while in the embayments *M. nervosa* was second most abundant and *A. plicata* third. Shorelines exhibited the greatest mussel density (0.522/m$^2$), while embayments had the lowest (0.212/m$^2$). The greatest density of *Q. quadrula* occurred at shoreline sites, while *A. plicata* and *Q. nodulata* had their greatest densities at floodplain sites. The highest percentages of mussels collected were in age classes 6 to 10 years. Legal harvest size for *Q. quadrula* (2.5 inch diameter) was reached between 7-9 years, and was 6-7 years for *A. plicata* (2.75 inch diameter). Shell morphology and allometric growth varied little between habitats; however, significantly larger *A. plicata* were found on the levees and embayments than the floodplains. *Q. quadrula* body weights were significantly greater in the embayments than the shoreline, while wet weights and shell weights were significantly greater in the embayments than any other habitats. Few mussels were gravid. These were evenly distributed betwee legal and illegal harvest size. No live Zebra mussels were found. This project is funded by the Kentucky Department of Fish and Wildlife Resources.**

# EFFECTS OF FISH PREDATION ON ZEBRA MUSSELS (*DREISSENA POLYMORHA)* IN LARGE REGULATED RIVERS

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**ABSTRACT. The effect of molluscivorous fish, such as freshwater drum (*Aplodiontis grunniens*) and the common carp (*Cyprinus carpio*), on the density of the invading zebra mussel (*D. polymorpha*) has been largely unmeasured. A predator exclusion experiment was conducted in the Ohio River above Louisville KY (ORM 573-579) from August 12 to October 19, 1994. This approach (predator exclusion cages) is untried in lotic systems as large as the Ohio River. Six-sided, vexar mesh (3 cm) cages and open control cages were used to determine the effects of fish predation on exotic and native species of invertebrates. Density and size frequency distribution of benthic invertebrates colonizing artificial snag and cobble substrates were determined monthly. Significant predator impacts were found on a recent invader and now dominant invertebrate species in the river, the bivalve *D. polymorpha*. Mean densities of *D. polymorpha* on snags were 7,370/m$^2$ and 4858/m$^2$ for exclusion and open control cages, respectively. Significant density differences were also found due to substrate type (snag at 4,858/m$^2$ versus cobble at 27,961/m$^2$). Density, size/frequency and substrate preference data from 30 predator exclusion cages were compared with 30 control cages. These experiments will continue April through October of 1995. Similar experiments are ongoing in the Mississippi River.**

# COMPARISON OF ZEBRA MUSSEL GROWTH IN TENNESSEE AND OHIO RIVER WATER AND IN TENNESSEE RIVER WATER WITH ELEVATED CALCIUM

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**ABSTRACT. Zebra mussels *Dreissena polymorpha*, were first reported in the lower Tennessee and Ohio rivers in the fall of 1991. As of the fall of 1993, zebra mussels had colonized the entire lower Ohio River but not the Tennessee River. Based on information from other investigations regarding the environmental requirements of *D. polymorpha*, we hypothesized that water quality, perhaps low dissolved calcium (ranging from 16-24 mg/L in the lower Tennessee River and 26-43 mg/L in the Ohio River) was the cause for the lack of colonization in Tennessee River. To determine if calcium concentration affects *D. polymorpha* growth, and possibly colonization, we measured mean length and weight changes of mussels held in tanks with various calcium concentrations. Two experiments were performed. The first included six sets of aquaria containing Tennessee River water with either 20, 40, or 80 mg/L $Ca^{2+}$ and 30 or 60 mg of food consisting of a mixture of spray-dried *Chlorella*, low-fat rabbit chow and soybean meal. Thirty *D. polymorpha* were measured and placed in each tank. Twice daily feeding and weekly water changes continued for a period of 4 months. Growth occurred in all tanks, however, significantly greater dreissenid growth occurred in tanks with a calcium level of 40 mg/L than in tanks having a calcium level of 20 mg/L. Of the remaining tanks which recieved 80 mg/L calcium, *D. polymorpha* showed better growth when fed 30 mg of food than 60 mg of food. This discrepancy in growth was not explained. The second experiment involved a comparison of *D. polymorpha* growth in Tennessee River and Ohio River water without added calcium. The mussels were fed 77 mg of food twice daily during this 2-month duration. Growth occurred in all tanks; however, growth was much greater in Ohio River water than in Tennessee River water. It appears that water quality differences between the Ohio and Tennessee rivers may result in significant differences in growth rates of *D. polymorpha*. We believe these differences are sufficient to prevent, or at least retard, zebra mussel colonization of the lower Tennessee River. This project is funded in part by the Murray State University Committee on Institutional Studies and Research and the Tennessee Water Resources Research Center subcontract with the University of Memphis.**

# ZOOPLANKTON OF KENTUCKY LAKE WITH EMPHASIS ON *DAPHNIA LUMHOLTZI*

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**ABSTRACT. *Daphnia lumholtzi* (Sars), an exotic cladoceran was first recorded August 1990 in Kentucky Lake. Lake level, hydraulic retention time, nutrients, potential primary productivity, chlorophyll *a* and crustacean zooplankton dynamics were examined from 1989 through 1993 to document the *D. lumholtzi* invasion and to assess potential effects on community structure. Seasonal plankton dynamics in Kentucky Lake were compared with the PEG (Plankton Ecology Group) model to define similarities and differences between natural lake and reservoir ecosystems. Kentucky Lake plankton dynamics conform well to the PEG model except in 1990 and 1991 when extreme fluctuations in hydraulic retention time occurred. Deviations from the PEG model were related to nutrient and algal dynamics reflecting the importance of hydrological factors for nutrient supply and distribution.**

# IMMUNE STATUS OF CATFISH FROM THE WARM-WATER DISCHARGE AT TVA'S CUMBERLAND CITY STEAM PLANT

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**ABSTRACT. Bacterial associations with fish play key roles in the development of fish disease as well as spoilage of fish intended for human consumption. Bacteria are ubiquitous in aquatic environments and most do not represent obligatory pathogens. Rather, clinical disease often is the result of overgrowth of a bacterium in a compromised fish. Fish become susceptible to bacterial infection when their environment deteriorates and the fish become stressed. A common stressor in many bacterial diseases is a change in water temperature. The water discharged from steam plants dramatically affects the temperature of the aquatic environment. Fish congregate in these areas and are thus subjected to extremes in water temperature. Catfish represent the most popular sportfish in these environments and thus were selected as the fish for this study. Bacterial immunoagglutination assays were used to analyze sera of catfish harvested from the warm-water discharge at TVA's Cumberland City steam plant. Sera were tested for antibodies against *Aeromonas hydrophilia, Edwardsiella tarda, Edwardsiella ictaluri* and *Escherichia coli.* Antibody titers against *A. hydrophilia, Edwardsiella ictaluri* and *Escherichia coli* were observed. Some fish had lesions characteristic of bacterial disease. Additional research is needed to clearly document the impact of warm-water discharges from steam plants on resident fish populations.**

# CALCIUM-REGULATED PROTEINS IN DIFFERENT ECOSYSTEMS: CA$^{+2}$-ATPASE AND CALMODULIN

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**ABSTRACT. A review is made of the plasma membrane calcium pump ($Ca^{2+}$-ATPase) and calmodulin (a calcium-dependent regulatory protein). Speculation is being provided as to how these molecules may be exploited in studies of organisms in different ecosystems. In essence, it is being suggested that organisms in different ecosystems may be compared by studying calcium-transporting molecules that arose early in evolution and that are present in a range of species. In addition, molecules regulated by the same cation (calcium) and that modulate diverse biological processes may be studied in different organisms. Such approaches may reveal how ancestral molecules have undergone changes to meet the needs of species occupying niches in different ecosystems.**

# COMPARATIVE ECOLOGY OF TWO MAP TURTLES, *GRAPTEMYS OUACHITENSIS* AND *G. PSEUDOGEOGRAPHICA*, IN KENTUCKY LAKE

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**ABSTRACT. Map turtles (*Graptemys*) form an economically intersting species complex inhabiting major rivers that empty into the Gulf of Mexico, with much of the range of the genus being inhabited by one "narrow-headed" and one "broad-headed" species. The ecology of two species in the Tennessee River drainage, the narrow-headed *G. ouachitensis* and the broad-headed *G. pseudogeographica kohnii*, was studied in Nickell Cove of Kentucky Lake. Dietary nonoverlap was pronounced, with *G. ouachitensis* feeding most heavily on dipteran larvae, other insects, and algae, and *G. p. kohnii* feeding most heavily on Asian clams, small snails, chironomid egg cases, and algae. In addition, both species showed low intraspecific dietary overlap values for juveniles, males, and females. Relative head size differences occurred between males and females within both species, and were greater than expected based on the allometry of sexual size dimorphism that strongly favors females.**

**Both species occurred predominately in the deeper habitat zones of the cove, with *G. p. kohnii* showing the greater tendency to also inhabit shallower habitat zones. Habitat-zone overlap was low within both species in comparisons of juveniles and adults, but high for males and females. Overlap in diet and seasonal use of basking time was high between and within species, with both species having broad time niches for basking. Thus the primary ecological differences between these two species was in diet, and was associated with trophic specializations that typify much of the composite range of the genus.**

# DEMOGRAPHICS OF A TURTLE COMMUNITY IN AN URBAN WETLAND

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**ABSTRACT. Trapping of turtles was conducted for fourteen months in a portion (6.5 ha) of Black Fox Wetland, Murfreesboro, Rutherford County, Tennessee (35°48'40"N, 86°21'30"W), with the intent of determining the community structure therein. The area studied is owned by Middle Tennessee State University and the City of Murfreesboro. The area surrounding this section of the wetland has become substantially urbanized over recent years. This study serves as a baseline of information for future assessments of the turtle community. Trapping was accomplished primarily with baited hoop traps. A few additional turtles were captured by hand, in a basking trap and in a fyke trap. Population estimates were calculated by the Schnabel method for multiple mark-recapture sampling. Five species of turtles were found within the wetland. These include *Chelydra serpentina serpentina* (255 captures, 220 recaptures, predicted 377), *Trachemys scripta elegans* (338, 127, 800), *Sternotherus odoratus* (34, 4, 155) *Kinosternon subrubrum subrubrum* (41, 11, 104), and *Apalone spinifera spinifera* (5, 4, 6). Density of turtles in the study area was estimated at 222 individuals ha$^{-1}$. Standing crop biomass was estimated at 345.2 kg ha$^{-1}$.**

# A HERPETOFAUNAL SURVEY OF SHELTON FERRY WETLAND, MONTGOMERY COUNTY, TENNESSEE

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**ABSTRACT. Shelton Ferry Wetland is a Tennessee Wildlife Resources Agency (TWRA) property situated in the floodplain of the Cumberland River, 13 kilometers southeast of Clarksville, Montgomery County, Tennessee. Purchased by TWRA in 1991, the area consists of 7 tracts totaling approximately 176 hectares. While little information on the herpetofauna of the wetland itself exists, information on these animals in surrounding areas is plentiful. This study's goals were to seasonally inventory the amphibians and reptiles within the wetland's boundaries and the major habitat types supporting them. Field work spanned the four seasons of 1994. Specimens were collected from all major habitats using a variety of techniques (e.g. drift fences, hand collecting, aquatic traps, and nets). Four major habitat types were identified on the study area: cultivated field, bottomland forest, fallow field, and two sub-types of wetland (scrub-shrub swamp and forested swamp). Thirty-four species (20 amphibians and 14 reptiles) were identified based on sightings, captures, and/or call. All were species previously reported for Montgomery County. One species, *Ambystoma talpoideum*, is listed in Tennessee by TWRA as "Deemed in Need of Management" and as "Special Concern" by the Department of Environment and Conservation. Funding for this project was provided by the Tennessee Wildlife Resources Agency and Austin Peay State University's Center for Field Biology.**

# THE AMPHIBIANS AND REPTILES OF ARNOLD AIR FORCE BASE IN SOUTH CENTRAL TENNESSEE

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**ABSTRACT. A field inventory of the herpetofauna of Arnold Air Force Base (AAFB), comprising ca. 15, 800 hectares in southern sections of the Eastern Highland Rim and Outer Central Basin physiographic regions, was conducted from May 1993 through December 1994. General field collecting techniques were used to survey all habitats of AAFB, including low lying hardwood, pine, and mixed forests subject to seasonal flooding, dry forested slopes, old fields, permanent and intermittent streams, permanent ponds, and a reservoir. This diversity of habitats supported a rich herpetofauna; 54 species were identified, including 13 species of frogs (2 bufonids, 4 hylids, 1 microhylid, 1 pelobatid, and 5 ranids), 11 species of salamanders (4 ambystomatids, 6 plethodontids, and 1 salamandrid), 17 species of snakes (16 colubrids, 1 viperid), 5 species of lizards (1 anguid, 1 iguanid, 2 skinks, and 1 teiid) and 8 species of turtles (1 chelydrid, 5 emydids, 2 kinosternids, and 1 trionychid). Amphibians and reptiles in needs of special protection included *Rana capito, Ambystoma talpoideum, Hemidactylium scutatum, Pituophis melanoleucus, and Ophisaurus attentuatus.* The occurrence of the following species at AAFB represented signficant extensions of their known range: *Nerodia erythrogaster, Virginia valeriae,* and *Pseudemys concinna.* The discovery of *Rana capito* at AAFB represented an addition to the herpetofauna of Tennessee. This project was support by funds provided by The Nature Conservancy.**

# A SURVEY OF BAT SPECIES IN TENNESSEE VALLEY AUTHORITY'S LAND BETWEEN THE LAKES

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**ABSTRACT. A mist-netting survey for bats was conducted in TVA's Land Between The Lakes to assess the presence of endangered, threatened or special concern species. Mist-netting procedures followed guidelines described by the Gray bat/Indiana bat recovery team. Twenty sites were sampled between 15 May and 15 August 1994. A total of 253 bats representing 9 different species was captured over 74 net nights. *Myotis grisecens* was the only federally listed species captured; 2 males and 6 females constituting 3.2% of the total capture. *Lasiurus borealis* was the most commonly captured species, constituting 68.3% (94 males and 80 females) of the total capture. Other species captured included: *Nycticeius humeralis*, 8.3% (11 males and 10 females); *Pipistrellus subflavus*, 7.9% (10 males and 10 females); *Myotis septentrionalis*, 7% (9 males and 8 females); *M. grisecens*, 3.2% (2 males and 6 females); *M. lucifugus*, 2.8% (2 males and 5 females); *L. cinereus*, 0.8% (2 males); *Lasionycteris noctivagans*, 0.8% ( 2 males); and *Eptesicus fuscus*, 0.4% (1 male). Using Shannon Weiner's index of species diversity, the Tennessee portion of LBL was found to be significantly more diverse in bat species than the Kentucky portion (H'=0.520 and H' = 0.338, respectively). Species evenness was also found to be greater in Tennessee than Kentucky (J'=-0.226 and J'=-0.558, respectively). Justifications for higher species diversity in TN include: juxtaposition of water source, roosting habitat, and foreaging habitat; location of highly traveled roads or other human activity; and location of crop lands.**

# AN ESTIMATION OF AVIFAUNA SPECIES RICHNESS USING THE FIXED-RADIUS POINT COUNT METHOD IN AN OLD-GROWTH WOODS ON THE PENNYROYAL PLAIN IN CHRISTIAN COUNTY, KENTUCKY

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**ABSTRACT. The avifauna of a 25-ha, old-growth woodland in Christian County, Kentucky, was surveyed on four days between May 25, 1994 and June 14, 1994, using the fixed-radius point count method to determine species richness. Twelve circular plots with 25-m radii were designated so that they would lie a minimum of 100 m apart and at least 60 m within the woodland margin. Two observers (same each count day) spent 10 minutes at each point and recorded three sets of data: (1) all species observed or detected audibly within the count radius, (2) the number of individuals of each species observed or detected audibly within the count radius, and (3) all species encountered within the woodland between points and outside count radii. All observations were made between 0700 and 1100. All count days were relatively windless, mild, and overcast with temperatures ranging from 70° to 90°F.**

**The 276 individuals counted within radii included 32 species. Eighteen additional species were encountered within the woodland between points and outside radii. Species with individual frequencies >5% were Brown-headed Cowbird, Northern Cardinal, Downy Woodpecker, Tufted Titmouse, Carolina Chickadee, White-breasted Nuthatch, Ruby-throated Hummingbird, and Eastern Wood-pewee. Species with average daily site-occurrence frequencies >20% were Northern Cardinal, Downy Woodpecker, Rufous-sided Towhee, Eastern Wood-pewee, Tufted Titmouse, White-breasted Nuthatch, Red-bellied Woodpecker, and Brown-headed Cowbird.**

**The woodland, relatively undisturbed since the 1850s, has a canopy dominated by *Carya ovata*, *Quercus falcata*, and *Acer rubrum*. The understory is dominated by *Ulmus alata*, *U. rubra*, *Acer rubrum*, and *Asimina triloba*. A dense layer of *Smilax rotundifolia* and *Rhus toxicodendron* covers much of the forest floor. Soils are of Smalley's Landtype Association G-Weakly Dissected Karst Plain and are composed of Robertsville silt loam, a deep, poorly drained, strongly acid residuum weathered from limestones and loess. Fragipans, at depths of 0.5-1 m, commonly result in ponding from January to April, but may result in droughty conditions in dry seasons because of shallow rooting zone. Throughout the count period, there was no standing water within any points, but water flowed in several small drainages within the woodland.**

# CONTRIBUTED PAPERS

## SESSION III: BOTANY

Saturday, March 4, 1995

Moderated by:

Edward W. Chester
Austin Peay State University

# OXYGEN METABOLISM IN GERMINATING *EQUISETUM HYEMALE* L. SPORES

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**ABSTRACT. Isolated *Equisetum hyemale* L. spores experienced virtually complete desiccation following exposure to two percent relative humidity for one-hour, 24-hour, 72-hour, one-week, two-week, or four-week periods. Spores from all desiccation-duration treatments exhibited respiratory oxygen consumption within 30 seconds upon hydration in the light (200 umol photons $m^{-2} s^{-1}$). Spores previously desiccated for one and 24 hours reached the oxygen compensation point very rapidly (3.1 ± 0.2 and 6.3 ± 0.3 minutes respectively). Even following 24 hours of light hydration, only spores previously desiccated for one week or less were able to recover photosynthetic competence. These results indicate that: (1) during desiccation, spore mitochondrial membrane integrity is more highly conserved relative to chloroplast membrane integrity; (2) the ability for photosynthetic recoverydecreases with increasing desiccation duration; and (3) rapid photosynthetic recovery is essential due to the limited amount of carbohydrates the small spores can store.**

# AN HISTORICAL AND FLORISTIC CHARACTERIZATION OF McGAUGHEY SWAMP, CHRISTIAN COUNTY, KENTUCKY

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**ABSTRACT. McGaughey Swamp is an upland wet forest/swamp complex on the Pennyroyal Plain in Christian County, Kentucky. The Swamp comprised about 2024 ha in the 1850s, but now has been reduced by clearing and draining to approximately 160 ha, including a 25 ha old-growth forest. Weekly collecting trips for vascular plants from February-October 1993-1994, yielded 442 taxa (368 herbaceous taxa) from 277 genera and 95 families. The flora was dominated by taxa of Asteraceae (58), Poaceae (52), and Cyperaceae (21). There were 76 county records found. Rare taxa include *Trillium pusillum* Michx., Least Trillium, listed C2 federally, and *Glyceria septentrionalis* Hitch., Eastern Mannagrass, under consideration for listing in Kentucky. Historical records show that portions of the Swamp were settled in the early 1820s by the Henry, Kincaid, Nance, Whitlock, Morris, and McGaughey families. A journal written by John McGaughey from 1852-1905 documents usage of the Swamp and conditions during that era. The McGaughey lands were sold and most forests clear-cut in the late 1970s. The old-growth woods has had three owners since settlement and is presently a part of the Beverly M. Greenwood, Sr. estate.**

## INTRODUCTION

A recent symposium on the vegetation and flora of Kentucky (Baskin *et al.* 1987), a comprehensive account of regional forest communities (Bryant *et al.* 1993), and others (e.g., Meijer 1970, Bougher and Winstead 1974) pointed out the paucity of information on forests of some areas of the state. Data are especially lacking on the upland wet to swampy forests of the Pennyroyal Plain, where demands for agricultural land and increased timber prices have resulted in the draining of many swamps and the removal of most mature forest stands.

McGaughey Swamp, an historic upland wet woods/swamp complex in Christian County, is a good example. The complex exceeded 2000 ha in the 1850s (McGaughey 1981), but now has been reduced to remnants totaling about 160 ha as a result of draining, clearing, and timber harvest. We began a series of studies in 1993 in order to characterize certain biological (especially botanical) features of this Swamp. Studies included a phytosociological analysis of a 25 ha old-growth woods in 1993. The results, including comparisons with published old-growth criteria from adjacent areas (Parker 1989, Martin 1992) will be presented elsewhere. A breeding bird species richness study was made to further determine old-growth significance and these results also will be presented elsewhere. The purpose of the present paper is two-fold: (1) to present an historical account of the Swamp, and (2) to give the results of a two-year study of the vascular flora.

## THE STUDY AREA

McGaughey Swamp (hereafter as MS) is in the Pee Dee Community of southwestern Christian County, western-central Kentucky, mostly between Kentucky Highways 117 and 164, but extending west of 164. It is a prominent feature of the Caledonia, KY, 1974, U.S. Geological Survey 7.5' topographic quadrangle.

The Swamp is in the Pennyroyal Plain (PP) Subsection of the Highland Rim Section of the Interior Low Plateaus Physiographic Province (Quarterman and Powell 1978). The PP and the Elizabethtown Plain Subsection (EP) are collectively designated the Kentucky Karst Plain (KKP) by Smalley (1980) and are nearly coincident with the Big Barrens Region (Baskin *et al.* 1994). The PP Subsection is a level to steeply rolling karst plain with elevations ranging from about 150-300 m a.s.l., much being 150-200 m a.s.l. Sinkholes are numerous and many are filled with several meters of sediment eroded from agricultural fields (Dicken and Brown 1938, Sauer 1929).

The KKP is drained by the Nolin (EP), Green, Barren, Red, and Little (PP) rivers. Drainage of the PP is mostly underground with numerous sinking streams (Baskin *et al.* 1994). According to Meacham (1930), one of the real curiosities of Christian County is the "Sinking Fork of Little River." This stream, the most westerly of the three forks of Little River, rises in the northern hills of the county, flows in a southwesterly direction, and suddenly disappears in a great sinkhole. After flowing a considerable distance underground it again emerges and continues to junction with Little River in Trigg County near confluence with the Cumberland River. Upland flats and depressions, such as MS, are distinctive features of the PP.

Most bedrock of the PP is Upper Mississippian limestone of the St. Louis and Ste. Genevieve formations. Quaternary deposits of alluvium and loess provide parent material for soil development (Baskin *et al.* 1994). Soils are divided into three broad categories: (1) deep, moderately-to well-drained soils on level to steeply rolling uplands; (2) deep, well to poorly-drained soils on floodplains, upland flats, and depressions; and (3) shallow to moderately deep, well-drained soils on ridges, knobs, and level to rolling parts of the Karst Plain proper (Baskin *et al.* 1994). The Robertsville-Lawrence soil group underlies MS and consists of deep, nearly level, poorly-drained loamy soils (Froedge 1980). Historically these soils have been described as "flat lake country" by Allen and Bushnell (1914) or as "pondy woods" or "crawfishy land" by Chester (1988). This soil is strongly acid, with bedrock at depths greater than 1.5 m and fragipans at depths of 0.5--1 m (Froedge 1980). Ponding is common from January to April, but droughty conditions may occur in dry seasons because of the shallow root zone (Chester 1988).

The KKP is in the Western Mesophytic Forest Region of Braun (1950) and the Oak Hickory/Bluestem Prairie Region of Küchler (1964). The landscapes are diverse and support a wide spectrum of natural and semi-natural plant community types, including limestone cedar glades, xeric limestone prairies, barrens, forests of dry, mesic, and wetland sites, aquatic vegetation of sinkhole lakes and ponds, farm woodlots, and old fields and pastures in various stages of secondary succession (Baskin *et al.* 1987, 1994). Most of the KKP is now agricultural and nearly all of the remaining native vegetation has been moderately to highly disturbed (Kingsley and Powell 1978, Worms 1993).

## METHODS

### Historical

Historical information was obtained from published state, regional, county, and family histories, courthouse records, county archives, and from interviews with landowners, county historians, and members of the McGaughey family.

### Floristic

The swamp, as shown on topographic maps, was divided into four areas: (1) Greenwood Forest (GF), the 25 ha old-growth forest, representing the least disturbed section and located to the west of Highway 164; (2) Morris Bottom (MB), a 55 ha forest adjacent and to the west of GF, was selectively timbered and some portions clear-cut in the 1960s (like GF this site is seasonally flooded but differs in that drainage ditches were opened in the fall of 1993 and some timber harvest is presently occurring); (3) Frank Mason Woodland (FM), a 4.4 ha woodland that has been minimally disturbed in the last 50 years; and (4) Henry property (HP), a 70-75 ha narrow strip of wet woods that was selectively harvested in the late 1970s. The two latter sites lie between Highway 164 and 117; all sites were contiguous as recently as the 1960s when portions northeast of Highway 164 were clear-cut, effectively isolating GF and HP. In addition to these sites, collections were made from wet meadows, drainage areas, roadsides, and other disturbed sites within the historic swamp area.

The floristic study extended through the growing season (February--October) of 1993-1994 and included weekly collecting trips. Specimens were identified, catalogued, and housed in the Austin Peay State University Herbarium in Clarksville, Tennessee. Nomenclature follows Wofford and Kral (1993). Used in identification and distribution analyses were Browne and Athey (1992), Cronquist (1980), Fernald (1950), Gleason and Cronquist (1991), Isley (1990), Steyermark (1975), and Wofford (1989).

## RESULTS AND DISCUSSION

### Historical

Occupants of the Ohio and Mississippi River valleys prior to the Anglo-Saxons and the latter-day Indians are known to us only by the relics and burial mounds they left. Rafinesque, as recorded in Marshall's History of Kentucky, listed 17 mounds in Christian County, 5 as "sites" and 12 as "monuments" (Perrin 1884). Analyses of materials from these mounds indicate that they were built by a pre-historic people of the Neolithic age (Funkhouser and Webb 1928).

These people were succeeded by the latter-day Indians, who may have exterminated the earlier residents. The Delaware Indian tradition holds that the Lenni-Lenape, in their sweep westward, were greeted by a mighty civilization east of the Mississippi (Perrin 1884). According to Collins (1847), Kentucky, during the pre-settlement years, was a favorite hunting ground for Delaware, Wyandots, Shawnees, and other tribes from beyond the Ohio River, and the Catawbas, Cherokees, and Creeks from the southern country (LaFarge 1956, Maxwell 1978). "They came to hunt deer, elk, and buffalo, roamed the forests, grazed the natural pastures, and frequented the salt-impregnated springs so common in the state" (Perrin 1884).

There is no record of permanent latter-day Indian settlements in Kentucky. Because of the bloody conflicts ensuing over the hunting grounds, superstitions may have prevented such occupancy. An old warrior speaking with Colonel Joseph Hamilton Davis in St. Louis in 1800 stated, "Kentucky is filled with the ghosts of its slaughtered inhabitants; how could the white man make it his home (Meacham 1930)?"

From 1763-1783, all of the county west of the Tennessee River was proclaimed an Indian Reservation by King George III. As a result, this section was settled later than eastern and central sections (Meacham 1930). John Filson's (1784) *Discovery, Settlement and Present State of Kentucke* was the first book on the Commonwealth and its now famous map of Kentucky did not attempt to describe the wilderness portions west of the Green River (Coleman 1971).

By the Treaty of Sycamore Shoals in 1775, Judge Richard Henderson and the Transylvania Company gained rights to 20 million acres from the Cherokee. This land lay in the triangle enclosed by the Cumberland, Kentucky, and Ohio rivers. Although an open violation of His Majesty's orders, the treaty opened the region to white settlement (Lester 1935, Kinkead 1896). After the Sycamore Shoals Treaty, Henderson dispatched Daniel Boone and 30 companions to blaze a trail from the Cumberland Gap to the Kentucky River. Boone, in his 1823 autobiography, describes his travels up the Cumberland to the Red River which crosses the southern border of Christian County. He and his party came through Cumberland Gap and down the Ohio and fought with Indians from both north and south who hunted in Kentucky (Lester 1935).

Prior to 1786, Kentucky was part of the Colony of Virginia and at that time had a population of approximately 30,000 persons. In 1789, a petition for separation from Virginia was granted and statehood was obtained on 1 June 1792. Entering the state at Cumberland Gap, more than 200 000 pioneers followed the Wilderness Road to settle Kentucky between 1776 and 1796. In these early settlement times, the Newstead area of Christian County was considered one of the finest sections of "The Barrens" because of the Little River, which provided water and fine timber along its course (Meacham 1930).

In 1792, Nelson County, Kentucky, which extended to the Mississippi River, was divided and Logan County formed from its western part. In 1796, Logan was divided, and while retaining the settled portion, Christian County was formed from all land west of the Green River and west of a line south of the Green River to the Tennessee line, which was the eastern boundary of Todd County. It contained 7,500 square miles and was larger than Connecticut, Delaware, and Rhode Island combined. This tract was later carved into 20 counties (Rone 1965).

From Boone's first foray into Kentucky in 1769, to the signing of the Treaty of Greenville in 1795, there was a continual struggle for supremacy between the Native Americans and the white explorers and pioneers. Despite many bloody confrontations in various parts of the state, there are no records of Indian outrages or atrocities in Christian County (Perrin 1884). The procession of 17,000 Native Americans, later named the Trail of Tears, passed through Hopkinsville in the fall of 1838 and ended forever the sojourn of the Indians in Kentucky's "Dark and Bloody Ground" (Meacham 1930).

According to Perrin (1884), prior to 1800 Christian County was a vast waste with only here and there meager settlements of hardy pioneers. Much of the county was an unbroken stretch of barrens or prairie land inhabited by wild animals, the settlements being confined to the timber. "Believing the barrens would never be worth anything, except pasturage, the good old pioneers of North Carolina sought the hills of the northern parts of the county where flowed perennial springs and grew towering forests" (Perrin, 1884). This opinion was not shared by all, however, and tales of Daniel Boone's exploits and the lure of "almost free" land to veterans of the Revolutionary War and War of 1812 proved to be hard to resist. Caravans of ox-carts brought settlers west (Meacham 1930).

The 2024 ha (in 1850) tract designated McGaughey Swamp has had a remarkably stable ownership history that can be traced readily from settlement. Tracts of property in the Newstead/Pee Dee Community, occupying a position in the southwestern section of the county and formerly a part of Union Schoolhouse District, were first owned by the Henry, Kincaid, Nance, Whitlock, Morris, and McGaughey families and entirely contain the McGaughey Swamp (Christian County Genealogical Society 1986).

Colonel William Henry, son of General William Henry, a near relative of Patrick Henry and a Revolutionary War Veteran, came to Kentucky in 1817 and in 1820 purchased 3000 acres one mile west of Newstead (Perrin 1884). This property was owned and farmed by the Henry family until the 1970s when it was purchased and further developed by William Hanson Williams, who, with his son-in-law, currently operate the farm.

Joel Nance, a Virginian and veteran of the War of 1812, settled in Shelby County, Kentucky, after the war, and in 1821 purchased property in the Newstead/Pee Dee Community (Perrin 1884). His son, Benjamin Bedford Nance, operated the farm until his death in 1914. This property is contiguous but not part of the swamp complex and no doubt influenced its flora.

Joseph Kincaid owned extensive property in the Newstead area and operated a store 11 miles southwest of Hopkinsville. In 1845, he sold a tract to Dr. J. C. Whitlock, who set up and maintained a medical practice in Christian County until his death in 1886 (Christian County

Genealogical Society 1986). He built the Whitlock home (now the late B.M. Greenwood, Sr. home) in 1851. The Whitlock land was purchased in 1894 by Ed and Matt Jones and sold to B.M. Greenwood, Sr. in 1919. In 1920, Mr. Greenwood, Sr. occupied the old Whitlock home and at his death owned 984 acres in that area (Christian County Genealogical Society 1986). His widow retained ownership of the property until her death in late 1993. The farm is now owned by the Greenwood heirs and is operated by B.M. Greenwood, Jr., who presently lives on the property.

A portion of the woodland/swamp complex joining the Greenwood property is presently owned by Douglas and Ann Mason Walker. This property was first settled in 1812 by Captain Eddin Morris, a Revolutionary War veteran, and has been owned by the Mason family for the past century. Many of the herbaceous species were collected on this cutover portion, known as "Morris Bottom," which had been left undisturbed following a selective timber harvest in 1965, but was harvested again in 1994 (Personal Communication, A. Mason, 1994).

Following the death of her husband,Charles McGaughey, in 1760, Lavinia McGaughey emigrated from Ireland in 1761 with her two young sons, Arthur and Thomas, remarried and settled in Pennsylvania. Her son Arthur married and in 1794, moved to Shelby County (then Hart County), Kentucky, when their son Arthur was four months old. At age 21, Arthur, Jr. served in the War of 1812 and fought with General Andrew Jackson in the Battle of New Orleans in 1814. He left his home in Shelby County in 1826 to purchase 1350 acres in the Newstead area of Christian County from George Loftus, who then owned 3000 acres. To reward the men who had served with him in the Battle of New Orleans, General Jackson, after becoming United States President in 1828, made it possible for veterans to purchase land at little cost in the unsettled portions of Kentucky, including large portions of Christian County (McGaughey 1981).

All except the Whitlock (now Greenwood) and McGaughey portions of the swamp had been cleared for agricultural use by the 1970s. In 1971, the McGaughey property was leased to Donald Moore from Evansville, Indiana, and was sold to him outright in 1976. "In 1979, a field of more than 200 acres of soybeans marked the area where once stood a forest of trees, vines, decayed logs covered with moss, the tract that remained of a swamp that bore the McGaughey name (McGaughey 1981). Only the small remnant woodland owned by the B. M. Greenwood Sr., heirs remains. Although the Greenwood acreage was never owned by the McGaughey family, it is a part of the swamp complex.

Arthur McGaughey, with his wife and four young children came to Christian County in 1826 and established the residence he named "Steadfast." Two additional children were born after arrival. The last, John, born in 1832, kept a journal of his life at Steadfast. His record from 1852-1905 is the main source of information about the Swamp, since the wettest portions (600 ha) were owned by the McGaughey family. In 1852 he survived a cholera epidemic which claimed his parents, a sister, and a number of the 15 farm and household slaves. At age 20, he and a slightly older brother were left to manage the business of the estate.

Being a sportsman, he took great pleasure in the Swamp and made numerous records of shooting wild turkeys, pigeons, and mallards and bagging or netting "paterages" for the table. In November, 1853, he writes ". . . had a delightful ride through the swamp. . .saw a drove of wild turkeys and squirrels. . .home is certainly the most pleasant place in the entire world." This entry was made two days after he returned from a trip east to visit Boston, New York, and Niagara Falls.

In the fall of 1857, McGaughey records his astonishment as he watched a tide of passenger pigeons three to four miles in length pass overhead. Acorns, their chief food, were available in abundance in this vast woodland. From November 1857, through January 1858, their morning and evening flights to and from their roosts were described as resembling the sound of thunder. McGaughey, as did many who witnessed this spectacle, shot into the clouds of pigeons and counted the toll. Meacham (1930) notes that the last known specimen of these birds in Christian County was captured in 1911, but McGaughey makes no further mention of them in his journal.

In addition to sport, the swamp woods provided necessities. McGaughey describes using oak and hickory logs and sawdust to produce the color and aroma of the "dark-fired" tobacco grown at Steadfast. He cut hickory and ash for firewood, oak saplings to make yokes for his teams of oxen, and vines from the swamp to bind the sheaves of wheat he cradled.

Frequent entries refer to bouts of dyspepsia and a condition referred to as "summer complaint." Among the treatments used to combat this malady were a round of "bitters" from dogwood and wild cherry cut in the swamp, or a dose of ipecac, an herb that still grows in the swamp woods, or sulfur water from a mineral spring at a nearby resort. Among those who succumbed to the condition were John McGaughey's brother and several children born to his sister, who lived near Steadfast. After her move to Hopkinsville, his sister's remaining infants survived. Water from the swamp and local wells may have been the culprit, as malaria and typhoid were commonly reported illnesses.

McGaughey, who suffered from chronic intestinal illness, reports in 1845 ". . . I rose at 4:00 a. m. and walked down to the cave spring with a pitcher before breakfast." This large spring served as the only outlet for the flood waters that collected after heavy rains. A public portion of the swamp road leading to Newstead and Pee Dee passed close to the cave spring situated under a ledge of rock at the base of a large sinkhole. Because it was inadequate to drain the surrounding area quickly, depths of 6-10 meters were not unusual following heavy rains and the road often became covered as several hundred acres flooded. McGaughey reports that on one occasion a team of mules drawing a wagon in such conditions plunged into the deep water and though the driver swam to safety, the mules, become entangled in the harness and drowned.

Remaining neutral during the Civil War, McGaughey carried out routine farm activities. In February 1862, amid rain, thunder, hail, and light snow, he stood on his porch at Steadfast and marvelled at the incessant cannonading of Fort Henry and Fort Donelson which rattled windows and doors, then quietly in the early morning hours had a Negro secure the farm horses in a safely wooded area to prevent their being pressed into service by a cavalry scouting party.

Winters found the young McGaughey driving large herds of hogs (several hundred) through the swamp to begin a 30 mile journey to Canton, Cumberland Furnace, Linton, or another shipping point along the Cumberland River, or on a more frivolous note, indulging in daring sleigh races along the swamp road with one of the local young ladies. In his more mature years, McGaughey found the swamp a place for contemplation. In 1875, he writes, "It affords me peculiar pleasure to be in the forest surrounded by trees that have been growing for a century or more. It is suggestive of sadness to me to see the old trees decaying and covered with marks of age. . . cycles of years have passed leaving their marks in view."

The serenity did not last. In November 1876, the entire swamp and contiguous woods were swept by a roaring fire. McGaughey describes setting a backfire to save some of his woodland fencing. "I shall never forget the two lines of fire approaching and meeting for a mile or more in extent. The roaring fire could be heard far away and the crashing and burning of trees at intervals on a tract of a thousand acres of tangled swamp. A vast destruction of timber has been caused and thousands of trees have been killed by the heat." The blaze was started by a neighbor's field hands who carelessly let the fire for a tobacco plant bed escape. In 1910, a steam sawmill operated by a Mr. White was set up on the ledge above the cave spring at Steadfast and timber was harvested for construction of additional farm buildings.

To those less familiar with the swamp, its vine-tangled trees presented a formidable and mysterious aspect. Local stories grew larger and larger even as the swamp diminished. Reports of monstrous snakes, wild boars, and wildcats circulated, as did tales of wanderers becoming lost for days in its sawbriar tangles (Kentucky New Era, 1981). The wild boars were no doubt feral hogs lost on drives to market; the wildcats (bobcats) were real and were seen on many local farmsteads as the swamp woodland was cleared in the 1970s; as to the snakes, they just seem to grow with each tale.

In one of his final diary entries (January 14, 1905), less than two months before his death, McGaughey writes ". . . reading old diaries of 50 years past . . .back into slavery time . . catching paterages in a net, and plenty of wild ducks, geese, and even wild turkeys . . . those days have long since passed and most of the people of that day with the fleeting years."

## Floristic

The vascular flora of the present McGaughey Swamp includes 442 taxa and 277 genera from 95 families. This includes 74 trees, shrubs, and woody vines from 47 genera and 29 families. There are 368 herbaceous species species, dominated by taxa of Asteraceae (58), Poaceae (52), Cyperaceae (21). The Pteridophyta include 12 genera, 8 families, and 15 species. Taxa of Ophioglossaceae, especially *Ophioglossum pycnostichum* and *Botrychium virginianum*, were most abundant. Of the 155 taxa from 111 genera and 65 families found in the old-growth forest, 136 species coincided with the list of 197 taxa compiled by Hannan and Lasseter (1982) from Brodhead Swamp in Rockcastle County, Kentucky.

Two listed taxa were found. *Trillium pusillum* Michx., Least Trillium, listed as C2 federally, grows in scattered colonies in old-growth woods in association with *Tipularia discolor, Platanthera peromoena, Cardamine rhomboidea, Lysimachia ciliata*, and *Poa sylvestris*. Secondly, *Glyceria septentrionalis* Hitchcock, Eastern Mannagrass, occurs in temporary shallow pools and is under consideration for listing in Kentucky (Jones 1993). When compared with wetland species listed for Kentucky by Beal and Thieret (1986), 76 collections from McGaughey Swamp constitute county records. Most of these are widely distributed species which have not been documented in the County. Of the 119 species encountered in wet meadows surrounding GF, 94 species are indicative of disturbance.

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**Appendix. Annotated list of vascular plants known from McGaughey Swamp, Christian County, Kentucky. Descriptors of distribution and abundance are: very rare (known from only a few sites, usually with only a few plants in each); rare (known from several sites, usually with only a few plants in each); occasional (irregular in occurrence and sometimes absent from the stated habitat(s) but generally scattered throughout); locally abundant (same as occasional but in large numbers when found); frequent (expected within the stated habitat, but often not in large numbers); abundant (expected in the type, often in large numbers). Species found at only one of the subdivisions of the Swamp are designated with GF, MB, HP, or FM to indicate the subdivision of occurrence. Non-indigenous taxa are indicated by an asterisk (*).**

## PTERIDOPHYTA: FERNS AND FERN ALLIES

### ASPLENIACEAE, Spleenwort Family

*Asplenium platyneuron* (L.) Britt., Sterns & Pog., Ebony Spleenwort. Occasional in wet thickets, streambanks.

### DENNSTAEDTIACEAE, Bracken Family

*Pteridium aquilinum* (L.) Kuhn, Bracken Fern. Occasional in wooded edges, thickets.

### DRYOPTERIDACEAE, Wood Fern Family

*Polystichum acrostichoides* (Michx.) Schott, Christmas Fern. Frequent throughout wet woods.

### OPHIOGLOSSACEAE, Adder's-Tongue Family

*Botrychium biternatum* (Sav.) Underwood, Southern Grape Fern. Occasional in mesic woods.
*Botrychium dissectum* Spreng. forma *obliquum* Fern., Common Grape Fern. Occasional in mesic woods.
*Botrychium dissectum* Spreng. forma *dissectum*, Dissected Grape Fern. Rare in wet woods of GF.
*Botrychium virginianum* (L.) Swartz, Rattlesnake Fern. Abundant in wet woods.
*Ophioglossum pycnostichum* (Fern.) Love & Love, Southeastern Adder's Tongue. Frequent in mesic woods.

### SELAGINELLACEAE, Spike-Moss Family

*Selaginella apoda* (L.) Spring, Meadow Spike-Moss. Occasional to frequent along shaded drainages, streambanks.

### OSMUNDACEAE, Royal Fern Family

*Osmunda regalis* L., Royal Fern. Locally abundant in disturbed wet woods of HP.

### THELYPTERIDACEAE, Marsh-Fern Family

*Thelypteris hexagonoptera* (Michx.) Weatherby, Broad Beech Fern. Occasional in mesic woods.

### WOODSIACEAE, Cliff Fern Family

*Athyrium asplenioides* (Michx.) A. A. Eaton, Southern Lady Fern. Occasional in wet woods.
*Cystopteris protrusa* (Weatherby) Blasdell , Southern Fragile Fern. Rare in HP woodland.
*Onoclea sensibilis* L., Sensitive Fern. Frequent throughout.
*Woodsia obtusa* (Spreng.) Torr., Common Woodsia. Occasional in disturbed wet woodland.

## SPERMATOPHYTA: GYMNOSPERMAE

### CUPRESSACEAE, Cedar Family

*Juniperus virginiana* L., Eastern Red Cedar. Rare in woods, occasional in thickets.

## SPERMATOPHYTA: ANGIOSPERMAE, MONOCOTYLEDONAE

### ALISMATACEAE, Water-Plantain Family

*Alisma subcordatum* Raf., Water-Plantain. Frequent in wet meadows, standing water.

### ARACEAE, Arum Family

*Arisaema dracontium* (L.) Schott, Green Dragon. Frequent in mesic woods, thickets.
*Arisaema triphyllum* (L.) Schott, Jack-in-the-Pulpit. Occasional in mesic woods.

### COMMELINACEAE, Spiderwort Family

**Commelina communis*, L., Dayflower. Occasional in mesic woods, clearings.
*Commelina diffusa* Burm. f., Diffuse Dayflower. Abundant in wet meadows.
*Tradescantia subaspersa* Ker, Harsh Spiderwort. Infrequent along streams, drainages.
*Tradescantia virginiana* L., Virginia Spiderwort. Rare in mesic woods, thickets.

### CYPERACEAE, Sedge Family

*Carex alata* Torr. Occasional in wet fields and ditches.
*Carex amphibola* Steud., Ambiguous Sedge. Frequent in wet fields and ditches.
*Carex annectens* (E.P. Bicknell), Connected Sedge. Frequent in wet fields and swamp margins.
*Carex cephalophora* Willd., Headed Sedge. Occasional in clearings and thickets.
*Carex frankii* Kunth, Frank's Sedge. Abundant in marshy fields and meadows.
*Carex grayi* J. Carey, Gray's Sedge. Frequent in moist thickets and marshy fields.
*Carex lupulina* Willd., Hop-Like Sedge. Frequent in swampy meadows and margins.
*Carex retroflexa* Willd., Reflexed Sedge. Occasional in open wet woods.
*Carex shortiana* Dewey, Short's Sedge. Occasional in wet meadows near GF.
*Carex squarrosa* L., Spreading Sedge. Abundant in wet woods, swampy fields and ditches.
*Carex stipata* Muhl. ex Willd., Crowded Sedge. Occasional in open wet woods.
*Carex tribuloides* Wahlenb., Tribulus-Like-Sedge. Frequent in wet woods and swampy fields.
*Carex vulpinoidea* Michx., Fox-Tail Sedge. Abundant in wet fields, ditches.
*Cyperus strigosus* L., Strigose Sedge. Occasional in marshy meadows, wet ditches.
*Cyperus ovularis* (Michx.) Torr., Egg-Shaped Sedge. Occasional in wet fields.
*Eleocharis erythropoda* Steud., Red-Stemmed Spike-Rush. Frequent in marshy meadows of MB.
*Eleocharis obtusa* (Willd.,) Schult., Blunt Spike-Rush. Frequent in wet ditches, marshy edges.
*Rhynchospora corniculata* (Lam.) Gray. Occasional in wet ditches, clearings.
*Scirpus atrovirens* Willd., Dark-Green Bulrush. Occasional in wet ditches, clearings.
*Scirpus cyperinus* (L.) Kunth., Red Bulrush. Occasional in marshy meadows, wet ditches.
*Scirpus pendulus* Muhl., Line-Scaled Bulrush. Occasional in marshy meadows, wet ditches.

### DIOSCOREACEAE, Yam Family

*Dioscorea villosa* L., Wild Yam. Frequent throughout in woods, thickets.

### IRIDACEAE, Iris Family

*Sisyrinchium angustifolium* Mill., Narrow-Leaf Blue-Eyed Grass. Occasional in wet fields, woods and thickets.

### JUNCACEAE, Rush Family

*Juncus biflorus* Ell., Two-Flowered Rush. Frequent in wet fields, meadows, ditches.
*Juncus canadensis* J. Gay ex Laharpe. Occasional in wet fields and ditches of MB.
*Juncus effusus* L., Soft Rush. Frequent in standing water, wet ditches.
*Juncus marginatus* Rostk., Margined Rush. Frequent in wet fields, ditches, marshy sites.
*Juncus tenuis* Willd., Path Rush. Abundant in mesic woods and thickets.

### LEMNACEAE, Duckweed Family

*Lemna minor* L., Duckweed. Frequent in standing water.

### LILIACEAE, Lily Family (including Amaryllidaceae)

*Allium canadense* L., Wild Onion. Frequent in thickets, field margins.
**Allium vineale* L., Field Garlic. Frequent in disturbed sites, field edges.
**Ornithogalum umbellatum* L., Star-of-Bethlehem. Occasional in field edges.
*Polygonatum biflorum* (Walt.) Ell., Two-Flowered Solomon's Seal. Occasional in mesic woods, thickets.
*Smilacina racemosa* (L.), False Spikenard. Occasional in mesic woods.
*Trillium pusillum* Michx., Least Trillium. Occasional, small colonies in swampy oak woods of GF.
*Trillium recurvatum* Beck, Recurved Trillium. Occasional in mesic woods.
*Uvularia sessilifolia* L., Wild Oats. Rare along streamsides of MB.

### ORCHIDACEAE, Orchid Family

*Platanthera peramoena* Gray, Purple Fringeless Orchid. Frequent in wet thickets.
*Spiranthes cernua* (L.) Rich., Nodding Ladies' Tresses. Rare in wet meadows of MB.
*Spiranthes vernalis* Engelm. & A. Gray, Spring Ladies' Tresses. Rare in wet meadows of MB.
*Tipularia discolor* (Pursh) Nutt., Cranefly Orchid. Occasional throughout mesic woods.

### **POACEAE**, Grass Family

*Agrostis perennans* (Walt.) Tuck., Upland Bent. Frequent in mesic woods.
*Alopecurus carolinianus* Walt., Carolina Foxtail. Frequent in wet meadows.
*Andropogon virginicus* L., Broom Sedge. Frequent in disturbed areas, meadows.
*Brachyelytrum erectum* (Shreb.) Beauv., Short Huskgrass. Occasional in open disturbed woods.
**Bromus commutatus* Schrad., Racemose Brome Grass. Frequent in fields and disturbed areas.
**Bromus japonicus* Thunb. ex Murray, Japanese Brome. Abundant in fields and disturbed sites.
*Bromus pubescens* Muhl. ex Willd. var. *pubescens,* Brome Grass. Occasional in wet thickets.
*Bromus purgans* L., Woodland Brome Grass. Occasional in swampy woods and wet ditches.
**Bromus tectorum* L., Brome Grass. Adundant in disturbed sites, open fields.
*Chasmanthium latifolium* (Michx.) H. O. Yates, Wild Oats. Occasional along streambanks.
*Cinna arundinacea* L., Wood Reedgrass. Occasional in open moist woods.
**Dactylis glomerata* L., Orchard Grass. Occasional in meadows.

*Danthonia spicata* (L.) Beauv. ex Roem. & Sch., Poverty Grass. Abundant in disturbed areas, ditches, roadbanks.
**Echinochloa colona* (L.) Link. Occasional in wet meadows.
**Echinochloa crusgalli* (L.) Beauv., Barnyard Grass. Abundant in wet fields, ditches.
*Elymus virginicus* L. var. *virginicus*, Wild Rye, Terrell Grass. Frequent in disturbed sites and thickets.
**Eragrostis cilianensis* (All.) Mosher., Stink Grass. Abundant in wet fields, disturbed sites.
*Eragrostis hypnoides* (Lam.) BSP., Creeping Love Grass. Abundant in wet fields.
**Eragrostis pilosa* (L.) Beauv., Pilose Love Grass. Frequent in disturbed wet areas.
*Eragrostis spectabilis* (Pursh) Steud., Tumble Grass. Occasional in well drained field edges.
*Erianthus giganteus* (Walt.) Muhl., Giant Beardgrass. Very rare, one plant in wooded edge at HP.
*Festuca subverticillata* (Pers.) E. B. Alexeev., Obtuse Fescue. Frequent in open wet woods.
*Glyceria septentrionalis* Hitchc. var. *septentrionalis*. Rare in standing water at GF.
*Glyceria striata* (Lam.) Hitchc., Manna-Grass. Frequent throughout wet woods, marshy edges.
*Hordeum pusillum* Nutt., Little Barley. Abundant in stands in disturbed areas, open moist fields.
*Leersia oryzoides* L. Swartz., Rice Cutgrass. Abundant in wet meadows.
*Leersia virginica* Willd., Woods Sawgrass. Frequent in wet fields and thickets.
*Leptochloa filiformis* (Lam.) Beauv., Feathergrass. Occasional in wet meadows.
**Lolium perenne* L., Common Ryegrass. Occasional in field margins, disturbed sites.
*Melica mutica* Walt., Melic Grass. Occasional in open wet woods.
*Muhlenbergia tenuiflora* (Willd.) BSP., Slender-Flowered Muhly. Occasional in moist open woods.
*Panicum agrostoides* Spreng. Frequent in wet meadows; occasional in disturbed wet woods.
*Panicum anceps* Michx. var. *anceps*, Two-Edged Panic Grass. Frequent in disturbed field edges.
*Panicum capillare* L. var. *sylvaticum* Torr., Philadelphia Panic Grass. Occasional in wet fields and swampy woods.
*Panicum clandestinum* L., Hidden Panic Grass. Frequent in mesic woods and thickets.
*Panicum commutatum* L., Changeable Panic Grass. Frequent in open mesic woods, thickets.
*Panicum dichotomiflorum* Michx., Forked-Flowered Panic Grass. Frequent in wet fields, ditches.
*Panicum dichotomum* L. var. *dichotomum*, Forking Panic Grass. Abundant in disturbed areas, wet ditches.
*Panicum lanuginosum* Ell. Occasional along drainage ditches and in wet fields.
*Panicum laxiflorum* Lam., Loose-Flowered Panic Grass. Frequent in drier sites, open woods.
*Panicum oligosanthes* Schult. Occasional in open woods, along streams and drainage ditches.
*Paspalum laeve* Michx., Smooth Knotgrass. Occasional in disturbed sites, wet fields.
**Phleum pratense* L., Timothy. Occasional in disturbed sites, open fields.
*Poa sylvestris* Gray., Woodland Bluegrass. Occasional in open wet woods.
*Setaria faberi* R.A.W. Herrm., Tall Foxtail. Frequent in disturbed areas, roadbanks, edges.
*Setaria parviflora* (Poir.) Kerguelen, Bent Bristly Foxtail. Frequent in wet fields, disturbed sites.
**Setaria viridis* (L.) P. Beauv., Green Foxtail. Frequent in open wet fields.
**Sorghum halepense* (L.) Pers., Johnson Grass. Occasional in disturbed field edges, ditches.
*Sphenopholis obtusata* (Michx.) Scribn. var. *obtusata*, Blunt Wedge Grass. Occasional in open wet woods.
*Tridens flavus* (L.) Hitchc., Purple-Top. Frequent in open fields, meadows.
**Triticum aestivum* L., Common Wheat. Planted as a crop, escaping to fencerows.
**Zea mays* L., Corn. Planted as a crop, escaping to fencerows.

### SMILACACEAE, Catbrier Family

*Smilax rotundifolia* L., Catbrier. Abundant throughout wet woods.

### TYPHACEAE, Cat-Tail Family

*Typha latifolia* L., Common Cat-Tail. Occasional in standing water, wet meadows.

## SPERMATOPHYTA: ANGIOSPERMAE, DICOTYLEDONAE

### ACANTHACEAE, Acanthus Family

*Ruellia caroliniensis* (Walt.) Steud., Carolina Wild Petunia. Rare in clearings in woods of MB.
*Ruellia strepens* L., Smooth Wild Petunia. Occasional in moist woods, thickets.

### ACERACEAE, Maple Family

*Acer negundo* L., Box Elder. Frequent throughout mesic woods.
*Acer rubrum* L., Red Maple. Abundant throughout.
*Acer saccharum* Marsh., Sugar Maple. Frequent in canopy.

### AMARANTHACEAE, Amaranth Family

**Amaranthus hybridus* L., Pigweed or Wild Beet. Occasional in field edges, disturbed sites.

### ANACARDIACEAE, Cashew Family

*Toxicodendron radicans* (L.) Kuntze, Poison Ivy. Abundant as groundcover throughout mesic woods.

### ANNONACEAE, Custard-Apple Family

*Asimina triloba* (L.) Dunal., Pawpaw. Abundant throughout.

### APIACEAE, Parsley Family

*Chaerophyllum tainturieri* Hook., Rough Chervil. Occasional in field edges.
*Cryptotaenia canadensis* (L.) DC., Honewort. Occasional in mesic woods.
**Daucus carota* L., Wild Carrot, Queen Anne's Lace. Frequent in field margins.
*Eryngium prostratum* Nutt., Prostrate Eryngo. Occasional in disturbed sites, drainages.
*Osmorhiza longistylis* (Torr.) DC., Anise-Root, Sweet Cicely. Occasional in mesic woods.
*Sanicula canadensis* L., Canada Black Snakeroot. Occasional in mesic woods.
**Torilis arvensis* (Huds.) Link, Hedge Parsley. Occasional in field edges, ditches.

### APOCYNACEAE, Dogbane Family

*Amsonia tabernaemontana* Walt., Bluestar, Blue Dogbane. Rare in mesic thickets of MB.
*Apocynum cannabinum* L., Indian Hemp. Infrequent in wet fields, wooded edges.

### AQUIFOLIACEAE, Holly Family

*Ilex decidua* Walt., Deciduous Holly. Rare in mesic woods at GF.

### ARALIACEAE, Ginseng Family

*Aralia spinosa* L., Devil's Walking Stick. Frequent throughout woods, thickets.
*Panax quinquefolius* L., Ginseng. Very rare; one plant encountered at FM.

### ASCLEPIADACEAE, Milkweed Family

**Asclepias incarnata* L., Swamp Milkweed. Abundant in wet meadows.

*Asclepias syriaca* L., Common Milkweed. Occasional in uncultivated fields.
*Asclepias tuberosa* L., Butterfly Weed. Rare in wet meadows.
*Cynanchum laeve* (Michx.) Pers., Honeyvine. Occasional in thickets throughout.

### ASTERACEAE, Composite Family

*Achillea millefolium* L., Common Yarrow. Occasional in meadows.
*Ambrosis artemesiifolia* L., Common Ragweed. Frequent in field edges, thickets.
*Ambrosia trifida* L., Great Ragweed, Buffalo Weed. Frequent in weedy thickets, field margins.
**Anthemis cotula* L., Mayweed, Dog-Fennel. Rare in field edges of HP.
**Arctium minus* (Hill) Bernh., Common Burdock. Frequent in margins or cultivated fields.
*Aster dumosus* L., Bushy Aster. Occasional in field edges, disturbed areas.
*Bidens frondosa* L., Leafy Sticktights. Frequent in wet fields, thickets.
**Chrysanthemum leucanthemum* L., Oxeye Daisy. Occasional in wet meadows.
**Cichorium intybus* L., Chicory. Rare in field edges, waste places.
*Cirsium discolor* (Muhl.) Spreng. Field Thistle. Occasional in disturbed sites, fallow fields.
*Cirsium vulgare* (Savi) Tenore, Bull Thistle. Occasional in disturbed sites, fallow fields.
*Conyza canadensis* (L.) Cronquist, Horseweed. Abundant in field edges, fencerows.
*Coreopsis tripteris* L., Tall Tickseed. Occasional in wet woods.
*Eclipta alba* (L.) Hassk., Yerba-De-Tago. Occasional in wet ditches.
*Elephantopus carolinianus* Willd., Carolina Elephant's Foot. Occasional in thickets.
*Erechtites hieracifolia* (L.) Raf. ex DC. Fireweed. Occasional in wooded borders.
*Erigeron annuus* (L.) Pers., Daisy Fleabane. Frequent in fields, disturbed sites.
*Erigeron philadelphicus* L., Philadelphia Fleabane. Frequent in disturbed areas.
*Eupatorium coelestinum* L., Mist Flower, Ageratum. Frequent in wet meadows, clearings.
*Eupatorium fistulosum* Barratt, Joe Pye Weed. Frequent in wet open meadows, thickets.
*Eupatorium hyssopifolium* L., Hyssop-Leaved Thoroughwort. Infrequent to rare in meadows.
*Eupatorium perfoliatum* L., Perfoliate Thoroughwort, Boneset. Occasional in open woods.
*Eupatorium purpureum* L., Joe-Pye Weed. Occasional in wet meadows, thickets.
*Eupatorium rugosum* Houtt., White Snakeroot. Frequent in wooded borders, thickets.
*Eupatorium serotinum* Michx., Late-Flowering Thoroughwort. Occasional in wet meadows.
*Gnaphalium obtusifolium* L., Rabbit-Tobacco, Catfoot. Occasional in thickets, drainage ditches.
*Gnaphalium purpureum* L., Purple Catfoot. Occasional in wet meadows.
*Helenium amarum* (Raf.) Rock, Slender-Leaved Sneezeweed. Rare in wet fields at GF.
*Helenium autumnale* L., Autumnal Sneezeweed. Rare in clearings, field margins of MB.
*Helenium flexosum* Raf. Sneezeweed. Occasional in wet meadows.
*Helianthus microcephalus* Torr. & Gray, Small Wood Sunflower. Occasional in clearings, wooded edges.
*Helianthus tuberosus* L., Jerusalem Artichoke. Occasional in wet thickets, streamsides.
*Heliopsis helianthoides* (L.) Sweet Oxeye. Occasional in wet meadows.
*Krigia biflora* (Walt.) Blake, Two-Flowered Dwarf Dandelion.
*Krigia oppositifolia* (Raf.), Opposite-Leaved Dwarf Dandelion. Occasional in wet meadows.
*Krigia virginica* (L.) Willd., Virginia Dwarf Dandelion. Occasional in wet meadows.
*Lactuca biennis* (Moench) Fern., Tall Blue Lettuce. Infrequent in fields, thickets.
*Lactuca canadensis* L., Canadian Wild Lettuce. Occasional in meadows.
*Lactuca floridana* (L.) Gaertn., Florida Wild Lettuce. Infrequent in waste areas, field edges.
**Lactuca saligna* L., Willow-Leaved Wild Lettuce. Infrequent in cultivated field margins.
**Lactuca serriola* L., Prickly Wild Lettuce. Occasional in meadows.
*Pluchea camphorata* (L.) DC., Camphor Weed, Marsh Fleabane. Occasional in wet meadows.
*Polymia uvedalia* L., Bearsfoot. Occasional in wooded margins.
*Pyrrhopappus carolinianus* (Walt.) DC., False Dandelion. Occasional in meadows.
*Rudbeckia hirta* L., Black-Eyed Susan. Infrequent in disturbed woods.
*Rudbeckia triloba* L., Black-Eyed-Susan. Occasional in wooded edges, fields.

*Senecio aureus* L., Golden Ragwort. Abundant in wet meadows.
*Senecio glabellus* Poir., Butterweed. Abundant in wet meadows.
*Solidago canadensis* L., Tall Goldenrod. Frequent in fields, edges.
*Solidago caesia* L., Bluestem Goldenrod. Occasional in open mesic woods, thickets.
*Solidago gigantea* Ait., Large Goldenrod. Occasional in wet meadows, clearing.
*Solidago rugosa* Aiton, Rugose Goldenrod. Occasional in clearings, well-drained sites.
**Taraxacum officinale* Weber, Common Dandelion. Occasional in fields, edges.
**Tragopogon dubius* Scop., Goat's-Beard. Very rare, one specimen from GF.
*Verbesina alternifolia* (L.) Britt. Wing-Stem. Frequent in field margins.
*Verbesina virginica* L., Occasional in thickets, wooded edges.
*Vernonia gigantea* (Walt.) Trel., Tall Ironweed. Occasional in wet fields, thickets.
**Xanthium strumarium* L., Cocklebur. Frequent in margins of cultivated fields.

### BALSAMINACEAE, Touch-Me-Not Family

*Impatiens capensis* Meerb., Spotted Touch-Me-Not. Abundant in wet woods, thickets.

### BERBERIDACEAE, Barberry Family

*Podophyllum peltatum* L., Mayapple. Abundant throughout mesic woods, thickets.

### BETULACEAE, Birch Family

*Carpinus caroliniana* Walt., Blue Beech, Ironwood. Frequent in understory.
*Corylus americana* Walt., Hazel Nut. Abundant throughout mesic woods.
*Ostrya virginiana* (Mill.) K. Koch., Hop Hornbeam. Frequent throughout in understory.

### BIGNONIACEAE, Bignonia Family

*Bignonia capreolata* L., Cross-Vine. Occasional in wooded edges, thickets.
*Campsis radicans* (L.) Seem., Trumpet Creeper. Frequent in open fields, thickets, margins.

### BORAGINACEAE, Borage Family

*Cynoglossum virginianum* L., Wild Comfrey. Rare in wet woods of MB.
**Heliotropium indicum* L., Turnsole. Occasional in cultivated fields, edges.
*Myosotis verna* L., Scorpion Grass. Frequent in open fields, edges, disturbed sites.

### BRASSICACEAE, Mustard Family

*Barbarea vulgaris* R. Browne, Yellow Rocket. Occasional in wet meadows, standing water.
**Capsella bursa-pastoris* (L.) Medic, Shepherd's Purse. Occasional in disturbed sites.
*Cardamine parviflora* L., Small-Flowered Bitter Cress. Abundant in wet meadows.
*Cardamine rhomboidea* (Pers.) DC., Spring Cress. Occasional in wet woods.
*Dentaria laciniata* Muhl. ex Willd., Laciniate Toothwort. Rare, in well-drained portions of woods at GF.
*Lepidium virginicum* L., Peppergrass, Poor-Man's Pepper. Occasional in field margins.
**Nasturtium officinale* R. Browne, Water Cress. Frequent in open water, drainage ditches.
*Rorippa palustris* (L.) Besser, Yellow Cress. Occasional in wet meadows, standing water.
**Sisymbrium officinale* (L.) Scop., Hedge Mustard. Infrequent in field edges.
*Thlaspi arvense* L., Field Penny-Cress. Infrequent in field edges.

## CALLITRICHACEAE, Water-Starwort Family

*Callitriche deflexa* A Browne., Deflexed Water-Starwort. Occasional at field edges, mudflats.
*Callitriche heterophylla* Pursh, Diverse-Leaved Water-Starwort. Occasional in drainage ditches and standing water.

## CAMPANULACEAE, Bluebell Family

*Campanula americana* L., American Bellflower. Occasional in wet thickets.
*Lobelia cardinalis* L., Cardinal Flower. Abundant in drainage areas, streamsides.
*Lobelia inflata* L., Indian Tobacco. Occasional in clearings, wooded edges.
*Lobelia puberula* Michx., Downy Lobelia. Occasional in wet meadows.
*Lobelia siphilitica* L., Great Blue Lobelia. Occasional along streams, drainage ditches, wet thickets.
*Triodanthus perfoliata* (L.) Nie. var *perfoliata*, Venus' Looking Glass. Frequent in fields, ditches, disturbed sites.

## CAPRIFOLIACEAE, Honeysuckle Family

**Lonicera japonica* Thunb., Japanese Honeysuckle. Occasional in wet woods; frequent in thickets.
*Lonicera sempervirens* L., Trumpet or Coral Honeysuckle. Occasional in wet woods, streamsides.
*Sambucus canadensis* L., Elderberry. Frequent in wet woods, thickets.
*Symphoricarpos orbiculatus* Moench, Coralberry, Buckbush. Frequent in mesic woods, thickets.
*Viburnum rufidulum* Raf., Blue Haw. Infrequent in wet woods.

## CARYOPHYLLACEAE, Pink Family

**Cerastium glomeratum* Thuillier, Sticky Mouse-Ear Chickweed. Frequent in meadows.
**Dianthus armeria* L., Deptford Pink. Occasional in meadows.
**Saponaria officinalis* L., Soapwort, Bouncing Bet. Occasional in field edges, fencerows
*Silene antirrhina* L., Sleepy Catchfly. Occasional in fields, fencerows.
**Stellaria media* (L.) Cyrillo, Common Chickweed. Frequent in meadows.

## CELASTRACEAE, Staff-Tree Family

*Euonymus americanus* L., Strawberry Bush. Abundant throughout mesic woods.

## CHENOPODIACEAE, Goosefoot Family

**Chenopodium album* L., Lamb's Quarters, Mexican Tea. Occasional in field edges.
**Chenopodium ambrosioides* L., Mexican Tea. Occasional in disturbed sites, fallow fields.

## CLUSIACEAE, St. John's-Wort Family

*Hypericum hypericoides* (L.) Crantz , St. Andrew's Cross. Frequent in drainage ditches, thickets.
*Hypericum mutilum* L., Slender St. John's-Wort. Occasional in edges of cultivated fields.
*Hypericum punctatum* Lam., Dotted St. John's-Wort. Occasional in open woods, thickets.
*Triadenum walteri* (Gmel.) Gleason, Walter's St. John's-Wort. Occasional in wet woods.

## CONVOLVULACEAE, Morning-Glory Family

*Calystegia sepium* (L.) R. Browne, Hedge Bindweed. Frequent in field edges.
*Cuscuta campestris* Yuncker, Prairie Dodder. Frequent in edges, thickets.
**Ipomoea hederacea* Jacq., Ivy-Like Morning-Glory. Frequent in cultivated fields.
*Ipomoea lacunosa* L., White Morning Glory. Occasional in cultivated fields.

*Ipomoea pandurata* (L.) Meyer, Wild Potato-Vine, Man of the Earth. Occasional in meadows.
**Ipomoea purpurea* (L.) Roth, Common Morning Glory. Occasional in cultivated fields.

### CORNACEAE, Dogwood Family

*Cornus amomum* Mill., Swamp Dogwood. Occasional in mesic woods.
*Cornus florida* L., Flowering Dogwood. Frequent in understory, thickets.
*Cornus foemina* Mill., Stiff Dogwood. Rare in wet woods of GF.

### CUCURBITACEAE, Gourd Family

*Sicyos angulatus* L., Bur Cucumber. Infrequent in mesic thickets, roadsides.

### EBENACEAE, Ebony Family

*Diospyros virginiana* l., Persimmon. Occasional in edges, thickets.

### EUPHORBIACEAE, Spurge Family

*Acalypha ostryaefolia* Ridd., Three-Seeded Mercury. Frequent in disturbed areas, cultivated fields.
*Acalyphya rhomboidea* Raf., Rhombic-Leaved Three-Seeded Mercury. Frequent in cultivated fields.
*Acalypha virginica* L., Virginia Three-Seeded Mercury. Occasional in field edges.
*Euphorbia corollata* L., Flowering Spurge. Occasional at field edges.
*Euphorbia dentata* Michx., Spurge, Wild Poinsettia. Infrequent in wet meadows, waste places.
*Euphorbia maculata* L., Eyebane. Frequent in meadows, waste places.
*Phyllanthus caroliniensis* Walt. Phyllanthus. Occasional in dried streambeds.

### FABACEAE, Legume or Pulse Family

*Apios americana*, Medik., American Potato Bean. Locally abundant at GF, forming dense canopies.
*Cercis canadensis* L., Redbud. Occasional in thickets and mesic woods.
*Chamaecrista fasciculata* (Michx.) Greene, Partridge Pea. Occasional in field edges.
*Chamaecrista nictitans* (L.) Monech, Sensitive Senna. Occasional in field edges.
*Desmodium canescens* (L.) DC., Hoary Tick Clover. Frequent in unplanted fields, edges.
*Desmodium pauciflorum* (Nutt.) DC., Few-Flowered Tick Clover. Occasional in meadows.
*Gleditsia triacanthus* L., Honey Locust. Rare in fencerows, edges.
**Glycine max* (L.) Merrill, Soybean. Cultivated in fields surrounding woods.
**Lathryus latifolius* L., Perennial Sweet Pea. Rare, one plant in wooded edge at FM..
**Lespedeza cuneata* (Dumont) G. Don, Sericea Lespedeza. Infrequent in disturbed areas.
*Lespedeza procumbens* Michx., Trailing Bush-Clover. Occasional in drier thickets, fencerows.
**Lespedeza stipulacea* Maxim., Korean Clover. Occasional in disturbed wooded edges.
**Lespedeza striata* (Thunb.). H & A., Japanese Clover. Occasional in sandy drainages.
**Medicago lupulina* L., Black Medic. Occasional in field margins.
**Medicago sativa* L., Alfalfa. Occasional in disturbed sites, fallow fields.
**Melilotus officinalis* (L.) Pallas, Yellow Sweetclover. Frequent in field margins, fencerows.
*Robinia pseudoacacia* L., Black Locust. Occasional in thickets, wooded edges.
*Strophostyles umbellata* (Muhl.) Britt., Wild Bean. Infrequent in disturbed areas, roadsides, cultivated fields.
**Trifolium campestre* Schreb., Hop Clover. Abundant in disturbed areas, field edges.
**Trifolium pratense* L., Red Clover. Frequent in field edges, fencerows.
**Trifolium repens* L., White Clover. Abundant in fields, disturbed sites.
**Vicia villosa* Roth., Hairy Vetch. Frequent in cultivated fields.

## FAGACEAE, Oak Family

*Fagus grandifolia* Ehrh., American Beech. Occasional beside streams of GF.
*Quercus alba* L., White Oak. Frequent in upland swamp.
*Quercus bicolor* Willd., Swamp White Oak. Frequent in upland wet woods.
*Quercus falcata* Michx., Southern Red Oak, Spanish Oak. Occasional throughout upland swamp.
*Quercus imbricaria* Michx., Shingle Oak. Occasional throughout upland swamp.
*Quercus lyrata* Walt., Overcup Oak. Occasional in wetter portions of woodland.
*Quercus michauxii* Nutt., Swamp Chestnut. Frequent in canopy of upland swamp.
*Quercus pagoda* Raf., Cherrybark Oak. Abundant throughout upland swamp.
*Quercus palustris* Muenchh., Pin Oak. Abundant throughout upland swamp.
*Quercus phellos* L., Willow Oak. Abundant in wetter portions of upland swamp woods.
*Quercus rubra* L., Northern Red Oak. Occasional large canopy specimens at GF.
*Quercus stellata* Wang., Post Oak. Infrequent in poorly drained sites.
*Quercus velutina* Lam., Black Oak. Frequent in canopy.

## GENTIANACEAE, Gentian Family

*Sabatia angularis* (L.) Pursh, Rose Pink. Infrequent in wet meadows of MB.

## GERANIACEAE, Geranium Family

*Geranium carolinianum* L., Wild Cranesbill. Occasional in field edges, disturbed sites.
*Geranium maculatum* L., Wild Geranium. Occasional in mesic woods of HP.

## HAMAMELIDACEAE, Witch-Hazel Family

*Liquidambar styraciflua* L., Sweetgum. Frequent throughout wooded portions and thickets.

## HYDROPHYLLACEAE, Waterleaf Family

*Hydrophyllum macrophyllum* Nutt., Large-Leaved Waterleaf. Locally abundant at HP.

## JUGLANDACEAE, Walnut Family

*Carya cordiformis* (Wang.,) K. Koch., Bitternut Hickory. Infrequent in old-growth woods.
*Carya glabra* (Mill.) Sweet, Pignut Hickory. Rare in old-growth woods.
*Carya ovata* (Mill.) K. Koch., Shagbark, Scalybark, Shellbark Hickory. Frequent in old-growth woods.
*Carya tomentosa* Nutt., Mockernut or White-Heart Hickory. Occasional in old-growth woods.

## LAMIACEAE, Mint Family

*Agastache nepetoides* (L.) Kuntze, Giant Hyssop. Infrequent in wet thickets.
*Lycopus rubellus* Moench., Stalked Water Horehound. Abundant in wet ditches.
*Perilla frutescens* (L.) Britt., Beefsteak Plant. Frequent in field edges, moist thickets.
**Prunella vulgaris* L., Heal-All. Occasional in mesic fields, streamsides.
*Pycnanthemum tenuifolium* Schrad., Slender Mountain Mint. Frequent in moist fields, open woods, thickets.
*Salvia lyrata* L., Lyre-Leaved Sage. Infrequent in thickets, edges.
*Scutellaria elliptica* Muhl., Hairy Skullcap. Occasional in moist thickets.
*Scutellaria lateriflora* L., Mad-Dog Skullcap. Occasional in clearings, thickets.
*Scutellaria parvula* Michx., Small Skullcap. Infrequent in open mesic woods, thickets.
*Stachys tenuifolia* Willd. var. *tenuifolia*, Smooth Hedge Nettle. Frequent in thickets, wooded edges.
*Teucrium canadense* L., American Germander. Frequent in wet thickets throughout.

## LAURACEAE, Laurel Family

*Lindera benzoin* (L.) Blume., Spicebush. Abundant throughout mesic woods.
*Sassafras albidum* (Nutt.) Nees, Sassafras. Infrequent, found in more well-drained sites.

## LYTHRACEAE, Loosestrife Family

*Ammannia coccinea* Rothb., Long-Leaved Ammannia. Occasional in swampy margins, drainage ditches.
*Cuphea petiolata* (L.) Koehne. Clammy Cuphea, Blue Waxweed. Occasional in wet meadows.
*Lythrum alatum* Pursh, Winged Loosestrife. Occasional forming colonies in wet meadows.
*Rotala ramosior* (L.) Koehne, Tooth-Cup. Occasional in wet depressions.

## MAGNOLIACEAE, Magnolia Family

*Liriodendron tulipifera* L., Tulip Tree or Yellow Poplar. Occasional in mesic woods.

## MALVACEAE, Mallow Family

**Abutilon theophrasti* Medik., Velvet-Leaf, Buttermold Plant. Occasional in field edges.
**Anoda cristata* L. Schltdl., Crested Anoda. Occasional in margins of cultivated fields.
*Hibiscus moscheutos* L., Swamp Rose Mallow, Swamp Cotton. Occasional in drainage ditches, wet meadows.
**Sida spinosa* L., Prickly Sida. Occasional in cultivated fields, waste areas.

## MELASTOMACEAE, Melastoma Family

*Rhexia mariana* var. *mariana* (L.), Maryland Meadow Beauty. Locally abundant in wet meadows of MB.

## MENISPERMACEAE, Moonseed Family

*Menispermum canadense* L., Moonseed. Occasional in mesic woods.

## MORACEAE, Mulberry Family

*Morus rubra* L., Red Mulberry. Occasional in understory.

## NYSSACEAE. Sour-Gum Family

*Nyssa sylvatica* Marsh., Black-Gum. Frequent throughout.

## OLEACEAE, Olive Family

*Fraxinus americana* L., White Ash. Frequent throughout.
*Fraxinus pennsylvanica* Marsh., Green Ash. Frequent in upland swamp woods.

## ONAGRACEAE, Evening Primrose Family

*Circaea lutetiana* ssp. *canadensis* (L.) Asch & Mag., Enchanter's Nightshade. Abundant throughout mesic woods.
*Ludwigia peploides* (Humb., Bonpl. & Kunth) Raven var. *glabrescens* (Kuntze) Raven, Smooth Primrose Willow.
*Ludwigia alternifolia* L. var. *alternifolia*, Seedbox. Abundant in wet meadows, thickets.
*Ludwigia palustris* L.(Ell.), Marsh Purslane. Frequent in open wet woods, clearings.
*Oenothera biennis* L., Biennial Evening Primrose. Occasional in disturbed sites, field edges.

## OXALIDACEAE, Wood-Sorrel Family

*Oxalis grandis* Small, Giant Wood Sorrel. Rare in mesic thickets of GF.
*Oxalis stricta* L., Yellow Wood Sorrel. Occasional in field edges, thickets.
*Oxalis violacea* L., Violet Wood Sorrel. Occasional in mesic woods, thickets.

## PASSIFLORACEAE, Passion-Flower Family

*Passiflora incarnata* L., Passion-Flower, Maypops. Occasional in wooded edges, thickets.
*Passiflora lutea* L., Small Passion-Flower. Infrequent in wooded borders of FM.

## PHRYMACEAE, Lopseed Family

*Phryma leptostachya* L., Lopseed. Occasional in wet thickets.

## PHYTOLACCACEAE, Pokeweed Family

*Phytolacca americana* L., Pokeweed. Occasional in wooded borders, field edges.

## PLANTAGINACEAE, Plantain Family

**Plantago lanceolata* L., Buckhorn, Lance-Leaved Plantain. Occasional in field edges.
*Plantago rugelii* Decne., Rugel's Plantain. Frequent in wet field margins.
*Plantago virginica* L., Virginia or Hoary Plantain. Frequent in wet meadows.

## PLATANACEAE, Plane-Tree Family

*Platanus occidentalis* L., Sycamore. Infrequent in upland swamp.

## POLEMONIACEAE, Phlox Family

*Phlox glaberrima* L., Swamp or Smooth Phlox. Occasional in moist thickets, wooded edges.

## POLYGALACEAE, Milkwort Family

*Polygala sanguinea* L., Field Milkwort. Occasional in wet meadows.

## POLYGONACEAE, Buckwheat Family

**Polygonum aviculare* L., Knotweed. Occasional in roadways, near cultivated fields.
**Polygonum cespitosum* Blume var. *longisetum* (Bruij.) Stewart, Bristled Smartweed. Abundant in wet meadows.
*Polygonum hydropiperoides* Michx., Mild Water Pepper. Frequent in drainage ditches, standing water.
*Polygonum lapathifolium* L., Dock-Leaved Smartweed. Frequent in wet field edges, marshy meadows.
*Polygonum sagittatum* L., Arrow-Leaved Tearthumb. Infrequent in wet meadows.
*Polygonum scandens* L., Climbing False Buckwheat. Infrequent in disturbed areas, thickets.
*Polygonum virginiana* L., Jumpseed. Occasional in mesic woods, moist thickets.
**Rumex crispus* L., Curly or Yellow Dock. Frequent in wet meadows, standing water.
*Tovara virginiana* (L.) Raf., Jumpseed. Occasional in mesic thickets.

### PORTULACACEAE, Purslane Family

*Claytonia virginica* L., Spring Beauty. Occasional in mesic woods.

### PRIMULACEAE, Primrose Family

*Lysimachia ciliata* L., Fringed Loosestrife. Occasional in wet woods, edges.
*Lysimachia lanceolata* Walt., Lance-Leaved Loosestrife. Occasional in wet fields.
*Samolus parviflorus* Raf., Brookweed, Water Pimpernel. Occasional in wet fields.

### RANUNCULACEAE, Crowfoot Family

*Cimicifuga racemosa* (L.) Nutt., Black Cohosh, Black Snakeroot. Occasional in mesic woods.
*Clematis virginiana* L., Virgin's Bower. Frequent in thickets, open woods.
*Myosurus minimus* L., Mousetail. Occasional in wet meadows.
*Ranunculus abortivus* L., Small-Flowered Crowfoot. Abundant in wet meadows.
*Ranunculus bulbosus* L., Bulbous Buttercup. Infrequent in disturbed sites, field edges.
*Ranunculus carolinianus* DC., Carolina Buttercup. Infrequent in swampy woods.
**Ranunculus parviflorus* L., Small-Flowered Crowfoot. Occasional in wet fields, ditches.
*Ranunculus pusillus* Poir., Low Spearwort. Frequent in wet fields.
*Thalictrum revolutum* DC., Waxy Meadow Rue. Occasional along streambanks in mesic woods.
*Thalictrum thalictroides* (L.) Eames & Boivin, Rue Anemone. Occasional in mesic woods, streamsides.

### ROSACEAE, Rose Family

*Agrimonia rostellata* Wallroth. Agrimony. Occasional in open wet woods.
*Agrimonia pubescens* Wallr., Hairy Harvest Lice. Occasional in mesic woods.
*Crataegus viridis* L. Hawthorn. Occasional in wooded edges, fencerows.
*Geum canadense* Jacq., Canada or White Avens. Occasional in wet woods, edges.
*Geum vernum* (Raf.) Torr. & Gray, Vernal Avens. Infrequent in mesic woods.
*Porteranthus stipulatus* (Muhl. ex Willd.) Britton, American Ipecac. Infrequent in mesic woods, thickets at GF.
*Potentilla norvegica* L., Norwegian Five-Finger. Occasional in disturbed areas, cultivated fields.
*Potentilla simplex* Michx., Cinquefoil. Infrequent in swampy meadows.
*Potentilla simplex* Michx., Old-Field Cinquefoil. Frequent in disturbed woods, fields.
*Prunus americana* L., American Plum. Occasional in wet woods.
*Prunus serotina* Ehrend., Wild Black Cherry. Frequent in understory.
**Rosa multiflora* Thunb. ex Murray, Multiflora Rose. Occasional in field edges, thickets.
*Rosa palustris* Marsh., Swamp Rose. Frequent in thickets, wooded edges.
*Rubus argutus* Link, Common Blackberry. Abundant in thickets, wooded edges.
*Rubus flagellaris* Willd., Dewberry. Occasional in mesic woods, thickets.

### RUBIACEAE, Madder Family

*Cephalanthus occidentalis* L. Button Bush. Occasional along streams, drainage ditches.
*Diodia teres* L., Poor-Joe, Buttonweed. Frequent in old fields, disturbed sites.
*Diodia virginiana* L., Virginia Buttonweed. Frequent in disturbed areas, field edges.
*Galium aparine* L., Cleavers, Bedstraw. Frequent in wet woods, thickets, fields.
*Galium circaezans* Michx., Wild Licorice. Occasional in moist woods, thickets.
*Galium tinctorium* L., Swamp Bedstraw. Frequent in wet fields and mesic woods.
*Hedyotis caerulea* (L.) Hook., Bluets. Occasional and forming colonies in clearings.
*Hedyotis purpurea* (L.) Torr. & Gray, Purple Bluets. Occasional and forming colonies in thickets, clearings at MB.

## RUTACEAE, Rue Family

*Zanthoxylum americanum* Mill., Prickly Ash. Rare, one small colony in mesic woods at GF.

## SALICACEAE, Willow Family

*Populus deltoides* Bartr., Cottonwood. Infrequent in upland wet woods.
*Salix nigra* Marsh., Black Willow. Infrequent along streams, drainages.

## SAXIFRAGACEAE, Saxifrage Family

*Penthorum sedoides* L., Ditch Stonecrop. Occasional in drainage ditches.

## SCROPHULARIACEAE, Figwort Family

*Agalinis tenuifolia* (Vahl.) Raf., Slender Foxglove. Occasional in wet meadows.
*Bacopa rotundifolia* (Michx.) Wettst., Round-Leaved Water-Hyssop. Infrequent in wet depressions.
*Conobea multifida* (Michx.) Benth. Occasional in wet fields, mudflats.
*Gratiola neglecta* Torr., Hedge-Hyssop. Abundant in wet meadows, ditches, marshes.
*Gratiola virginiana* L., Virginia Hedge Hyssop. Rare in standing water, wet ditches at GF.
*Lindernia dubia* (L.) Penn., False Pimpernel, Frequent in wet ditches, mudflats.
*Mimulus alatus* Ait., Winged Monkey Flower. Frequent along drainage ditches, streamsides.
*Penstemon laevigatus* (L.) Aiton, Smooth Beard Tongue. Occasional in clearings, wet meadows.
*Scrophularia marilandica* L., Carpenter's Square. Occasional in wooded edges, thickets.
**Verbascum blattaria* L., Moth-Mullein. Infrequent in meadows.
**Verbascum thapsus* L., Common Mullein. Occasional in field edges, fencerows.
**Veronica arvensis* L., Common Speedwell. Abundant in fields, edges, disturbed sites.
**Veronica peregrina* L., Neckweed. Frequent in fields, edges.

## SOLANACEAE, Nightshade Family

*Physalis longifolia* Nutt., var. *subglabrata* M. & B., Glabrous Ground Cherry. Frequent, wet fields, fencerows.
*Solanum carolinense* L., Horse Nettle. Occasional in wet meadows.
*Solanum ptycanthum* Dunal, Eastern Black Nightshade. Occasional in cultivated fields.

## ULMACEAE, Elm Family

*Celtis laevigata* Willd., Sugarberry. Frequent throughout mesic woods.
*Celtis occidentalis* L., Hackberry. Frequent in understory.
*Ulmus alata* Michx., Winged Elm. Abundant throughout.
*Ulmus americana* L., American Elm. Occasional in canopy in wet woods.
*Ulmus rubra* Muhl., Slippery Elm. Frequent in canopy.

## URTICACEAE, Nettle Family

*Boehmeria cylindrica* (L.) Sw., False Nettle, Bog-Hemp. Abundant in open wet woods, along streams, thickets.
*Parietaria pennsylvanica* Muhl. ex Willd., Pennsylvania Pellitory. Occasional in wet meadows, streamsides.
*Pilea pumila* (L.) A. Gray, Clearweed. Frequent in wooded borders, field edges.

## VALERIANACEAE, Valerian Family

*Valerianella radiata* (L.) Dufr., Corn-Salad. Occasional in small stands in poorly drained fields.

## VERBENACEAE, Vervain Family

*Phyla lanceolata* (Michx.) Greene, Fog Fruit. Abundant in wet meadows, ditches.
*Verbena hastata* L., Blue Vervain. Occasional in field edges.
*Verbena urticifolia* L. var. *urticifolia*, White Vervain. Occasional in fields, disturbed areas.

## VIOLACEAE, Violet Family

*Viola cucullata* Aiton, Hooded Violet. Occasional in wet woods.
*Viola lanceolata* L., Lance-Leaved Violet. Rare in wet meadows near GF.
*Viola pubescens* Ait. var. *eriocarpa* (Sch.) Russell, Yellow Violet. Occasional in mesic woods, streambanks at FM. *Viola rafinesquii* Greene, Field Pansy. Occasional in field edges, disturbed sites.
*Viola sororia* Willd., Meadow Violet. Occasional in open wet woods, streamsides.

## VISCACEAE, Mistletoe Family

*Phoradendron leucarpum* (Raf.) Reveal & M.C. Johnson, Mistletoe. Rare, epiphyte in trees of upland swamp.

## VITACEAE, Grape Family

*Ampelopsis cordata* Michx., Heart-Leaved Ampelopsis. Occasional in wooded edges, fencerows.
*Parthenocissus quinquefolia* (L.) Planch., Virginia Creeper. Frequent in wooded edges, thickets.
*Vitis aestivalis* Michx., Summer Grape. Frequent in upland swamp woods.
*Vitis vulpina L.*, Frost Grape. Frequent throughout wet woods.

# THE ANNUAL DORMANCY CYCLE IN BURIED SEEDS OF THE SUMMER ANNUAL *BIDENS POLYLEPIS* BLAKE (ASTERACEAE)

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**ABSTRACT. Achenes (seeds) of *Bidens polylepis* were dormant at maturity in autumn, and they came out of dormancy while buried in moist soil (1) in a nonheated greenhouse in Lexington, Kentucky, during winter or (2) at 5 or 15/6°C for 12 weeks. As seeds came out of dormancy, they first germinated at 30/15 and 35/20°C in light and at 30/15°C in darkness. With additional loss of dormancy, the minimum temperature for germination in light and darkness decreased to 15/6°C. Nondormant seeds re-entered dormancy (secondary dormancy) when (1) kept in the greenhouse during summer, (2) subjected sequentially to simulated March to October temperatures in incubators or (3) exposed to 25/15 or 30/15°C for 24 and 12 weeks, respectively. As seeds entered dormancy, they first lost the ability to germinate at 15/6°C and then at higher and higher temperatures, until they could not germinate even at 35/20°C. Buried seeds exposed to seasonal temperature changes for 28 months in the nonheated greenhouse exhibited an annual dormancy/nondormancy cycle, with full dormancy occurring in September to November. Seeds came out of dormancy in December to March, and they germinated to 85-96% in light at simulated habitat temperatures from April to July. Thus, unlike buried seeds of the summer annual Asteraceae *Ambrosia artemisiifolia* L., which enter dormancy in early spring (J. and C. Baskin. 1980. Ecology 61: 475-480), entrance of *B. polylepis* seeds into dormancy is delayed until early summer. Although a high percentage of the *B. polylepis* seeds germinated when tested in darkness at simulated habitat temperatures in March to June, only 2% of them germinated while buried in soil in the nonheated greenhouse. In the field, seeds of this species have the potential to germinate from early spring to early summer and to form a persistent seed bank.**

# USING LEAF SHAPE TO IDENTIFY TAXA IN A MIXED-OAK COMMUNITY IN LAND BETWEEN THE LAKES, KENTUCKY

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**ABSTRACT. Most species of oaks (*Quercus*) can be readily identified by their leaf morphology, which is also a good indicator of putative hybridization. One characteristic of hybrids is that their leaves often are of irregular and asymmetric shapes. While these features are readily discernible to the naked eye, it is difficult to quantify leaf shapes for more objective comparison. In this study, leaves from 14 oaks (including four species and one putative hybrid) growing in a mixed community were compared on the basis of several simple morphological measurements as well as several types of shape descriptors. The latter consisted of two single-value descriptors (fractal dimension, leaf dissection) and two multiple-value descriptors (40 coefficients or 10 amplitudes derived from the first 10 elliptic Fourier harmonics for each leaf). For each tree, the two-dimensional outlines of five randomly chosen leaves were used to generate mean shape descriptors. In addition, the mean for each of four simple morphological characters (leaf length, leaf width, petiole length, number of bristle tips) was generated. The data were used for UPGMA cluster analysis to determine the groupings revealed by each set of features. The results indicate that the taxonomic structure of the data set is easily recaptured by the simple morphological features. The shape descriptors provide additional insights into relationships. Of these, fractal dimension and leaf dissection appear to best reflect relationships among the trees.**

## INTRODUCTION

The great diversity of oaks in Land Between The Lakes (LBL) has often proved problematic for taxonomists and ecologists alike. Nineteen species of oaks have been found in LBL (Chester *et al.* 1987) and many of these are known to produce hybrids (*e.g.*, Jensen 1988b). While the species are generally morphologically distinct, there are numerous cases in which trees of uncertain taxonomic affinity are encountered. In such cases, there is great temptation to declare the tree a hybrid. This is an easy out and in most cases is not necessary. Generally, careful observation of the morphological features of the leaves, twigs, and fruits will allow species designation for most trees encountered. Unfortunately, mature fruits often are not available and only the leaves and twigs can be used for identification.

In previous studies (*e.g.*, Jensen 1988a,b), I have relied upon multivariate analyses of a suite of quantitative leaf characters in an attempt to sort out variation within mixed-oak communities. What I wish to demonstrate here is that in many communities, the taxonomic affinities of individual trees can be easily determined by using a small set of quantitative leaf characters. In addition, I wish to provide insights into problems of identification by demonstrating how quantitative measures of leaf shape can be used for differentiating species.

I have elsewhere (Jensen 1990) discussed the problems associated with subjective descriptions of leaf shapes. A variety of procedures have been proposed for conducting quantitative comparisons of leaf shapes, including variants of principal components analysis (PCA) of linear measures (*e.g.*, Jensen *et al.* 1993), rotational-fit analyses of landmark configurations (*e.g.*, Jensen 1990), and analysis of leaf outlines (McLellan 1993). The first of these is based on the assumption that the first component of a PCA will reflect general size differences and that subsequent components will reflect something other than size, *i.e.*, shape. While this is certainly a reasonable expectation for some data sets (Somers 1989), it cannot be viewed as a general solution to the problem of quantifying shape variation (Bookstein 1989). The second approach is applicable only when the objects being compared can be described by sets of three or more homologous landmarks (landmarks are points, such as the juncture of leaf blade and petiole, that may be considered biologically equivalent from leaf to leaf). While sets of such landmarks can be found for some comparisons, there are many situations in which a leaf has only two non-arbitrary landmarks (*i.e.*, the base and apex of the blade) or in which the leaves being compared do not have the same architecture. This leaves us with outlines.

Leaves may be viewed as two-dimensional objects (they are, in fact, three-dimensional; the third dimension, often negligible, can be physiologically and taxonomically important). The shape of a two-dimensional object, as represented by an outline, can be quantified by any of a number of mathematical operations. Rohlf and Archie (1984) provide a good overview of methods for conducting quantitative studies of outlines, concluding with a recommendation for analysis of elliptic Fourier coefficients. White *et al.* (1988) compared several methods for analyzing outlines and concluded that elliptic Fourier analysis (EFA) was the method of choice. McLellan (1993) observed that the first few EFA harmonics summarize overall shape and that the amplitudes of these harmonics reflect the "roughness" of the outline. McLellan (1993) also found that a measure of leaf dissection, derived from the area and length of the perimeter of the leaf, could be used to recognize different shapes.

In the study reported here, I utilized several different approaches for examining taxonomic structure in a group of red and black oaks (*Quercus* section *Lobatae*) occurring in a community of trees in which I discovered a putative hybrid. The taxa in this community are *Q. falcata* Michx., *Q. imbricaria* Michx., *Q. pagoda* Raf., and *Q. palustris* Muenchh. Each tree sampled (other than the hybrid) was assigned to one of these four species. In addition, the trees of *Q. falcata* were assigned to two forms of this species: f. *falcata* Trel. (leaves are ovate with 5-7 lobes separated by deep sinuses) and f. *triloba* Ashe (leaves are elliptic to obovate with three lobes).

## MATERIALS AND METHODS

Mature leaves were collected from 14 oaks growing in a mixed community at Cravens Bay (Lyon County, Kentucky). For each tree, three or more twigs with leaves were collected at heights of 2-5 meters. All intact leaves were harvested and pressed in standard plant presses. Data were recorded for five randomly chosen leaves for each tree. Four morphological characters were recorded for each leaf: leaf blade length (base to apex), leaf blade width (maximum extent of blade measured perpendicular to the length), petiole length, and the number of bristle tips.

Leaf outlines were captured using SigmaScan (version 3.92; Jandel Scientific) with a digitizing tablet interfaced with a microcomputer. Each leaf was placed on the tablet with abaxial surface up and the length of the blade parallel to the y-axis. Outlines were traced in a counterclockwise direction, beginning and ending at the base of the blade. The x,y coordinates for each outline were stored in an ASCII file. Perimeter length (cm) and area ($cm^2$) for each leaf (automatically calculated by SigmaScan) were recorded by hand. Each file of x,y coordinates was converted to a form suitable for analysis using a program written by the author (this program read the original SigmaScan files, deleted redundant x,y pairs, and created new files used as input for NTSYS-pc or Fractal-D; see below).

NTSYS-pc (version 1.8; Rohlf 1993) was used for elliptic Fourier analysis of each leaf outline. The first ten EFA harmonics were generated and saved in individual files. Programs written by the author were used to create a mean EFA outline for each tree and calculate mean EFA amplitudes for each tree. These analyses yielded two sets of data for each tree: a 14 x 40 matrix consisting of the mean coefficients for the first ten EFA harmonics (each harmonic is defined by four coefficients) and a 14 x 10 matrix consisting of the mean EFA amplitudes.

The fractal dimension of an outline can be viewed as a measure of outline complexity. As examined here, the fractal dimension can vary between 1 (for a circle) and 2 (for a plane-filling infinite random walk). Three different fractal dimensions were calculated by varying the power function for increasing step lengths for iterated walks of the outline. In each case, the outline was traversed 25 times to create 25 estimates of outline length. The fractal dimension (D) is derived by a least squares solution for the slope of the line defined by the relationship between the log of step length (= x) and the log of the estimated outline length (= y):

$$D = 1 - b$$

where b is the slope of the line of best fit. All calculations were performed using the Fractal-D program (a test version provided to the author by D. Slice). For all leaves, each walk started at the base of the blade and proceeded in a counter-clockwise direction. Inspection of the three different estimates of D revealed that the first (based on the smallest power function for increasing step length) yielded a non-linear curve when step length was plotted against estimated outline length. The other two yielded very similar estimates of D (the Pearson correlation for the two sets of 70 estimates was 0.936) and only one is reported here. The mean values of D were calculated for each tree.

Perimeters and areas of each leaf were used to generate a second descriptor of outline complexity (here referred to as a measure of leaf dissection):

$$\text{dissection} = (\text{perimeter} / (2 * \text{area})) * \sqrt{(\text{area} / \text{pi})}$$

This provides a standardized function of the area so that any circle will have a value of 1.0 and more complex outlines will have values greater than 1.0. As with D, leaf dissection was calculated for each leaf and the mean leaf dissection was calculated for each tree.

Phenetic relationships among the 14 trees (= OTUs; operational taxonomic units) were examined by cluster analysis of several different distance matrices. In all cases, a 14 x 14 matrix of average taxonomic distances was used as input for unweighted pair-group using arithmetic averages cluster analysis. Distances for EFA harmonics and amplitudes were derived from raw values while distances for analyses involving the morphological characters, D, and leaf dissection were derived from standardized (0 mean, unit variance) data. All cluster analyses were performed using NTSYS-pc (version 1.8; Rohlf 1993).

Finally, a one-way analysis of variance followed by pairwise comparisons (Tukey's HSD) was performed to compare means for D and leaf dissection among the 14 trees (using the ANOVA program in SYSTAT, version 5 for Windows).

## RESULTS AND DISCUSSION

One surprising result of this study is that the five taxa can be readily differentiated by a small set of simple morphological measurements. This is illustrated in Figure 1, (all Figures are given in the Appendix) the phenogram derived from the four morphological characters. There are three primary clusters corresponding to *Q. imbricaria*, *Q. palustris*, and the *Q. falcata* - *Q. pagoda* complex (plus the one putative hybrid). The only discrepancy in *species* recognition involves the two OTUs of *Q. falcata* f. *falcata*, which cluster separately from the three other OTUs of this species. The placement of the putative hybrid would suggest that one parent species is either *Q. falcata* or *Q. pagoda*.

Figures 2-5 present phenograms based solely on information derived from the leaf outlines. Analysis of the coefficients from EFA (Figure 2) produces one cluster consisting of *Q. imbricaria* plus the putative hybrid, a second cluster corresponding to *Q. falcata* f. *falcata*, and two additional clusters comprising a mixture of species, *i.e.*, the two individuals of *Q. pagoda* cluster either with *Q. falcata* f. *triloba* or with *Q. palustris*. Despite the failure of this analysis to depict well-defined species clusters, it does suggest that *Q. imbricaria* may be one parent of the putative hybrid.

Figure 3 is the phenogram derived from EFA amplitudes. In a sense, this is the least acceptable analysis. That is, the clusters seen are rather poor representations of the taxa present. As in Figures 1 and 2, the two *Q. falcata* f. *falcata* OTUs and the three *Q. falcata* f. *triloba* OTUs form distinct clusters, but OTUs of the other three species fail to cluster together and the putative hybrid links to a cluster containing OTUs representative of these three species.

The phenograms depicted in Figures 4 and 5 are derived from data sets consisting of a single variable: D and leaf dissection, respectively. Both phenograms are reasonably good reflections of the taxonomic relationships among these OTUs. In Figure 5, three taxa, *Q. imbricaria*, *Q. falcata* f. *triloba* and *Q. pagoda*, form distinct clusters; in Figure 4 only the first two of these form distinct clusters. In both phenograms, the putative hybrid clusters with *Q. imbricaria*.

Figures 2-5 represent analyses that may be viewed as reflections of shape only. That is, the characters in each are functions solely of the leaf outlines - there is no information about size differences or any other morphological features. What is revealing about these four analyses is that both D and leaf dissection, representing simple univariate shape descriptors, appear to be equally as effective as EFA for detecting the taxonomic structure of the sample. None of these shape analyses perfectly recaptures the taxonomic structure of this data set, but the discrepancies seen (*e.g.*, an OTU of *Q. falcata* f. *falcata* clustering with an OTU of *Q. palustris*; Figs. 4, 5) are consistent with the degree of leaf dissection of these OTUs. As shown in Tables 1-2 and Figs. 6-7, analysis of variance of D and leaf dissection (a one-way analysis with tree as the grouping variable), followed by pairwise comparison of group means, yields essentially the same groups as seen in Figs. 4 and 5.

One advantage of using either D or leaf dissection as a shape descriptor is that both can be easily calculated and both can be added to a data set consisting of other morphological characters without unduly influencing the phenetic relationships among the OTUs. That is, the EFA analyses presented here yield a multivariate set of shape descriptors: either 40 coefficients or 10 amplitudes. If either were combined with the set of 4 morphological measures used to produce Figure 1, the resulting phenetic relationships would be dominated by shape. The addition of D or leaf dissection, however, provides a single shape character that contributes no more or less to the phenetic relationships than do any other characters. This is illustrated in Figs. 8 and 9, phenograms derived by adding D or leaf dissection, respectively, to the original morphological data set.

Comparison of these phenograms with Figure 1 reveals that the addition of a shape character subtly alters the relationships among the OTUs. It would appear that leaf dissection (Figure 9) has less effect on the pattern in Figure 1 than does D, but the decision of which to use is arbitrary. I suggest that leaf dissection is the better of the two because there is a unique dissection value associated with any leaf outline. On the other hand, the value of D will be a function of (1) the number of steps used to walk the outline, (2) the function used to increase step length for subsequent walks, and (3) the point on the outline at which the walks are initiated.

**Table 1. Analysis of variance of the fractal dimension (D) among trees.**

**A. Analysis of variance table**

| Source | Sum-of-squares | DF | Mean-square | F | P |
|---|---|---|---|---|---|
| Tree | 0.520 | 13 | 0.040 | 28.45 | 0.00 |
| Error | 0.079 | 56 | 0.001 | | |

**B. Trees ordered by means (smallest to largest; trees not connected by an underscore have means that differ at $\alpha = 0.05$)**

I1 I2 I4 I3 H F3 F5 F4 PG2 PG1 F2 PL1 F1 PL2

**Table 2. Analysis of variance of leaf dissection among trees.**

**A. Analysis of variance table**

| Source | Sum-of-squares | DF | Mean-square | F | P |
|---|---|---|---|---|---|
| Tree | 20.843 | 13 | 1.603 | 45.97 | 0.00 |
| Error | 1.953 | 56 | 0.035 | | |

**B. Trees ordered by means (smallest to largest; trees not connected by an underscore have means that differ at $\alpha = 0.05$)**

I1 I2 I4 I3 H F3 F5 F4 PG1 PG2 F2 PL1 PL2 F1

Finally, these analyses cannot be viewed as proof of the parentage of the putative hybrid. The characteristics of this tree are clearly consistent with it having *Q. imbricaria* as one parent. The other parent is almost assuredly either *Q. falcata* or *Q. pagoda*, but I don't believe morphology alone can resolve the issue. These analyses do demonstrate that (1) it is possible to readily differentiate these taxa using a small number of quantitative morphological features and (2) it is possible to derive simple shape descriptors (either or both D and leaf dissection) that can be viewed as additional quantitative characters for a morphological analysis.

## ACKNOWLEDGMENTS

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# APPENDIX: FIGURES

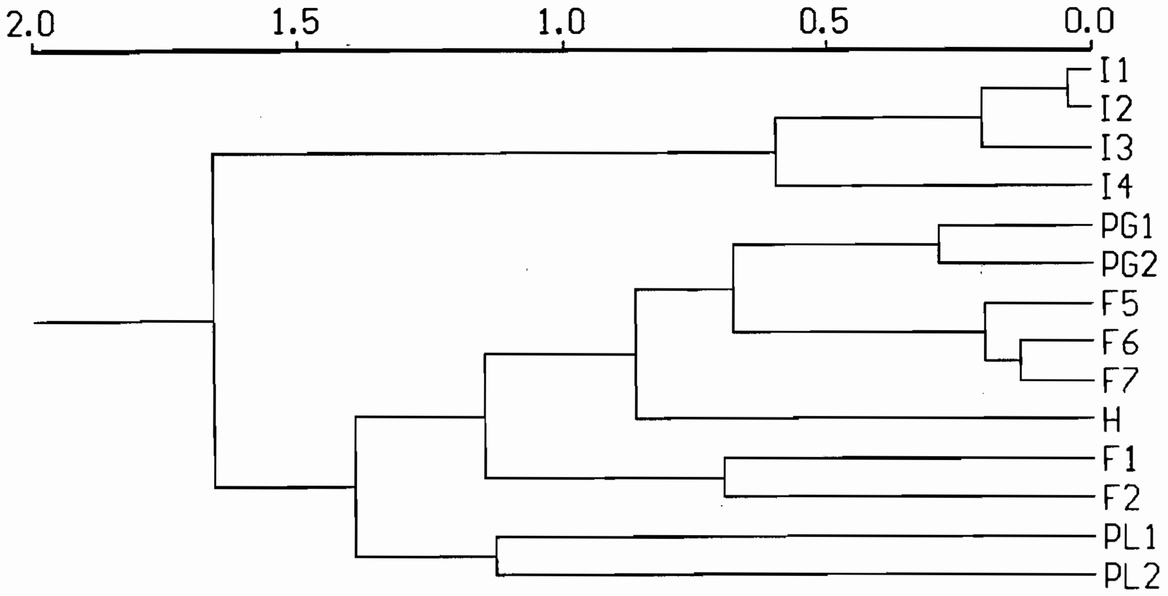
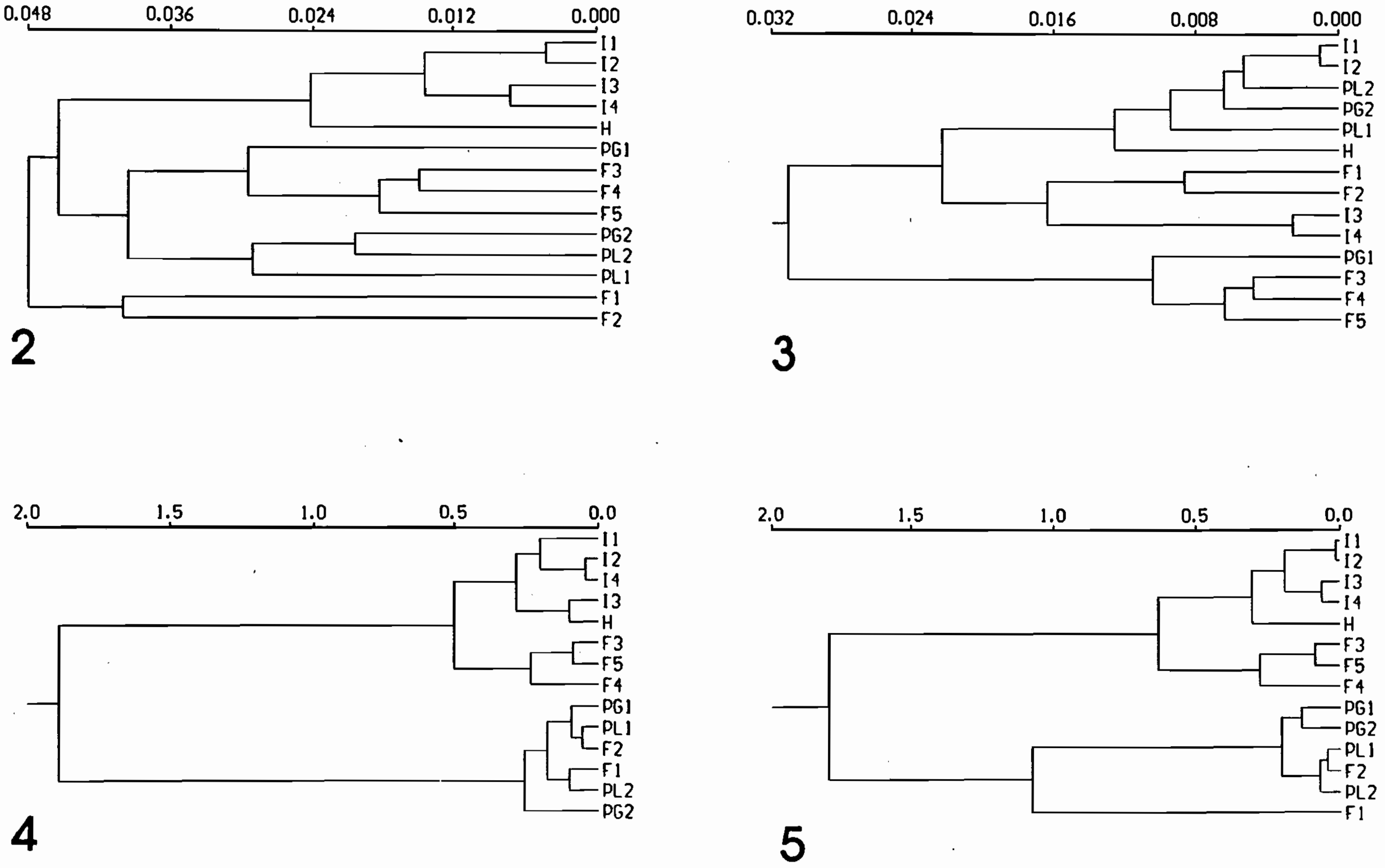


**Figure 1.** **Phenogram derived from cluster analysis based on four morphological characters. Key: F1 - F2 = *Q. falcata* f. *falcata*; F3 - F5 = *Q. falcata* f. *triloba*; H = putative hybrid; I1 - I4 = *Q. imbricaria*; PG1 - PG2 = *Q. pagoda*; PL1 - PL2 = *Q. palustris*.**



**Figures 2-5 (keyed as in Figure 1). 2. Phenogram derived from cluster analysis based on 40 elliptic Fourier coefficients. 3. Phenogram derived from cluster analysis based on 10 elliptic Fourier amplitudes. 4. Phenogram derived from cluster analysis of fractal D. 5. Phenogram derived from cluster analysis of leaf dissection.**

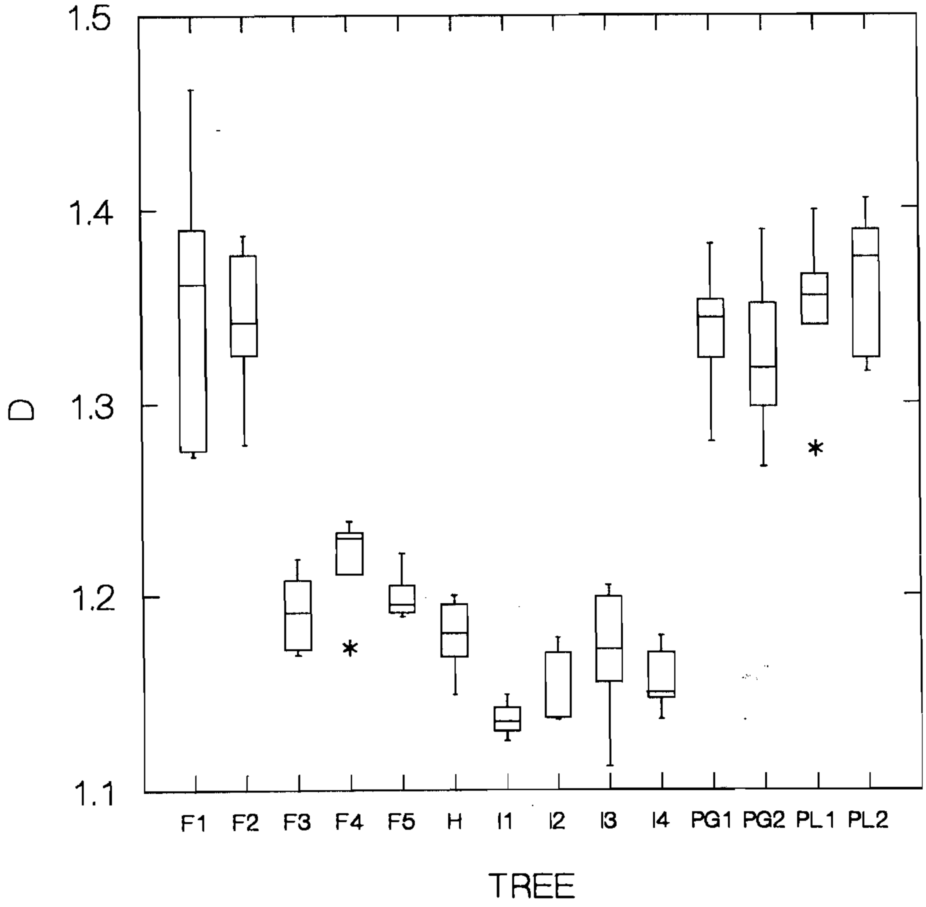


**Figure 6.** **Box plots of fractal D for each tree. Box interpretation: the lower and upper edges of the box represent the 25th and 75th percentiles, the line inside the box represents the median, the whiskers extend as far as values that fall within 1.5 spreads of the median (the spread is the distance from the 25th to the 75th percentile), asterisks mark outliers (between 1.5 and 3 spreads from the median), and circles mark extreme outliers (beyond 3 spreads from the median).**

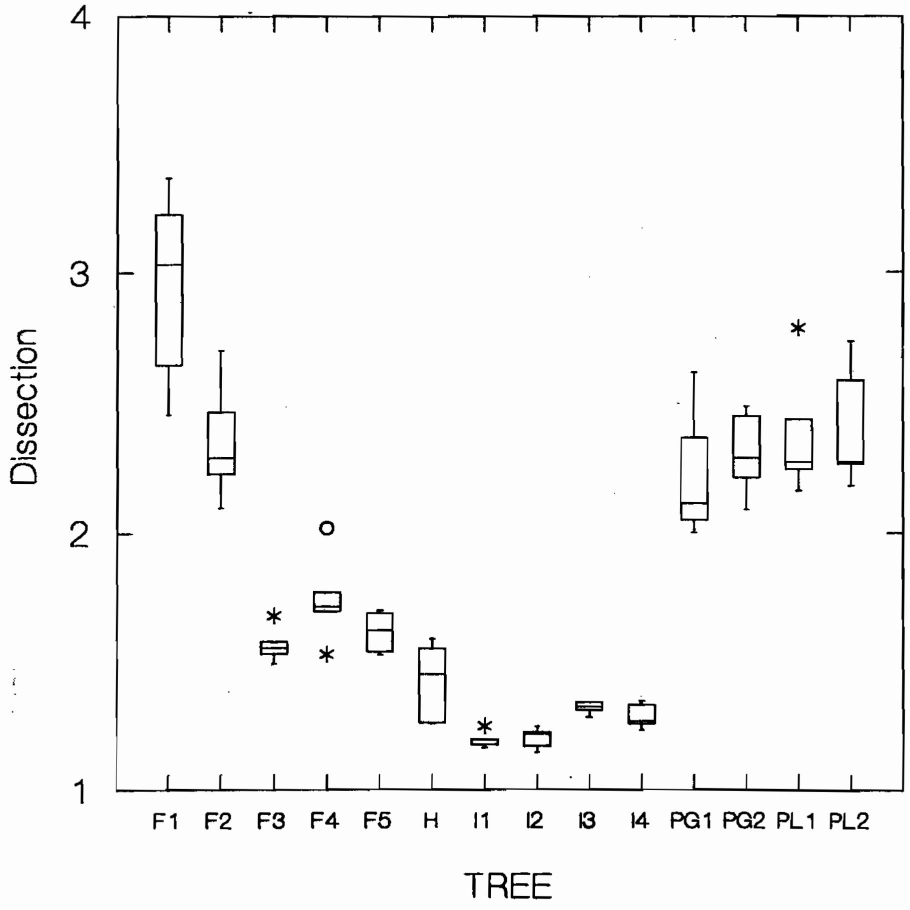
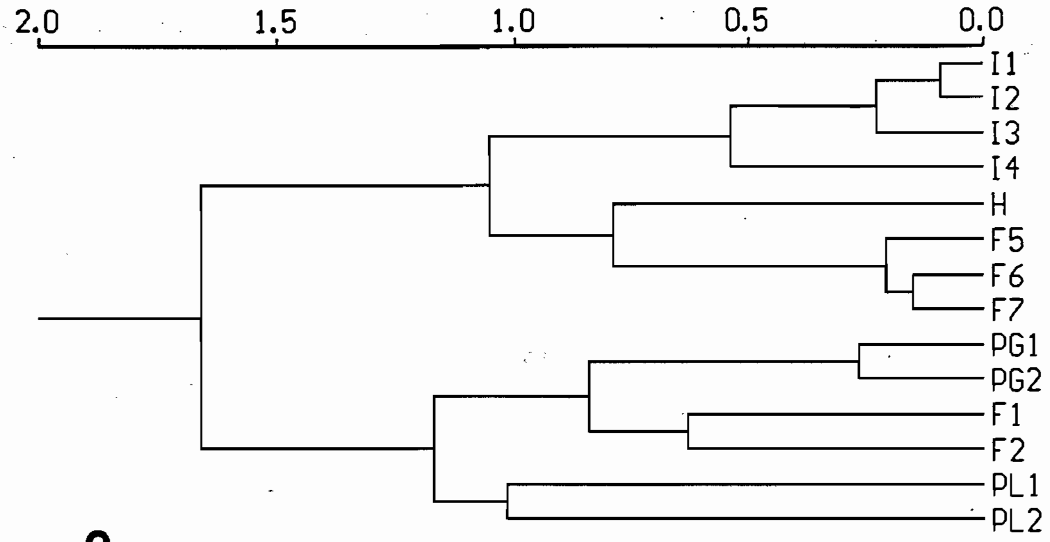
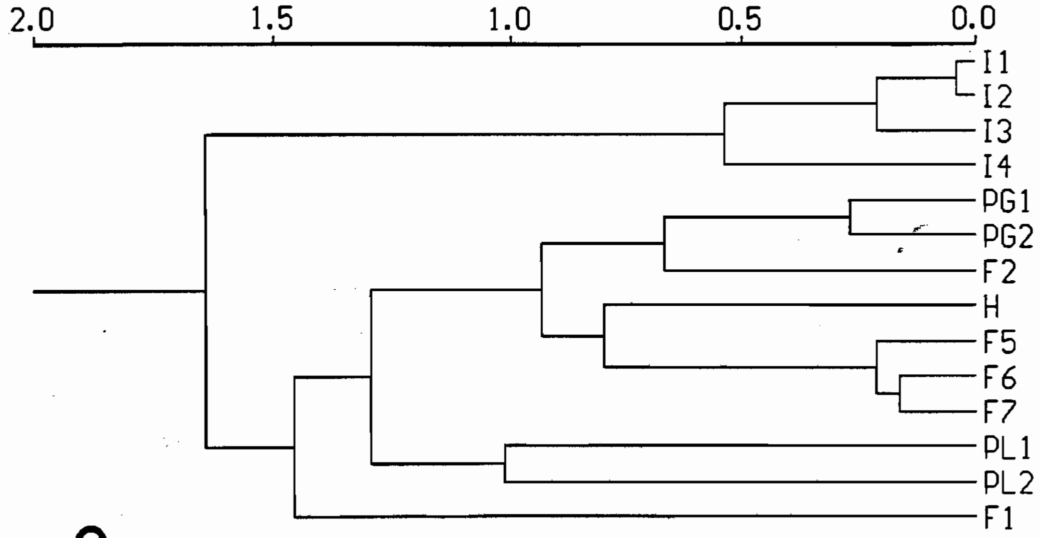


**Figure 7. Box plots of leaf dissection for each tree. See Figure 6 for explanation.**



**8**



**9**

Figures 8-9 (keyed as in Figure 1). 8. Phenogram derived from cluster analysis of four morphological characters plus fractal D. 9. Phenogram derived from cluster analysis of four morphological characters plus leaf dissection.

# STUDIES ON THE SEED BIOLOGY OF THREE NORTH AMERICAN SPECIES OF *RHUS* (ANACARDIACEAE). I. SOME PRELIMINARY RESULTS OF THE EFFECTS OF SEED DORMANCY-BREAKING PRETREATMENTS, TEMPERATURE, AND LIGHT ON GERMINATION

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**ABSTRACT. Ripe fruits of fragrant sumac *(Rhus aromatica)* were collected in 1994 from Fayette Co, KY; smooth sumac (*R. glabra*) in 1993 from Robertson Co, KY; and skunk sumac *(R. trilobata)* in 1994 from Santaquin Canyon, UT. Their water-impermeable seeds (*sensu lato*) vary greatly in size, with the 1000-seed (including endocarp) weight being 22.50 ± 0.29 (MEAN ± SE) g, 7.09 ± 0.03 g, and 14.15 ± 0.35 g, respectively.**

**Endocarp permeability was lost gradually in skunk sumac by incubating seeds for 20 weeks on wet sand at room temperature; 93.5 ± 1.5% of them imbibed water during this period. For fragrant and smooth sumac, however, 92 ± 2.9% and 98 ± 0% of the seeds, respectively, remained impermeable at the end of the 20-week soaking period.**

**The three species responded differently to various dormancy-breaking treatments. In smooth sumac, the most effective scarification treatment was boiling in water for 1 min, which resulted in imbibition of 98 ± 0.82% of the seeds. On the other hand, soaking seeds in conc. $H_2SO_4$ proved to be the most effective treatment for breaking hard seed coat dormancy in fragrant and skunk sumac seeds. Percentage of imbibed seeds of skunk sumac reached 100 after soaking in conc. $H_2SO_4$ for 2, 1, or 0.5 h. Similar results were obtained with seeds of fragrant sumac, except for the 0.5-h soaking, which rendered 81.5 ± 2.22% of the seeds permeable. Dry-heating at 100°C for 10 min did not significantly increase the percentage of imbibed seeds in any of the three species.**

**Physiological dormancy was detected in fragrant sumac seeds only. Stratification of scarified seeds at 5°C for 15 days resulted in 93.4 ± 1.29% germination, after two weeks of incubation at 25/15°C in white light. The lack of combinational dormancy (i.e., hard seed coat plus physiologically-dormant embryo) in seeds of skunk sumac is contrary to previous reports.**

**In general, seed germination of the three sumac species was rather insensitive to either temperature or light conditions, once dormancy was broken. High germination percentages were obtained at 30/15, 25/15, and 23°C (room temperature). The very highest germination percentages occurred at 20/10°C (12-h day/12-h night); 35/20°C appeared to be supraoptimal. As expected, the germination rate at 15/6°C was slow, but given enough time high germination percentages also were obtained at this temperature. Light quality (white, red, far-red) or darkness did not significantly affect the germination of either smooth or fragrant sumac seeds. However, seeds of skunk sumac germinated to significantly higher percentages in white light than in darkness at 15/6°C, though not at any of the other temperatures tested.**

# THE EFFECT OF PRESCRIBED BURNING ON FUEL AND SOIL NUTRIENTS OF UPLAND *QUERCUS* COMMUNITIES

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**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 (nonsuccessional) 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.**

## INTRODUCTION

Fire is a mechanism that speeds up the decomposition process (Ahlgren and Ahlgren 1960, Hall 1972, Wright and Bailey 1982) which is estimated at little more than a year for litter fuels of the eastern deciduous forest (Meentemeyer 1978, Peterson and Rolfe 1982). However, an understanding of the tradeoff between forest floor fuel decomposition by fire which may add mineral elements to the soil, and the loss of the litter layer which provides a sink for nutrients and is a medium for decomposition and mineralization processes is essential. The purpose of this research was to: 1) determine the effects of prescribed burning and mechanical thinning on fuel loads in a typical upland *Quercus alba* L. stand, 2) determine the effect of prescribed burning on soil nutrient levels in typical upland hardwood stands, and 3) determine if prescribed fire effects nutrient levels differently than a single fire in typical upland hardwood stands. To better understand the effects of fire, the following is a brief review of the decomposition process, nutrient sources, and nutrient sinks.

## Forest Nutrient Cycling and the Effect of Fire

Moisture is the most important consideration in decomposition (Kelly and Beauchamp 1987). Meentemeyer (1978) found that actual evapotranspiration accounted for 51% of variance in litter decomposition. Upland stands tend to have a less favorable moisture regime and, thus, slower decomposition rates than bottomland forests (Peterson and Rolfe 1982). Leaf characteristics may further differentiate between upland and lowland decomposition rates. The thick cuticle and high tannin concentrations in litter of some species (*e.g. Quercus*) may inhibit decomposition by inhibiting growth of microorganisms. *Acer saccharum* Marsh. leaf litter has more soluble material and less cellulose and lignin, which makes it less difficult to break down (Alexander 1973) than *Quercus rubra* L. litter (Aber and Mellilo 1991). Thus, *A. saccharum* leaves are more easily leached and decomposed (Aber and Mellilo 1991). Similar differences were found between *A. rubrum* L. (more easily decomposed) and *Q. prinus* L. leaves (Blair 1988). Litter of mesophytic species generally has a greater decomposition rate than *Quercus* litter (Swift *et al.* 1976) which contributes to the more rapid nutrient turnover on mesophytic sites than on more xeric *Quercus* sites (Waring and Schlesinger 1985).

A great majority of the annual supply of nutrients comes from leaves, as opposed to stems, acorns, and flowers (Cromack and Monk 1975). Due to their high leachability, throughfall contributes most of the K and Na (Cromack and Monk 1975, Patterson 1975). In contrast, decaying litter contributes most of the Ca and Mg, as these nutrients are structural components of the leaf (Cromack and Monk 1975).

Natural decomposing processes stratify the litter layer both structurally and chemically into the L layer ($O_1$), F layer, and H layer (F and H together = $O_2$). Yount (1975) defined the material of the L layer as loose and undecomposed, material of the F layer as ranging from easily distinguishable to too small to distinguish and bound by fungal hyphae, and material of the H layer as amorphous and indistinguishable. Due to high rates of decomposition, the H layer is generally nonexistent in eastern hardwood forests. Higher concentrations of P, N, Na, and Ca are present in the F layer than in the L layer (Richter *et al.* 1982, Yount 1975). Much of the decomposition takes place in the forest floor litter rather than in the soil profile due to higher concentrations of decomposing organisms (Bollen and Wright 1961, Anderson *et al.* 1983). The forest floor accounts for 75% of the total N input through biological fixation and has higher rates of nitrogen fixation and denitrification than soils (Todd *et al.* 1975). Potassium, Mg, and organic matter are more concentrated in the L layer than in the F and H layers (Yount 1975). Yount (1975) found Mg, Ca, and P decomposition rates were closely tied to litter biomass loss, while N and K were found to be highly mobile. Eleven percent of Ca and 3% of K are processed by leaf litter animals (Cornaby *et al.* 1975) which tend to enhance existing patterns of nutrient release (Anderson *et al.* 1983). The influence of litter feeding animals is greatest on freshly fallen or decayed (low C:N ratio) litter; these litter types are generally limiting to microbial growth (Wensem *et al.* 1993).

Fire induced nutrient level changes may be negligible (Harvey *et al.* 1979), reduced but eventually return to a normal level (Lewis 1974, McKee 1982), or increase (Vance and Henderson

1984, Gilliam 1990). McKee (1982) noted that burning accelerated mineralization and subsequent organic matter build-up, and cations were quickly recycled (Lewis 1974). Burning has been shown to convert P to an inorganic form readily useable by plants (Seasteadt and Ramundo 1990). Kelly and Beauchamp (1987) consider P to be one of the most important nutrients controlling decomposer populations. Both Vance and Henderson (1984) and McKee (1982) agree that fire may benefit soils by increasing fertility. Lewis (1974) notes that soils take over the job of the litter layer in providing a nutrient sink, although they are not as adequate. Richter *et al.* (1982) indicates minor effects of fire on mineral soil.

The exception to increases in nutrients following fire may be nitrogen, which volatilizes at temperatures > 200°C and can also be released with particulate matter (Agee 1993, Gillon *et al.* 1995). Vance and Henderson (1984) show declining amounts of ammonium and extractable N after repeated burning. They also note that it is the primary growth-limiting nutrient of hardwood forests. When litter is burned, 1/4 to 1/2 of the N is volatilized (Lewis 1974) which may equal as much as a 40 year input from precipitation. Even small portions of fixed N lost due to fire in a longleaf pine stand made up substantial portions (2/3) of annual atmospheric input (Lewis 1974). Lewis (1974) indicated an initial nutrient loss, but in part, as a result of microbial activity, nitrate and phosphorous slowly increased to preburn levels.

The major effectops of fire may be due to litter removal and associated changes in the microclimate rather than to direct soil heating or fire induced nutrient changes (Dhillion *et al.* 1988, Dobrowolski 1992). Depth of litter alone has been shown to effect regeneration of *Quercus* species which reproduce best in moderate to light litter cover (Minkler and Jensen 1944, Burns and Honkala 1990). Wells *et al.* (1979) argued that reduced competition between plants and microorganisms may be a better explanation for increases in plant biomass following fire than the incorporation of ash into the soil. Moreover, nutrients, especially K, Mg, and Na, may be largely leached from litter material long before a burn (Best and Monk 1975, Peterson and Rolfe 1982, Dwyer and Merriam 1984, Dhillion *et al.* 1988). Dhillion *et al.* (1988) found no differences in nutrient content of vegetative material between burned and unburned sites, but greater vegetative biomass did occur on the burned sites. Ohmann and Grigal (1979) found vegetation to be an effective sink for nutrients released by fire.

Fire also will effect decomposer populations, particularly of the litter, and thus the potential decomposition rate on a site. The general pattern following fire is a decrease in soil microbes followed by an increase (Armson 1977, Harvey *et al.* 1979). Microorganisms may decrease or be largely eliminated (depending on fire temperature and fuel consumption) from the litter, duff, and upper soil layers, but will be reestablished following the burn (Dunn *et al.* 1979). Generally, bacteria are more heat resistant than fungi (Dunn *et al.* 1979, Wells *et al.* 1979) with most microorganisms unable to withstand temperatures > 100°C (Hartford and Frandsen 1992). Fire has the greatest effect in moist soils, when microorganisms are more sensitive (Dunn and DeBano 1977, Dunn *et al.* 1979, Wells *et al.* 1979). Here again, effects of burning show varying results. Spore counts in burned areas of prairie were significantly different than unburned areas, but this difference was attributed to changes in host plants and not directly to fire (Dhillion *et al.*

1988). Jorgensen and Hodges (1970) found burning to have no effect on soil fungi in a South Carolina forest following 20 years of prescribed burning. Fire significantly reduced soil microarthropods in chaparral communities (Sgardelis and Margaris 1993).

## STUDY AREA

The data were collected at Land Between The Lakes National Recreation Area (LBL), Kentucky and Tennessee, a 67,000 ha highly dissected interfluve between Kentucky Lake and Lake Barkley. The area ranges from 6-13 km wide and is approximately 64 km long. The center of LBL is 36°47' N latitude and 88°04' E longitude. Mean annual precipitation is 1210 mm. Average temperatures are 3°C in the winter and 28°C in the summer. Prevailing wind is from the southwest. Average number of growing days is 195 between April and October (U.S.D.A. 1941).

Braun (1950) described the forest region as western mesophytic, a combination of mixed mesophytic and oak-hickory. A general description of oak-hickory forests for the southeastern United States is provided by Bryant *et al.* (1993). LBL is over 80% second-growth forest dominated by *Quercus* species with much of the area succeeding to mesophytic dominance. Forest vegetation and soils (Harris 1988, Schibig and Chester 1988, Fralish *et al.* 1993, Franklin *et al.* 1993), geology (Potter 1955, Harris 1988), and history (Gildrie 1992, Wallace 1992, Franklin 1994) of LBL have been described.

## METHODS

Two forest conditions were studied: 1) a *Quercus alba* L.-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 following treatments and on two oak/oak sites which contained all five 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 only from 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 - .64 cm Class 1 (0 - .25"), .64 - 2.54 cm Class 2 (.25 - 1"), and 2.54 - 7.62 cm Class 3 (1 - 3") intersecting the planar transect were counted and fuel load by weight (w) was calculated by the following formula for each size class:

$$\text{w (tons/acre)} = (11.64 \text{ X } n \text{ X } d^2 \text{ X } s \text{ X } a \text{ X } c)/N \text{ X } L$$

where: n = total 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 = .70, 2 = .70, and 3 = .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 = $\sqrt{1 + [\text{Percent Slope}/100]^2}$
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 were 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:

$$\text{w (tons/acre)} = (11.64 \text{ X } \sum d^2 \text{ X } s \text{ X } a \text{ X } c)/N \text{ X } L$$

where: $\sum d^2$ = 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 = .30 (Anderson 1978).
a = as above, 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:

$$w \text{ (kg/ha)} = \Sigma [w_i(1 + P_1 + P_2 + P_3 + P_4 + P_5)]/6$$

where: $w_i$ = 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.* 1982).

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 lbs/acre), 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.

## RESULTS

### Burns

Weather data and characteristics of prescribed burns are presented in Table 1. No data were taken from Site 6 and no soil data were obtained from Site 2. There are no clear differences in weather conditions between the two forest conditions (*i.e.* oak/oak and oak/maple). It should be noted that wind speeds were very low for all burns. One conspicuous result is the generally greater headfire rate and maximum flame height in the oak/maple sites, even though fuel moisture levels were less and vapor pressure deficits were greater on the oak/oak sites. Greater slope angles on the oak/maple sites (> 20° vs. < 20° on oak/oak sites) are likely responsible for an apparently more severe fire. However, litter consumption did not vary considerably between sites. In all cases, only portions of the L layer and the F layer were consumed (visual observations).

### Fuels

Litter samples averaged 27.67% moisture by weight while duff and herbaceous averaged 45.04% and 39.77%, respectively (Table 2). Percent moisture for litter and duff during burns ranged from 17.11% to 36.16% by weight. The 17.11% value was far below all other values, but was also the only site that had been previously burned.

Litter and duff fuel biomass decreased sharply following burning, but increased to 75% of preburn levels by the second summer following all treatments (Figure 1). Data indicate a 50-60% reduction in litter and duff fuel biomass (Table 3). Litter and duff biomass data from control plots following all treatments are indicative of preburn levels (Mean Litter = 591 g/m$^2$; Mean Duff = 694 g/m$^2$), suggesting an equilibrium of fuel levels in these upland stands.

Herbaceous fuel biomass decreased to zero immediately following the burn, but increased to above preburn levels in the second summer following all treatments (Figure 1). In the thinned and burned plots, herbaceous vegetation increased 100 times.

Results from dead and down material were less definitive. Typical upland preburn loadings averaged 6.0 tons/acre (13,500 kg/ha) while thinned areas containing slash averaged 43.54 tons/acre (97,965 kg/ha) (Table 3). An average of 31.65% of dead and down fuels > 7.62 cm (Class 4) were consumed by the fire in the uncut plots while only 12.83% were consumed in the cut plots.

**Table 1. Date, time, prescibed burning weather, and fire behavior data for first burn treatments, Land Between The Lakes, Kentucky and Tennessee.**

| | | Oak/maple Sites (1-4) | | | | Oak/oak Sites (5-8) | | |
|---|---|---|---|---|---|---|---|---|
| Variable | | 1 | 2 | 3 | 4 | 5 | 7 | 8 |
| Date | | 2/92 | 2/92 | 11/91 | 2/92 | 11/91 | 11/90 | 11/91 |
| Time | | 1100 | 1300 | 1100 | - | 1300 | 1445 | 1300 |
| Weather | | | | | | | | |
| | Temp. (°C) | 21 | 22 | - | - | 12 | 27 | - |
| | % Cl. Cover | 100 | 15 | 0 | 50 | 100 | 0 | 0 |
| | Rel. Humidity | 67 | 49 | 55 | 65 | 53 | 37 | 55 |
| | VPD (mm Hg) | 1.36 | 3.10 | 1.71 | 1.41 | 2.54 | 4.54 | 3.13 |
| | % Fuel Moist. | 15.0 | - | 15.5 | 13.5 | - | 7.1 | 13 |
| | Wind Sp.(km/hr) | < 5 | < 5 | 6.86 | < 5 | < 5 | 15.91 | 6.86 |
| Fire Behavior | | | | | | | | |
| | Min. Flame Ht.(cm) | 15 | 10 | 10 | - | 15 | 10.2 | 6 |
| | Max. Flame Ht. (cm) | 80 | 61 | 76 | - | 91 | 45.7 | 20 |
| | Headfire Rate (km/hr) | 1.1 | 0.550 | 0.439 | - | 0.274 | 0.274 | 0.056 |
| | Backfire Rate (km/hr) | 0.026 | 0.026 | 0.027 | - | 0.036 | 0.137 | 0.014 |

**Table 2. Moisture content in forest floor fuels for an upland oak stand at Land Between The Lakes, Kentucky and Tennessee. Weights are given in g/m².**

| Treatment: Burn | | | |
|---|---|---|---|
| | Litter | Duff | Herbaceous |
| Preburn (wet) | 800.20 | 1082.41 | 0.0 |
| Preburn (O.D.W.) | 568.24 | 581.00 | 0.0 |
| % Moisture | 28.99 | 46.32 | 0.0 |
| Treatment: Burn Twice | | | |
| Preburn (wet) | 861.75 | 1526.42 | 1.51 |
| Preburn (O.D.W.) | 614.22 | 807.38 | 0.85 |
| % Moisture | 28.72 | 47.11 | 43.71 |
| Treatment: Cut & Burn | | | |
| Preburn (wet) | 490.54 | 948.54 | 0.67 |
| Preburn (O.D.W.) | 366.50 | 553.08 | 0.43 |
| % Moisture | 25.29 | 41.69 | 35.82 |
| Mean % Moisture | 27.67 | 45.04 | 39.77 |

Conversion: tons/acre = (g/m²) * 0.0044;

Table 3. **Fuel loading data for one upland oak/oak site, Land Between The Lakes, Kentucky and Tennessee. Forest floor fuel values are g/m$^2$; Dead & Down values are kg/ha; Dead & Down class sizes are: (1) 0.0 - 0.64 cm; (2) .64 - 2.54 cm; (3) 2.54 - 7.62 cm; (4) > 7.62 cm.**

| | Forest Floor Fuels | | | Dead & Down Material | | | | Total |
|---|---|---|---|---|---|---|---|---|
| | Litt | Duff | Herb | (1) | (2) | (3) | (4) | |
| **Treatment: Burned** | | | | | | | | |
| Preburn | 568.18 | 581.82 | 0.00 | 553.50 | 1512.00 | 1957.50 | 15869.25 | 19892.25 |
| Immediately Postburn | 202.27 | 250.00 | 0.00 | 837.00 | 2031.75 | 2214.00 | 11164.50 | 16247.25 |
| Consumption | 365.91 | 331.82 | 0.00 | (283.50) | (519.75) | (256.50) | 4704.75 | 5764.50 |
| % Consumption | 64.4 | 57.0 | 0.00 | 0.00 | 0.00 | 0.00 | 29.7 | 28.98 |
| Postburn | 331.82 | 670.45 | 6.27 | | | | | |
| % of Total Fuels - Preburn | | 36.40 | | | 12.86 | | 50.74 | |
| % of Total Fuels - Immediately Postburn | | 21.61 | | | 24.53 | | 53.88 | |
| **Treatment: Burn Twice** | | | | | | | | |
| Preburn | 613.64 | 806.82 | 0.91 | 704.25 | 1701.00 | 1428.75 | 3172.50 | 21082.50 |
| Immediately Postburn | 327.27 | 329.55 | 0.00 | 922.5 | 3397.50 | 1350.00 | 2115.00 | 14287.50 |
| Consumption | 286.37 | 477.27 | 0.91 | (218.25) | (1696.50) | 78.75 | 1057.50 | 6795.00 |
| % Consumption | 46.67 | 59.15 | 100.0 | 0.0 | 0.0 | 5.51 | 33.33 | 32.23 |
| Postburn | 479.55 | 538.64 | 1.01 | | | | | |
| % of Total Fuels - Preburn | | 66.74 | | | 18.19 | | 15.05 | |
| % of Total Fuels - Immediately Postburn | | 45.51 | | | 39.69 | | 14.80 | |
| **Treatment: Cut & Burn** | | | | | | | | |
| Preburn | 365.91 | 552.27 | 0.45 | 5287.50 | 5490.00 | 5715.00 | 81472.50 | 107055.0 |
| Immediately Postburn | 338.64 | 347.73 | 0.00 | 4522.50 | 9967.50 | 8932.50 | 71032.50 | 101250.0 |
| Consumption | 27.27 | 204.54 | 0.45 | 765.00 | (4477.50) | (3217.50) | 10440.00 | 5805.0 |
| % Consumption | 7.45 | 37.04 | 100.0 | 14.47 | 0.0 | 0.0 | 12.81 | 5.42 |
| Postburn | 484.09 | 1.95 | 45.45 | | | | | |
| % of Total Fuels - Preburn | | 8.50 | | | 15.41 | | 76.10 | |
| % of Total Fuels - Immediately Postburn | | 6.71 | | | 23.13 | | 70.16 | |

Conversion of Forest Floor Fuels: tons/acre = (g/m$^2$) * 0.0044;
Conversion of Dead and Down material: tons/acre = (kg/ha) / 2250;

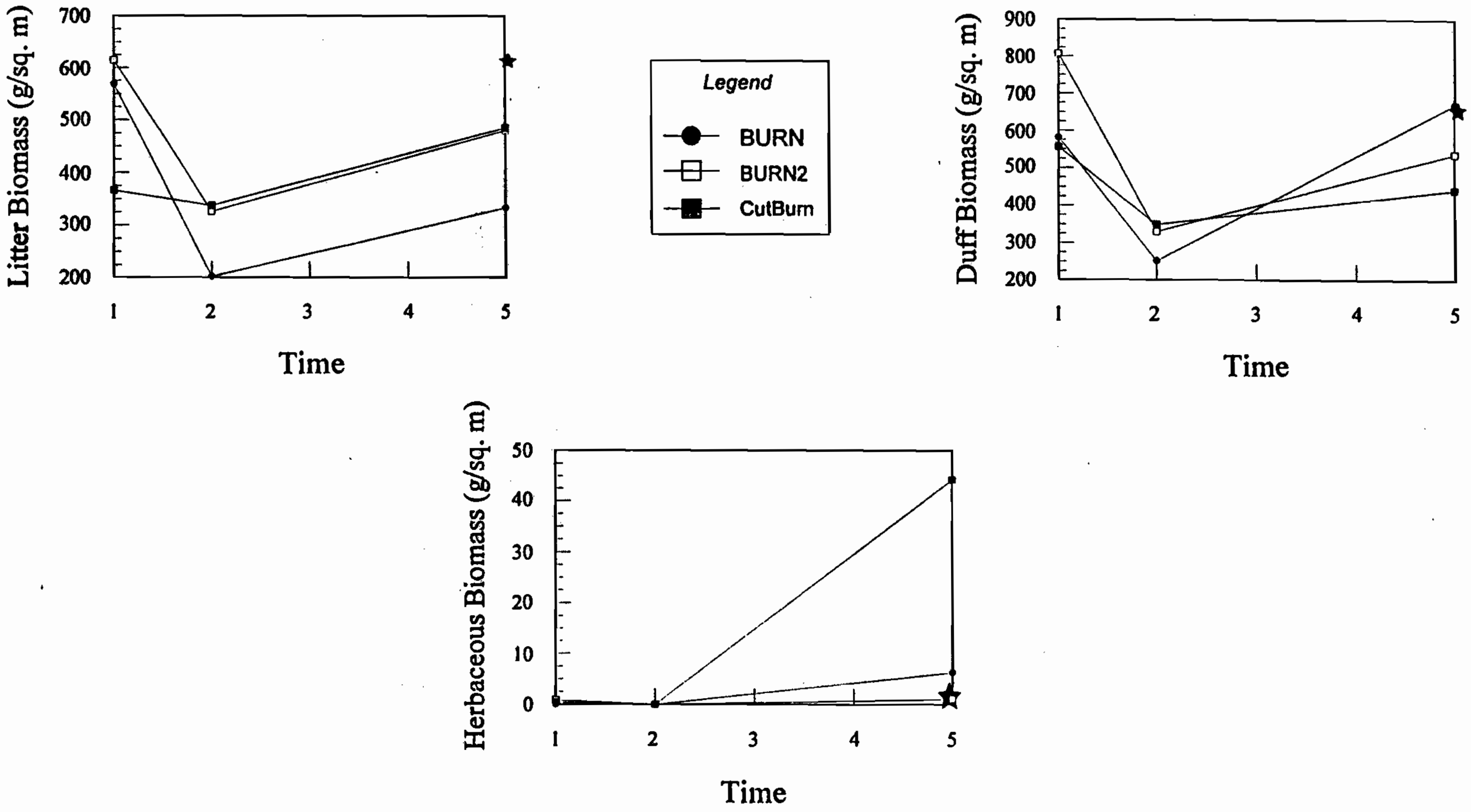

**Figure 1. Effect of fire on forest floor fuels from Land Between The Lakes, Kentucky and Tennessee. The first burn took place+ at time 1.5. The second burn took place at time 4. BURN = plots that received one burn, BURN2 = plots that received two burns, CutBurn = plots that were mechanically thinned and burned. Star indicates control plots at final sample period.**

**Nutrients**

Nutrient data for oak/oak sites suggested little significant effect of prescribed burning (Figure 2). Although significant changes were witnessed between time periods (FH), control plot data reacted similarly to burn plot data. However, burning seemed to augment nutrient increases or decreases in pH, exchangeable P, ENR, % organic matter, and exchangeable H. Exchangeable H was the only variable that decreased. Exchangeable nitrate and soil pH were the only variables with a significant overall time*treatment interaction (PH). All treatments increased following burning, but contrary to control plot nitrate concentrations, burned plot nitrate concentrations decreased between the second and third sampling periods.

Overall significant time*treatment interactions (PH) for exchangeable P, total P, and exchangeable K were found for the oak/maple sites (Figure 3). Only exchangeable P had a significant ($\alpha = 0.033$) time*treatment effect for the first time interval. Again, however, some variables were noticeably augmented by burning (*e.g.* exchangeable Mg, exchangeable Ca, % organic matter, ENR, CEC, and exchangeable H). Variables that decreased were % organic matter, exchangeable H, ENR, and CEC.

Most of the nutrients had returned or were progressing toward preburn levels by the third sampling period. CEC for both sites and % organic matter for oak/oak sites may be exceptions.

## DISCUSSION

**Fuels**

Even though preburn fuel loads are biased underestimates, loadings were comparable to other studies in the eastern United States. Sanders and Van Lear (1988) estimated slash loads for southeastern Appalachian mixed conifer-hardwoods between 36,000 & 115,875 kg/ha. Fire consumed an average of 54.5% of these fuels. Because the burns in this study were of low intensity, only 12-31% of fuels were consumed. Wade *et al.* (1993) examined post-hurricane dead and down fuels in South Carolina mixed conifer-hardwood stands. There, total fuel loading was similar to the present study, but percentage of fuels consumed generally was much greater. However, as in the present study, Wade *et al.* (1993) had greater or equal fuel loadings following fire in smaller dead and down size classes of material for one of their samples.

Litter and duff fuel loadings and their reduction due to fire were also comparable to loadings from the mixed pine-hardwood stands (Sanders and Van Lear 1988, Wade *et al.* 1993). As expected, litter/duff loadings decreased 22.2-60.7% following burning, and thus were the greatest overall influence on fire intensity and magnitude (*i.e.* litter and duff were the main fuel source). Lewis (1974) noted a 33% reduction in pine litter following burning. Sanders and Van Lear (1988) found up to 100% reduction in litter and 22-73% reduction in the duff layer following

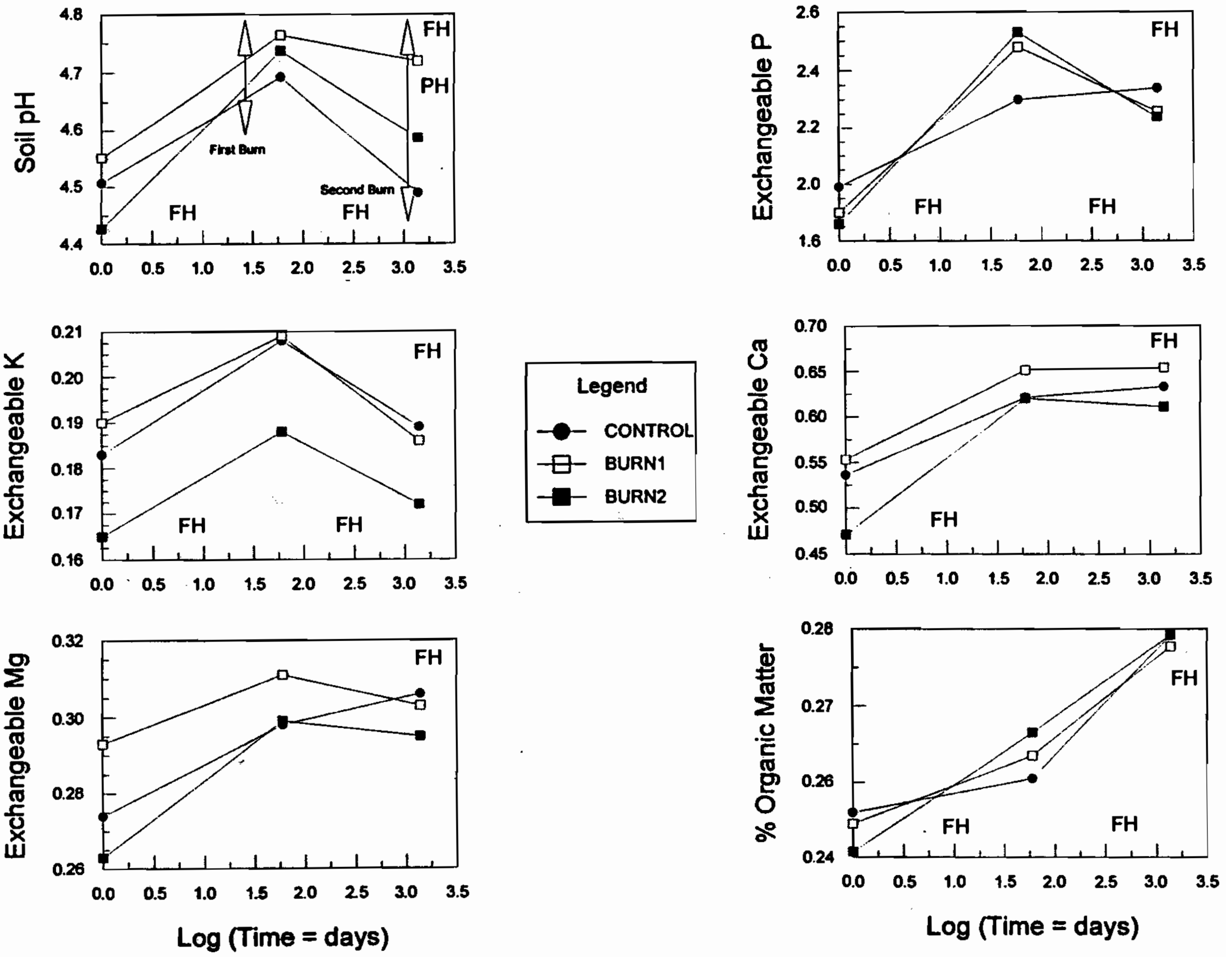

**Figure 2.** Effects of prescribed burning on soil nutrients in upland oak/oak sites (non-successional) at Land Between The Lakes, Kentucky and Tennessee. Treatments include: 1) control, 2) burned once, and 3) burned twice (burns were during the dormant season). Repeated measures analyses results are given: FH = flatness hypothesis (time effect), PH = parallel hypothesis (time*treatment effect). An FH or PH in the upper right hand corner of each graph represent significance of the overall test (∝ = 0.10); an FH or PH just above the x-axis represents significance (∝ = 0.33) between each sampling period.

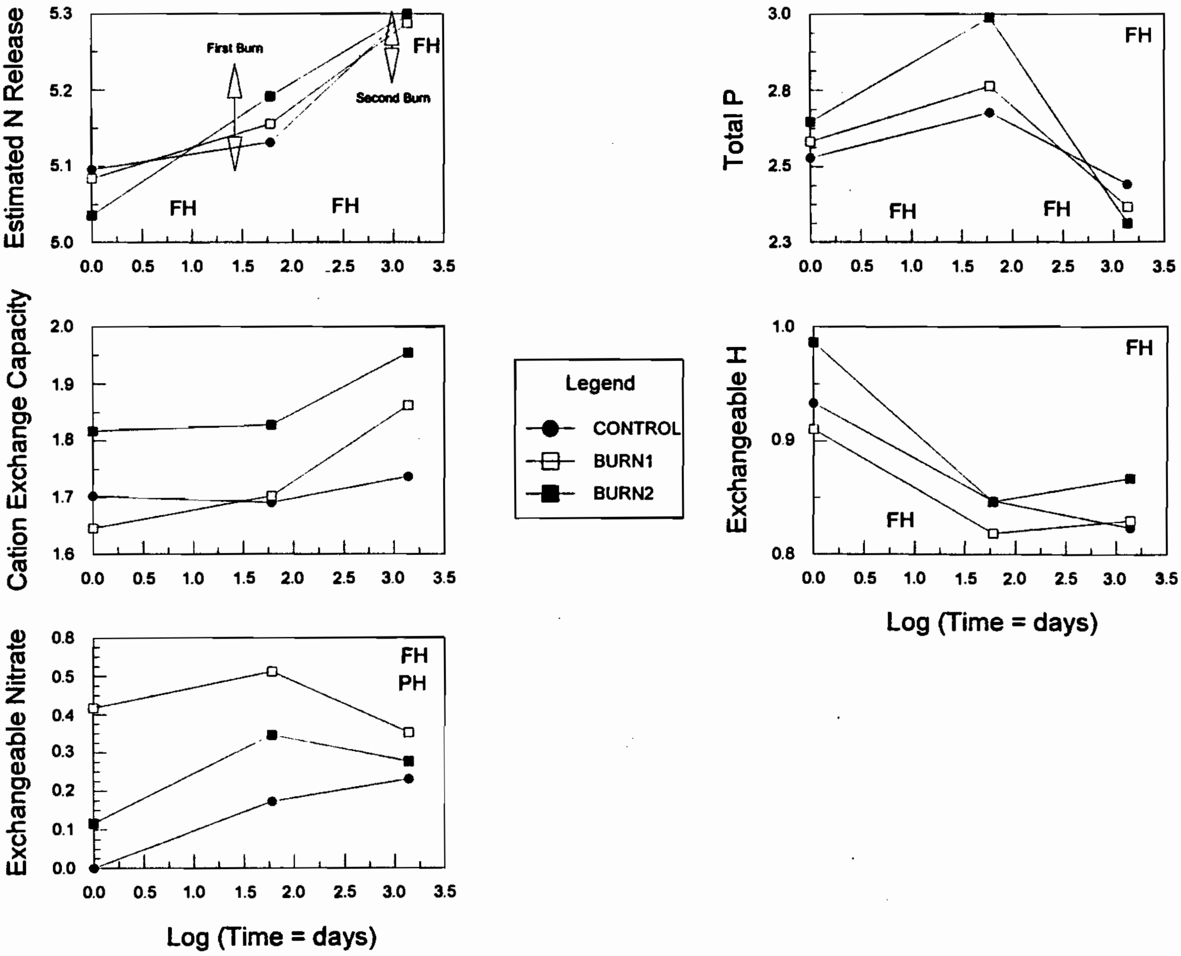

**Figure 2, continued.**

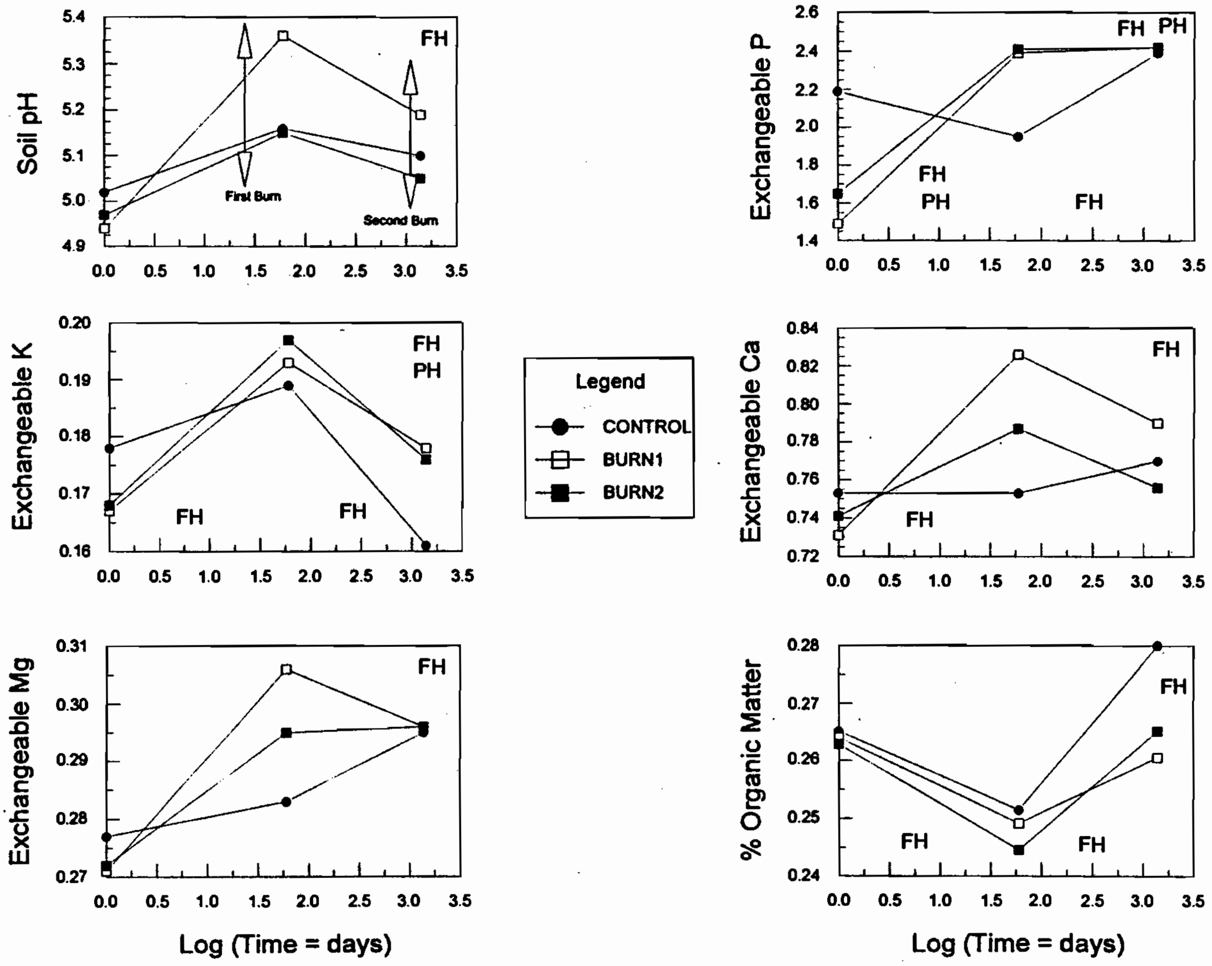

**Figure 3.** Effects of prescribed burning on soil nutrients in upland oak/maple sites (succes-sional) at Land Between The Lakes Kentucky and Tennessee. Treatments include: 1) control, 2) burned once, and 3) burned twice (burns were during the dormant season). Repeated measures analyses results are given: FH = flatness hypothesis (time effect), PH = parallel hypothesis (time*treatment effect). An FH or PH in the upper right hand corner of each graph represent significance of the overall test (∝ = 0.10); an FH or PH just above the x-axis represents significance (∝ = 0.33) between each sampling period.

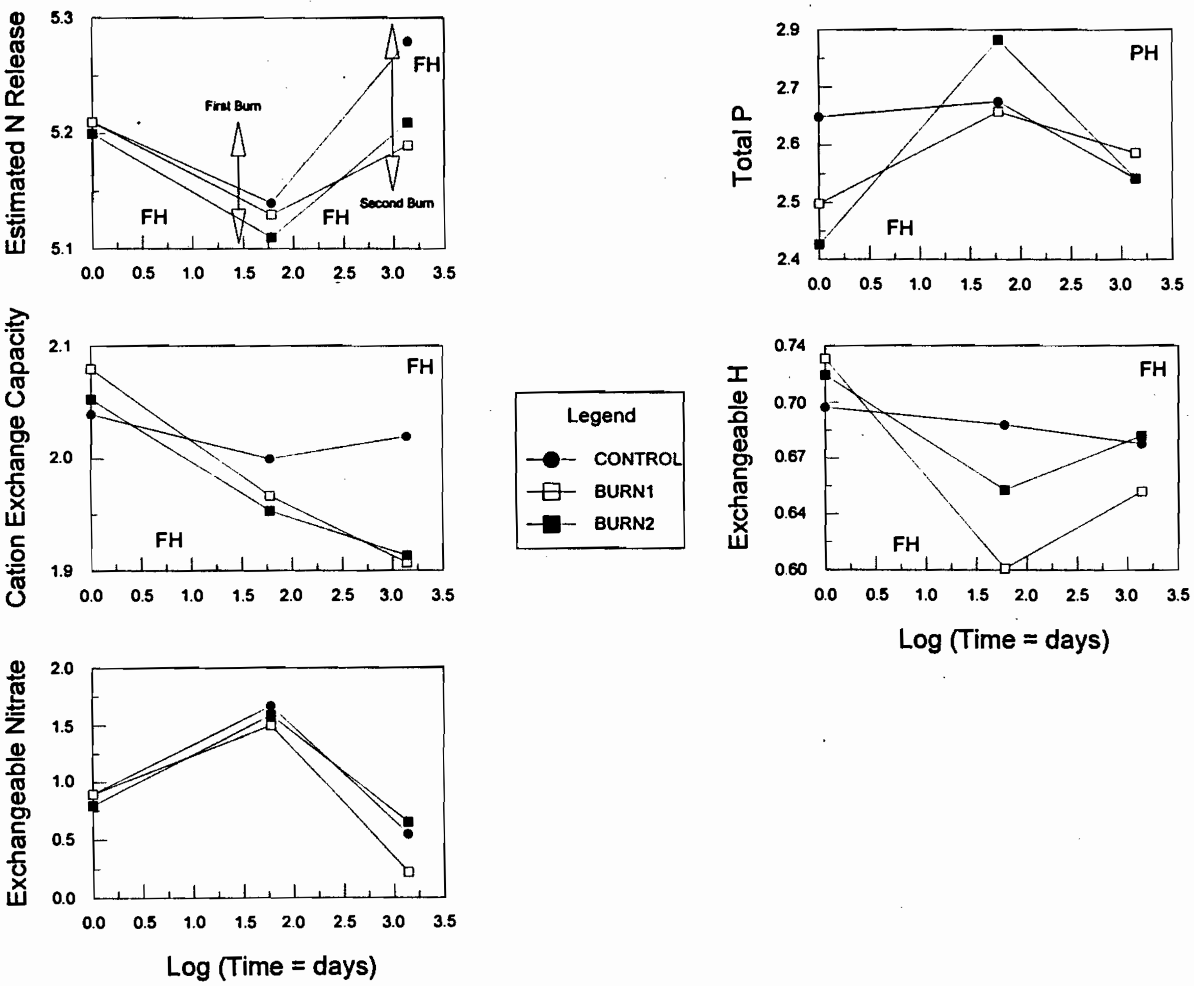

**Figure 3, continued.**

Appalachian slash fires. On our sites, visual observations 30 days following burns indicated nearly complete loss of these fuels. In the summer following the second burn, litter was absent and duff biomass was negligible on plots that received a second burn.

Peterson and Rolfe (1982) and Meentemeyer (1978) estimate eastern deciduous litter turnover rates at just over 1 year. This figure has been disputed by Kelly and Beauchamp (1987), who estimated 4.4-6.8 years for decomposition. Based on the similarity between data collected from control plots during the final sample period and data taken prior to treatments, our data corroborate decomposition rates at close to 1 year for forest floor fuels.

## Nutrients

Nutrient cycling in forests is a complex and variable phenomenon. Site to site differences occur due to the initial elemental content in litter and microbial demand (Luvall 1976; Kelly and Beauchamp 1987). Even within site differences can be high. Luvall (1976) found that increasing the sample size above 6 within 0.04 ha plots did not decrease variability of soil nutrients, which remained high. Bell *et al.* (1993) concluded that the variance of Wisconsin forest edaphic properties increased continually with distance between samples. Data from the present study indicate that the response of soil variables within sites and treatments was not always uniform. This variability along with significant differences between sites tended to obscure treatment effects.

Two points merit discussion before pursuing specific nutrient changes due to prescribed burning: 1) the increase in nutrients between preburn and immediately postburn samples for control plots as well as burn treatments, and 2) the response difference between oak/oak and oak/maple sites between preburn and immediately postburn samples.

Over all sites, there is a significant increase in nutrients during the 60 day first time interval (*i.e.* from the first sampling period to the second sampling period). Although nutrient increases would not be expected from normal decomposition processes during the dormant season (B. Klubek, pers. comm.), and thus nutrient content in control sites would not be expected to increase, precipitation may play a role. Mean monthly precipitation from the last ten years at the Golden Pond, Kentucky, weather station shows an general increase from September (9.0 cm) to October (9.5 cm) to November (13.7 cm). Mean precipitation then decreases in December (12.1 cm) and January (8.8 cm), followed by an increase in February (15.0 cm) (climate data provided by Glen Conner, Kentucky Climate Center, Western Kentucky University). The increase in precipitation provides a source for nutrients as well as a medium for leaching from forest floor fuels, both of which would result in an increase in soil nutrients. Likens *et al.* (1977) noted that H ions accounted for 70% of the total cationic strength in precipitation. The remaining 30%, in order of abundance, were $NH_4$, Ca, Na, Mg, and K. Precipitation data indicate that total ionic concentrations from December to February were much less than concentrations during October and November, which were only slightly less than spring and summer months (Likens *et al.* 1977). Precipitation concentrations reported by Likens *et al.* (1977) are greater than increases recorded between preburn and immediately post burn soil samples in this study. However, these data were taken from the northeastern United States, and may only be minimally comparable to the LBL area. Precipitation is also a source for nitrate and dissolved organic carbon.

Yount (1975) showed that litter weight and forest floor nutrients (Ca, Mg, K, Na, N, P) peaked in November (litter fall) and then decreased from November to March. Best and Monk (1975) found that water flow-through from litter contained high amounts of K, Ca, Mg, and Na. Gosz *et al.* (1975) ranked the leachability of nutrients from the litter layer: K > Mg > Ca > N > Na. They further noted that 80-90% of K could be leached within the first 7 days due to the fact that it is not structurally bound. Several researchers have noted the ease of leaching both K and Mg (Day and McGinty 1975, Patterson 1975, Peterson and Rolfe 1982, Kelly and Beauchamp 1987). Losses of other elements (*e.g.*Ca and P), and losses of K and Mg following initial leaching, are closely tied with biomass loss rates (Yount 1975, Peterson and Rolfe 1982, Kelly and Beauchamp 1987). Kuitters and Sarink (1986) found that most of the water-soluble phenolics, an important source of organic compounds, leached from the litter layer during the period from October to January.

While burns only directly consumed the loose leaf litter, site observations one month later revealed near complete forest floor fuel consumption. Because there was no evidence of mass erosion, we attribute this to decomposition. Increases in pH and cation saturation increase the diversity of microbial organisms. Bacteria are less tolerant than fungi to acidity and grow much faster (Wright and Bailey 1982, Alexander 1973). Thus, an increase in pH following burning would cause a burst in microbial populations and activity, and thus, decomposition rates would increase (Lewis 1974, Fritz *et al.* 1994). Bacterial populations may increase 3- to 10-fold within one month following burning (Swift *et al.* 1976, Wright and Bailey 1982, Kelly and Beauchamp 1987). Both prescribed burning and these decomposition processes increase the soil nutrient pool while decreasing the forest floor biomass and nutrient pool, thus leaving the top soil unprotected from wind and water erosion.

Increased precipitation during burn months could also add to subsurface water flow (Miyazaki 1993) and erosion (Brady 1984), providing a possible explanation for the transport of nutrients across plots, and an additional explanation for nutrient increases over all treatments (Wright and Bailey 1982, Jeffrey 1987). Likens *et al.* (1977) show a general relationship between precipitation input and streamflow output for several nutrients. Treatment plots were separated by only 4 m. Nutrient transport in systems is controlled by soil particle and water transport.

Several processes of erosion may be applicable. There is no evidence of rill erosion thus far, but sheet erosion is likely with an unprotected surface (Jeffrey 1987, Agee 1993). The LBL area falls within the most highly erodible lands (sheet and rill) in the United States (Brady 1984). Lack of transpiration and exposed soil surfaces would increase water movement velocity and thus increase the potential for erosion (Wright and Bailey 1982, Bormann and Likens 1979). Most of the nutrients are found in the top soil horizon and nutrient losses (nutrients are attached to the particles) can be significant (Brady 1984). The lack of a canopy during the dormant season would also leave these areas vulnerable to soil-splash effects from raindrops, which include: 1) detachment of soil, 2) destruction of granulation, and 3) transport of particles, especially with the help of wind (Brady 1984, Agee 1993). Wind erosion, especially saltation, may also be possible with an exposed soil surface. Due to the decrease in wind velocity within the forest (Kimmins 1988), however, it is likely less of a factor than water erosion. Evidence for increased erosion due to burning in southeastern forests exists, but is debated (Wells *et al.* 1979). There is no clear pattern in the raw data to support erosion and nutrient transfer between plots, but it should not be ruled out a this time. We attribute increases in nutrients during the 60 day interval to precipitation and leaching along with the possibility of erosion.

The second major point of discussion involves the difference in nutrient responses to burning between the oak/oak sites and oak/maple sites. The oak/maple sites, two of which were burned in February and one in November, are comparable to the oak/oak sites as exchangeable H decreased while pH and exchangeable cations, exchangeable P, and total P increase. Contrary to the pattern on oak/oak sites burned in November, all variable changes on the oak/maple sites were augmented by burning. Fire tends to increase the structural vulnerability of the litter layer to decomposition, thus increasing microbial activity (Lewis 1974). In addition, burned litter retains less rainwater, thus runoff and seepage are greater (Lewis 1974). Lewis (1974) found that the solubility of ions increased several times following burning, and that the total amount of leachable material was greatly increased by fire. Richter *et al.* (1982) found concentrations of water soluble K, Mg, and Ca in burned forest floor litter were significantly reduced by the initial 15 cm of rainfall, while N, P, and S were not significantly reduced. In addition, precipitation has lower concentrations of cations during the months from December-February than during October and November (Likens *et al.* 1977). Apparently, fire plays a greater role in nutrient cycling in the spring because natural nutrient cycling events in the fall render similar nutrient changes as fire. Following initial leaching, however, the role of fire in nutrient cycling increases. Thus, light burning may be analogous to the role of litter macrofeeders.

Also contrary to the pattern on oak/oak sites, % organic matter, CEC, and ENR decreased between pretreatment and immediately posttreatment samples on oak/maple sites. They are acting in consort, as one would expect, but opposite of exchangeable cations. Fire has been shown to increase organic matter in the top soil layer, but generally at the expense of the litter and humus layers suggesting only a redistribution and not direct increases or decreases (Wells *et al.* 1979). Reductions in organic matter seem to be greatest in unproductive or submarginal forests or due to high intensity fires (Wells *et al.* 1979) where the structural matrix or organic matter may be destroyed (Lewis 1975). Organic matter was not altered when the litter was charred but not removed by fire in the coastal range of Oregon (Wells *et al.* 1979). Fire may be the reason for the discrepancy in the response of organic matter between oak/oak and oak/maple sites only if greater amounts of litter and duff were consumed due to a slightly more severe fire (*i.e.* if combustion processes were greater and more duff was consumed). Another possibility may be faster decomposition rates in mesophytic versus oak forests (Swift el al. 1976) in combination with the time of year samples were extracted. The increase of % organic matter, CEC, and ENR in oak/oak sites may be explained by organic matter and N input from precipitation (Kuitters and

Sarink 1986). Likens *et al.* (1977) presented increasing concentrations of nitrate during the last 3-4 months of each year.

The initial flush of elements, with an excess of basic ions over anions, neutralizes soil acidity (Wells *et al.* 1979). Both sites show a significant decrease in exchangeable H and simultaneous increase in soil pH. This is a typical response to burning, but is also apparently a response to leaf fall as a pulse of nutrients is released into the soil. Soil microbial activity (decomposition and mineralization) has been shown to increase due to nutrient flush (Wells *et al.* 1979, Fritz *et al.* 1994, Gillon *et al.* 1995).

There is little evidence for the volatilization of nitrate on either site. These cool to moderate burns at best consumed the loose leaf litter and very top of the microbial matted leaf litter. It is in this lower horizon ($O_2$), due to natural decomposition processes, that N accumulates (Yount 1975). Thus, fire had little direct impact. In addition, surface fire temperatures taken during two LBL burns ranged from 83-260°C; mean surface temperature was 206°C (Franklin unpublished data). Thus, burns often fell below the 200°C temperature for volatilization of N (Lewis 1974). Oak/maple sites have a noticeably greater increase in $NO_3$ than oak/oak sites, which is likely due to the greater mineralization on mesophytic sites versus *Quercus* sites (Plymale *et al.* 1987).

Phosphorus is the one nutrient that is noticeably enhanced by burning on the oak/oak sites and is significantly different on the oak/maple sites. This follows because very little P comes from rainfall. Trees get most of their P from litter (Correll and Miklas 1975). Seastead and Ramundo (1990) found that burning converted P to an inorganic form readily useable by plants.

In conclusion, our results indicate that fire may have a short-term impact on organic matter and nutrients, which depends on the time of year burns are administered and fire severity. The impact of light burning, however, is confined to releasing nutrients that are bound as opposed to nutrients easily leached from the litter layer. Thus, light fire mimics the role of macrofauna decomposers through litter breakdown and subsequent nutrient release in upland *Quercus* forests.

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# SEED GERMINATION ECOLOGY OF *SOLIDAGO NEMORALIS* AITON (ASTERACEAE)

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**ABSTRACT. Most freshly-matured seeds of *Solidago nemoralis* ssp. *nemoralis* collected on 10 November 1991 in northcentral Kentucky were conditionally dormant at maturity. Seeds germinated to 0-32% after two weeks incubation at 15/6, 20/10, 25/15, 30/15, and 35/20°C in light, with highest percentages at 30/15 and 35/20°C. Seeds cold-stratified at 5°C for 12 weeks gained the ability to germinate to 36-100% over the range of thermoperiods; 0-7% of the seeds germinated during stratification. Seeds required light to germinate at all thermoperiods, but the light requirement could be fulfilled either during stratification or incubation.**

**Germination results with freshly-matured seeds collected on 25 November 1992 at a second site in northcentral Kentucky were somewhat different than those above. After two weeks incubation, highest germination percentages for 1992 seeds were at 25/15 and 30/15°C. During stratification, 6-58% of the seeds germinated.**

**Seeds collected in 1992, buried in soil in a nontemperature-controlled greenhouse (T2) in Lexington, Kentucky, in December 1992, and exhumed and incubated over the range of thermoperiods in April 1993, germinated to 65-100% in light. However, seeds exhumed in September 1993 germinated to only 22-57% in light at 25/15, 30/15, and 35/20°C, and no seeds germinated at 20/10 and 15/6°C. Seeds exhumed in April and September 1993 and incubated in darkness germinated to only 0-1% regardless of the thermoperiod.**

**Seeds collected on 31 October 1993 at the same site as the 1992 collection, buried in soil in T2 in December 1993, and exhumed and incubated over the range of thermoperiods in April 1994, germinated to 94-100% in light. However, seeds exhumed in September 1994 germinated to only 0-5% in light at 15/6 and 20/10°C and 22-62% in light at 25/15, 30/15, and 35/15°C. Seeds exhumed in April and September 1994 and incubated in darkness germinated to only 0-1% regardless of the thermoperiod. The results from the 1992 and 1993 burials demonstrate that seeds of *S. nemoralis* exhibit an annual conditional dormancy/nondormancy cycle.**

**Seeds collected in 1991 and stored dry in the laboratory for 9.5 months germinated to 0-6% in light at 15/6 and 20/10°C and to 21-32% in light at 25/15, 30/15, and 35/20°C. However, only 0-4% of the seeds germinated in darkness over the range of thermoperiods. After 21.5 months of storage, seeds germinated to 25-72% in light at 20/10, 25/15, 30/15, and 35/20°C; no seeds germinated at 15/6°C. In darkness, 21.5-month-old seeds germinated to 0-6% at 15/6 and 20/10°C and to 17-26% at 25/15, 30/15, and 35/20°C.**

**Seeds collected in 1992 and stored dry in the laboratory for 9 months germinated to 29% in light at 15/6°C and to 85-98% in light at 20/10, 25/15, 30/15, and 35/20°C; however, no seeds germinated in darkness at any of the thermoperiods. After 21 months of storage, seeds germinated to 33% in light at 15/6°C and to 87-98% in light at 20/10, 25/15, 30/15, and 35/20°C. In darkness, 21-month-old seeds germinated to 0-2% at 15/6, 25/15, 30/15, and 35/20°C and to 15% at 20/10°C. Thus, 1991- and 1992-collected seeds afterripened in dry storage.**

**Peak germination of 1991-collected seeds sown in flats in T2 on 14 November 1991 occurred between 3 and 9 March 1992, when the average daily maximum and minimum temperatures were 22.5 and 11.7°C, respectively; these seeds had received 1702 hours of cold-stratifying temperatures (0-10°C). Peak germination of 1992-collected seeds sown on 26 November 1992 occurred between 23 and 29 March**

1993, when the average daily maximum and minimum temperatures were 21.2 and 9.5°C, respectively; these seeds had received 1800 hours of cold-stratifying temperatures.

Seeds collected in 1991, buried in soil in T2, and exhumed after 32.5 months (in September 1994), germinated to 96% in light after two weeks incubation at 30/15°C. Further, during the second germination season (spring 1994), 52 ± 10 and 667 ± 103 seedlings/$m^2$ emerged from soil samples collected February 1993 and September 1993, respectively. These results show that *S. nemoralis* can form a persistent seed bank, i.e., seeds remain viable until at least the second germination season.

# FACTORS AFFECTING THE DISTRIBUTION OF WATERWILLOW (*JUSTICIA AMERICANA*) IN KENTUCKY LAKE

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**ABSTRACT. Hydrology and water chemistry of the littoral zone were compared at two adjacent sites, one with a waterwillow [*Justicia americana* (L.) Vahl] bed (Site A) and the other without (Site B) from May 1993 to October 1994 to investigate groundwater factors (i.e., groundwater seepage and nutrient flux) that may affect plant distributions. Seepage meters confirmed that groundwater discharge occurred during the growing season and that seepage rates were similar for the two littoral sites. Wells were used to both estimate hydraulic gradients between surface water and groundwater, and to sample well groundwater for water chemistry analyses. Mini-piezometers were used to sample interstitial water at the littoral zone. Significant differences in dissolved nutrient concentrations were found between well sites. Alkalinity was significantly higher at Site A wells than Site B wells and may have influenced the distribution of *J. americana* which is a calciphilous species. Interstitial water nutrient concentrations were variable but had higher levels of soluble reactive phosphorus, nitrate and ammonium than groundwater or surface water indicating that the littoral zone may be a source for these nutrients. Littoral sediment cores (30 cm) showed a higher clay/silt percentage at Site B. Clay complexing with nutrients may have reduced the dissolved nutrient availability for waterwillow at Site B.**

# A COMPARISON OF CLEARCUT FOREST COMMUNITIES AND THE UNDERSTORY OF MATURE FOREST COMMUNITIES AT LAND BETWEEN THE LAKES, KENTUCKY AND TENNESSEE

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**ABSTRACT. In 1992 and 1993, twenty 10-12 year old clearcut stands (recovering forest) were studied to determine if the composition is similar to that of the understory of mature forest communities. In each stand, six to eight points were located 20 m apart and along the contour. Each point was used as the center of two nested circular quadrats. The number of woody stems of seedlings (stems greater 9.0 cm DBH) were recorded by species on a 0.003 and a 0.006 ha plot, respectively. If stems of tree size (DBH > 9.0 cm) were present, they were sampled on the 0.006 ha plot. Stands were located across a range of sites from ridgetops to slopes of various aspects to stream terraces. Density was calculated by tree species, size class and plot, and averaged for each clearcut stand. The densities for *Diospyros virginiana, Nyssa sylvatica, Prunus serotina* and *Sassafras albidum* were analyzed separately as these species seldom obtain the stature of mature forest overstory species. COMPAH, a clustering program, was used to classify plots and identify community types, and DECORANA was used to generate a coenocline (continuum).**

**Four community types similar to those studied by Franklin (1990) and Kettler (1990) were identified: Chestnut Oak-Scarlet Oak, Mixed Black Oak, White Oak-Black Oak-Post Oak, White Oak-Black Oak-Mesophytic and Sugar Maple-Red Elm. One type that appeared from the analysis but which did not appear in previous studies was the Sweetgum-Mesophytic community. It appears that communities which have developed after clearcutting are reasonably similar (percent similarity 48-69%) to the understory of mature stands and that clearcutting does not substantially disrupt community development. As further evidence of similarity, a coenocline of plot data showed the same sequence of major species in compositionally stands as reported by Franklin (1990) and Fralish et al. (1993) although *Fagus gradifolia* was a minor species in recovering forest and *Quercus velutina* was less important in compositionally stable forest.**

# CONTINUED STUDIES ON BARRENS VEGETATION

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**ABSTRACT. This paper includes data from sampling of barrens vegetation using 43 sets of sample plots at 32 sites in the Central Basin, on the Cumberland Plateau, and in the Ridge and Valley of Tennessee and northwestern Georgia. Nearly three-fourths of the stands are dominated by *Schizachyrium scoparium, Andropogon gerardii,* or *Panicum virgatum*. The vegetation was arrayed on a moisture axis from wet-mesic *Panicum virgatum* stands to subxeric stands dominated by *Schizachyrium scoparium*. A few intermediate and cedar-pine glade stands were sampled. Low species richness occurred at both ends of the site array--the peak richness occurred in the intermediate 30-70 base unit range. Here several stands occurred which had experienced little land use or vegetation use or damage in the past few decades. The "reserve" nature of these sites contributes greatly to species persistence and perhaps to increased richness.**

## INTRODUCTION

The Tennessee barrens are small openings in the forest wherein the vegetation is dominated largely by perennial grasses. The term barrens was used by the early explorers and diarists for this vegetation in Kentucky and Tennessee (cf. Michaux 1793-1796). The vegetation in Tennessee resembles the prairies and barrens of Kentucky (Bryant 1977, 1982, Baskin *et al.* 1994) and of the Middle West (Heikens and Robertson 1994, Hutchinson 1994, Homoya 1994). In Tennessee the floristics of 119 sites have been documented. Plot sampling of 59 sites was done but sampling results have only been published on 17 sites (DeSelm 1988, 1990, 1992a, 1992b, 1993, DeSelm and Chester 1993). In addition, in the Plateau study (DeSelm 1992b), data from several data sets were merged into three "sites." Abbreviated lists were provided for eight sites (DeSelm 1989). This paper includes data from 43 sets of sample plots from 32 sites in Tennessee and northwestern Georgia. These include full data expanded from previously merged or abbreviated data. Also, certain data from Finn (1968) at Mascot in the Ridge and Valley are included. Data are included here from and this paper is focused on the Central Basin, the Cumberland Plateau, and the Ridge and Valley.

## THE STUDY AREAS

Tennessee and adjacent Georgia are marked by diverse topographic and geologic features which result in a variety of habitats. The Basin is an elliptical depression in the Highland Rim, a plateau surface of exposed Mississippian limestones. Ordovician bedrocks are exposed in the Basin on which develop cedar barrens and glades on shallow soils (DeSelm 1989, 1992a, 1994). The Cumberland Plateau rises over 1000 feet above the eastern Highland Rim and Ridge and Valley and is capped by sandstones and shales where barrens occur on both shallow and deep soils. Those on soils developed from sandstone are sandy, rocky, acid and infertile. The Plateau barrens are already described (DeSelm 1989, 1992b, 1994). The Ridge and Valley Province extends from Alabama to New York and features folded and faulted geologic beds resulting in ridges and valleys extending northeast-southwest. In eastern Tennessee and northwestern Georgia, most barrens occur on the Chickamauga limestone and occur in valley-bottom or side-slope positions (DeSelm 1989, 1993, 1994).

After the expulsion of the Shawnee Native Americans by the Cherokee and Chickasaw tribes in 1714 (Williams 1937), this area was used mainly as a hunting ground by the Cherokee. European-Americans began settling the area from 1770 to 1806 in the Basin, after 1805-1809 on the Plateau, and after 1790-1835 in the Ridge and Valley (Folmsbee *et al.* 1960). Land with deep soils and gentle topography was cleared of forest and converted to row crops. Areas of steeper topography were cleared and pastured or simply pastured. Livestock were fenced out of dwelling areas and fields (Killebrew *et al.* 1874). Open range persisted until about 1940 (Ploskonke 1993). It was common to burn (surface fires) the underbrush of stock ranges to encourage early forage growth. The spread of the fires was controlled mainly by the topography and weather change (DeSelm 1989). Many additional characteristics of the study areas are found in the papers cited above.

## METHODS

Reconnaissance for and on barrens began in 1955 but plot sampling did not begin until 1968 with the work of Finn on the Mascot glade and forest (Finn 1968). She sampled five communities there--two herbaceous communities are reported here on which she used a one-foot square quadrat. Finn estimated cover in square inches or parts thereof, converted these to percentages and therefore had mean cover of less than one for some species. Sampling by the author begin in autumn 1985 when I used at first a 40 x 40 cm frame, and later a 50 x 50 cm frame. During the period 1986-1989, I used a 0.5 x 1.0 m frame; the elongate shape is recommended by Daubenmire (1968). Samples were placed on a straight line through aspectually homogeneous vegetation at one m spacing. Size of the opening and time available dictated sample plot number; reported here are plot numbers per set from 10 to 35 (mean 22.2). Sampling was carried out August-October because of the later developing flora but doubtless some spring and early summer taxa were missed. Unknowns, such as seedlings, were recorded at an average rate of two per plot. Surface cover of rock, gravel, soil, bryophytes, lichens, and tree litter were estimated to the nearest one percent beginning in 1986. Cover of plant species also was estimated to the nearest percent. In the tables, some data, as frequencies, are rounded to the nearest whole number. Nomenclature used in the tables and text follows that in the regional papers cited above.

## RESULTS AND DISCUSSION

Tabular data from the Basin (Appendix 1), for the Plateau (Appendixes 1-6), for the Ridge and Valley of Tennessee (Appendixes 7-11), and for Georgia (Appendixes 12-14) are appended. Locational information for the numbered sites in the tables are, for the Basin (in DeSelm 1992a), for the Plateau (in DeSelm 1992b), and for the Ridge and Valley (in DeSelm 1993).

The conclusion has previously been drawn (DeSelm 1989, 1994) that a moisture gradient supports a series of barrens communities: the wettest is a hydric sedge-dominated community (DeSelm 1992b). This gives way upslope to one dominated by *Panicum virgatum* (DeSelm 1992b, 1993) or mixed tall *Panicum* (DeSelm 1990). On mesic uplands *Andropogon gerardii* stands occur (1990, 1992b, 1993); this is replaced on drier sites by the widespread *Schizachyrium scoparium* vegetation. On even drier sites this passed through an intermediate vegetation (DeSelm 1992a), or rocky prairie (Baskin *et al.* 1994), to cedar glades (DeSelm 1992a) or cedar-pine glades (DeSelm 1988, 1993). The data in the following tables support the occurrence of all but the hydric community, which is not documented here.

Floristic richness of the plot sets varies from 15 to 92 native taxa. On sites which were seen only one-few times, the native flora tabulated is more than 90% of the total known flora. However, on sites such as Gladeview, which was seen many times over a period of three decades, the tabular flora (of 49 native taxa) is only 24% of the known native flora (cf. DeSelm 1992b).

A comparison of the richness of native taxa per data set (mean richness 38.2) with numbers of square meters sampled (mean 8.5) indicated a linear relationship which passed through the origin and with a slope of 4.3 species added per square meter of an additional sampling. In this data plot no curvature was seen, although in previous species/area curves flexure was seen at about 20 square meters. This suggests that species area curves should be drawn for both species-poor and species-rich barrens vegetation or that a running count of species number added be made (Daubenmire 1968, Mueller-Dombois and Ellenburg 1974).

## The Moisture Gradient

A direct gradient relating native species number number/m$^2$ to site aridity, calculated as the sum of bedrock, gravel, and soil frequency and cover (herein after called base units) was constructed (Figure 1). Rock in the soil profile decreases its moisture-supplying power (Brady 1974) and here rock and gravel cover is a surrogate for profile rock content. Between base units of 50 and 200, a negative relationship was obtained, indicating a loss of about 7.6 taxa in 150 base units or one taxon per 19.7 base units. Below 50 base units a different slope is suggested; the line intersects the ordinate at 3.0 species/m$^2$ with a species loss rate of one per 10 base units. The slopes and flexure toward lowered base units is soil series induced. On the Plateau, for example, the series above 50 base units are from sites with fine sandy loam and stony, fine sandy loam soils of the Muskingham and Hartsells series. Less than 50 base unit sites are underlain by Crossville loams and the Lickdale silt loam--the Lickdale is poorly drained (Hubbard *et al.* 1950). The improved moisture conditions facilitates the heavy growth of the sod-forming grasses *Panicum virgatum* and *Andropogon gerardii*, the leaves and litter of which cover the soil surface.

The response to more moist soils is shown; two-thirds of the stands with base values of less than 50 are dominated by *Panicum virgatum* and *Andropogon gerardii*, where above 50 base units only 21% of the stands are so dominated. All of the stands dominated by the xerophytes

*Bouteloua curtipendula* and 88% of the annual and perennial *Sporobolus* spp. occur on the base line between 50 and 200. Similar environmental gradient arrays for prairie species (Curtis 1955) and barrens species (DeSelm 1988) have appeared.

In the base unit range 30-70 (Figure 1) where native species numbers per m$^2$ is 6 or more, the peak richness is seen. Three sites are dominated by the mesic prairie dominant *Andropogon gerardii*, two by *Schizachyrium,* and two with other grasses. Thus, richness is not a function of available water since richness declines on wetter soils than base unit 50. Instead, peak richness is achieved with little stand use--four of these stands are virtual reserves: Gladeview, the two at Mascot, and the Vinyard-Alexander Road area. In addition one is bush-hogged, which damages herbaceous vegetation little when done late in the year. The other two sites are mowed--both of these are on US70 N, West of Crossville. Mowing is suspected as a cause of decreased richness (DeSelm 1989, 1994). Effects of land use would be better measured directly where current stands receive currently known use-treatment or where the past history of stand uses are exactly known. However, past land uses are rarely known and even present-day land use often is difficult to determine and so estimates become the alternative available here.

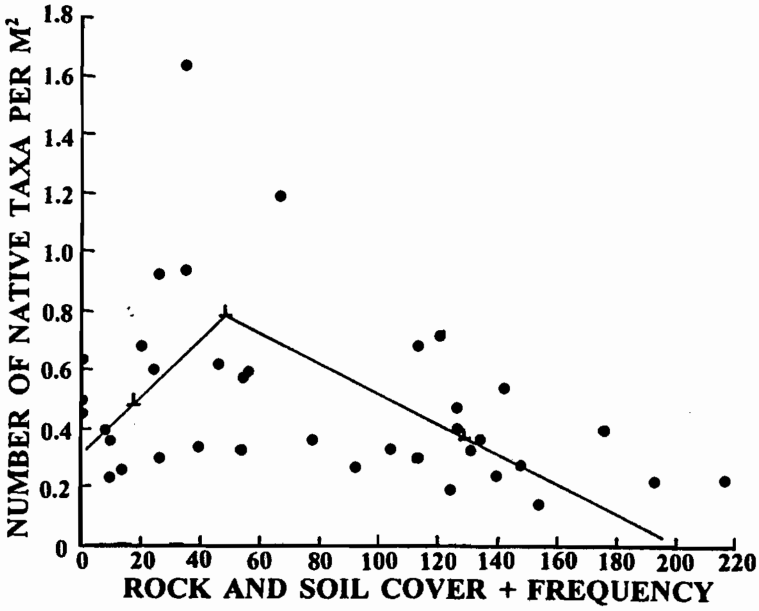

**Figure 1. Plot of most stands' richness, mean number of native species m$^2$, based on sum of cover and frequency of rock and soil. The line passes through three averages: left, less than 30 on abcissa; middle, 30-70 on abcissa and 6.0 and over on ordinate; and right, 71 and more on abcissa**

## Vegetation Classes

The tabular data (Appendixes 1-14) may be used to assign vegetation type names to the vegetation represented by the various data sets. While the grasses are usually aspectually dominate, usually the sum of forb importance values exceeds that of grasses; strictly speaking most of these stands are of forb-grass types. The reason for the high forb importance value is the use of one percent as the lowest cover estimate; this inflates the importance of forbs (DeSelm 1994). Seven stands (Table columns) occur where the sum of important grass I.V.'s are 1.0 or larger. In Appendix 2, column 2, *Schizachyrium* is clearly the most important plant with an I.V. of 1.023 (a *Schizachyrium*-forb type). Six other stands have grass importance values that exceed 1.0, but two to five grasses are involved so the stands should be called mixed grass-forb types.

Because of the aspect importance of the grasses and the relatively few species compared to hundred of forb species, it seems relevant to name the types by their grass dominants. Among stands with grass importance totalling less than 1.0, 12 stands with only one important grass are dominated by *Andropogon gerardii, Panicum virgatum. Schizachyrium*, *Sorghastrum nutans*, *Sporobolus asper* or *Sporobolus vaginiflorus*. The remaining stands have two-four important grasses as leading dominants, and, may be called mixed grass-forb stands. Three stands are dominated by mixed grasses and must be called cedar-pine glades, the Mascot glade (Appendix 11) and in Appendix 14: Fort Oglethorpe High School (column 2) and Vinyard-Alexander Road (column 1). Two other sites may be called intermediates, with high annual *Sporobolus* cover, but some perennial grass cover: Appendix 10 column 3 at Fezzell Road, and Appendix 14 column 2 at Rt. 146 at 218.

Most stands were dominated by *Schizachyrium scoparium* (40%) by *Andropogon gerardii* (21%). *Panicum virgatum* dominated 12%, *Sorghastrum nutans* and *Sporobolus asper* (both at 5%) and *Bouteloua curtipendula* (2%). Three stands were glades and two or three were intermediate with both annual and perennial grasses important. Stand types were named after their leading dominant grass although some are mixed grass-forb types.

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## Appendix 12 Frequency, mean cover (where they occur), and Importance Value 200 of species of two Basin Barrens and two Plateau barrens. Also shown is the frequency and cover (where exposed) of bedrock, gravel, soil, and bryophytes, fungi, lichens, and tree litter where they occur.

| Site (number) | Gladeview Savannah (62) | Mt. Juliet Rd. (108) | Lee Station (88) | Daddy's Creek Boulder Bar (46) |
|---|---|---|---|---|
| Plot number (size, $m^2$) | 30 (0.5) | 16 (0.5) | 25 (0.5) | 20 (0.5) |
| Frequency-Mean Cover | | | | |
| Rock and gravel | 20-8.0 | 63-30.0 | | 85-34.0 |
| Soil | 23-3.0 | 13-9.0 | 90-15.4 | 5-10.0 |
| Bryophytes | 10-1.0 | | | 35-7.0 |
| Fungi | 3-1.0 | | | |
| Lichens | 17-1.0 | | | |
| Tree litter | 83-26.0 | | | |
| Frequency-Mean Cover-Importance Value 200 | | | | |
| Agave virginica | 23-1.0-.038 | | 12-1.0-.019 | |
| Alnus serrulata | | | | 20-15.0-.081 |
| Amorpha fruticosa | | | | 5-10.0-.041 |
| Andropogon gerardii | 33-12.0-.045 | | 16-5.0-.047 | 40-43.0-.216 |
| Asclepias verticillata | 3-1.0-.013 | | 4-1.0-.010 | |
| A. viridiflora | 3-1.0-.013 | | | |
| Aster dumosus | 20-1.0-.035 | 25-1.0-.089 | 28-1.6-.040 | 65-1.0-.065 |
| A. linariifolia | | | | 35-1.0-.037 |
| A. patens | 10-1.0-.021 | | | |
| A. pilosus | | | 4-1.0-.010 | |
| Baptisia australis | 10-3.0-.038 | | | |
| Berchemia scandens | 23-2.0-.046 | | | |
| Betula nigra | | | | 5-1.0-.009 |
| Calamovilfa arcuata | | | | 5-20.0-.088 |
| Carex spp. | | 19-1.0-.070 | 16-1.0-.023 | 10-2.0-.017 |

(Appendix 1, cont.)

| | | | | |
|---|---|---|---|---|
| Celtis occidentalis | | | 4-1.0-.010 | |
| Clematis virginiana | | | | 20-8.0-.052 |
| Coreopsis pubescens | | | | 20-1.0-.023 |
| C. tripteris | | | | 70-1.0-.070 |
| Danthonia spicata | | | 20-6.6-.060 | |
| Daucus carota | | | 4-1.0-.010 | |
| Desmodium ciliare | 13-1.0-.026 | | 4-1.0-.010 | |
| D. dillenii | 3-1.0-.013 | | | |
| D. marilandicum | 3-1.0-.013 | | | |
| Elymus virginicus var. glabriflorus | | | | 20-18.0-.094 |
| Euonymus americanus | | | | 5-1.0-.009 |
| Euphorbia corallata | 69-1.0-.097 | 31-1.0-.108 | | 5-1.0-.009 |
| Festuca pretensis | | | 4-1.0-.010 | |
| Fraxinus americana | 10-2.0-.029 | | | |
| Galactia volubilis | 40-1.0-.060 | | 48-1.3-.060 | |
| Galium pilosum | 7-1.0-.018 | | | |
| Gaura filipes | | | 20-1.0-.027 | |
| Gerardia gattingeri | 7-1.0-.018 | | | |
| G. purpurea | | 6-1.0-.030 | | |
| G. tenuifolia | | | 4-10.0-.064 | |
| Hamamelis virginiana | | | | 5-1.0-.009 |
| Hedyotis nigricans | 10-1.0-.021 | 56-7.0-.254 | | |
| Helianthus occidentalis | 89-9.0-.192 | | 76-12.5-.157 | |
| Heliotropium tenellum | | 6-1.0-.030 | | |
| Hexastylis sp. | | | | 5-1.0-.009 |
| Houstonia longifolia | | | 4-1.0-.010 | |
| Hypericum dolabriforme | | | 20-1.8-.032 | |

**(Appendix 1, cont.)**

| | | | | |
|---|---|---|---|---|
| H. prolificum | | | | 20-1.0-.023 |
| H. sphaerocarpon | 17-1.0-.031 | 6-1.0-.030 | | |
| Ipomoea pandurata | 3-1.0-.013 | | | 20-1.0-.023 |
| Isanthus brachiatus | | | 8-4.0-.033 | |
| Juniperus virginiana | 33-4.0-.076 | | 24-1.3-.034 | |
| Kuhnia eupatorioides | 3-10.0-.090 | | | |
| Lespedeza intermedia | | | 4-1.0-.010 | |
| L. procumbens | | | 4-1.0-.010 | |
| L. repens | 13-2.0-.034 | | | |
| L. virginica | 3-1.0-.013 | | | |
| Liatris aspera | | | 48-3.3-.072 | |
| L. graminifolia | | | | 40-1.0-.042 |
| Linum sulcatum | | | 8-1.0-.015 | |
| Lithospermum canescens | 7-1.0-.018 | | 16-1.5-.026 | |
| Lobelia spicata | 7-1.0-.018 | 6-1.0-.030 | 20-1.0-.027 | 5-1.0-.009 |
| Lysimachia lanceolata | | | | 10-1.0-.012 |
| Marshallia grandiflora | | | | 20-1.0-.023 |
| Melilotus sp. | | | 12-1.0-.019 | |
| Muhlenbergia tenuifolia | | | | 25-1.0-.028 |
| Nyssa sylvatica | | | | 10-1.0-.013 |
| Oenothera fruticosa | | | | 10-1.0-.013 |
| Opuntia humifusa | 3-2.0-.021 | | | |
| Osmunda regalis | | | | 5-1.0-.009 |
| Oxalis priceae | 3-1.0-.013 | | | |
| O. stricta | | | | 5-1.0-.009 |
| Panicum commutatum | 3-1.0-.013 | | | |
| P. polyanthes | | | 4-1.0-.010 | |
| P. villosissimum | 3-1.0-.013 | | 8-1.0-.015 | |

(**Appendix 1, cont.**)

| | | | | |
|---|---|---|---|---|
| Parthenium integrifolium | 7-2.0-.018 | | | |
| Penstemon laevigatus | 17-1.0-.070 | 19-1.0-.010 | | |
| Petalostemum gattingeri | 17-1.0-.031 | 19-1.0-.070 | | |
| Phlox sp. | | | | 5-1.0-.009 |
| Physocarpus americanus | | | | 5-1.0-.009 |
| Physostegia virginiana | 26-1.0-.041 | | 24-1.7-.036 | |
| Pinus virginiana | | | | 10-30.0-.134 |
| Polygala ambigua | | | 8-1.0-.015 | |
| Potentilla canadensis | | | | 5-1.0-.009 |
| P. simplex | 17-1.0-.031 | | | 55-1.0-.056 |
| Prunella vulgaris | 3-1.0-.013 | | | 40-1.0-.042 |
| Pteridium aquilinum | | | | 40-11.0-.084 |
| Pycnanthemum tenuifolium | | | 48-4.5-.079 | 50-2.0-.055 |
| Quercus falcata | 13-1.0-.026 | | | |
| Q. muhlenbergii | 3-1.0-.026 | | | |
| Q. shumardii | 3-1.0-.013 | | | |
| Ratibitta pinnata | | | 4-1.0-.010 | |
| Rhododendron arborescens | | | | 30-4.0-.045 |
| Rhus aromatica | 10-1.0-.021 | | | |
| Rosa carolina | 10-1.0-.021 | 19-1.0-.070 | | 15-1.0-.018 |
| R. setigera | | 6-1.0-.030 | | |
| Rubus sp. | | | | 20-1.0-.023 |
| Rudbeckia fulgida | | | 16-2.0-.029 | |
| R. laciniata | | | | 10-1.0-.013 |
| Ruellia humilis | 13-1.0-.027 | | 20-1.0-.027 | |
| Salvia lyrata | | | | 30-1.0-.032 |
| Schizachyrium scoparium | 100-24.0-.335 | 84-67.0-1.023 | 100-62.6-.481 | 60-17.0-.127 |
| Scleria oligantha | 26-1.0-.042 | | | |

**(Appendix 1, cont.)**

| | | | | |
|---|---|---|---|---|
| Senecio anonymus | 3-1.0-.013 | | | 10-1.0-.013 |
| S. aureus | | | | 15-1.0-.018 |
| Sisyrinchium sp. | | 6-1.0-.030 | 28-1.0-.036 | |
| Smilax bona-nox | 3-1.0-.013 | | | |
| S. glauca | | | | 5-1.0-.009 |
| Solidago erecta | | | | 30-1.0-.032 |
| S. gattingeri | 7-6.0-.061 | | | 30-1.0-.032 |
| S. nemoralis | 3-1.0-.013 | 6-1.0-.030 | 16-3.3-.037 | |
| S. rigida | | | 68-4.5-.100 | |
| Silphium trifoliatum | | | | 5-1.0-.009 |
| Sorghastrum nutans | | | 8-12.5-.084 | 25-17.0-.095 |
| Spigelia marilandica | | | | 25-1.0-.028 |
| Sporobolus neglectus | | 13-1.0-.051 | | |
| S. vaginiflorus | 10-6.0-.064 | | 16-5.5-.050 | |
| Stylosanthes biflora | 7-1.0-.018 | | | 5-1.0-.009 |
| Thalictrum revolutum | | | | 25-1.0-.028 |
| Thaspium trifoliatum | | | | 10-1.0-.013 |
| Tomanthera auriculata | | | 20-1.0-.027 | |
| Trifolium pretense | | | 8-1.0-.015 | 5-1.0-.013 |
| Unknown forb | 7-1.0-.018 | 13-1.0-.051 | 28-1.0-.037 | 65-1.0-.065 |
| Vaccinium arboreum | | | | 5-1.0-.009 |
| Veronicastrum virginianum | | | | 25-1.0-.028 |
| Viola pedata | | | | 15-1.0-.018 |
| V. sp. | | | | 15-1.0-.018 |
| Zizia aptera | | | 68-4.9-.102 | |

Appendix 2. **Frequency mean cover (where they occur) and Importance Value 200 of species of three wet Plateau barrens. Also shown is frequency and cover (when present) of soil and bryophyte cover.**

| Site (Number) | Under Powerline (141) | Under Powerline (141) | US70N bottom of big swale (110) |
|---|---|---|---|
| Plot Number (size, $m^2$) | 25 (0.50) | 20 (0.50) | 15 (0.50) |
| Frequency-Mean Cover | | | |
| Soil | 4-10 | | |
| Bryophytes | 68-29.7 | | |
| Frequency-Mean Cover-Importance Value 200 | | | |
| Acalypha virginica | | | 21-1.0-.024 |
| Acer rubrum | 48-11.3-.132 | 35-8.9-.086 | 40-17.0-.110 |
| Agrostis perennans | | | 7-1.0-.011 |
| Alnus serrulata | 4-5.0-.039 | | 7-10.0-.049 |
| Ambrosia artimisiifolia | | 30-2.5-.045 | 7-1.0-.011 |
| Amphicarpa bracteata | | | 20-1.0-.023 |
| Andropogon gerardii | | | 20-47.0-.218 |
| A. glomeratus | 4-1.0-.011 | | |
| Angelica venenosa | 20-1.6-.033 | 15-2.0-.028 | |
| Apios americana | | 45-3.6-.071 | 67-1.0-.067 |
| Aster dumosus | 36-1.0-.046 | 25-1.0-.034 | 40-1.0-.042 |
| A. pilosus | | 5-1.0-.011 | 13-1.0-.016 |
| A. solidagineus | | 15-7.3-.055 | |
| A. umbellatus | 24-6.3-.070 | 40-2.1-.058 | |
| Bartonia virginica | 4-1.0-.011 | | |
| Bidens polylepis | | | 35-3.0-.046 |
| Buchnera americana | | 5-1.0-.011 | |
| Calamogrostis cinnoides | 28-2.3-.047 | | |
| Calopogon pulchellus | 4-1.0-.011 | | |
| Cassia fasciculata | | 25-1.0-.034 | |

(Appendix 2, cont.)

| | | | |
|---|---|---|---|
| C. nictitans | | 10-1.0-.017 | |
| Coreopsis major | | 5-1.0-.011 | |
| C. tripteris | | 5-1.0-.011 | |
| Cyperaceae, unknown | | 10-1.0-.017 | 7-1.0-.011 |
| Danthonia sericea | | 20-3.3-.041 | |
| D. spicata | 4-1.0-.011 | | |
| Desmodium obtusun | | 5-1.0-.011 | |
| Eupatorium fistulosum | | 10-3.0-.027 | 13-1.0-.016 |
| E. perfoliatum | | 5-1.0-.011 | 20-1.0-.023 |
| E. rotundifolium | 40-1.0-.051 | 10-1.0-.017 | |
| E. rotundifolium var. saundersi | 84-2.4-.109 | | |
| Fimbristylis autumnalis | | | 27-25.0-.132 |
| Forb, unknown | | 10-1.0-.017 | |
| Galium tinctorium | | | 47-1.0-.049 |
| Gerardia purpurea | | 15-1.0-.023 | 40-1.0-.042 |
| Gramineae, unknown | | 10-3.0-.027 | |
| Habenaris ciliaris | 4-1.0-.011 | | |
| Helianthus angustifolius | 44-1.0-.055 | 10-1.0-.027 | 7-1.0-.011 |
| Hypericum canadense | | | 27-1.0-.030 |
| H. gymnanthum | | 25-1.0-.034 | |
| H. mutilum | | | 27-1.0-.030 |
| H. stans | 4-1.0-.011 | | |
| Juncus debilis | | | 20-7.0-.049 |
| J. marginatus | | 5-1.0-.011 | |
| Lespedeza capitata | | 20-1.5-.032 | |
| Lilium michiganense | | 10-1.0-.017 | |
| Linum striatum | | | 7-1.0-.011 |
| Liriodendron tulipifera | | 5-3.0-.021 | |

(Appendix 2, cont.)

| | | | |
|---|---|---|---|
| Lobelia canbyi | 20-1.0-.029 | | |
| L. puberula | | 15-1.0-.023 | |
| Lonicera japonica | | 5-3.0-.021 | |
| Ludwigia hirtella | 16-1.0-.025 | | |
| Lycopus virginicus | | | 13-1.0-.016 |
| Lyonia ligustrina | 16-2.0-.032 | | |
| Lysimachia lanceolata | | 25-1.0-.034 | |
| Lythrum alatum | | | 7-1.0-.011 |
| Monarda fistulosa | | 15-3.0-.031 | |
| Nyssa sylvatica | | 10-4.0-.032 | 13-6.0-.037 |
| Oxalis stricta | | | 7-1.0-.011 |
| Oxopolis rigidior | | | 35-1.0-.037 |
| Panicum lanuginosum | | | 7-1.0-.011 |
| P. longifolium | 4-2.0-.018 | | 7-1.0-.011 |
| P. lucidum | 90-17.1-.217 | | |
| P. microcarpon | 24-13.7-.122 | 25-7.6-.067 | 87-18.0-.158 |
| P. virgatum | 100-55.8-.498 | 100-64.0-.440 | 47-41.0-.219 |
| Pilea pumila | | 5-1.0-.011 | |
| Platanthera integrifolia | 24-1.0-.033 | | |
| Polygala cruciata | 8-1.0-.016 | 15-1.0-.023 | |
| Potentilla simplex | 60-1.1-.073 | 40-1.0-.052 | 27-6.0-.051 |
| Prunella vulgaris | | 5-1.0-.011 | |
| Pteridium aquilinum | | 15-10.7-.072 | |
| Pycnanthemum muticum | | 10-1.0-.017 | 35-1.0-.037 |
| Pyrus melanocarpa | 60-3.1-.088 | 65-7.0-.111 | |
| Rhexia mariana | | 15-1.0-.023 | 27-1.0-.030 |
| Rhynchspora capitellata | | | 7-1.0-.011 |
| R. gracilienta | 40-1.4-0.540 | | |

(Appendix 2, cont.)

| | | | |
|---|---|---|---|
| Rubus sp. | | 5-1.0-.011 | 35-1.0-.037 |
| Salix tristis | | 5-1.0-.011 | |
| Scirpus atrovirens | | | 40-7.0-.068 |
| Scleria minor | | 5-1.0-.011 | |
| S. pauciflora | 24-1.0-.033 | | |
| Scutellaria elliptica | | 5-1.0-.011 | 7-1.0-.011 |
| Setaria geniculata | | 10-1.0-.017 | |
| Smilax bona nox | | 20-2.3-.036 | |
| S. glauca | 4-1.0-.011 | | 7-1.0-.011 |
| Solidago canadensis var. scabra | 4-1.0-.011 | 60-18.8-.102 | 35-3.0-.036 |
| S. rugosa var. aspera | | 20-4.3-.046 | 13-1.0-.016 |
| Spirea tomentosa | | 20-4.3-.046 | 27-5.0-.047 |
| Unknown forb | 64-1.2-.078 | | 35-1.0-.037 |
| Vernonia noveboracensis | | 5-10.0-.056 | 20-11.0-.066 |
| Xyris torta | 4-1.0-.011 | | |

**Appendix 3. Frequency, mean cover (where they occur) and Importance Value 200 of species of mesic Plateau barrens. Also shown is frequency and cover (where present) of exposed soil.**

| Site (number) | Under Powerline (141) | Slopes of Big Swale, US70N (109) | US70S near airport entrance (106) |
|---|---|---|---|
| Plot number (size m$^2$) | 20 (0.5) | 30 (0.5) | 20 (0.5) |
| Frequency-Mean Cover | | | |
| Soil | 5-5.0 | 10-30.0 | 5-5.0 |
| Frequency-Mean Cover-Importance Value 200 | | | |
| Acer rubrum | | 7-6.0-.031 | |
| Achillea millifolium | | 3-1.0-.009 | |
| Agrostis gigantea | | 7-1.0-.014 | |
| Alnus serrulata | | 3-1.0-.009 | |
| Amphicarpaea bracteata | | 3-1.0-.009 | |
| Andropogon gerardii | 95-86.8-.670 | 100-55.7-.364 | 5-80.0-.277 |
| A. gyrans | | | 5-20.0-.075 |
| Anthoxanthum odoratum | | | 45-2.0-.078 |
| Apios americana | 5-3.0-.028 | 7-1.0-.014 | |
| Aster dumosus | 5-1.0-.018 | 17-1.0-.029 | |
| A. umbellatus | 5-1.0-0.18 | | |
| A. surculosus | | 3-1.0-.009 | |
| Carex hirsutella | | | 10-1.0-.019 |
| Cassia fasciculata | 5-1.0-.018 | | |
| C. nictitans | | 3-1.0-.009 | |
| Chrysanthemum leucanthemum | | | 35-1.0-.010 |
| Chrysopsis camporum | | 7-1.0-.014 | 5-1.0-.011 |
| C. mariana | | 3-1.0-.009 | |
| Coreopsis major | | 7-1.0-.014 | |
| C. tripteris | 5-1.0-.018 | | |
| Desmodium ciliare | | 3-1.0-.009 | |

**Appendix 4. Frequency, mean cover (where they occur) and Importance Value 200 of species of three xeric Plateau barrens. Also shown is frequency and cover (where present) of exposed soil, lichens and tree litter.**

| Site (number) | Under Powerline (141) | Crossville US 70 (50) | US 70 N West of Big Swale (111) |
|---|---|---|---|
| Plot number (size m²) | 18 (0.5) | 20 (0.16) | 35 (0.5) |
| Frequency-Mean Cover | | | |
| Soil | 17-3.7 | | 63-15.0 |
| Lichens | 44-6.5 | | |
| Tree litter | 6-5.0 | | |
| Frequency-Mean Cover-Importance Value 200 | | | |
| Acer rubrum | 22-1.0-.019 | | |
| Achillea millifolium | | | 3-1.0-.009 |
| Aletris farinosa | 56-1.0-.040 | | |
| Ambrosia artimisiifolia | | 5-1.0-.017 | 6-2.0-.018 |
| Andropogon gerardii | 39-25.0-.175 | 15-40.0-.261 | 3-30.0-.176 |
| A. gyrans | | 5-1.0-.017 | |
| A. virginicus | | 10-3.0-.040 | |
| Angelica venenosa | 11-1.0-.013 | | |
| Antennaria plantaginifolia | 6-1.0-.010 | 5-1.0-.017 | |
| Aristida dichotoma | 6-10.0-.064 | | |
| A. longispica | 6-10.0-.064 | | |
| A. purpurescens | 56-16.6-.135 | 20-1.0-.050 | |
| Aster dumosus | 83-1.0-.056 | 5-1.0-.017 | 14-2.0-.026 |
| A. linariifolius | 17-1.0-.016 | | 9-1.0-.015 |
| A. patens | 28-1.0-.023 | 5-1.0-.017 | |
| A. solidagineus | 17-1.0-.016 | | |
| A. umbellatus | 6-1.0-.010 | | |
| A. undulatus | 28-1.0-.023 | | |
| Botrychium dissectum var obliquum | | 5-1.0-.017 | |

**(Appendix 4, cont.)**

| | | | |
|---|---|---|---|
| Calamogrostis cinnoides | 6-1.0-.010 | | |
| Carex hirsutella | | 5-1.0-.017 | |
| C. sp. | | 5-1.0-.017 | |
| Cassia fasciculata | | | 3-1.0-.009 |
| C. nictitans | 17-1.0-.016 | | 9-1.0-.015 |
| Ceanothus americana | 6-1.0-.010 | | 3-5.0-.032 |
| Chrysopsis camporum | | 35-2.3-.090 | |
| C. mariana | 28-1.0-.023 | | 17-1.0-.022 |
| Chrysanthemum leucanthemum | | 15-1.0-.040 | 31-1.0-.036 |
| Composite, unknown | | | 20-1.0-.025 |
| Coreopsis major | 61-1.0-.043 | | 3-1.0-.009 |
| Croton monanthogynus | | | 3-1.0-.009 |
| Cyperaceae, unknown | 11-1.0-.013 | | |
| Danthonia sericea | 22-1.0-.019 | | 14-1.0-.020 |
| Daucus carota | | | 14-1.0-.020 |
| Desmodium ciliare | 11-1.0-.013 | 20-1.0-.052 | 17-1.0-.022 |
| D. dillenii | 6-1.0-.010 | | 9-1.0-.015 |
| D. marilandicum | 39-1.0-.029 | 10-1.0-.029 | 26-1.0-.031 |
| D. paniculatum | 6-1.0-.010 | | 6-3.0-.024 |
| Diospyros virginiana | 6-20.0-.124 | 5-10.0-.068 | |
| Erigeron strigosus | | | 6-1.0-.012 |
| Eupatorium altissimum | | | 3-1.0-.009 |
| E. rotundifolium | 11-1.0-.013 | | 3-5.0-.032 |
| Festuca pretensis | | 20-2.0-.057 | 46-3.0-.062 |
| Galactia volubilis | | 25-1.0-.063 | 43-2.0-.053 |
| Galium circaezans | | 5-1.0-.017 | |
| G. pilosum | 39-1.0-.029 | | 43-2.0-.053 |
| Gentiana saponaria | 6-1.0-.010 | | |

(Appendix 3, cont.)

| | | | |
|---|---|---|---|
| D. marilandicum | | 17-1.0-.029 | 15-1.0-.027 |
| D. obtusum | 5-1.0-.018 | | |
| D. paniculatum | | 10-4.0-.029 | |
| Eragrostis spectabilis | | | 5-30.0-.109 |
| Eupatorium fistulosum | 15-5.0-.063 | 7-6.0-.013 | |
| E. perfoliatum | 5-1.0-.018 | | |
| E. rotundifolium | | 7-1.0-.014 | |
| Euphorbia corollata | 5-1.0-.018 | | |
| E. nutans | 25-1.0-.070 | | |
| Festuca pretensis | 25-9.6-.112 | 13-6.0-.040 | 30-9.0-.078 |
| Galactia volubilis | | | 10-1.0-.019 |
| Galium pilosum | | 7-1.0-.014 | 5-1.0-.011 |
| Gaylussacia baccata | | 3-5.0-.023 | |
| Gerardia purpurea | | 3-1.0-.009 | |
| Helianthus hirsutus | 10-3.0-.041 | 13-1.0-.024 | |
| Hypericum punctatum | | 10-1.0-.019 | |
| Juncus secundus | | 7-16.0-.064 | |
| J. tenuis | | | 20-1.0-.035 |
| Lactuca canadensis | | 7-1.0-.014 | |
| Lespedeza cuneata | 10-1.0-.041 | | |
| L. procumbens | | | 5-10.0-.043 |
| L. repens | | 7-1.0-.014 | 15-2.0-.031 |
| L. striata | | 3-10.0-.038 | |
| Liatris spicata | 5-1.0-.018 | | |
| Lobelia siphilitica | | 3-1.0-.009 | 5-1.0-.011 |
| Lysimachia lanceolata | | | 5-1.0-.011 |
| Melilotus alba | 10-1.0-.031 | | |
| Muhlenbergia schreberi | | 3-1.0-.009 | |

(Appendix 3, cont.)

| | | | |
|---|---|---|---|
| Nyssa sylvatica | | 3.0-20.0-.072 | |
| Oenothera sp. | | 10-1.0-.072 | |
| Oxopolis rigidior | | 3-1.0-.009 | |
| Panicum lanuginosum | | | 5-1.0-.011 |
| P. laxiflorum | | | 5-1.0-.011 |
| P. microcarpon | | 3-1.0-.009 | |
| P. sphaerocarpon | | | 5-1.0-.011 |
| P. virgatum | 10-70.0-.367 | | |
| Paspalum laeve | | | 5-1.0-.01 |
| Penstemon brevisepalus | | 3-1.0-.009 | |
| Phlox amoena | | 7-1.0-.014 | |
| Plantago lanceolata | | | 5-1.0-.011 |
| Poa compressa | | 10-1.0-.019 | |
| P. pretensis | | | 10-1.0-.019 |
| Potentilla simplex | 5-1.0-.018 | 19-4.0-.044 | |
| Prunella vulgaris | | 7-1.0-.014 | |
| Prunus serotina | | | 5-1.0-.011 |
| Pteridium aquilinum | | 17-5.0-.043 | |
| Pycnanthemum muticum | 5-1.0-.018 | 7-1.0-.014 | 40-2.0-.071 |
| Pyrus melanocarpa | 15-3.7-.057 | | 5-1.0-.011 |
| Rhus copallina | | 3-10.0-.039 | 5-1.0-.011 |
| R. radicans | | | 5-1.0-.011 |
| Rhynchospora capitellata | | 3-1.0-.009 | |
| Rosa carolina | | 3-10.0-.039 | |
| Rubus sp. | 15-2.3-.050 | 46-4.0-.088 | 35-1.0-.100 |
| Rudbeckia hirta | | 7-1.0-.014 | |
| Salix tristis | 10-1.0-.031 | 40-21.0-.133 | 5-2.0-.015 |
| Schizachyrium scoparium | | 3-40.0-.138 | 75-36.0-.240 |

(Appendix 3, cont.)

| | | | |
|---|---|---|---|
| Scirpus atrovirens | | 3-1.0-.009 | |
| Scrophulariaceae, unknown | | | 10-5.0-.033 |
| Scutellaria elliptica | | 3-1.0-.009 | 5-1.0-.011 |
| Setaria geniculata | | 3-1.0-.009 | 60-1.0-.098 |
| Smilax glauca | | 30-2.4-.055 | 80-1.0-.130 |
| Solidago canadensis var. scabra | 75-5.0-.219 | 17-2.8-.036 | |
| S. nemoralis | | 3-1.0-.009 | |
| S. rugosa | 5-1.0-.018 | | |
| Sorghastrum nutans | | 3-5.0-.023 | 80--63.0-.339 |
| Strophostyles umbellata | | | 20-1.0-.035 |
| Stylostanthes biflora | | 3-1.0-.009 | |
| Tephrosia virginica | 5-1.0-.018 | | |
| Tridens flavus | | | 15-4.0-.038 |
| Unknown forb | | | 10-1.0-.019 |
| Vaccinium stamineum | | | 10-1.0-.019 |
| V. vacillans | | | 5-1.0-.011 |
| Vernonia noveboracensis | 5-1.0-.018 | | |

**(Appendix 4, cont.)**

| | | | |
|---|---|---|---|
| Gerardia purpurea | 17-1.0-.016 | | |
| Gnaphalium obtusifolium | | | 3-1.0-.009 |
| Gratiola pilosa | 6-1.0-.010 | | |
| Helianthus angustifolius | 11-1.0-.013 | | |
| H. atrorubens | 28-7.0-.060 | 30-10.0-.91 | 11-3.0-.029 |
| H. hirsutus | 28-1.0-.023 | | |
| H. microcephalus | 11-1.0-.013 | | |
| Hieracium gronovii | 17-1.0-.016 | | 3-1.0-.009 |
| Houstonia purpurea var. calycosa | | | 3-1.0-.009 |
| Hypericum punctatum | | | 6-1.0-.012 |
| H. stragalum | 6-1.0-.010 | | 6-3.0-.024 |
| Krigia biflora | 6-1.0-.010 | | |
| Kuhnia eupatorioides | 6-1.0-.010 | | |
| Lactuca candensis | | | 3-1.0-.009 |
| Lechea minor | 11-1.0-.013 | | 3-1.0-.009 |
| L. racemulosa | 22-1.0-.019 | | |
| Lespedeza cuneata | | | 3-1.0-.009 |
| L. procumbens | | | 17-3.0-.034 |
| L. repens | 6-1.0-.010 | 20-1.0-.052 | 11-2.0-.023 |
| L. striata | | | 3-1.0-.009 |
| L. virginica | 6-1.0-.010 | | |
| Linum medium | 6-1.0-.010 | | |
| Lobelia puberula | 6-1.0-.010 | | |
| L. spicata | | | 3-1.0-.009 |
| Medicago sp. | | | 3-1.0-.009 |
| Melilotus sp. | | 5-1.0-.017 | |
| Monarda fistulosa | 61-1.0-.043 | 5-1.0-.017 | 14-1.0-.020 |
| Nyssa sylvatica | 6-1.0-.010 | | |

**(Appendix 4, cont.)**

| | | | |
|---|---|---|---|
| Oenothera sp. | | | 54-1.0-0.58 |
| Oxalis stricta | | | 3-1.0-.009 |
| Oxydendron arboreum | 6-5.0-.034 | | |
| Panicum commutatum | 6-1.0-.010 | | |
| P. depauperatum | 11-5.5-.040 | | |
| P. lanuginosum | | | 3-1.0-.009 |
| P. laxiflorum | 6-1.0-.010 | | 3-1.0-.009 |
| P. microcarpon | 28-6.4-.056 | | |
| P. sphaerocarpon | 6-1.0-.010 | | 8-1.0-.015 |
| P. sp. | 17-1.0-0.16 | | |
| P. villosissimum | | | 3-1.0-.009 |
| Parthenium integrifolium | 6-1.0-.010 | | 6-6.0-.041 |
| Paspalum setaceum | | | 11-1.0-.017 |
| Phlox amoena | 17-1.0-.016 | | |
| Physalis sp. | | | 6-1.0-.012 |
| Plantago lanceolata | | | 31-1.0-.036 |
| P. virginica | | | 6-1.0-.012 |
| Poa compressa | | 10-5.5-.054 | 9-6.0-.044 |
| Polygala ambigua | 11-1.0-.013 | | |
| P. cruciata | 6-1.0-.010 | | |
| Potentilla canadensis | | | 14-2.0-.026 |
| P. simplex | 39-1.0-.029 | 35-1.0-.086 | 11-4.0-.017 |
| Prenanthes serpentaria | | | 6-1.0-.012 |
| Prunella vulgaris | | 10-1.0-.029 | 11-1.0-.017 |
| Psoralea psoralioides | 22-1.0-.019 | 20-1.0-.052 | |
| Pteridium aquilinum | | | 9-10.0-.068 |
| Pycnanthemum muticum | | | 6-1.0-.012 |
| P. tenuifolium | | 5-1.0-.017 | |

(Appendix 4, cont.)

| | | | |
|---|---|---|---|
| Pyrus melanocarpa | 17-1.0-.016 | | |
| Rhododendron nudiflorum | 6-1.0-.010 | | |
| Rosaceae, unknown | | | 3-1.0-.009 |
| Rubus spp. | 11-8.0-.013 | 10-1.0-.029 | 40-2.0-.041 |
| Rudbeckia hirta | 6-1.0-.010 | | |
| Salix humilis | 11-1.0-.013 | | |
| S. tristis | 6-20.0-.124 | | |
| Sassafras albidum | | | 14-3.0-.090 |
| Schizachyrium scoparium | 100-56.1-.401 | 90-42.8-.449 | 100-53.0-.406 |
| Schrankia uncinata | 11-1.0-.013 | | |
| Scleria pauciflora | | 15-1.0-.040 | |
| Scutellaria incana | 11-1.0-.013 | | |
| S. integrifolia | 6-1.0-.010 | | |
| Senecio anonymus | 33-1.0-.026 | 5-1.0-.017 | 14-1.0-.020 |
| Setaria geniculata | | | 11-4.0-.034 |
| Smilax glauca | 17-1.0-.016 | 5-5.0-.039 | 74-4.0-.094 |
| Solidago canadensis var. scabra | | | 3-1.0-.009 |
| S. erecta | 22-1.0-.019 | | |
| S. hispida | 6-1.0-.010 | | |
| S. juncea | | 5-1.0-.019 | |
| s. nemoralis | 22-1.0-.019 | 10-1.0-.029 | |
| S. odora | 22-1.0-.019 | | |
| S. sp. | 6-1.0-.010 | | |
| Sorghastrum nutans | 11-5.5-.040 | 10-15.0-.108 | 9-15.0-.097 |
| Spirea tomentosa | 11-3.0-.025 | | |
| Sporobolus neglectus | | 5-1.0-.017 | |
| Strophostyles umbellata | 6-1.0-.010 | | |
| Stylosanthes biflora | 28-1.0-.023 | 10-1.0-.029 | 71-1.0-.074 |

(**Appendix 4, cont.**)

| | | | |
|---|---|---|---|
| Tephrosia virginica | | | 20-9.0-.072 |
| Tridens flavus | | | 17-23.0-.151 |
| Trifolium pretense | | | 6-1.0-.012 |
| Unknown forb | | 10-1.0-.029 | 14-1.0-.020 |
| Vaccinium vacillans | 17-2.3-.024 | | 3-1.0-.009 |
| Viola sagittata/triloba | 11-1.0-.013 | 10-1.0-.024 | |
| V. triloba | | | 3-1.0-.009 |
| Zizia aptera | | 15-13.0-.108 | |

**Appendix 5. Frequency, mean cover (where they occur) and Importance Value 200 of species of Plateau barrens. Also shown is the frequency and cover (where exposed or present) of rock/gravel and lichens.**

| Site (number) | US 70 N West of Crossville (112) | US 70 N at Expt. Station (115) | US 70 N West of Crossville (114) | US 70 N at I40 (113) |
|---|---|---|---|---|
| Plot number (size, m$^2$) | 18 (0.16) | 20 (0.16) | 20 (0.16) | 20 (0.16) |
| Frequency-Mean cover | | | | |
| Rock/gravel | 6-30 | | | |
| Lichens | | 10-75 | | |
| Frequency-Mean Cover-Importance Value 200 | | | | |
| | | | | |
| Acalypha graciliens | | | 5-1.0-.018 | |
| Achillea millifolium | 6-1.0-.020 | | | |
| Andropogon gyrans | 6-1.0-.020 | | | |
| A. ternarius | 6-1.0-.020 | | | |
| A. virginicus | | 5-1.0-.016 | | |
| Antennaria plantaginifolia | 11-1.0-.222 | | | 15-1.0-.032 |
| Aristida longispica | | | 5-1.0-.018 | |
| Aster dumosus | 56-1.8-.123 | 5-1.0-.016 | 20-1.0-.058 | |
| A. hemisphericus | | | | 5-1.0-.017 |
| A. patens | | | 10-2.0-.037 | |
| A. surculosus | | 5-1.0-.016 | | 5-1.0-.017 |
| A. undulatus | | | | 5-1.0-.017 |
| Botrichium dissectum var. obliquum | | 5-1.0-.016 | | |
| Cassia nictitans | 6-1.0-.020 | | | 5-1.0-.017 |
| C. fasciculata | | | | 5-1.0-.017 |
| Chrysanthemum leucanthemum | 6-1.0-.020 | | | 5-1.0-.017 |
| Chrysopsis camporum | 11-1.0-.029 | | 10-1.0-.032 | |
| C. mariana | | | | 30-1.0-.054 |

**(Appendix 5, cont.)**

| | | | | |
|---|---|---|---|---|
| Coreopsis major | 6-1.0-.020 | 60-1.8-.131 | | 20-1.0-.039 |
| Cuphea villosissima | | 5-1.0-.016 | | |
| Danthonia spicata | 22-1.0-.051 | 5-5.0-.040 | | 5-1.0-.017 |
| Daucus carota | 6-3.0-.044 | | | |
| Desmodium ciliare | | | 5-1.0-.018 | 15-1.0-.032 |
| D. marilandicum | | | 5-1.0-.018 | 15-1.0-.032 |
| D. paniculatum | | | | 10-1.0-.024 |
| D. sp. | 6-1.0-.020 | | | |
| Elephantopus carolinianus | | | 15-1.0-.045 | |
| Eupatorium altissimum | | | 15-1.0-.045 | |
| E. rotundifolium | 6-1.0-.020 | 20-4.0-.064 | | |
| Euphorbia corollatta | 11-1.0-.029 | | 15-1.0-.045 | 15-1.0-.032 |
| Festuca pratensis | 10-10.0-.088 | | | |
| Galactia volubilis | 6-1.0-.020 | | 5-1.0-.018 | 15-1.0-.032 |
| Galium circaezans | 6-1.0-.020 | | | |
| G. pilosum | | | 5-1.0-.018 | |
| Gerardia purpurea | | | | 5-1.0-.017 |
| Gnaphalium obtusifolium | | | 5-1.0-.018 | |
| Helianthus atrorubens | | 15-3.0-.048 | | |
| Hieracium gronovii | | | | 15-1.0-.032 |
| Houstonia purpurea var. calycosa | | | 5-1.0-.018 | |
| Hypericum gentianoides | | | 5-1.0-.018 | |
| Ipomoea pandurata | 6-1.0-.020 | | | |
| Lechea minor | | | | 15-1.0-.032 |
| Lespedeza cuneata | | | 5-1.0-.018 | |
| L. intermedia | | | | 10-1.0-.024 |
| L. repens | 33-1.0-.072 | 5-1.0-.016 | | 5-1.0-.017 |

| | | | | |
|---|---|---|---|---|
| Liatris microcephala | | 10-1.0-.026 | | |
| Lobelia puberula | | | 5-1.0-.018 | |
| L. inflata | | | 5-1.0-.032 | |
| Lonicera japonica | 6-1.0-.020 | | | |
| Monarda fistulosa | | 10-1.0-.026 | 20-1.0-.058 | 20-1.0-.043 |
| Panicum commutatum | 6-1.0-.020 | | | |
| P. lanuginosum | | | 5-1.0-.018 | 40-1.0-.077 |
| P. meridionale | | | | 20-1.0-.043 |
| P. sp. | | 5-1.0-.016 | 5-1.0-.018 | |
| Parthenium integrifolium | 6-2.0-.165 | | | |
| Paspalum setaceum | | | | 5-1.0-.017 |
| Plantago aristata | | | 5-1.0-.018 | |
| Poa compressa | | | 15-1.0-.045 | |
| Potentilla canadensis | 33-5.8-.108 | | | 15-1.0-.032 |
| P. simplex | 33-3.2-.088 | 35-1.0-.077 | | 30-1.0-.054 |
| Prunella vulgaris | | | 5-1.0-.018 | 5-1.0-.017 |
| Psoralea psoralioides | | | | 10-1.0-.024 |
| Pyrus angustifolia | | | | 5-1.0-.017 |
| Quercus falcata | 6-1.0-.020 | | 5-1.0-.018 | |
| Q. stellata | | 5-10.0-.070 | | |
| Rubus, sp. | 28-3.6-.083 | 75-6.1-.188 | 10-1.0-.032 | 25-1.0-.047 |
| Schizachyrium scoparium | 100-56.1-.624 | 95-35.8-.406 | 65-74.0-.556 | 100-39.5-.534 |
| Senecio anonymus | 33-1.0-.072 | 15-4.0-.054 | 15-3.0-.056 | 35-1.0-.061 |
| Sericocarpus asteroides | | 65-1.7-.141 | | |
| Smilax glauca | 6-1.0-.020 | 10-6.0-.056 | 10-3.0-.043 | 40-1.0-.069 |
| Solidago juncea | | | | 10-1.0-.024 |
| S. nemoralis | 17-5.3-.074 | | 10-1.0-.032 | 5-1.0-.017 |
| S. odora | | 20-2.0-.052 | 5-1.0-.018 | 5-1.0-.017 |

(Appendix 5, cont.)

| | | | | |
|---|---|---|---|---|
| Sorghastrum nutans | | | 35-77.0-.492 | 45-19.0-.372 |
| Spiranthes gracilis | | | | 5-1.0-.019 |
| Stylosanthes biflora | | 10-1.0-.026 | 10-1.0-.032 | 20-2.0-.053 |
| Tephrosia virginana | | 20-1.0-.046 | | |
| Tridens flavus | | | 5-10.0-.065 | |
| Unknown forb | 6-1.0-.020 | | 5-1.0-.018 | 40-2.5-.267 |
| Vaccinium vacillans | | | | 10-1.0-.024 |
| Vernonia gigantea | 6-1.0-.020 | 5-1.0-.016 | | |
| Viola sagittata | | | | 10-1.0-.024 |

**Appendix 6. Frequency, mean cover (where they occur) and Importance Value 200 of species of two xeric Plateau barrens. Also shown is frequency and cover (where present) of exposed bedrock, gravel, soil, lichens and tree litter.**

| Site (number) | Roosevelt Mountain (45) | US 70 S, south end of airport (106) |
|---|---|---|
| Plot numbers (size m$^2$) | 20 (0.5) | 25 (0.5) |
| Frequency-Mean Cover | | |
| Bedrock | 10-15.0 | |
| Gravel | 20-38.0 | 16-20.0 |
| Soil | 20-11.0 | 80-27.0 |
| Lichens | 30-12.0 | |
| Tree litter | 20-18.0 | |
| Frequency-Mean Cover-Importance Value 200 | | |
| Ambrosia artimisiifolia | 15-1.0-.017 | 20-1.0-.022 |
| Andropogon virginicus | | 16-20.0-.108 |
| A. gerardii | 50-31.0-.128 | |
| Antennaria plantaginifolia | | 12-1.0-.015 |
| Aristida purpurescens | 5-2.0-.010 | 4-1.0-.008 |
| Asclepias sp. | 5-1.0-.008 | |
| Aster concolor | 5-1.0-.008 | |
| A. dumosus | 25-1.0-.026 | 20-1.0-.022 |
| A. linariifolius | 10-1.0-.012 | 8-1.0-.012 |
| A. patens | 40-1.0-.041 | 48-1.0-.046 |
| A. pilosus | | 8-1.0-.012 |
| A. sp. | 10-1.0-.012 | |
| A. surculosus | | 4-1.0-.008 |
| A. undulatus | 10-1.0-.012 | 8-1.0-.012 |
| Carex sp. | 15-27.0-.085 | |
| Carya glabra | 5-1.0-.008 | |
| Cassia nictitans | 15-1.0-.017 | 24-1.0-.026 |

(**Appendix 6, cont.**)

| | | |
|---|---|---|
| Ceanothus americanus | 5-20.0-.057 | |
| Chrysanthemum leucanthemum | | 72-1.0-.066 |
| Chrysopsis camporum | 5-1.0-.008 | 76-1.0-.070 |
| C. mariana | | 8-1.0-.012 |
| C. nervosa | 25-1.0-.026 | |
| Coreopsis major | 15-1.0-.017 | 4-1.0-.008 |
| Croton monanthogynous | 5-1.0-.008 | |
| Crotonopsis elliptica | | 8-2.0-.016 |
| Danthonia sericea | 5-20.0-.057 | |
| D. spicata | 30-10.0-.054 | 32-8.0-.064 |
| Daucus carota | 25-1.0-.026 | 24-1.0-.026 |
| Desmodium ciliare | 10-1.0-.012 | 4-1.0-.008 |
| D. dillenii | 5-10.0-.031 | 8-1.0-.012 |
| D. marilandicum | 10-1.0-.012 | 16-1.0-.019 |
| Diodia teres | | 28-19.0-.113 |
| Diospyros virginiana | 10-1.0-.012 | 4-1.0-.008 |
| Eragrostis spectabilis | | 44-1.0-.043 |
| Erigeron strigosus | 25-1.0-.026 | |
| Eupatorium album | 5-1.0-.008 | 4-1.0-.008 |
| Euphorbia corallata | 25-1.0-.006 | 20-1.0-.022 |
| E. humistrata | | 12-1.0-.015 |
| Festuca pretensis | 10-6.0-.025 | 12-10.0-.057 |
| Galactia volubilis | 30-1.0-.031 | |
| Galium pilosum | 5-1.0-.008 | 8-1.0-.012 |
| Gnaphalium obtusifolium | 5-1.0-.008 | 4-1.0-.008 |
| Helianthus atrorubens | | 20-1.0-.022 |
| H. hirsutus | 25-1.0-.026 | 4-1.0-.008 |
| Houstonia purpurea var. calycosa | 5-1.0-.008 | 20-1.0-.022 |

(**Appendix 6, cont.**)

| | | |
|---|---|---|
| Hypericum gentianoides | | 8-1.0-.012 |
| Ipomoea pandurata | 5-1.0-.008 | |
| Kuhnia eupatorioides | 5-1.0-.008 | |
| Lechea minor | | 4-1.0-.008 |
| Legume, unknown | 10-1.0-.012 | |
| Lespedeza hirta | 5-1.0-.008 | |
| L. intermedia | | 4-1.0-.008 |
| L. repens | | 44-1.0-.043 |
| L. virginica | 55-1.0-.055 | 32-1.0-.032 |
| Liatris microcephala | 5-1.0-.008 | |
| L. squarrosa | 25-1.0-.026 | |
| Oxalis stricta | | 16-1.0-.019 |
| Panicum bicknellii | 5-1.0-.008 | |
| P. commutatum | 5-1.0-.008 | 4-1.0-.008 |
| P. depauperatum | 5-1.0-.008 | 16-1.0-.019 |
| P. lanuginosum | 5-1.0-.008 | 12-1.0-.015 |
| P. laxiflorum | 5-1.0-.008 | 4-1.0-.008 |
| P. longiligulatum | | 4-1.0-.008 |
| P. microcarpon | 5-1.0-.008 | |
| P. oligosanthes | 10-1.0-.012 | |
| P. polyanthes | 15-1.0-.017 | 8-1.0-.012 |
| P. sp. | | 4-1.0-.008 |
| P. sphaerocarpon | | 32-1.0-.032 |
| P. villosissimum | | 4-1.0-.008 |
| Parthenium integrifolium | | 8-1.0-.012 |
| Paspalum laeve | | 12-1.0-.015 |
| Phlox amoena | | 4-1.0-.008 |
| Physalis, sp. | | 4-1.0-.008 |

(Appendix 6, cont.)

| | | |
|---|---|---|
| Pinus echinata | 5-1.0-.008 | |
| Plantago lanceolata | | 12-1.0-.015 |
| Polygala verticillata | | 12-1.0-.015 |
| Potentilla canadensis | 5-1.0-.026 | 60-1.0-.056 |
| P. simplex | 10-1.0-.012 | |
| Pteridium aquilinum | 20-2.0-.024 | |
| Rhus copallina | 5-1.0-.008 | 16-1.0-.019 |
| Rubus sp. | 10-1.0-.012 | 4-1.0-.008 |
| Salvia lyrata | 5-1.0-.008 | 4-1.0-.008 |
| Sassafras albidum | | 4-1.0-.008 |
| Schizachyrium scoparium | 70-33.6-.138 | 96-62.0-.343 |
| Schrankia uncinata | 5-1.0-.008 | |
| Senecio anonymus | | 76-1.0-.071 |
| Sida spinosa | 5-1.0-.008 | |
| Smilax glauca | 15-2.0-.009 | 32-1.0-.032 |
| Solidago canadensis var. scabra | | 4-1.0-.008 |
| S. nemoralis | 10-1.0-.012 | 32-1.0-.032 |
| Sorghastrum nutans | 5-50.0-.136 | 8-28.0-.155 |
| Spiranthes gracilis | | 4-1.0-.008 |
| Sporobolus asper | 5-50.0-.136 | |
| Stylosanthes biflora | 5-1.0-.008 | 32-1.0-.032 |
| Taraxicum officinale | | 8-1.0-.012 |
| Trichostemum dichotomum | | 4-1.0-.008 |
| Tridens flavus | 10-6.0-.025 | |
| Unknown forb | 60-1.0-.059 | 96-1.0-.087 |
| Unknown woody plant | 15-4.0-.030 | |
| Vaccinium arboreum | 10-1.0-.012 | |
| V. vacillans | | 4-1.0-.008 |

(Appendix 6, cont.)

| | | |
|---|---|---|
| Viola pedata | 5-1.0-.008 | |
| V. sagittata | 5-1.0-.008 | |
| V. triloba | | 4-1.0-.008 |
| Vitis sp. | 5-30.0-.014 | |

**Appendix 7. Frequency, mean cover (where they occur) and Importance Value 200 of species of three mesic Ridge and Valley barrens. Also shown is frequency and cover (where present) of exposed rock, gravel, soil, and the occurrence of bryophytes and tree litter.**

| Sites (number) | Oak Ridge Fairbanks Road (9) | Fezzell Road near road (33) | Fezzell Road Cedar area (33) |
|---|---|---|---|
| Plot number (size m$^2$) | 20 (0.5) | 20 (0.25) | 20 (0.25) |
| Frequency-Mean Cover | | | |
| Bedrock/gravel | 30-36 | 10-15 | |
| Soil | 35-26 | | |
| Bryophytes | 5-50 | | |
| Tree litter | 20-1 | | |
| Frequency-Mean Cover-Importance Value 200 | | | |
| Agave virginica | 35-1.0-.047 | 15-1.0-.029 | |
| Andropogon gerardii | 100-57.0-.503 | 95-30.5-.321 | 100-39.3-.758 |
| Anemone virginica | | 5-1.0-.013 | |
| Asclepias verticillata | 5-1.0-.013 | 5-1.0-.013 | |
| A. pilosus | | 5-1.0-.013 | |
| Carex hirsutella | 10-1.0-.018 | | |
| Cassia nictitans | 10-1.0-.018 | | 10-1.0-.043 |
| Cocculus carolinus | 5-1.0-.013 | | |
| Danthonia spicata | 40-13.0-.132 | | |
| Daucus carota | 5-1.0-.013 | | |
| Desmodium ciliare | | | 10-1.0-.043 |
| D. dillenii | | | 5-1.0-.027 |
| D. marilandicum | 5-1.0-.013 | | |
| D. paniculatum | | | 5-1.0-.027 |
| Dicot, unknown | 10-1.0-.018 | | |
| Elymus virginicus | | 10-15.0-.098 | 10-1.0-.043 |
| Erigeron strigosus | 5-1.0-.013 | | |

(**Appendix 7, cont.**)

| | | | |
|---|---|---|---|
| Eupatorium altissimum | 5-1.0-.013 | | |
| Euphorbia corallata | 15-1.0-.024 | | |
| Fragaria virginiana | 15-1.0-.024 | 20-1.0-.038 | |
| Galactia volubilis | 40-1.0-.052 | 5-1.0-.013 | |
| Galium pilosum | | 5-1.0-.013 | 10-1.0-.043 |
| Gaura filipes | | 10-1.0-.021 | |
| Helianthus hirsutus | 45-1.0-.058 | 30-2.5-.083 | |
| Houstonia canadensis | 5-1.0-.013 | | |
| Hypericum dolabriforme | 30-1.0-.041 | | |
| Ipomoea pandurata | 10-1.0-.018 | | |
| Isanthus brachiatus | 5-1.0-.013 | | |
| Juniperus virginiana | 20-1.0-.030 | 35-23.6-.186 | 5-1.0-.027 |
| Kuhnia eupatorioides | 10-1.0-.018 | | |
| Legume, unknown | 5-1.0-.013 | | |
| Lespedeza cuneata | 25-1.0-.035 | | |
| L. intermedia | 5-1.0-.013 | | |
| L. procumbens | | 80-3.9-.146 | 20-1.0-.076 |
| L. repens | 5-1.0-.013 | | |
| L. virginica | 5-1.0-.013 | 35-5.1-.085 | 25-1.0-.090 |
| Liatris aspera | 60-1.0-.075 | | |
| L. cylindracea | 25-1.0-.035 | 20-1.0-.038 | |
| Lithospermum canescens | | 5-1.0-.013 | |
| Lobelia spicata | | 15-1.0-.029 | 5-1.0-.027 |
| Lonicera japonica | 25-1.0-.035 | | |
| Panicum anceps | 5-1.0-.013 | | |
| P. lanuginosum | 25-1.0-.035 | | |
| P. oligosanthes | 5-1.0-.013 | | |
| P. sp. | | 10-1.0-.021 | |

(Appendix 7, cont.)

| | | | |
|---|---|---|---|
| Penstemon brevisepalus | | 5-1.0-.013 | |
| P. laevigatus | 10-1.0-.018 | | |
| Potentilla simplex | 20-1.0-.030 | | 5-1.0-.027 |
| Prunella vulgaris | 10-1.0-.018 | | |
| Prunus serotina | 5-1.0-.013 | | |
| Pycnanthemum virginianum | 20-1.0-.030 | | |
| Ratibitta pinnata | 50-1.0-.063 | 25-1.0-.046 | |
| Rhamnus caroliniana | 5-1.0-.013 | | |
| Rhus radicans | 5-1.0-.013 | | |
| Rubus, sp. | | | 5-10.0-.128 |
| Rudbeckia fulgida | 10-1.0-.030 | 10-1.0-.021 | |
| Ruellia humilis | 30-1.0-.041 | | |
| Salvia lyrata | | 5-1.0-.013 | 15-10.3-.163 |
| Schizachyrium scoparium | | 15-11.2-.085 | |
| Senecio anonymus | | | 5-1.0-.027 |
| Silphium terebinthinaceum | | 30-17.0-.142 | 20-6.3-.136 |
| Solidago canadensis var. scabra | 20-1.0-.030 | | 10-1.0-.043 |
| S. nemoralis | 5-1.0-.013 | 5-1.0-.013 | |
| S. ptarmicoides | 30-1.0-.041 | | |
| S. rigida | | 70-7.1-.153 | 20-5.3-.124 |
| S. ulmifolia | | | 10-3.0-.066 |
| Sporobolus asper | 10-1.0-.018 | | |
| S. vaginiflorus | 25-11.0-.101 | 10-15.5-.101 | |
| Tridens flavus | | 5-1.0-.013 | 10-1.0-.043 |
| Ulmus alata | 15-14.0-.110 | | |
| Unknown forb | | 25-2.8-.055 | |
| Unknown gramineae | | 5-30.0-.173 | |

Appendix 8. **Frequency, mean cover (where they occur) and Importance Value 200 of species of three xeric Ridge and Valley barrens. Also shown is frequency and cover (where present) of exposed bedrock, gravel, and soil and bryophytes, lichens and tree litter.**

| Sites (numbers) | New Hope (149) | Strong Mailbox (150) | Rt. 130 x I40, Covington (139) |
|---|---|---|---|
| Plot number (size m$^2$) | 25 (0.5) | 25 (0.5) | 25 (0.5) |
| | Frequency-Mean Cover | | |
| Bedrock | 74-12.1 | | |
| Gravel | 100-30.5 | 40-53.0 | 8-17.5 |
| Soil | | 24-10.0 | 52-14.7 |
| Bryophytes | 4-3.0 | | 48-2.6 |
| Lichens | 8-2.0 | | 16-1.0 |
| Tree litter | 12-2.7 | | |
| | Frequency-Mean Cover-Importance Value 200 | | |
| Agave virginica | 72-1.1-.109 | | |
| Ambrosia artimisiifolia | | 8-1.0-.015 | |
| Andropogon gerardii | | 72-56.0-.114 | |
| Anemone virginica | | | 24-1.0-.035 |
| Arabis laevigata | | | 4-1.0-.013 |
| Asclepias tuberosa | | 4-1.0-.011 | |
| Asparagus officinale | | | 4-1.0-.013 |
| Aster dumosus | 4-1.0-.017 | | |
| A. patens | 4-1.0-.017 | 4-1.0-.011 | |
| A. pilosus | | 4-2.0-.023 | 4-1.0-.013 |
| A. undulatus | 16-1.0-.033 | 12-1.0-.019 | |
| Carex hirsutella | | | 4-1.0-.013 |
| C. sp. | | | 24-1.0-.035 |
| Cassia fasciculata | | | 4-1.0-.013 |
| Centrosema virginiana | | 4-1.0-.011 | |
| Cercis canadensis | 32-1.6-.062 | | |

(Appendix 8, cont.)

| | | | |
|---|---|---|---|
| Chrysanthemum leucanthemum | | 24-1.4-.033 | 32-1.0-.044 |
| Chrysopsis camporum | | 4-1.0-.011 | |
| Coreopsis tripteris | | 12-1.0-.019 | |
| Croton monthanogynous | | 8-1.0-.015 | |
| Danthonia spicata | | 24-11.0-.129 | 16-3.5-.045 |
| Daucus carota | | 12-1.0-.019 | 4-1.0-.013 |
| Desmodium ciliare | 12-1.0-.028 | 8-1.0-.015 | |
| Echinacea purpurea | | 28-1.7-.041 | |
| Erigeron strigosus | | | 4-1.0-.013 |
| Eupatorium altissimum | | 12-3.0-.035 | 8-1.0-.017 |
| Euphorbia corallata | 12-1.0-.028 | 4-1.0-.011 | |
| E. maculata | | 8-1.0-.015 | |
| Fabaceae, unknown | | | 12-1.0-.022 |
| Fragaria virginiana | | 12-1.0-.019 | 28-1.0-.040 |
| Galactia volubilis | 80-1.2-.121 | 20-1.0-.027 | |
| Galium circaezans | 8-1.0-.023 | 4-2.0-.019 | 4-1.0-.013 |
| Gaura biennis | | | 4-1.0-.013 |
| Helianthus hirsutus | | 52-1.2-.061 | 44-1.0-.058 |
| Houstonia purpurea var. calycosa | 24-1.0-.044 | 4-1.0-.013 | 12-1.0-.022 |
| Hypericum perforatum | | | 4-1.0-.013 |
| H. sphaerocarpon | 4-1.0-.017 | | |
| Isanthus brachiatus | 8-1.0-.023 | | |
| Juniperus virginiana | 40-3.1-.089 | 92-8.3-.156 | 44-2.2-.067 |
| Lespedeza cuneata | | | 12-1.7-.027 |
| L. procumbens | 8-1.0-.023 | 32-1.0-.039 | 20-1.8-.037 |
| L. virginiana | | 12-1.0-.019 | 24-1.0-.035 |
| Linum sulcatum | 8-1.0-.023 | | |
| Lithospermum canescens | 64-1.1-.098 | 12-1.0-.019 | 4-1.0-.013 |

(Appendix 8, cont.)

| | | | |
|---|---|---|---|
| Lobelia spicata | 32-1.0-.055 | | 12-1.0-.022 |
| Lonicera japonica | | | 12-1.0-.022 |
| Melilotus alba | | 20-1.0-.027 | 28-1.0-.040 |
| Monarda fistulosa | | 28-1.0-.035 | 72-1.0-.089 |
| Nostoc commune | 8-1.0-.023 | | 4-1.0-.013 |
| Panicum commutatum | | 8-1.0-.015 | |
| P. flexile | | 0-1.0-.011 | |
| P. lanuginosum | 8-1.0-.023 | | |
| Pinus virginiana | 16-1.0-.033 | | |
| Plantago lanceolata | | 4-1.0-.011 | |
| Poa compressa | | 4-1.0-.011 | |
| P. pratensis | | 4-1.0-.011 | |
| Polygala ambigua | 4-1.0-.017 | | |
| P. verticillata | | | 4-1.0-.013 |
| Potentilla simplex | | 52-1.0-.059 | 16-1.0-.024 |
| Prunella vulgaris | | 8-1.0-.015 | 4-1.0-.013 |
| Pycnanthemum tenuifolium | | 4-1.0-.011 | 8-1.0-.017 |
| Quercus falcata | 8-1.0-.023 | | |
| Rhus copallina | | 4-1.0-.011 | |
| R. radicans | | 8-1.0-.015 | |
| Rosa carolina | | 12-2.3-.030 | 40-1.0-.053 |
| Rudbeckia fulgida | | 4-1.0-.011 | |
| Ruellia humilis | 8-1.0-.023 | | |
| Salvia lyrata | | 4-1.0-.011 | 12-1.0-.022 |
| Schizachyrium scoparium | 100-53.8-.766 | 60-28.0-.277 | 100-84.1-.750 |
| Scleria oligantha | | 4-1.0-.011 | |
| Scutellaria leonardii | 12-1.0-.028 | | |
| Senecio anonymus | | 4-1.0-.011 | 20-1.0-.031 |

(Appendix 8, cont.)

| | | | |
|---|---|---|---|
| Silphium terebinthinaceum | | 44-3.3-.070 | 72-1.8-.089 |
| Sisyrinchium albidum | | 4-1.0-.011 | |
| Solidago canadensis var. scabra | | | 4-1.0-.013 |
| S. nemoralis | 68-2.1-.116 | 12-1.0-.019 | 72-1.2-.090 |
| S. rigida | | 68-2.1-.084 | |
| Sorghastrum nutans | | 24-7.0-.078 | |
| Sporobolus neglectus | 32-1.0-.055 | 20-8.4-.085 | |
| Tridens flavus | | 8-1.5-.020 | |
| Unknown forb | 48-1.0-.076 | 64-1.1-.063 | 52-1.7-.072 |
| Viburnum rufidulum | | 16-3.3-.042 | |
| Vitis vulpina | | 12-10.0-.089 | |

**Appendix 9. Frequency, mean cover (where they occur) and Importance Value 200 of species of three xeric Ridge and Valley barrens. Also shown is frequency and cover (where present) of bedrock, gravel, bryophytes, lichens, an alga, and tree litter.**

| Site (number) | G. Porter (155) | Yeary (146) | Exxon (154) |
|---|---|---|---|
| Plot number (size m$^2$) | 25 (0.5) | 25 (0.5) | 25 (0.5) |
| Frequency-Mean Cover | | | |
| Bedrock | 32-10.0 | 52-16.0 | 28-11.4 |
| Gravel | 76-36.1 | 36-9.7 | 100-53.6 |
| Bryophytes | | 8-1.5 | |
| Lichens | | | 8-8.0 |
| Alga (Nostoc) | 4-1.0 | | |
| Tree litter | 12-5.3 | 48-6.0 | 8-12.5 |
| Frequency-Mean Cover-Importance Value 200 | | | |
| Agave virginica | | | 20-1.0-.043 |
| Andropogon gerardii | | 44-21.5-.187 | |
| Anemone virginica | | 8-1.0-.018 | |
| Asclepias verticillata | | 16-1.0-.029 | |
| Aster dumosus | 8-2.0-.031 | 56-3.1-.099 | |
| A. sp. | | 4-1.0-.012 | |
| A. undulatus | | 40-1.2-.065 | |
| Asteraceae, unknown | | 8-1.0-.018 | |
| Campsis radicans | | 20-1.6-.028 | |
| Cercis canadensis | | 12-3.7-.038 | |
| Daucus carota | 4-1.0-.015 | | |
| Desmodium ciliare | 8-1.0-.022 | 16-1.0-.029 | 4-1.0-.021 |
| Diospyros virginiana | | 12-4.3-.042 | |
| Euphorbia corallata | | 32-1.0-.052 | |
| E. dentata | | | 20-1.0-.043 |
| E. maculata | | | 8-1.0-.026 |
| Fragaria virginiana | | 4-1.0-.012 | |

(**Appendix 9, cont.**)

| | | | |
|---|---|---|---|
| Galactia volubilis | 28-1.4-.057 | 72-2.6-.019 | 16-1.0-.037 |
| Gaura filipes | 24-1.3-.050 | | |
| Heliotropium tenellum | 40-1.0-.072 | | 12-1.0-.032 |
| Hedyotis nigricans | 52-1.0-.071 | | 52-1.2-.090 |
| Helianthus hirsutus | | 4-2.0-.017 | |
| H. microcephalus | | 8-2.0-.023 | |
| Hypericum punctatum | | 4-2.0-.017 | |
| H. sphaerocarpon | 12-1.0-.028 | | 36-1.0-.065 |
| Juniperus virginiana | 40-13.4-.185 | 36-3.0-.059 | |
| Kuhnia eupatorioides | | 4-1.0-.012 | 8-1.0-.026 |
| Lespedeza procumbens | 12-2.0-.037 | 4-1.0-.012 | 20-1.2-.046 |
| L. virginica | | 40-2.4-.072 | |
| Linum sulcatum | | | 4-1.0-.021 |
| Lithospermum canescens | | 8-1.0-.018 | 20-1.0-.043 |
| Lobelia spicata | 4-1.0-.015 | | 44-1.0-.076 |
| Lonicera japonica | 20-1.0-.041 | | |
| Monarda fistulosa | | 8-1.0-.018 | |
| Panicum flexile | | | 28-1.0-.054 |
| Physostegia virginiana | | 8-1.0-.018 | |
| Polygala verticillata | | | 4-1.0-.021 |
| Potentilla simplex | 4-1.0-.015 | 4-1.0-.012 | |
| Prunella vulgaris | | 4-1.0-.012 | |
| Pycnanthemum tenuifolium | | 12-4.3-.037 | |
| Rhus radicans | | | 4-1.0-.021 |
| Rosa carolina | | 28-1.0-.046 | 4-1.0-.021 |
| Rudbeckia fulgida | | 8-1.5-.021 | |
| Ruellia humilis | 24-1.0-.048 | | 44-1.3-.080 |
| Salvia lyrata | | 8-1.0-.018 | |

**(Appendix 9, cont.)**

| | | | |
|---|---|---|---|
| Schizachyrium scoparium | 100-61.4-.715 | 100-58.6-.482 | 100-40.4-.738 |
| Scleria oligantha | | 8-6.0-.046 | |
| Scutellaria leonardii | | | 8-1.0-.026 |
| Senecio anonymus | 52-1.0-.091 | 16-1.0-.029 | 60-1.1-.099 |
| Silphium trifoliatum | 8-10.5-.108 | | |
| Sisyrinchium albidum | 16-1.0-.034 | | 20-1.0-.043 |
| Smilax bona-nox | | 12-2.3-.030 | |
| Solidago canadensis var. scabra | | 4-2.0-.017 | |
| S. nemoralis | 8-3.0-.040 | 48-3.0-.086 | 28-1.1-.055 |
| S. ptarmicoides | 76-1.1-.130 | | 68-1.1-.110 |
| Sporobolus neglectus | 64-1.0-.110 | | |
| S. vaginiflorus | | | 44-1.0-.076 |
| Strophostyles umbellata | | | 4-1.0-.021 |
| Ulmus alata | | 8-10.0-.069 | |
| Unknown forb | 24-1.0-.047 | | 40-1.0-.071 |
| Viburnum rufidulum | | 4-20.0-.121 | |

## Appendix 10. Frequency, mean cover (where they occur) and Importance Value 200 of species of two xeric Ridge and Valley barrens, and a glade. Also shown is frquency and cover (where present) of bedrock, gravel, soil and bryophytes/algae.

| Site (number) | Rt. 58 x 60 (120) | Eidson (148) | Fezzell (33) |
|---|---|---|---|
| Plot number (size $m^2$) | 20 (0.25) | 25 (0.5) | 20 (0.25) |
| Frequency-Mean Cover | | | |
| Bedrock | | 40-8.3 | |
| Gravel | | 40-20.3 | |
| Soil | | 32-8.0 | |
| Gravelly Soil | 10-10.0 | | 85-36.0 |
| Bryophytes/algae | | | 35-4.0 |
| Frequency-Mean Cover-Importance Value 200 | | | |
| Achillea millifolium | | | 5-1.0-.015 |
| Agave virginica | | | 65-2.0-.106 |
| Ambrosia artimisiifolia | | | 5-1.0-.015 |
| Andropogon gerardii | | | 15-12.0-.116 |
| Anemone virginica | 10-1.0-.024 | 56-1.9-.088 | 5-5.0-.047 |
| Anisostichus capreolata | 10-1.0-.024 | | |
| Aristida oligantha | | | 20-1.0-.037 |
| Aristolochia serpentaria | | 8-1.0-.017 | |
| Asclepias verticillata | | 4-1.0-.011 | |
| Aster dumosus | 5-1.0-.016 | | |
| A. pilosus | | | 10-1.0-.022 |
| A. undulatus | 20-1.0-.041 | | |
| Asteraceae, unknown | | 48-2.0-.077 | |
| Campsis radicans | 5-1.0-.016 | | |
| Carya ovata | 5-1.0-.016 | | |
| Cassia nictitans | 30-1.0-.058 | | |
| Ceanothus americanus | 10-3.0-.039 | | |
| Cercis canadensis | 15-7.0-.077 | 20-5.6-.059 | |

**(Appendix 10, cont.)**

| | | | |
|---|---|---|---|
| Chrysanthemum leucanthemum | 20-1.0-.041 | | |
| Danthonia spicata | 5-5.0-.046 | | |
| Daucus carota | | 12-2.3-.029 | |
| Desmodium ciliare | 5-1.0-.016 | | |
| D. paniculatum | | 8-5.5-.042 | |
| D. sp. | | 16-1.3-.029 | |
| Diospyros virginiana | | 16-6.8-.060 | |
| Eragrostis spectabilis | | | 5-20.0-.166 |
| Erigeron strigosus | | 8-1.0-.017 | 15-1.0-.029 |
| Eupatorium hyssopifolium | 35-1.0-.066 | | |
| Fragaria virginiana | | 48-1.8-.076 | 25-1.0-.042 |
| Galactia volubilis | 45-2.0-.091 | 16-6.0-.056 | 5-1.0-.015 |
| Galium circaezans | | 8-1.0-.017 | |
| G. pilosum | | 5-1.0-.016 | |
| Gaura filipes | | | 25-1.0-.043 |
| Gnaphalium obtusifolium | 5-1.0-.016 | | |
| Helianthus hirsutus | 10-1.0-.024 | | |
| Houstonia longifolia | | | 45-1.0-.071 |
| H. purpurea var. calycosa | | | 5-1.0-.015 |
| Hypericum punctatum | | 8-1.0-.017 | |
| Ipomoea pandurata | | 20-1.0-.037 | |
| Isanthus brachiatus | | | 30-1.0-.050 |
| Juniperus virginiana | | | 5-10.0-.086 |
| Kuhnia eupatorioides | | 8-3.0-.028 | |
| Lespedeza procumbens | 45-5.0-.111 | 80-14.3-.190 | 45-1.0-.071 |
| L. repens | 5-1.0-.016 | 4-1.0-.011 | |
| L. stipulacea | | 16-1.0-.028 | |
| L. virginica | | | 20-1.0-.037 |

(Appendix 10, cont.)

| | | | |
|---|---|---|---|
| Liatris cylindracea | | | 10-15.0-.054 |
| Lithospermum canescens | 5-1.0-.016 | | |
| Lobelia spicata | 5-1.0-.016 | | 60-1.0-.091 |
| Lonicera japonica | | 8-7.5-.053 | |
| Monarda fistulosa | | 60-2.6-.097 | |
| Panicum boscii | 25-2.0-.057 | | |
| P. flexile | | | 5-1.0-.015 |
| P. lanuginosum | | 4-1.0-.011 | 5-1.0-.015 |
| Penstemon brevisepalus | | | 5-1.0-.015 |
| P. laevigatus | | 4-1.0-.011 | |
| Physalis heterophylla | | 4-1.0-.011 | |
| Physostegia virginiana | | | 5-1.0-.015 |
| Polygala verticillata | | | 5-1.0-.015 |
| Potentilla simplex | 25-1.0-.049 | | |
| Prunella vulgaris | | 8-1.5-.019 | |
| Prunus serotina | | | 5-1.0-.015 |
| Pycnanthemum tenuifolium | | | 40-1.0-.064 |
| Quercus muhlenbergii | 5-1.0-.016 | | |
| Ratibida pinnata | | | 10-1.0-.022 |
| Rhus glabra | | | 5-1.0-.015 |
| R. radicans | | 4-1.0-.011 | |
| Rosa carolina | 10-3.0-.039 | | |
| Rubus, sp. | | 12-1.0-.022 | |
| Ruellia humilis | | 8-1.0-.017 | |
| Salvia lyrata | 15-1.0-.032 | 12-2.3-.029 | |
| Schizachyrium scoparium | 100-73.0-.707 | | |
| Senecio anonymus | 25-1.0-.049 | 24-1.0-.039 | 25-1.0-.043 |
| Silphium asteriscus | | 4-3.0-.022 | |

(**Appendix 10, cont.**)

| | | | |
|---|---|---|---|
| S. terebinthinacium | | | 40-2.0-.072 |
| Solidago canadensis var. scabra | 5-1.0-.016 | 12-3.7-.037 | 5-1.0-.015 |
| S. nemoralis | 10-1.0-.024 | 24-2.5-.047 | 20-1.0-.037 |
| S. rigida | | | 50-4.0-.101 |
| Sporobolus asper | | 100-76.4-.569 | |
| S. vaginiflorus | | | 100-28.0-.361 |
| Stytosanthes biflora | 10-1.0-.024 | | |
| Tridens flavus | 30-10.0-.125 | 20-3.8-.048 | |
| Trifolium repens | | 4-1.0-.011 | |
| Unknown forb | 20-1.0-.041 | | 55-1.0-.084 |
| Verbesina occidentalis | | 4-2.0-.016 | |
| Vernonia gigantea | 5-1.0-.016 | | |
| Viola sororia var. missouriensis | | 28-1.0-.042 | |
| V. triloba | 5-1.0-.016 | | |
| Vitis sp. | | 4-5.0-.032 | |

**Appendix 11. Frequency, mean cover (where they occur) and Importance Value 200 of species of the Mascot cedar-pine glade herb and herb-moss ecotone communities. Also shown is the mean cover of rock and soil where exposed (data from Finn 1968).**

| Site Mascot (16) | Glade | Cedar border |
|---|---|---|
| Plot number (size m$^2$) | 23(.093) | 24(.093) |
| Mean Cover (percent) | | |
| Rock and soil | 67 | 35 |
| Frequency-Mean Cover-Importance Value 200 | | |
| Agave virginica | 17.4-1.7-.112 | 12.5-0.6-.029 |
| Anemone virginica | | 8.3-0.3-.019 |
| Aristida purpurescens | | 8.3-3.4-.075 |
| Asclepias verticillata | 4.3-<0.1-.011 | |
| Ascyrum hypericoides | | 4.2-0.1-.012 |
| Aster oblongifolius | 43.5-3.0-.225 | 62.5-10.9-.304 |
| Croton moranthogynous | 17.4-0.3-.053 | 4.2-0.1-.009 |
| Desmodium ciliare | 13.0-1.6-.094 | 20.8-0.9-.052 |
| D. paniculatum | | 20.8-3.8-.104 |
| Diodia teres | 13.0-0.1-.037 | |
| Eragrostis capillaris | | 4.2-<0.1-.008 |
| E. spectabilis | 8.7-0.3-.030 | 4.2-0.3-.012 |
| Euphorbia corallata | 21.7-0.7-.096 | |
| E. dentata | | 4.2-0.1-.008 |
| E. nutans | 4.3-0.8-.043 | 8.3-0.3-.019 |
| Fragaria virginiana | | 12.5-1.0-.030 |
| Galium pilosum | | 4.2-0.1-.008 |
| Helianthus hirsutus | | 16.7-1.5-.057 |
| Houstonia purpurea var. calycosa | 13-0.1-.037 | 4.2-<0.1-.008 |
| H. purpurea x H. tenuifolia | 4.3-0.1-.013 | |
| Hypericum dolabriforme | 21.7-1.7-.133 | 12.5-2.2-.238 |
| H. punctatum | 13.0-0.3-.045 | 12.5-0.6-.033 |

(**Appendix 11, cont.**)

| | | |
|---|---|---|
| Isanthus brachiatus | 17.4-1.6-.105 | |
| Lespedeza cuneata | | 4.2-<0.1-.008 |
| L. virginica | 8.7-0.2-.027 | 4.2-0.1-.010 |
| Linum sulcatum | 8.7-0.1-.024 | 8.3-0.1-.018 |
| Lithospermum canescens | | 8.3-0.1-.019 |
| Lonicera japonica | | 4.2-0.7-.053 |
| Opuntia humifusa | 4.3-.05-.030 | |
| Panicum anceps | | 4.2-0.7-.020 |
| P. flexile | 21.7-0.3-.083 | 25.0-1.0-.061 |
| P. sp. | | 4.2-<0.1-.008 |
| Potentilla recta | 8.7-0.2-.027 | 8.3-0.3-.019 |
| Prunella vulgaris | 4.3-0.1-.014 | 45.8-3.1-.135 |
| Rosa sp. | 4.3-0.1-.013 | |
| Rudbeckia fulgida | | 4.2-1.1-.026 |
| Ruellia humilis | 82.6-6.4-.453 | 75.0-6.7-.253 |
| Schizachyrium scoparium | 4.3-0.2-.016 | 12.5-0.7-.034 |
| Scleria oligantha | | 33.3-1.3-.081 |
| Sisyrinchium albidum | 4.3-<0.1-.011 | |
| Solidago nemoralis | 8.7-0.1-.026 | 45.8-2.5-.124 |
| Sporobolus asper, S. clandestinus | | 37.5-5.2-.158 |
| S. vaginiflorus | 39.1-2.0-.175 | 16.7-0.3-.033 |
| Stylosanthes biflora | | 4.2-0.2-.011 |
| Viola pedata | | 4.2-0.2-.010 |

**Appendix 12. Frequency, mean cover (where they occur) and Importance Value 200 of species of three Georgia Ridge and Valley barrens. Also shown is the frequency and mean cover (where it appears) of bedrock, gravel, soil, bryophytes, lichens and tree litter.**

| Site (number) | Ft. Oglethorpe High School (119) | Rt. 146 at 218 Barren (117) | Rt. 138 (92) |
|---|---|---|---|
| Plot number (size m$^2$) | 30 (0.25) | 20 (0.25) | 20 (0.25) |
| Frequency-Mean Cover | | | |
| Rock and soil | 3-5.0 | | |
| Bryophytes - Algae | | 30-16 | |
| Lichens | | 5-5 | |
| Frequency-Mean Cover-Importance Value 200 | | | |
| Acalypha graciliens | | 5-1.0-.014 | |
| Allium cernuum | 17-1.0-.041 | 10-1.0-.023 | |
| Andropogon gerardii | 20-47.0-.121 | | |
| Aristida purpurescens | 7-1.0-.019 | 15-1.0-.032 | 10-1.0-.023 |
| Aster dumosus | 7-1.0-.019 | 20-1.0-.041 | 15-1.0-.033 |
| Berchemia scandens | 13-3.0-.040 | 10-5.0-.043 | |
| Bouteloua curtipendula | 23-34.0-.179 | 50-35.0-.262 | |
| Commandra umbellata | | 15-1.0-.032 | |
| Croton capitatus | | 5-1.0-.014 | 5-1.0-.014 |
| C. monanthogynus | 26-1.0-.061 | 5-1.0-.014 | 5-1.0-.014 |
| Galactia volubilis | 13-1.0-.033 | 10-1.0-.023 | 5-1.0-.014 |
| Gaura filipes | 20-1.0-.048 | | |
| Helianthus hirsutus | | 5-1.0-.014 | |
| H. occidentalis | | 25-1.0-.050 | |
| Heliotropium tenellum | | 5-1.0-.014 | |
| Hypericum dolabriforme | 10-3.0-.033 | | |
| Juniperus virginiana | 3-1.0-.011 | | |
| Liatris cylindracea | | 65-2.0-.128 | |
| L. spicata | 10-1.0-.026 | 12-1.0-.026 | 10-1.0-.023 |

(Appendix 12, cont.)

| | | | |
|---|---|---|---|
| Lobelia spicata | | | 5-1.0-.014 |
| Lonicera japonica | 3-1.0-.011 | | |
| Panicum flexile | 17-1.0-.041 | 60-1.0-.112 | 45-1.0-.091 |
| P. microcarpon | 7-1.0-.019 | 5-1.0-.014 | 5-1.0-.014 |
| P. virgatum | 20-65.0-.288 | | 15-90.0-.396 |
| Petalostemum gattingeri | | | 15-1.0-.033 |
| Pinus taeda | | 5-1.0-.014 | 5-1.0-.014 |
| Physostegia virginiana | 3-1.0-.011 | | 40-2.1-.087 |
| Potentilla simplex | 3-1.0-.011 | | |
| Prunella vulgaris | 3-1.0-.011 | | |
| Quercus falcata | | 5-1.0-.014 | |
| Ratibida pinnata | 7-3.0-.026 | | |
| Rosa carolina | 7-1.0-.019 | 30-1.0-.058 | |
| R. setigera | 13-1.0-.033 | | |
| Rudbeckia fulgida | 36-1.0-.083 | 5-1.0-.014 | 65-6.4-.152 |
| Schizachyrium scoparium | 43-40.0-.245 | 50-36.0-.267 | 75-44.7-.328 |
| Senecio anonymus | 3-1.0-.008 | | |
| Setaria geniculata | 23-1.0-.055 | | 20-.62.8-.295 |
| Silphium pinnatifidum | | 15-10.0-.077 | 50-7.1-.126 |
| Smilax bona-nox | | 10-1.0-.023 | |
| Solidago ptarmicoides | 17-1.0-.041 | 15-1.0-.032 | 35-1.0-.072 |
| Sorghastrum nutans | 17-43.0-.199 | 60-21.0-.211 | |
| Sporobolus heterolepis | 23-6.0-.074 | 10-70.0-.365 | |
| S. vaginiflorus | 30-1.0-.070 | 5-1.0-.013 | 55-12.5-.158 |
| Tragia cordata | 10-1.0-.026 | 5-1.0-.014 | 10-1.0-.023 |
| Unknown forb | | 25-1.0-.050 | 20-6.8-.067 |
| Viola sp. | | | 5-1.0-.014 |

**Appendix 13. Frequency, mean cover (where they occur) and Importance Value 200 of species of three Georgia Ridge and Valley barrens. Also shown is the frequency and mean cover (where it appears) of bedrock, gravel, soil, bryophytes, lichens or tree litter.**

| Site (number) | Powerline Rt. 218 (128) | Powerline Rt. 218 (128) | Vinyard Alexander Rd. (130) |
|---|---|---|---|
| Plot Number (size m$^2$) | 15 (0.5) | 30 (0.5) | 15 (0.5) |
| Frequency - Mean Cover | | | |
| Rock/gravel | 7-20.0 | 10-28.3 | 20-13.3 |
| Gravel/soil | | | |
| Soil | | 3-5.0 | 07-15.0 |
| Bryophytes | | | 27-25.0 |
| Lichens | | | 07-05.0 |
| Frequency - Mean Cover - Importance Value 200 | | | |
| Agave virginica | | 6-1.0-.017 | 20-1.0-.035 |
| Agrimonia pubescens | | 3-1.0-.010 | |
| Allium cernuum | | 20-1.0-.049 | |
| Ambrosia artimisiifolia | | 6-1.0-.017 | |
| A. bidentata | | 6-1.0-.017 | |
| Andropogon gerardii | 20-37.3-.278 | 60-35.9-.255 | 13-75.0-.297 |
| A. gyrans | | 3-5.0-.023 | |
| Anemone virginica | | 6-1.0-.017 | |
| Antennaria plantaginifolia | | | 7-1.0-.015 |
| Asclepias verticillata | | | 7-1.0-.015 |
| Aster dumosus | | 9-1.0-.024 | 27-2.0-.046 |
| A. patens | | | 13-1.0-.024 |
| A. pilosus | 53-13.4-.239 | | |
| Baptisia australis | | 6-10.5-.049 | |
| Berchemia scandens | | 37-8.4-.112 | |
| Bidens sp. | 7-10.0.079 | | |

**(Appendix 13, cont.)**

| | | | |
|---|---|---|---|
| Bouteloua curtipendula | | 3-20.0-.073 | 40-31.7-.179 |
| Campsis radicans | 7-1.0-.027 | | 7-1.0-.015 |
| Carex sp. | | 3-1.0-.010 | |
| Cassia fasciculata | | 9-1.0-.024 | |
| C. nictitans | | 9-1.0-.024 | |
| Ceanothus americanus | | 9-5.0-.037 | |
| Cercis canadensis | | 13-14.0-.076 | |
| Commandra umbellata | | 23-1.1-.056 | |
| Composite, unknown | 07-1.0-.027 | | |
| Cornus florida | | 3-50.0-.172 | |
| Crotalaria sagittalis | | 13-1.3-.034 | |
| Croton capitatus | | | 27-1.0-.046 |
| C. monanthogynus | | 9-1.0-.024 | 60-1.0-.096 |
| Danthonia spicata | | 3-10.0-.040 | |
| Desmanthus illinoensis | 13-5.5-.071 | 3-1.0-.010 | |
| Desmodium ciliare | | 9-1.0-.024 | |
| D. dillenii | | 3-1.0-.010 | |
| Dicot, unknown | 07-1.0-.027 | 9-1.0-.024 | 20-1.0-.046 |
| Diodia teres | | | 13-1.0-.024 |
| Diospyros virginiana | | 6-1.0-.017 | |
| Elymus virginicus var. glabriflorus | | 3-1.0-.010 | |
| Eragrostis spectabilis | | 3-1.0-.010 | |
| Eupatorium altissimum | | 3-1.0-.010 | |
| Euphorbia nutans | | | 7-1.0-.015 |
| Fraxinus americana | 07-5.0-.050 | | |
| Galactia volubilis | | 37-1.0-.087 | 27-1.0-.046 |
| Gaura sp. | | 23-2.9-.062 | |
| Helianthus hirsutus | | 23-1.6-.057 | 40-1.0-.066 |

**(Appendix 13, cont.)**

| | | | |
|---|---|---|---|
| H. mollis | | 03-1.0-.010 | |
| Heliotropium tenellum | | | 7-1.0-.015 |
| Houstonia longifolia | | 9-1.0-.024 | 7-1.0-.015 |
| Hybiscus sp. | 07-1.0-.027 | | |
| Hypericum denticulatum | | 3-1.0-.010 | |
| H. dolabriforme | | | 33-1.0-.055 |
| Ipomoea pandurata | 07-1.0-.027 | 13-3.0-.040 | |
| Juniperus virginiana | | 9-1.7-.027 | 7-1.0-.015 |
| Lespedeza cuneata | 07-8.0-.024 | 9-1.0-.024 | |
| L. procumbens | | 9-1.0-.024 | |
| L. repens | | 6-1.0-.017 | |
| L. virginiana | | 3-1.0-.010 | |
| Liatris sp. | | 9-1.0-.024 | |
| Ligustrum vulgare | 07-1.0-.027 | 3-3.0-.017 | |
| Linum sulcatum | | | 7-1.0-.015 |
| Lithospermum canescens | | 3-1.0-.010 | |
| Lobelia spicata | | 9-1.0-.024 | 7-1.0-.015 |
| Lonicera japonica | | | 7-1.0-.015 |
| Lysimachia lanceolata | | 3-1.0-.010 | |
| Monarda fistulosa | 07-1.0-.027 | 13-2.0-.037 | |
| Oxalis stricta | | 3-1.0-.010 | 7-1.0-.015 |
| Panicum anceps | 07-1.0-.027 | 9-8.3-.049 | |
| P. annulum | | 33-1.0-.078 | |
| P. flexile | | 3-1.0-.010 | |
| P. lanuginosum | | 9-1.0-.024 | 7-1.0-.015 |
| P. laxiflorum | | 3-1.0-.010 | 7-1.0-.015 |
| P. microcarpon | | 6-1.0-.017 | |
| P. oligosanthes | | 6-1.0-.017 | |

(Appendix 13, cont.)

| | | | |
|---|---|---|---|
| P. virgatum | 100-71.3-.717 | 37-9.9-.117 | |
| Parthenium integrifolium | | 3-1.0-.010 | |
| Paspalum setaceum var. ciliatifolium | | | 7-1.0-.015 |
| Petalostemum gattingeri | | | 7-1.0-.015 |
| Phlox amoena | | 6-1.0-.017 | |
| Pinus taeda | | 3-1.0-.010 | |
| Poa pretensis | | | 7-1.0-.015 |
| Poaceae, unknown | | | 7-1.0-.015 |
| Potentilla simplex | | 17-1.0-.042 | 7-1.0-.015 |
| Prunella vulgaris | | 3-1.0-.010 | 7-1.0-.015 |
| Prunus americana | | 17-1.0-.042 | |
| Pycnanthemum tenuifolium | | 23-1.0-.055 | |
| Quercus phellos | | 17-1.0-.042 | |
| Q. stellata | | 6-15.5-.065 | |
| Ratibida pinnata | | 3-1.0-.010 | 13-3.0-.031 |
| Rhus aromatica | | 3-20.0-.073 | |
| R. copallina | | 3-1.0-.010 | |
| R. radicans | | 6-3.0-.024 | |
| Rosa carolina | | 57-1.2-.134 | |
| R. setigera | | | 7-1.0-.015 |
| Rubus spp. | 20-7.0-.102 | 27-3.2-.073 | |
| Rudbeckia fulgida | | 30-2.4-.077 | |
| Ruellia humilis | | 30-1.0-.072 | 7-1.0-.015 |
| Salvia lyrata | | 9-1.0-.024 | |
| Schizachyrium scoparium | | 57-34.9-.245 | 80-32.1-.242 |
| Scleria sp. | | 27-1.0-.065 | |

**(Appendix 13, cont.)**

| | | | |
|---|---|---|---|
| Scutellaria elliptica | | 3-1.0-.010 | |
| Senecio anonymus | | 3-1.0-.010 | |
| Setaria geniculata | 13-1.0-.045 | | 7-10.0-.051 |
| Sida elliottii | | | 27-1.0-.046 |
| Silphium asteriscus | | 3-1.0-.010 | |
| S. pinnatifidum | | 30-3.9-.082 | |
| Smilax bona-nox | 07-1.0-.027 | 3-1.0-.010 | 7-1.0-.015 |
| Solanum caroliniense | 07-1.0-.027 | 3-1.0-.010 | |
| Solidago canadensis var. scabra | 20-3.7-.082 | 6-1.0-.017 | |
| S. nemoralis | | 20-1.0-.049 | |
| S. ptarmicoides | | 3-1.0-.010 | |
| S. rigida | | 80-4.6-.197 | |
| S. sp. | | 3-1.0-.010 | |
| Sorghastrum nutans | | | 7-20.0-.085 |
| Sporobolus asper | | | 47-37.9-.212 |
| S. heterolepis | | 23-42.8-.193 | |
| S. neglectus/vaginiflorus | | 9-1.0-.024 | 7-20.0-.085 |
| Symphoricarpus orbiculatus | | | 7-5.0-.029 |
| Tragia cordata | | 20-1.0-.149 | 7-1.0-.015 |
| Ulmus alata | | 9-1.0-.024 | 7-1.0-.015 |
| Vernonia gigantea | | 3-1.0-.010 | |
| Viola sp. | | | 7-1.0-.015 |
| Vitis sp. | | 3-20.0-.073 | |

**Appendix 14. Frequency, mean cover (where they occur) and Importance Value 200 of species of four Georgia Ridge and Valley gladelike sample areas. Also shown is the frequency and mean cover (where it occurs) of bedrock, gravel, soil, bryophytes, lichens, or tree litter.**

| Sites (numbers) | Vinyard-Alexander Rd. (131) | Ft. Oglethorpe High School (119) | Rt. 146 at Rt. 218 (118) | Rt. 146 at Rt. 218 (118) |
|---|---|---|---|---|
| Plot number (size $m^2$) | 10 (0.5) | 20 (0.25) | 20 (0.25) | 35 (0.5) |
| Frequency - Mean Cover | | | | |
| Bedrock and gravel | 80-51.3 | | | 83-43.1 |
| Gravel and soil | | 75-34.0 | 100-20.8 | |
| Soil | | | | 06-7.8 |
| Bryophytes | 40-68.8 | | 15-20.0 | 20-15.7 |
| Tree litter | | | | 26-6.0 |
| Frequency - Mean Cover - Importance Value 200 | | | | |
| Allium cernuum | | | | 14-2.8-.039 |
| A. sp. | | | 5-1.0-.020 | |
| Ambrosia artimisiifolia | 20-4.0-.100 | | | 3-1.0-.009 |
| Aristida dichotoma | | 25-11.0-.205 | | |
| A. purpurescens | | 5-1.0-.025 | | |
| Aster dumosus | | 25-1.0-.078 | 90-14.6-.337 | 77-4.1-.155 |
| A. pilosus | | | | 9-1.0-.020 |
| Belamcanda chinensis | | | | 3-2.0-.013 |
| Berchemia scandens | | | | 3-1.0-.009 |
| Bouteloua curtipendula | | | 15-36.7-.290 | 3-50.0-.217 |
| Coreopsis tinctoria | | | | 3-1.0-.009 |
| Croton capitatus | 80-1.0-.125 | | | |
| C. monanthogynus | 100-1.0-.052 | 5-1.0-.025 | 5-1.0-.020 | 60-1.0-.112 |
| Crotonopsis elliptica | 30-1.0-.059 | | | 6-2.0-.019 |

(**Appendix 14, cont.**)

| | | | | |
|---|---|---|---|---|
| Daucus carota | | | | 3-1.0-.009 |
| Dicots, Unknown | 30-1.0-.059 | | | 3-1.1-.010 |
| Diodia teres | 20-1.0-.045 | | | |
| Eleocharis compressa | | 5-1.0-.025 | | |
| Erigeron strigosus | | | 5-10.0-.081 | 17-6.0-.056 |
| Euphorbia nutans | 40-1.0-.072 | | | |
| Festuca pretensis | | | | 3-10.0-.047 |
| Galactia volubilis | | | 5-1.0-.020 | |
| Helianthus hirsutus | | | | 11-2.0-.028 |
| H. occidentalis | | | 30-9.3-.143 | |
| Heliotropium tenellum | 100-1.0-.152 | | | 9-1.0-.020 |
| Houstonia longifolia | 10-1.0-.032 | | | |
| Hypericum denticulatum | | | | 3-1.0-.009 |
| H. dolabriforme | 10-1.0-.032 | | | 31-46.5-.253 |
| H. sp. | | 15-5.0-.102 | 15-4.0-.066 | |
| Isanthus brachiatus | 80-1.3-.132 | | | 11-1.0-.026 |
| Lespedeza stipulacea | | | 10-2.0-.040 | 17-1.3-.037 |
| Liatris cylindracea/squarrosa | | | 5-10.0-.081 | 6-5.5-.034 |
| Lithospermum canescens | | | | 6-1.0-.015 |
| Lobelia spicata | | | 5-1.0-.020 | |
| Lonicera japonica | | | | 3-1.0-.009 |
| Panicum flexile | 30-2.3-.083 | 40-1.0-.117 | 5-1.0.020 | |
| P. sp. | | | | 3-1.0-.009 |
| Petalostemum gattingeri | 60-6.1-.194 | 10-3.0-.063 | 10-3.0-.046 | 26-17.0-.119 |
| Physostegia virginiana | | 15-1.0-.052 | | |
| Plantago aristata | | | | 9-1.0-.020 |
| P. virginica | | | | 9-1.0-.020 |
| Poaceae, unknown | | | | 9-1.0-.020 |

**(Appendix 14, cont.)**

| | | | | |
|---|---|---|---|---|
| Potentilla simplex | | | 5-1.0-.020 | 6-1.0-.015 |
| Ratibida pinnata | 10-5.0-.106 | | | |
| Rosa carolina | | | | 3-1.0-.009 |
| Rudbeckia fulgida | | 25-1.0-.078 | | 6-20.5-.098 |
| Ruellia humilis | 90-1.0-.139 | 5-1.0-.025 | 10-3.5-.050 | 29-3.2-.066 |
| Sabattia angularis | | 5-1.0-.025 | | 14-1.0-.029 |
| Schizachyrium scoparium | | 60-4.0-.204 | 45-12.2-.201 | 3-1.0-.009 |
| Senecio anonymus | | | | 14-1.0-.029 |
| Setaria geniculata | | 10-1.0-.038 | | 3-1.0-.009 |
| Sida elliottii | | | | 3-1.0-.009 |
| Silphium pinnatifidum | | | 20-10.0-.121 | |
| Solanum carolinense | | | 10-1.0-.033 | |
| Solidago ptarmicoides | | 20-1.0-.065 | 15-12.0-.121 | 3-1.0-.009 |
| Sporobolus asper | | | | 3-1.0-.009 |
| S. neglectus/vaginiflorus | 80-25.0-.572 | | | 94-31.5-.303 |
| S. vaginiflorus | | 90-46.0-.807 | 65-21.1-.315 | |
| Symphoricarpos orbiculatus | | | | 3-4.0-.022 |
| Unknown forb | | 20-1.0-.065 | 5-1.0-.020 | |
| Verbena simplex | | | | 9-1.0-.020 |
| Viola pedata | | | | 3-1.0-.009 |

# VEGETATION RESULTS FROM THE 1807-1810 LAND SURVEYS IN THE FIFTH SURVEY DISTRICT OF TENNESSEE

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**ABSTRACT. This is a study of floristic composition of forests extracted from metes and bounds survey records from the Fifth Survey District of East Tennessee. The surveys were made during the 1807-1810 period. It was found that the trees most often serving as survey corners were oaks. The moderately strong associates of the oaks were hickories and pines. On moist lower slopes or in draws, beech, maple and tulip poplars represented the mesic forests. Chestnut was not well represented. These proportions (except chestnut) are within a few percentages of 1931 or 1946 inventory values following which upward or downward trends, caused by disease and modern forest use, modify comparative percents. The taxonomic understanding of the red oak species was doubtless faulty among the surveyors. Comparison of species abundance between early surveyor records and modern inventories also is made more difficult by the reporting of species groups in both the surveys and the inventories.**

## INTRODUCTION

Vegetation ecologists seek to understand the causes of species and community distribution patterns using known environmental and historical facts (Mueller-Dombois and Ellenburg 1974). Present distributions may be markedly different from those of the recent past and reflect species and community range and structural disruption caused by modern and presettlement human land uses. The environmental relationships between species and community distributions may be logically sought from landscape records where disturbances have been minimal. This need for minimal disturbance records has fostered the use of species abundance data from old land surveys. These are of two types. The most commonly used are those of rectilinear surveys, including those of the Congressional land survey of the middle west (cf. Shanks 1953) and southeast (cf. DeSelm 1994). Metes and bounds surveys, with little or no chronological or geographic pattern between entries and with the difficulty in knowing the location of survey starting points, have been used less. Thus the latter survey records constitute a great untapped source of information about plants and community distributions of the survey period (DeSelm and Rose, in press).

This paper reports vegetation results gleaned from land surveys in the 1807-1810 period of East Tennessee and compares them with modern inventories. The area is the Fifth Survey District, which lies between the Tennessee and French Broad rivers and the Kentucky border (Crouch 1968; Figure 1).

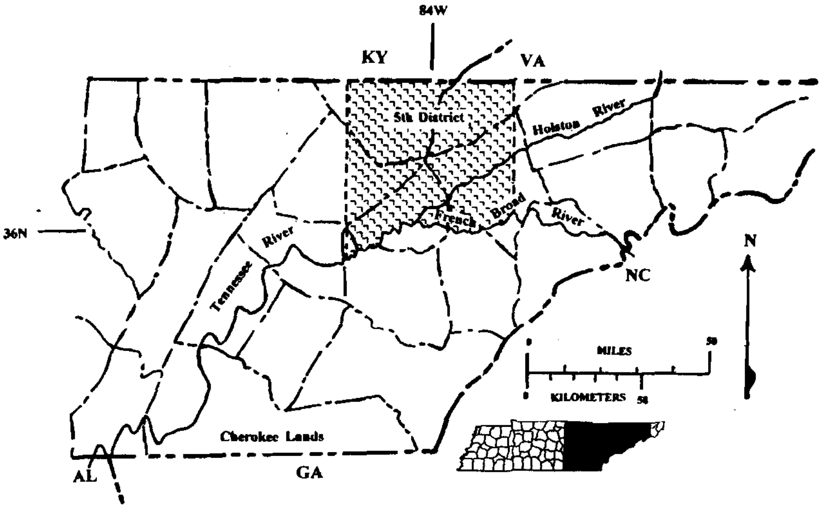

**Figure 1.** Part of East Tennessee showing the location of the Fifth Survey District. District boundaries are from Crouch (1968). Base map is interpreted from that of Lucas (1822). Boundaries are somewhat approximate, being based chiefly on legislation rather than a comprehensive survey. Some boundaries have changed by legislative action or by treaty since 1822.

## CHARACTER OF THE SURVEYED AREA

The Fifth Survey District was an approximately 2200-square-mile area centered at 36°15'N/83°30'W. It included all of the present Claiborne and Union counties, most of Grainger, Jefferson, and Knox counties, the eastern portions of Anderson and Campbell counties, and the western portions of Hamblen and Hancock counties, Tennessee. This is a moderately rugged area topographically, composed partly of the Cumberland Mountains and partly of the Ridge and Valley Provinces (Fenneman 1938). Elevations rise above 3500 feet on the west and northwest side in the Cumberlands; in the Ridge and Valley, elevations rise to above 2200 feet on Clinch and Powell mountains to about 1400 feet on most other ridges and fall to 800-1100 feet in the valleys.

Bedrocks of the Cumberland Mountains are chiefly Pennsylvanian sandstones and shales. Ridges in the Ridge and Valley extend northeast-southwest and are underlain by several Silurian, Ordovician, or Cambrian sandstones or Ordovician and Cambrian dolomites. Several Ordovician and Cambrian shales weather to knob, rolling, or valley topography. The Ordovician Chickamauga limestone also weathers to valleys (Rodgers 1953, Hardeman 1966).

Soils of the Cumberlands are mainly Dystrochrepts and are usually steep, rocky, sandy, often shallow, and acid. Soils of the Valley sandstone ridges are similar. Soils of the limestone valleys are chiefly Hapludalfs--some of these are very shallow and stony. Soils of the dolomitic ridges and rolling lands are chiefly Paleudults--usually very deep but they may be cherty. Rolling to valley landscapes derived from shales are Eutrochrepts, Hapludults, and Paleudults and may be steep to shallow sloped, stony or not so, loamy or clayey, shallow or deep, and acid or calcareous (at least at depth). Everywhere the major and most minor streams have deposited alluvial flood plains and terraces where soil materials are deep enough that bedrock does not influence the soils. These soils are Paleudults, Haplaquepts and Haplaquents; they may be quite fertile and moist but may be poorly drained (Springer and Elder 1980).

Climate is of the warm tempetate type (Dickson 1960). Tornado winds are rare (Vaiksnoras 1971) but winter and spring flooding (Tennessee Valley Authority 1957) and growing season droughts are common (Safley and Parks 1974).

The flora of the area is well known (Wofford and Kral 1993). General descriptions of the vegetation are found in Braun (1950), DeSelm (1984), Hinkle *et al.* (1993), and Stephenson *et al.* (1993). The forest communities were examined in detail in Knox and adjacent counties (Hinkle 1975, Martin 1971, 1978, Martin and DeSelm 1976). Barrens and glades were studied by DeSelm (1993) and Finn (1968). Most forests examined were dominated by oaks (*Quercus* spp.); of these *Q. prinus* dominated ridges and *Q. alba* dominated open slopes. On some ridges, oaks were replaced by pine forests (*Pinus* spp.). On shallow or pan soils, *Q. stellata* was dominant and such stands vary, with shallower soils, to stands dominated by *Pinus* and *Juniperus*, and these, on even more shallow soils, were replaced by open glades and barrens. Also sometimes barrens occurred as the result of regular fires. Ravine forests were dominated by mesic species such as *Fagus grandifolia, Liriodendron tulipifera, Fraxinus americana*, and others. Floodplains and flat terrace were forested by swamp taxa of several kinds.

## HUMAN HISTORY OF THE AREA

The area was occupied by Native Americans not long after the end of the last Pleistocene cold period. Hunter-gatherers (Paleoindians) were replaced by more sedentary types who established villages, fields, and cemeteries and moved over land from place to place using the large animal trails already in existence. While habitat destruction occurred near the villages, which were chiefly along major rivers, hunters and herb gatherers ranged widely and employed the use of fire which modified habitats on slopes above the river terraces (Hudson 1976, Lewis and Kneberg 1958, Williams 1989).

European-Americans entered the area about 1780 to establish settlements. Treaties with Native Americans during the period 1770-1791, the First Treaty of Tellico of 1798 and the Third Treaty of Tellico of 1805, made land available (Folmsbee *et al.* 1969). Bottoms and other gentle topography were cleared and drained for agricultural use. Most slopes were logged for farm wood, pastured, and burned (surface fires) in the spring to increase stock forage (Killebrew *et al.* 1874, DeSelm 1993). Surveying and settlement of the best lands proceeded rapidly; surveys were registered in the District Survey Office in Knoxville. By 1790, the human population of the State was only 35,691, but by 1950, it had risen to 3.2 million--with proportional land use conversions (Brunsman 1951).

## NATURE OF THE RECORDS AND METHODS

The Survey Book for the Fifth Survey District for the period 1807-1810 was found in the Special Collections of the Library, University of Tennessee, Knoxville. Surveyors recorded topography but it was seldom linked to a particular plant species. Trees were recorded by name, rarely as dead, as a stump, as being forked, or rarely as "a bunch of" (probably) stump sprouts. "Bunches" of sycamores, poplars, lynns, maples, and dogwoods were noted. Trees already "marked" (chopped) sometimes were recorded at the adjacent property line. Surveys ran to Walker's line, the Kentucky border, and across an Indian path.

Surveys were of the metes and bounds type. Irregular shapes were usual and starting points were generally relative to a previous survey boundary point. Mostly surveying was done from tree to tree, but some stakes were recorded instead of trees. Distances were in poles or chains and apparently both 33 and 66 foot chains were used (Rose 1993). Distances between named tree corners were generally so large that rarely did all trees fall within one community type. Occasionally it was noted that when two surveys were sequentially recorded, the corner trees from the first survey were repeated in the second. These duplications were eliminated from the data. No tree diameters nor point-to-tree distances were given. Since the precise location of so few surveys is known, no attempt was made to follow survey lines on the ground. Fifty species or species groups are recorded in the data. About 70% can be distinguished to a single, modern, known species; the other survey names represent groups of species. A total of 455 surveys were used, yielding 3143 named plant stems. These records form the basis of this study.

Using stem density per acre in Hinkle (1975) and McCarthy (1976), an average stem density of 101,000 per square mile is calculated. The survey sample of 3143 stems in 2200 square miles of the Fifth District calculates to 1.4 trees per square mile. Surely this is a very small sample of the forest trees.

## RESULTS

For many species and/or species groups, no modern abundance data is available in the District (Appendix). Such species as *Asimina triloba*, which are generally common understory small trees, are not sampled in timber inventories because of their size. Uncommon species, as *Aesculus octandra,* are reported as part of "other" or "other hardwoods." Such survey taxa as *Malus pumila* (apple) and *Prunus persica* (peach) were probably planted but *Prunus* (cherry and plum) includes nearly a dozen native and now naturalized shrub and tree taxa (Wofford and Kral 1993), but I have no good basis for knowing which taxa were included in the surveyor names.

In some taxa percentages have changed little between the survey and the last inventory used here; these include *Fraxinus, Liquidambar, Carya,* and *Platanus*. The beech-maple (*Fagus-*

*Acer*) combination used by Peterson has also varied only slightly but this is the result of the canceling of the loss of *Fagus* by the gain in *Acer rubrum*.

Another group of taxa had one to a few percentage increases between the surveys and later inventories. These were *Juniperus virginiana, Pinus* spp., and *Liriodendron tulipifera,* which all increase with forest disturbance or enter in old field succession (Burns and Honkala 1990, Smith 1968). Other increasers are *Nyssa sylvatica, Robinia pseudoacacia,* and *Acer rubrum*. The second of these (like *Pinus* spp.) may have been planted--but all increase with forest disturbance (Burns and Honkala 1990). The "increase" in *Quercus prinus*, a ridge dominant, may reflect the increased proportion of ridge forests among all sites available to modern inventories as other landforms pass into agricultural use, or it may reflect the low numbers of early surveys on the often stony ridges. It is also possible that the *Q. prinus* category includes *Q. muhlenbergii*, a species of shallow limestone soils. These forests, near cedar-pine glade and barren communities, may get little use and may be increasing proportionally as deeper soil sites are converted to agriculture. On the other hand, the "increase" in *Tsuga canadensis* may reflect the low numbers of narrow ravines surveyed. They may have been seldom surveyed because of their lack of value as crop fields. The ravines persist today and may form a larger proportion of available-to-sample forest land now than formerly.

The taxa which have declined in prominence, in the face of the increasers noted above, are the oaks (*Quercus* spp.). Both red and white oak group percentages have decreased. The percentage of *Juglans nigra* may have decreased because of its preference as furniture and gun stock wood. The large increase in the much-favored *Castanea* by 1931 was followed by its demise due to fungus disease (Hepting 1971).

Barrens were recorded in Grainger County between the Holston River and both Buffalo and Richland creeks. Bedrock here is Knox dolomite and certain calcareous shales and limestones on which barrens occur--though rarely (DeSelm 1993). These may have been fire-caused forest openings. In Claiborne County, west of Tazewell, the Taupak (spelling?) glade was recorded. Barrens and glades are known in the Tazewell area (DeSelm 1993), but this place-name cannot be located.

## DISCUSSION

Based on probable community presence from detailed studies by DeSelm (1993), Hinkle (1975), and Martin (1971), certain general classes of vegetation may be discerned from the survey data (Appendix). Surveyors were doubtless seeking out good land, sites with flat or low slope topography--so one could expect swamp and mesophytic taxa to be well represented. Indeed there were 5.4% swamp taxa and 17.2% mesophytes counted among the total.

The surveyors actually saw mostly oak forests; 50.9% of the trees were oaks; post oak and white oak suggest forests of gentle topography. The black oak category may have included scarlet oak common here on ridges and the mesophyte or xero-mesophyte northern red oak. In studies on mostly second growth forest stands in the Cumberland Mountains, Hinkle (1975) reported that 53% of community types there had black, scarlet, or northern red oaks as first or second dominant. The same kind of number from similar Ridge and Valley stands was 19%. In the Ridge and Valley, these species occurred on 80% of all landforms (Soil-Parent Material Units) and 90% of landforms above the bottomland hardwoods (Martin 1971). Clearly these were important and widespread species (then and now). A study of Middle Tennessee (DeSelm 1994) suggests that certain communities known from modern studies can be interpreted from survey records, indicating their long continuity. But the grouping of oak species, such as "black" oak in the surveys, impedes such understandings.

Problems also exist with the yellow pines. In 1807 the pines probably would have been prominent in glade and barren borders, and on steep slopes or ridges and in disturbed areas. The low percentage of cedar, chinquipin oak, redbud and red elm suggests that glade and barren borders were rarely surveyed. Thus, the pines probably occurred chiefly in pine or oak-pine communities; Hinkle (1975) and Martin (1971) saw pine as the first or second dominant in seven percent of the communities that they sampled. Dr. Thomas Walker had seen ridge pine in 1750 in upper East Tennessee (Walker's Journal, in Williams 1928). Also, lands disturbed by lightning and by fires set by Native Americans, where pines invade, are well known (Williams 1989).

The hickory group, composed of species that range from wet mesic to xeric sites, doubtless occurred across the landscape as they do today. Martin (1971) and Hinkle (1975) found them first or second dominant in 19 and 20% of their community types, respectively.

The low percentages of chestnut oak, sourwood and blackgum argues for little surveying on the xeric ridgetops. In the Cumberlands, Hinkle (1975) found 27% of the stands with chestnut oak first or second dominant. In the Ridge and Valley, the comparable figure was 31% (Martin 1971). But chestnut was seldom used as a corner in the early surveys (1.9%, only 17% of hickory and 28% of pine). This suggests that chestnut and chestnut oak grew together on the little surveyed ridges. But in second growth Ridge and Valley stands, Martin (1971) found chestnut stumps or sprouts in 68% of his types which had a much wider site distribution than ridgetops. This disparity of percentages is not understood.

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**Appendix. Data showing percentages of species and species groups for Survey District 5; the average of Anderson, Grainger and Hancock counties from Peterson data of 1931 in Woolrich (1934) and Woolrich and Neeley (1934a, 1934b), the average composition in Anderson, Campbell, Claiborne, Grainger, Hamblen, Hancock, Jefferson, Knox, and Union counties in Cowan (1946) and average composition in Campbell County (Tennessee Valley Authority 1967), the Anderson-Knox-Union county unit (Tennessee Valley Authority 1964), Grainger County (Tennessee Valley Authority 1961a), Hancock County (Tennessee Valley Authority 1961b) and Claiborne County (Tennessee Valley Authority 1960).**

| | District 5 | Peterson 1931, Anderson, Grainger and Hancock cos. | Cowan 1946 | TVA 1960-67 |
|---|---|---|---|---|
| Apple (Malus pumila, also two native crabapples are possible) | 0.1 | | | |
| Ash (Fraxinus, F. americana is most common) | 2.1 | 1.7[a] | | 1.9 |
| Ash, white (Fraxinus americana) | 0.1 | | | |
| Beech (Fagus grandifolia) | 4.0 | 9.2[b] | 4.5 | 1.7 |
| Buckeye (Aesculus octandra) | 0.4 | | | |
| Cedar (Juniperus virginiana) | 0.2 | | 1.5 | 3.5 |
| Cherry (Prunus serotina probably, six other native and now naturalized cherries are possible) | 0.2 | | | |
| Chestnut (Castanea dentata, possibly also C. pumila) | 1.9 | 13.5 | | |
| Cucumber (Magnolia acuminata) | 0.2 | | | |
| Dogwood (Cornus florida probably, four other species occur) | 3.7 | | | |
| Elm (Allum, Ulmus, five species occur) | 1.1 | | | |
| Elm, red (Ulmus rubra) | 0.1 | | | |
| Gum (Liquidambar styraciflua probably) | 0.1 | | 0.4 | |
| Gum, black (Nyssa sylvatica) | 0.5 | | 2.6 | 2.3 |
| Hackberry (Celtis, three species occur) | <0.1 | | | |
| Hickory (Carya, eight species occur) | 11.3 | 5.6 | 12.8 | 12.3 |
| Hornbeam (Carpinus caroliniana) | 0.2 | | | |
| Ironwood (Ostrya virginiana) | 0.2 | | | |
| Linden (Linn, Lynn, Tilia heterophylla, T. americana) | 1.3 | | | |
| Locust (Robinia pseudoacacia and/or Gleditsia triacanthos) | 0.5 | | | 1.3 |
| Maple (Acer rubrum, A. saccharinum) | 0.6 | | | 3.2 |
| Maple, boxelder (Acer negundo) | 0.1 | | | |
| Maple, sugar (Acer saccharum, A. nigrum) | 2.8 | | | 1.5 |
| Mulberry (Morus rubra) | 0.4 | | | |
| Oak (Quercus spp.) | 0.2 | | | |
| Oak, blackjack, jack oak (Quercus marilandica) | 0.1 | | | |

## Appendix (cont.)

| | | | | |
|---|---|---|---|---|
| Oak, black (Quercus velutina, perhaps also Q. coccinea, Q. shumardii, rubra) | 16.7 | | | |
| Oak, chestnut (Quercus prinus) | 0.8 | | | 9.6 |
| Oak, chinquipin (Quercus muhlenbergii) | 0.2 | | | |
| Oak, post (Quercus stellata) | 15.4 | | | |
| Oak, Spanish (Quercus falcata) | 2.3 | | | |
| Oak, swamp white (Quercus bicolor) | <0.1 | | | |
| Oak, water white (Overcup oak, Quercus lyrata) | <0.1 | | | |
| Oak, water (Quercus sp.) | 0.1 | | | |
| Oak, white (Quercus alba) | 14.9 | | 13.9 | 7.1 |
| Pawpaw (Asimina triloba) | <0.1 | | | |
| Peach (Prunus persica) | 0.1 | | | |
| Persimmon (Diospyros virginiana) | 0.3 | | | |
| Pine (Pinus, five species occur) | 6.7 | 10.4[c] | 10.6 | 19.4 |
| Pine, white (Pinus strobus) | | 3.0[d] | | |
| Plum (Plumbush, Prunus, five native plums occur) | <0.1 | | | |
| Poplar (Tulip tree, Liriodendron tulipifera) | 3.4 | 12.4 | 9.3 | 10.0 |
| Redbud (Cercis canadensis) | 0.2 | | | |
| Sassafras (Sassafras albidum) | 0.5 | | | |
| Serviceberry (Service, Amelanchier arborea) | <0.1 | | | |
| Sourwood (Sowerwood, Oxydendrum arboreum) | 0.4 | | | |
| Spicewood (Spicebush Lindera benzoin) | <0.1 | | | |
| Spruce pine (Eastern hemlock, Tsuga canadensis) | <0.1 | 3.8 | | 3.5 |
| Sycamore (Platanus occidentalis) | 0.4 | | | 0.4 |
| Walnut (Black walnut, Juglans nigra) | 2.2 | | | 1.2 |
| Walnut, white (Juglans cinerea) | 0.3 | | | |
| Oaks, total | 50.9 | 40.4 | 19.3 | 29.7 |
| Beech and all maple | 7.4 | 9.26 | 7.7 | 6.4 |
| Ash, total | 2.2 | 1.7 | | 1.9 |
| Maple, total | 3.5 | | 3.2 | 4.7 |
| Oaks, "red" | 1.8 | | 5.4 | 13.0 |
| Oaks (Erythrobalanus) | 20.9 | | 5.4 | 13.0 |
| Oaks (Lepidobalanus) | 31.4 | | 13.9 | 16.7 |

[a] Anderson County only
[b] Beech-Maple, Anderson County only
[c] Yellow pines
[d] Grainger and Hancock counties

# VEGETATION RESULTS FROM EARLY LAND SURVEYS OF NORTHERN SEVIER COUNTY, TENNESSEE

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**ABSTRACT. Metes and bounds surveys from the 1806-07 and the 1824-30 period were used to reconstruct forest composition in northern Sevier County, Tennessee, during those periods. Percentage composition agreement between those and modern inventories is relatively good. Oak, oak-hickory, and oak-pine forests prevailed on most upland sites. Ravines contained mixed mesophytic forests seen in the coves of the Ridge and Valley, and stream and river border forests are suggested by some surveys. Non-forested corners occurred but were rare.**

## INTRODUCTION

The cover of vegetation on the landscape at or near the time of settlement is of interest to field scientists. Information of this type is used by anthropologists (Chapman and Shea 1981), historians (Williams 1989), paleoecologists (Delcourt *et al.* 1986), pedologists (Jenny 1980), and vegetation biomass modelers (Waring and Schlesinger 1985). The information is of particular interest to vegetation ecologists who interpret present vegetation in terms of known environmental and historical factors (Mueller-Dombois 1974). Old land surveys are useful in establishing vegetation pattern (Shanks 1953, Lindsey *et al.* 1965) because of line descriptions and the naming of trees or recording of other vegetation features at prescribed regular intervals.

Congressional Land Survey records have been used extensively in *e.g.*, midwestern vegetation, with considerable success (Gordon 1969, Inverson *et al.* 1989, Lindsey *et al.* 1965). Somewhat 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 are relatively easy to use compared to metes and bounds surveys, which records have less chronological and geographic pattern. Metes and bounds survey records have been little used in early vegetation study and, as such, constitute a great untapped wealth of knowledge of plant distribution during the survey period.

This paper reports the vegetation results from early metes and bounds surveys in a 45-square-mile area of northern Sevier County, Tennessee, and compares them to those of modern systematic inventories. The survey district is that area "South of the French Broad and Holston Rivers" (Crouch 1968). The study area centers at about 35°15' N and 83°37' W and is included in the Boyds Creek, Douglas Dam, Pigeon Forge, Shooks Gap, Walden Creek and Wildwood U.S.G.S. 7.5 minute quadrangles (Figure 1). Reported here is the average forest composition seen by surveyors in the study area. They are compared with results from more modern inventories.

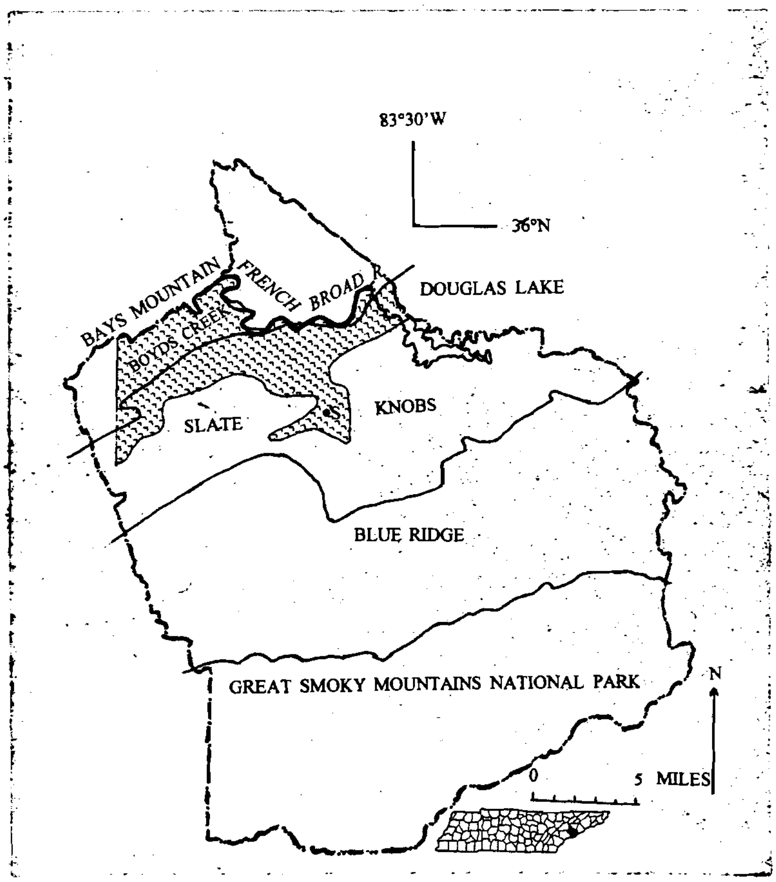

**Figure 1. Map of Sevier County, Tennessee, showing approximate location (hachured) of surveyed area (after Rose 1993). Boyds Creek is the Boyds Creek-Dry Creek-Gap Creek drainages. Slate Knobs and Blue Ridge boundaries are from Rodgers (1953). S is location of Sevierville. Base from Tennessee Department of Transportation map of Sevier County, 1990, scale 1/125,000.**

## Character of the Surveyed Area

The study area is within the Ridge and Valley Province (Fenneman 1938). The surveys lie south of the French Broad River and Bays Mountain and extend south toward the edge of the Blue Ridge Province. Elevations vary from about 870 to 1170 feet, but higher elevations occur to the north (Bays Mountain to 1340 feet), and to the south (Great Smoky Mountains to 6643 feet). Drainage is to the north and east to the French Broad River by way of the Pigeon River and smaller streams. The northern half of the area is the Boyds Creek-Dry Creek-Gap Creek valley and the southern half is called the "slate knobs."

Geologic beds in the Boyds Creek-Dry Creek-Gap Creek valley are the Knox Group consisting of five named dolomitic limestone members, and the Conasauga Group consisting of six named limestone, and calcareous and dolomitic shale members. Most of these members are narrow beds with little topography and are partly overlain by alluvium of various ages (Swingle *et al.* 1967). The knobs to the south constitute a much dissected topography underlain by calcareous shale with some sandstone and calcareous sandstone, the Tellico Formation (King 1964).

The Dandridge silt loam and shaley silt loam cover the slate knobs; slopes are 12-60%, profiles are 10-30 inches deep, are well to excessively drained and are about neutral. This series is an Alfic Eutrocrept. In the Boyds Creek-Dry Creek-Gap Creek valley lie the Fullerton silt loam and silty clay loam soils which may be cherty; slopes are 5-60%, profiles extend to 40 or more inches, and they are generally well drained and acid. Occurring with the Fullerton is the Dewey silty clay loam derived from old limestone alluvium or valley fills; it is a well drained acid soil with low slope angles. The Decatur silty clay loam is a similar soil derived from old limestone valley fill; it has slopes of 12-60%. The above three soils series are Paleudults. Other soils of this area include high river terrace soils, the Cumberland silty clay loam, the Waynesboro loam, and the Holston loam--all Paleudults. Low terrace and flood plain soils (of the knobs and northward) are the Whitesburg silt loam, Hamblen silt loam, Congaree loam, Staser fine sandy loam and Sequatchic fine sandy loam. These soils are Eutrochrepts, Hapludolls and Hapludults (Hubbard *et al.* 1956).

Woody floras of the study area are well known (Wofford and Kral 1993). Studies of forest vegetation include the general statements of Braun (1950), DeSelm (1984), and Stephenson *et al.* (1993). The Tennessee Valley Authority (1941) maps upland hardwood (chiefly oak forests), yellow pine hardwood, and cedar-hardwood types in the area. Martin (1971, 1978) and Martin and DeSelm (1976) sampled forests in a six-county area of the Ridge and Valley, including Sevier County. Martin (1971, 1978) found white oak and chestnut oak forests commonly on upland landforms similar to those of the study area. He also found mixed mesophytic, white pine, Virginia pine, northern red oak, southern red oak, black oak, and swamp community types on landforms somewhat similar to those of northern Sevier County.

Parts of the Ridge and Valley, in and around the study area, were occupied by Native American cultures at least 10,000 years PB (Archaic culture) but these were preceded by Paleoindian hunters. Later cultures had settlements along major streams while the uplands were used for hunting and gathering (Hudson 1976). Small bands of Cherokee apparently lived/camped in the study area (Matthews 1960). Following the Battle of Boyds Creek in 1780, white settlement began (Matthews 1960). An Entry Office (land claim) was opened in Knoxville in 1806 (Rose 1993) and settlement followed. Forests were cleared in the valleys and row crops were cultivated. Slopes were logged for farm timber and the forests were grazed (DeSelm 1993).

## METHODS

Rose (1993) acquired the land survey records for this area from the Tennessee State Archives and Library, Nashville, in photocopy form. Using natural landform features and adjoining ownership on the several distance and angle calls per survey, Rose was able to reconstruct the location of 195 surveys chiefly from the 1806-1807 and 1824-1830 periods (Rose 1993). These are supplemented here by data from 53 other surveys, locations of which were known less precisely. The citation of tree names at survey corners makes compilation of an average forest composition possible. Tree (and some shrub) stems totalled 2438 in 148 surveys.

The study area has been part of the land of four separate governments since 1780, each selling land: the State of North Carolina, the State of Franklin, the Territory South of the Ohio River, and the State of Tennessee. Conflicting and missing records abound but hand copying of surveyors' records in the office of the Secretary of State has saved many from destruction--as from the Sevier County Courthouse fire in 1855 (Rose 1993).

In each survey, generally recorded at corners was a tree, or rarely a rock, or more than one tree, or the edge of a stream or river. At about three corners per survey, a stake was recorded. Surveyors used the tools of the period, compass and a 33 or 66 foot chain. Nothing is known of the botanical qualifications of the surveyors. No point to tree distances nor tree diameters are given. No attempt has been made to find survey lines on the ground.

Percentage composition from all surveys is compared with composition of later inventories. U. S. Forest Service inventories have not been used because of "differences in standards of tree measurement" (Hedlund and Earles 1971) between the 1971 and earlier inventories. Also there are few "species" categories.

## RESULTS

The surveys record most of the streams currently mapped and named some which cannot be verified on available maps. The "poor valley" in the Gap Creek area of the survey is apparently Union Valley. Their geographic/topographic vocabulary included: branch, creek, fork, hill, hollow, knob, lick, mudlick, ridge, river, and spring. Trees were recorded simply by name though occasionally described as large, or sapling (saplin), or double, or stump, bush/sprout, or dead. Dead and burned trees are so rare in the surveys, however, as to suggest that they were not used as corners probably by reason of lack of permanence. Plants named in the surveys were usually overstory trees, but a few understory tree names appear in the records (as dogwood, *Cornus florida*). Shrubs as *Lindera benzoin*, "spicewood" appear rarely. Most individual surveys crossed landforms and a variety of soil series and are not expected to represent a single community type. Some surveys, however, included trees suggestive of upland oak, ravine, and river border communities.

The Appendix contains the probable scientific name corresponding to the plant names used by surveyors; spelling variations are noted. Note the high percentage composition of oak (*Quercus* spp.), pines (*Pinus* spp.), and hickories (*Carya* spp.) in the forests of the period. Oak percentage exceeds the sum of hickory and pine by more than two. The high percentage of *Quercus alba* and *Q. velutina* suggests the possibility of the occurrence of the *Quercus alba-Q. velutina* community type (as seen by Martin 1971) or of separate types dominated by each of these taxa (both also seen by Martin 1971). The percentage of *Quercus stellata* is nearly as high as that of *Q. velutina* suggesting its importance in the types noted above (seen by Martin 1971). Pines and hickories were also important associates of the oaks (as seen by Martin 1971). Taxa, such as *Fagus, Liriodendron, Acer saccharum,* and *Fraxinus americana*, which dominate more mesic sites, have percentages which reflect the restricted development of these sites. Taxa with even more restricted site requirements, *Aesculus, Tilia* and *Tsuga* are ever less common. Mesic types with these taxa were seen by Martin (1971). Other mesophytes, as *Lindera*, also occurred. Stream and river border taxa are uncommon but include *Acer negundo, Celtis* sp. *Platanus, Salix* sp. and *Ulmus* sp. in the survey records.

Comparison with percentages from later inventories are appended (probably none of these inventories included data from the Great Smoky Mountains National Park). Species which usually increase in abundance after forest disturbance appear in this record: *Acer rubrum, Carya* (apparently recovery is occurring), *Juniperus, Liriodendron, Pinus* and *Robinia*. Increase in *Pinus* and *Robinia* (1956, 1971) also may be due to planting. *Castanea, Quercus prinus* and *Tsuga* also appear to increase but this represents the difference in sampling area: The Surveys were chiefly from the less rugged landforms north of Sevierville, the later inventories through 1971 included the mountainous Blue Ridge southward to the edge of the Park.

The relatively constant pine percentage (Survey versus 1931 and 1945 inventories) during the period of settlement, forest cutting and conversion of much of the landscape to agricultural uses, suggests that there may have been some forest disturbances, as by Native Americans, prior to the surveys. The use of fire has been suggested (Delcourt *et al.* 1986) but fire evidence reported by surveyors was extremely rare.

Species whose abundance which have decreased are *Juglans nigra, Quercus alba, Q. stellata*, red oaks, all oaks, and hickories. These changes probably represent increased severity of logging in the slate knobs. Comparison of species and species groups between columns sometimes shows non-trend numbers for the 1931 and 1945 inventories; it seems possible that those were based on few sample plots compared to those later. The high red oak percentage in 1946 may be an example.

Non-forest vegetation was rarely seen in the surveys. The 1841 survey for G. W. Rogers and H. L. Andes note a "rock in an old field." While Indian old fields were occasionally seen by early explorers and settlers (Putnam 1859), this one is late enough to be a turned out (abandoned) field - a result of common agricultural practices of the period (Killebrew *et al.* 1874). The 1778 survey for Samuel Loomips notes a spot where, "the Indian Pathe crosses the same" (Boyds Creek). The path is the north-south Great Indian Warpath (Myer 1928). Abraham Swaggerty's survey of 1784 notes, "a long grassy glade above the spring" on Sinking Creek. Non-forested springs and licks are reported elsewhere (Putnam 1859) - the openings are believed to be the result of heavy use by large animals, Native Americans, and early American hunters.

## DISCUSSION

The absence of rectilinear Congressional type land surveys in Tennessee has limited attempts to reconstruct vegetation cover at the time of these early surveys (roughly the time of settlement). The 1807 survey data (DeSelm 1994) in southern Middle Tennessee is an exception; no such records have been found in East Tennessee. The use of metes and bounds surveys in this study is the first attempt at reconstruction of early forest composition in East Tennessee.

But what is there available with which to compare such information representing modern truth? Modern surveys are produced by two types of scientists for different purposes. The foresters (State and TVA) placed plots in all types of forest lands at rigidly determined distances. Martin (1971), on the other hand, sampled only selected old growth forests - the least disturbed that he could find. These represent the forest closest to those of the early survey. Martin recorded trees, overstory and understory, to species for a total of 23-40 taxa. The Tennessee Valley Authority reports data for some species and species groups for a total of 15-19 categories including two "other." Numbers of tree taxa of about 46 occur in the surveys and up to 40 per community occur in the Martin study; clearly these are the most comparable. But the survey includes categories (species groups) such as pine, hickory, red oak, willow, and elm; each of these contain multiple species making comparison with detailed studies difficult. Some of these categories are used in modern forest inventories making them more comparable to the surveys. Clearly it is fortunate to have both kinds of modern studies available for comparison.

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**Appendix. Plant taxa seen in the early survey with their percentage occurrences, and with percentages from four later inventories.**

| | This Survey | 1931[1] | 1946[2] | 1956[3] | 1971[4] |
|---|---|---|---|---|---|
| Acer negundo (boxelder) | 0.1 | | | | |
| A. rubrum (maple) | 0.2 | | | 3.3 | |
| A. saccharum (sugar tree) | 1.2 | | | | |
| All maples | 1.5 | | 2.0 | | |
| Aesculus octandra (buckeye) | 0.8 | | | | |
| Amelanchier arborea (servicetree) | 0.1 | | | | |
| Asimina triloba (pawpaw) | 0.1 | | | | |
| Betula cf. lenta (mountain birch) | 0.2 | | | | |
| Carpinus caroliniana (hornbeam) | 1.2 | | | | |
| Carya ovata (white hickory) | 0.1 | | | | |
| Carya spp. (hickory) | 12.6 | 4.0 | 5.3 | 7.8 | 10.1 |
| Castanea dentata (chestnut, chisnut) | 1.4 | 20.0 | | | |
| Celtis spp. (hackberry) | 0.1 | | | | |
| Cercis canadensis (redbud) | 0.1 | | | | |
| Cornus florida (dogwood) | 3.6 | | | | |
| Crataegus spp. (Hawthorn, thornbush) | 0.2 | | | | |
| Diospyros virginiana (persimmon) | 0.4 | | | | |
| Fagus grandifolia (beech, beach) | 4.3 | | 7.9 | 1.5 | |
| Fraxinus cf. americana (ash) | 2.3 | | | | |
| Gleditsia triacanthos (honey locust) | 0.5 | | | | |
| Juglans cinerea (white walnut) | 0.4 | | | | |
| J. nigra (walnut, black walnut) | 1.2 | | | | 0.8 |
| Juniperus virginiana (cedar) | 0.1 | | | 2.0 | |
| Lindera benzoin (spicewood) | 0.1 | | | | |
| Liquidambar styraciflua (sweetgum) | 0.5 | | | | |
| Liquidambar/Nyssa (gum) | 0.8 | | | | |
| Liriodendron tulipifera (poplar, popular) | 2.9 | 8.0 | 4.6 | 5.8 | 4.3 |

**Appendix (cont.)**

| | This Survey | 1931[1] | 1946[2] | 1956[3] | 1971[4] |
|---|---|---|---|---|---|
| Magnolia acuminata (cucumber) | 0.1 | | | | |
| Morus cf. rubra (mulberry) | 0.1 | | | | |
| Nyssa sylvatica (blackgum) | 1.8 | | 3.3 | 1.3 | |
| Ostrya virginiana (ironwood) | 1.0 | | | | |
| Oxydendrum arboreum (sourwood, sowerwood) | 1.9 | | | | |
| Pinus spp. (yellow pines) | 10.8 | 10.0 | 13.8 | 36.4 | 41.7 |
| Pinus strobus (white pine) | | 3.0 | 0.7 | 1.7 | |
| Platanus occidentalis (sycamore) | 0.4 | | | | |
| Prunus serotina (cherry) | 0.2 | | | | |
| Quercus sp. (oak) | 0.1 | | | | |
| Q. alba (white oak) | 14.7 | | | 6.8 | 3.3 |
| Q. stellata (post oak) | 12.4 | | | 0.6 | 1.5 |
| All white oaks | 27.3 | | 17.1 | | |
| Q. falcata (Spanish oak) | 1.0 | | | | |
| Q. coccinea, Q. rubra (red oak) | 0.8 | | | | |
| Q. marilandica (blackjack) | 0.2 | | | | |
| Q. prinus (chestnut oak) | 0.2 | | | 10.0 | 10.3 |
| Q. velutina (black oak) | 16.4 | | | | |
| All red oaks | 18.2 | | 38.2 | 11.7 | 10.1 |
| All oaks | 55.8 | 40.0 | 55.3 | 29.1 | 25.2 |
| Oaks and pines | 66.6 | 53.0 | 69.1 | 65.5 | 66.9 |
| Oaks and hickory | 68.6 | 44.0 | 60.6 | 36.9 | 35.3 |
| Robinia pseudoacacia (locust) | 0.2 | | | 3.5 | 3.0 |
| Salix spp. (willow) | 0.1 | | | | |
| Sassafras albidum (sassafras) | 0.4 | | | | |
| Tilia heterophylla (lynn, lyn, lin, red lin) | 0.3 | | | | |
| Tsuga canadensis (spruce pine) | 0.2 | 7.0 | | 2.2 | |

**Appendix (cont.)**

| | This Survey | 1931[1] | 1946[2] | 1956[3] | 1971[4] |
|---|---|---|---|---|---|
| Ulmus spp. (elm) | 0.9 | | | | |
| Viburnum prunifolium, V. rufidulum (blackhaw) | 0.2 | | | | |

[1] Percent of commercial board feet, Peterson data 1931 (Woolrich and Neely 1934)
[2] Percent volume (Cowan 1946)
[3] Percent of trees ≥ 5 inches (Tennessee Valley Authority (1956)
[4] Percent of trees ≥ 5 inches (Tennessee Valley Authority (1971)

# CHARACTERISTIC NATIVE PLANTS OF TENNESSEE BARRENS

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**ABSTRACT. The extensive flora of the Tennessee barrens has been listed in several papers, mostly by physiographic region. This paper consolidates some of the 1095 known taxa into one list of 113 characteristic taxa which have been selected in more or less equal numbers from several of the State's physiographic-geologic regions. The list includes 16 woody taxa, a few weeds, several midwestern Tallgrass Prairie dominants, and some species that also occur on cedar and cedar-pine glades.**

## INTRODUCTION

Vegetation is characterized by site, floristic composition, and structure, among other attributes. The Tennessee barrens occur widely across the State--known in all physiographic areas except the Mississippi Alluvial Plain and the Blue Ridge (DeSelm and Murdock 1993). The absolute floristic composition is large, being about 39.3% of the State's vascular flora (DeSelm 1993). The barrens flora from specific physiographic areas is known from several studies (*e.g.*, DeSelm 1993). In the papers listed below the site location known for each species was coded to the species name. However, the sites of some physiographic units differ in their geology (and thus have somewhat different floras) so the extraction of characteristic taxa is best accomplished using physiographic-geologic units, as is done herein.

## METHODS

The published papers on the Tennessee barrens used herein include: West (DeSelm 1989), western and northern Rims (DeSelm and Chester 1993), Central Basin (DeSelm 1992a), eastern Rim (DeSelm 1990), Cumberland Plateau (DeSelm 1992b), and Ridge and Valley (DeSelm 1993). From these papers, native species with a presence of at least 50% were compiled into a composite list using the physiographic units as above except the western Rim was separated as upland and Silurian limestone parts, the Plateau as sandstone and limestone, and the Ridge and Valley as barrens and glades. This produced a list of over 700 taxa which was consolidated to a list of 346. This list contained only taxa which had at least 50% presences and at least one physiographic-geologic subunit. Representation of all physiographic-geologic subunits eliminated the bias that would result from only choosing species from many sites since the Plateau and Ridge and Valley had about two-thirds of the sample sites.

To make the final list more manageable, cut-offs were used for ultimate inclusion. These were:

West, 6 sites, 33 taxa, cutoff at 67% presence = 15 taxa

Western Rim upland, 6 sites, 37 taxa, cutoff at 67% = 14 taxa
Western Rim Silurian limestone, 12 sites, 53 taxa, cutoff at 67% = 24 taxa
Northern Rim, 6 sites, 82 taxa, cutoff at 83% = 26 taxa
Eastern Rim, 6 sites, 100 taxa, cutoff at 67% = 34 taxa
    Total Rim, 30 sites, 183 taxa consolidated to 88 taxa

Basin, 4 sites, 146 taxa, cutoff at 75% = 25 taxa

Plateau surface, 19 sites, 46 taxa, cutoff at 63% = 29 taxa
Plateau limestone, 2 sites, 104 taxa. Number of sites here is too few to extract a smaller representative group.

Ridge and Valley barrens, 39 sites, 65 taxa, cutoff at 69% = 18 taxa
Ridge and Valley gladey sites, 6 sites, 120 taxa, cutoff at 83% = 27 taxa

Barrens on limestone, 57 sites, 255 taxa consolidated to 84 taxa.

Lists are compared using the Sorenson species presence coefficient (2c/a+b) (Mueller-Dombois and Ellenberg 1979). Nomenclature follows Gleason and Cronquist (1991) or Wofford and Kral (1993).

## RESULTS AND DISCUSSION

The procedure detailed yielded a list of 113 most characteristic species of Tennessee barrens, including some regularly-occurring woody taxa (Appendix). Five Tallgrass Prairie dominants or characteristic species (Weaver 1954) are included, *i.e.*, *Andropogon gerardii, Panicum anceps, Schizachyrium scoparium, Sorghastrum nutans,* and *Sporobolus asper.*

Certain taxa characteristic of cedar glades occur in the barrens (and on Ridge and Valley glades). From the glade lists (Baskin *et al.* 1968, Baskin and Baskin 1975) 57 native herbaceous taxa were found to co-occur. This is a Sorenson species presence coefficient of 31.6%. When compared to the Basin cedar glade plot study flora (Somers *et al.* 1986), the coefficient is 21.9%. The Ridge and Valley glade flora here compares with the Basin cedar glade plot study flora (Somers *et al.* 1986) at 23.2%. Some of the characteristic barrens flora are weeds (Underwood 1965); the coefficient is 11.4%, but these and other taxa persist on mown roadsides, on road cuts, and on field and forest borders.

The effort to keep the total taxa list near 100 by using stringent presence cutoffs has produced a modest length list but it has also unfortunately excluded low percent presence species characteristic of the largest and most floristically rich barrens sites. Excluded are such families as the Orchidaceae, such characteristic genera as *Liatris* and *Silphium*, and such widely occurring species as *Solidago rigida*. Rare plants (Somers *et al.* 1989), except for a few cedar glade endemics (Baskin and Baskin 1986), are excluded, as are western taxa (Bridges and Orzell 1986) and many southern taxa (as in DeSelm 1993).

Seventy-seven percent of the characteristic species occur on the Highland Rim. The northern Rim has a rich barrens flora (Chester 1988, DeSelm and Chester 1993)--much of it part of the Big Barrens of Kentucky (Baskin *et al.* 1994). Overland movement of the barrens flora from the north to the eastern and western Rims, with their small barrens, is hypothesized. A nearly equally large percent (75) of the barrens taxa occurs on limestone. Most of these taxa also occur on the Rim so movement between most limestone areas may be relatively easy. However, 21 limestone taxa do not occur on the Rim and their mechanism of movement between the (1) Silurian limestone of the western Rim (on the Tennessee River), (2) the Basin, (3) the upper Mississippian limestones of the Plateau, and (4) the Chickamauga limestone and calcareous shales of the Ridge and Valley, is unknown. Migration routes between the Basin and the western Rim barrens are unknown but the Elk or Duck River basins may be involved. Piercing the Highland Rim and Plateau, each with acid surface soils, would seem to be formidable. Direct access to the limestone Plateau slopes and valleys of the Ridge and Valley is possible, however, by way of the Tennessee River slopes and bluffs. Paucity of barrens sites from the Plateau limestone (only two, DeSelm 1992b) has made the understanding of this migration difficult (migrations such as western taxa eastward, DeSelm *et al.* ms.). Locating and examining Plateau limestone barrens is a prime future objective of the writer. One cannot rule out, however, the possible role of long distance dispersal in migration of taxa. A barrens species less common than those on the Characteristic Species List, *Sporobolus heterolepis*, is disjunct from the west to the Ridge and Valley by about 400 km. Other examples are known (DeSelm *et al.* ms.).

## CONCLUSIONS

The procedure used produced a list of 113 characteristic taxa of Tennessee barrens. While this is a useful list for reconnaissance and study, it should be used in conjunction with other more extensive published lists that include less common species, especially rare, western, southern and endemic floristic elements.

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**Appendix. List of characteristic taxa of Tennessee barrens. Numbers are presence percentages (most have presence >50% in at least one physiographic region); maximum possible presence sum for all AR and BL each is 400. Location notations are arranged west to east with the following abbreviations: AR (all Rim units); B (Basin); BL (Barrens on limestone, excludes RVG); ER (eastern Rim); NR (northern Rim); PL (Plateau on limestone); PS (Plateau on sandstone or shale); RVB (Ridge and Valley barrens); RVG (Ridge and Valley glades); W (West Tennessee); WRS (western Rim on Silurian limestone); WRU (western Rim upland).**

*Acer rubrum* L.: WRU-50, NR-83, ER-50, PS-79, AR-183
*Agalinus tenuifolia* (M. Vahl) Raf.: NR-100, PL-50, RVG-50, AR-100, BL-50
*Allium cernuum* Roth: B-100, PL-50, BL-150
*Ambrosia artimisiifolia* L.: W-50, NR-50, B-50, PS-63, PL-50, RVB-67, RVG-83, AR-50, BL-167
*Andropogon gerardii* Vitman: W-83, WRU-50, WRS-75, NR-50, ER-67, PS-68, PL-50, RVB-49, RVG-50, AR-282, BL-174
*A. gyrans* Ashe: WRU-50, NR-83, AR-133
*Anemone virginica* L.: WRS-58, B-50, RVB-77, RVG-100, AR-58, BL-185
*Arenaria patula* Michx.: B-100, RVG-67, BL-100
*Aronia melanocarpa* (Michx.) Elliott: ER-67, AR-67
*Aristida dichotoma* Michx.: NR-67, B-100, AR-67, BL-100
*Asclepias verticillata* L.: WRS-58, B-100, RVB-67, RVG-83, AR-58, BL-225
*A. viridis* Walter: B-100, BL-100
*Aster dumosus* L.: NR-67, B-50, PS-89, PL-50, AR-67, BL-100
*A. hemisphericus* Alexander: WRV-50, ER-67, PL-50, AR-117, BL-100
*A. patens* Ait.: W-83, WRU-67, WRS-50, B-50, PS-65, PL-100, RVG-67, AR-117, BL-200
*A. pilosus* Willd.: W-67, B-50, PL-50, RVB-59, RVG-50, BL-159
*A. solidagineus* Michx.: WRU-50, NR-67, ER-67, AR-184
*A. undulatus* L.: PL-50, RVG-83, BL-50
*Astragalus tennessensis* A. Gray: B-100, BL-100
*Carex hirsutella* Mackenzie: WRU-83, NR-67, B-75, RVB-72, RVG-67, AR-150, BL-147
*Chamaecrista fasciculata* (Michx.) Greene: W-67, NR-67, B-75, ER-67, RVB-51, AR-134, BL-126
*C. nictitans* (L.) Moench.: W-50, WRU-50, NR-50, PS-63, AR-100
*Celtis tenuifolia* Nutt.: WRS-75, RVG-50, AR-75, BL-75
*Cercis canadensis* L.: WRS-75, B-100, PL-50, RVG-67, RVG-83, AR-75, BL-292
*Chasmanthium laxum* (L.) Yates: ER-67, AR-67
*Chrysopsis mariana* (L.) Ell.: ER-67, PS-74, AR-67
*Coreopsis major* Walt.: WRU-50, NR-50, PS-63, PL-50, AR-100, BL-50
*C. tripteris* L.: NR-83, B-50, AR-83, BL-50
*Croton monanthogynus* Michx.: WRS-67, B-50, PL-50, RVG-8E, AR-67, BL-167
*Dalea gattingeri* (A. Heller) Barneby: B-100, BL-100
*Danthonia spicata* (L.) Beauv. ex R. and S.: WRU-83, WRS-58,NR-50, B-75, PS-74, PL-50, RVB-74, RVG-83, AR-191, BL-257
*Desmanthus illinoensis* (Michx.) MacM. ex Robin S.: B-100, BL-100
*Desmodium ciliare* (Willd.) DC.: W-67, WRS-50, B-75, ER-50, PS-63, RVB-59, RVG-67, AR-100, BL-184
*Diospyros virginiana* L.: W-50, WRU-67, WRS-58, NR-83, B-50, PL-50, RVB-67, RVG-50, AR-150, BL-225
*Elymus virginicus* L. var. glabriflorus (Vasey) Bush: NR-50, B-100, PL-50, RVG-50, AR-50, BL-150
*Eragrostis spectabilis* (Pursh) Steud.: W-83, B-100, RVB-51, RVG-50, BL-151

*Erigeron strigosus* Muhl. ex Willd.: WRU-50, WRS-50, NR-83, B-100, ER-67, PS-74, PL-50, RVB-82, RVG-67, AR-250, BL-282
*Eupatorium altissimum* L.: NR-50, B-100, RVB-51, AR-50, BL-151

*E. rotundifolium* L.: WRU-67, ER-67, PS-79, AR-134
*Euphorbia corallata* L.: W-67, WRU-67, WRS-67, NR-100, B-100, PS-74, PL-50, RVB-59, RVG-67, AR-234, BL-276
*E. maculata* L.: PS-67, RVB-64, RVG-67, AR-67, BL-131
*Galactia volubilis* (L.) Britt.: W-50, WRS-83, B-75, PL-50, RVB-79, RVG-83, AR-83, BL-282
*Galium pilosum* Ait.: WRU-50, NR-83, PS-68, RVG-75, AR-133
*Gaura filipes* Spach.: WRS-75, B-75, PL-50, AR-75, BL-200
*Gnaphalium obtusifolium* L.: WRU-50, B-100, RVG-50, AR-50, BL-100
*Helianthus hirsutus* Raf.: W-50, WRU-50, NR-50, B-75, ER-75, PL-50, RVB-56, RVG-50, AR-175, BL-181
*H. mollis* Lam.: W-50, NR-50, ER-75, AR-125
*Houstonia nigricans* (Lam.) Fern.: B-100, BL-100
*H. purpurea* L. var. *calycosa* Gray: WRS-75, B-75, PS-53, RVG-75, AR-75, BL-150
*Hypericum gentianoides* (L.) BSP.: NR-50, ER-75, PS-63, AR-125
*H. stans* (Michx.) P. Adams and Robson: ER-75, AR-75
*Ipomoea pandurata* (L.) Meyer: PL-50, RVB-59, RVG-83, BL-109
*Isanthus brachiatus* (L.) BSP.: WRS-75, ER-50, PL-50, RVB-67, RVG-100, AR-125, BL-192
*Juncus scirpoides* Lam.: ER-75, AR-75
*Juniperus virginiana* L.: WRU-50, WRS-50, NR-83, B-100, PL-50, RVB-85, RVG-100, AR-183, BL-285
*Lespedeza hirta* (L.) Hornemann: ER-75, PS-53, AR-75
*L. procumbens Michx.*: WRU-50, WRS-58, NR-50, PL-50, RVB-77, RVG-75, AR-158, BL-185
*L. repens* (L.) Bart.: NR-50, B-50, ER-50, PS-68, RVG-56, AR-100, BL-50
*L. virginica* (L.) Britt.: W-67, NR-100, B-100, ER-83, PL-50, RVG-51, RVG-50, AR-183, BL-201
*Linum sulcatum* Riddell: WRS-83, B-75, PL-50, AR-83, BL-208
*Lithospermum canescens* (Michx.) Lehmann: WRS-83, PL-50, RVG-75, AR-83, BL-133
*Lobelia appendiculata* A. DC. var. Gattinger (A. Gray) McVaugh: B-100, BL-100
*L. puberula* Michx.: NR-83, ER-50, AR-133
*L. spicata* Lam.: WRS-83, B-50, PL-50, RVB-72, RVG-83, AR-83, BL-255
*Manfreda virginica* (L.) Rose: WRU-75, WRS-92, NR-50, B-75, ER-50, PL-50, RVB-69, RVG-100, AR-267, BL-296
*Monarda fistulosa* L.: WRU-50, WRS-75, B-50, RVB-64, RVG-100, AR-125, BL-189
*Nothoscordum bivalve* (L.) Britt.: B-100, BL-100
*Nyssa sylvatica* Marsh.: NR-50, ER-50, PS-68, AR-100
*Panicum anceps* Michx.: W-67, NR-83, B-75, ER-50, PL-50, RVB-62, RVG-50, AR-133, BL-187
*P. flexile* (Gatt.) Scribner: B-75, RVB-72, RVG-100, BL-147
*P. lanuginosum* Ell.: W-50, NR-50, B-100, ER-83, PS-74, PL-50, RVB-69, RVG-83, AR-133, BL-219
*P. microcarpon* Muhl.: NR-100, ER-50, PS-68, AR-150
*P. sphaerocarpon* Ell.: WRU-75, B-75, ER-50, PS-58, PL-50, AR-125, BL-125
*Paspalum laeve* Michx.: W-67, ER-50, AR-50
*Penstemon brevisepalus* Pennell: RVG-83
*Physostegia virginiana* (L.) Benth.: WRS-75, RVG-75, AR-75, BL-75
*Polygala verticillata* L. var. *ambigua* (Nutt.) A. W. Wood: WRU-50, NR-83, B-50, ER-50, AR-183, BL-50
*P. curtissii* Gray: ER-67, AR-67
*Potentilla canadensis* L.: W-50, PS-74
*P. simplex* Michx.: WRS-50, NR-83, B-50, ER-67, PS-74, RVB-79, RVG-75, AR-200, BL-179
*Prunella vulgaris* L. var. *lanceolata* (Barton) Fern.: WRS-50, PS-63, RVB-77, RVG-83, AR-50, BL-127
*Pediomelum subacaule* (Torr. and Gray) Rydb.: B-100, BL-100
*Pycnanthemum muticum* (Michx.) Pers.: ER-67, PS-63, AR-67
*P. tenuifolium* Schrader: WRU-75, NR-100, B-50, ER-100, RVG-83, AR-275, BL-50
*Quercus marilandica* Muenchh.: WRU-75, WRS-58, ER-83, PL-50, AR-166, BL-108
*Q. muhlenbergii* Engelm.: WRS-67, B-50, PL-50, RVB-67, RVG-75, AR-67, BL-234
*Q. shumardii* Buckl.: WRS-50, B-50, PL-50, RVB-59, RVG-83, AR-50, BL-209

*Q. stellata* Wang.: WRU-75, WRS-58, NR-67, B-75, ER-67, PL-50, RVB-62, RVG-75, AR-159, BL-245
*Rhamnus caroliniana* Walt.: WRS-75, B-50, RVB-51, RVG-75, AR-75, BL-176
*Rhexia mariana* L.: NR-50, ER-67, AR-117
*Rhus copallina* L.: WRU-50, WRS-50, NR-83, B-75, ER-67, PS-53, PL-50, RVB-69, PG-75, AR-250, BL-244
*R. glabra* L.: W-67, B-75, RVB-51, RVG-50, BL-126
*Robinia pseudoacacia* L.: WRS-67, NR-100, B-50, PL-50, RVB-56, RVG-83, AR-167, BL-223
*Rudbeckia fulgida* Ait.: PL-50, RVB-72, RVG-75, BL-122
*R. hirta* L.: WRU-75, AR-75
*Ruellia humilis* Nutt.: WRS-83, B-75, PL-50, RVB-64, RVG-50, AR-83, BL-272
*Salvia lyrata* L.: WRU-50, WRS-50, B-50, RVB-74, RVG-50, AR-50, BL-187
*S. urticaefolia* L.: RVG-83
*Schizachyrium scoparium* (Michx.) Nash: W-67, WRU-100, WRS-100, NR-100, B-100, ER-83, PS-89, PL-100, RVB-72, RVG-83, AR-383, BL-372
*Scutellaria australis* (Fassett) Epling: B-100, RVG-50, BL-100
*Senecio anonymus* A. Wood: B-75, ER-50, PS-79, PL-50, RVB-87, RVG-100, AR-50, BL-221
*Sisyrinchium albidum* Raf.: WRS-75, NR-50, B-50, ER-50, PL-50, RVB-67, RVG-83, AR-175, BL-242
*Smilax glauca* Walt.: PS-84
*Solidago erecta* Pursh: ER-75, AR-75
*S. nemoralis* Aiton: W-100, WRS-75, NR-75, B-50, ER-75, PS-74, PL-50, RVB-72, RVG-83, AR-225, BL-247
*S. odora* Aiton: ER-75, PS-53, AR-75
*Sorghastrum nutans* (L.) Nash: W-100, NR-50, ER-75, PS-79, PL-50, AR-125, BL-50
*Sporobolus asper* (Michx.) Kunth.: B-100, PL-50, RVB-49, RVG-100, BL-179
*Stylosanthes biflora* (L.) BSP.: WRU-50, WRS-50, NR-83, ER-83, PS-74, AR-266, BL-50
*Tephrosia virginiana* (L.) Pers.: WRU-83, WRS-58, ER-83, PS-63, AR-224, BL-58
*Tridens flavus* (L.) Hitchc.: B-50, PL-50, RVB-69, RVG-83, BL-169
*Ulmus alata* Michx.: WRS-75, B-50, RVB-64, RVG-50, AR-75, BL-189
*Verbena simplex* Lehmann: WRS-50, B-75, RVG-61, RVG-100, AR-50, BL-186

# USE OF THE TERM "CEDAR GLADES" FOR A TYPE OF VEGETATION IN THE CENTRAL BASIN OF TENNESSEE: AN HISTORICAL PERSPECTIVE AND SOME MISINTERPRETATIONS

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**ABSTRACT. Use of the term "cedar glades" by geologists, botanists, zoologists, and soil scientists to describe a type of vegetation in the Central Basin of Tennessee from 1851 to present is reviewed. Originally, the term referred to the rocky openings-redcedar forest complex (primarily) on the Lebanon limestone. However, "cedar glades," "limestone glades," and "limestone cedar glades" increasingly are being used by botanists and plant ecologists for the rocky openings only, which have a $C_4$ annual grass-Ç annual/perennial forb-cryptogam-dominated vegetation. Some erroneous statements in the literature that resulted from misinterpretation/ misunderstanding of "cedar glades" and other terms will be discussed.**