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

HELD AT BRANDON SPRING GROUP CAMP
LAND BETWEEN THE LAKES
MARCH 6, 1993

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

and

Murray State University
Center for Reservoir Research

and

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

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PREFACE

On March 5th and 6th, 1993 over 120 students of regional natural history and field biology gathered at Brandon Spring Group Camp in TVA's Land Between The Lakes to participate in the Fifth Symposium on the Natural History of Lower Tennessee and Cumberland River Valleys. Sponsors of this symposium were The Center for Field Biology at Austin Peay State University, the Center for Reservoir Research at Murray State University, and Land Between The Lakes.

On Friday afternoon the symposium attendees were welcomed by Dr. Ben Stone, Director of The Center for Field Biology at APSU and Dr. Gary Boggess, Dean of the College of Sciences at Murray State University. Representing Land Between The Lakes was Mr. John Mechler, manager of Land Management. In his welcoming presentation Mr. Mechler described LBL's three-pronged environmental mission of resource management, research, and education. Stream ecology was the theme of Friday afternoon's invited papers presented by Dr. Art Benke of the University of Alabama and Dr. Ike Schlosser of the University of North Dakota. Dr. Benke presented information about what is probably the most poorly studied lotic environment, large rivers. Dr. Benke's studies of coastal plain blackwater rivers in southeastern Georgia have provided critical insights into the function of large rivers and the importance of floodplain inundation. Dr. Schlosser, applying landscape ecology perspectives to stream fish ecology, discussed the importance of large scale habitat heterogeneity, the effects of ecotonal barriers, and the interactions of adjacent habitats on stream fish distributions and life histories. The full text of Dr. Benke's and Dr. Schlosser's papers are presented in these proceedings.

Following the evening meal, Dr. Ray Norris, coordinator of Tennessee Save Our Streams, Izaak Walton League of America, gave an informative and enjoyable slide presentation on the Adopt-A-River program in Tennessee. This program educates the public about water quality problems, sponsors river "clean-up" projects, trains volunteer groups to monitor water quality via sampling of aquatic macroinvertebrates, and even initiates litigation against water quality violators. An informal social followed the presentation by Dr. Norris.

The Saturday morning program was filled with two concurrent sessions, each comprised 15 contributed papers. Session I, moderated by Dr. Cindy Taylor of Austin Peay State University, consisted of papers on general zoology and aquatic biology. Dr. William Ellis, Dean of the College of Graduate and Professional Programs and Professor of Biology at Austin Peay, served as moderator for Session II, which included papers on botany and microbiology. The contributors were invited to publish an abstract or a complete paper in these proceedings. The 15 contributors to Session I opted to publish abstracts only. Five of the contributors to Session II chose to publish complete papers, while the remaining ten elected to publish only abstracts.

The style and format of these proceedings follow, for the most part, the style established by earlier proceedings. Dr. Floyd Scott served as the organizer and editor for Contributed Papers Session I and Dr. Wayne Chester was the organizer and editor for Session II. I organized and edited the Invited Papers session and acted as the managing editor for these proceedings.

Steve Hamilton
July 1993

ACKNOWLEDGMENTS

The editors would like to thank Ms. Cathy Hoback and Ms. Dorothy Reed for assistance in organizing and coordinating the activities before and during the symposium. We also must recognize the participation of the many APSU undergraduate and graduate research assistants for their help during this event. Manuscripts were typed and corrected by Ms. Reed and Ms. Marilyn Griffy, and Ms. Griffy helped with the final format. Their assistance is greatly appreciated. All complete papers were reviewed by at least one anonymous reviewer. We acknowledge all reviewers for their contribution to the quality of these papers. While we hope these proceedings are error free, experience suggests that this is not the case.

SYMPOSIUM REGISTRANTS

Following, in alphabetical order, is a list of those individuals who registered at the 1993 symposium. Institutional affiliation (when available), city (of the person's institution or home), and state are also given.

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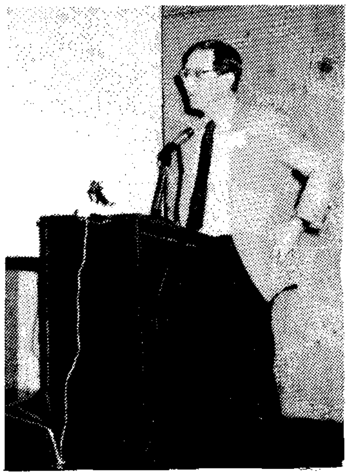
SYMPOSIUM PARTICIPANTS

INVITED SPEAKERS



Arthur Benke

Isaac Schlosser

SPEAKERS - CONTRIBUTED PAPERS SESSION I: AQUATIC BIOLOGY AND ZOOLOGY

Front row (from left) Charles Nelson, Jennifer Harrison, Colleen White. Middle row (from left) Thomas Kind, Eugene Zirkle, John Koons, Patricia Stinger, Donald Green. Back row (from left) Bob Moser, Burl Naugle, Brian Sharp, Steve Hamilton, Dave White.

SPEAKERS - CONTIBUTED PAPERS SESSION II: BOTANY AND MICROBIOLOGY

Front row (from left) Hal DeSelm, Jeffery Walck, Patricia Grimes, Carol Baskin, Jerry Baskin, William Ellis, Ed Zimmerer, Wayne Chester. Back row (from left) Richard Clements, Scott Franklin, James Joyner, Paul Florence, Jonathan Dey, Joe Schibig.

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INVITED PAPERS

STREAM ECOLOGY

Friday, March 5, 1993

Moderated by:

Steven W. Hamilton
The Center for Field Biology
Austin Peay State University

INVERTEBRATE PRODUCTION DYNAMICS OF LARGE RIVERS - DEVIATIONS FROM THE STREAM PARADIGM

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ABSTRACT. Our current views (conceptual model or paradigm) of lotic ecology are strongly influenced by research done in small streams. From an ecosystem perspective, the paradigm incorporates ideas from the River Continuum Concept, but also includes other views such as the role of floods as a disturbance to biotic communities. More specific aspects of the stream paradigm deal with the invertebrate consumers, including their relationship to habitat type, responsiveness to floods, magnitude of secondary production and biomass turnover, utilization of leaves and algae as food sources, and drift dynamics. Relatively little research has been done on larger rivers which appear to differ significantly from the paradigm based on small streams. Future investigations in river ecology are made extremely difficult, however, since most large rivers in temperate North America are strongly regulated by channels, dams and levees.

Medium-size rivers (6th order) of the southeastern Coastal Plain, appear to approximate the functioning of what we might expect for large, low-gradient, floodplain rivers before they were modified. Our studies on the Satilla and Ogeechee rivers, in southeastern Georgia, show they possess unstable sandy bottoms, broad forested swamps that are inundated for weeks to months each year, and woody debris (snags) as the major stabilized habitat type in the channel. Significant exchanges of organic matter occur between river and swamp, and the system is heterotrophic throughout the year. Freshwater invertebrates in these systems also depart substantially from our view of small streams. Rather than having a rocky substratum, distinctly different invertebrate communities are distributed among three main habitats (sand, mud, and snags). Although high benthic densities are found in the sandy habitat of the main channel and the muddy habitat of backwaters, the greatest diversity and production are found on snags. Many taxa have substantially higher annual production/biomass ratios than previously found. Analysis of literature production values demonstrated a significant relationship between community production and stream size, with the highest production on snags from the Satilla River. The great majority of invertebrate production in Coastal Plain rivers is by collector organisms (gathering collectors in sand and mud, and filtering collectors on snags), that primarily consume amorphous detritus and microbes that are flushed from floodplain soils.

Flooding is not a disturbance to invertebrates in large floodplain rivers, but is a vital aspect of periodic habitat expansion in two dimensions. Flooding increases snag habitat in the main channel in the vertical dimension, and inundates vast floodplain areas in the horizontal dimension. The floodplain offers at least two other major habitat types for invertebrates: the benthic zones with heavy organic deposition, as well as the surfaces of wood (including tree trunks). Drift densities in the main channel are extremely high, with snag-dwelling aquatic insects and microcrustaceans from swamps predominating. Drift distances, drift times, and the percentage of organisms drifting are substantially greater than has previously been found for invertebrate populations in smaller streams. Thus, unlike the stream paradigm, high invertebrate production and drift levels are dependent on an abundance of snag habitats, the occurrence of natural flooding regimes and mobilization of organic matter between habitats.

INTRODUCTION

Much of our understanding of lotic ecology comes from studies of relatively small streams (e.g., Hynes 1970, 1989, Cummins 1992). Ecological studies of rivers are relatively few and we often tend to extrapolate our views (conceptual model or paradigm) of the small to the large lotic ecosystems (Hynes 1989). We have been slow in recognizing that large systems can behave quite differently (e.g., Sedell *et al.* 1989, Ward 1989). Although more attention has been paid to large rivers in recent years, most large-river research has a decidedly fisheries-based perspective (e.g., see several papers in Dodge 1989), and is conducted on highly-regulated rivers. Not only has our view of rivers as ecosystems been slow to develop, but parallel notions of invertebrates and their functional role are weak. In this paper, I present an overview of some fundamental differences in large rivers, in contrast to the stream paradigm based on small systems, using data from unregulated rivers in the southeastern U.S.A. Coastal Plain. Then I focus on the distinct differences in invertebrate dynamics and function in these rivers compared to most streams.

A stream paradigm typically envisions lotic ecosystems as shallow waters with alternations of riffles and pools, and a rocky substratum (cobbles, boulders, etc.). Beyond such a physical description, it can encompass ecosystem, community, and population perspectives. Much of the ecosystem perspective is embodied within the River Continuum Concept (RCC), which incorporates a catchment perspective in proposing that lotic organisms have evolved and function in a consistent manner in response to the physical conditions imposed by geomorphology (Vannote *et al.* 1980, Cummins 1992). Although its originators described a rather definitive sequence of changes along the continuum, subsequent descriptions recognized that there can be considerable variation (e.g., Minshall *et al.* 1983, 1985). In low-order, shaded reaches of streams (order 1-4), allochthonous matter (leaves) from riparian vegetation falls into streams for consumption by leaf-shredders which dominate the invertebrate community. As the stream increases in size (5-6th order) and becomes more exposed to sunlight, in-stream autotrophy is thought to become dominant over heterotrophic processes (i.e., gross primary production exceeds community respiration), and herbivorous scraping invertebrates are believed to replace shredders. As the river gets wider and deeper (> 6th order), autotrophy declines with increased turbidity and food is thought to be delivered as seston derived from the upstream processing of organic matter. Other aspects of the stream paradigm concern the frequency and significance of floods as a factor determining the structure of lotic communities (e.g., Resh *et al.* 1988), the importance of patch dynamics (e.g., Pringle *et al.* 1988, Townsend 1989), and the degree of resource spiralling (e.g., Elwood *et al.* 1983). While it is becoming recognized that this stream paradigm, based largely on small-stream studies, must be greatly modified for large rivers that are unconstrained in their geomorphology and have broad forested floodplains (e.g., Sedell *et al.* 1989, Ward 1989), relatively little research on large natural systems has actually been done.

A major part of the problem of studying natural large-river ecosystems is exemplified by the condition of rivers in the United States and many other developed countries. There are simply no major river systems left in the contiguous 48 states that are undisturbed by human activity from their headwaters to the sea (Benke 1990). All large river systems in the U.S. (except in Alaska, and the Yellowstone River) are strongly regulated by dams, channels, and levees (Benke 1990). These include such rivers as the Tennessee, Ohio, Missouri, and Mississippi. For future management and restoration purposes, how are we to determine the natural functioning of large rivers that were unstudied prior to damming and channelization? Do we study our already-modified systems in areas that seem natural? Do we study undisturbed rivers from other parts of the globe (e.g., subarctic or tropical zones)? Or do we study medium-size lotic systems that seem to have characteristics in common with the larger systems (i.e., low gradient, soft bottoms, floodplain swamps). Perhaps all of these approaches will contribute insight toward understanding large temperate rivers, but in this paper, I will examine what we might learn from medium-size rivers.

ECOLOGY OF BLACKWATER RIVERS IN THE SOUTHEASTERN U.S.A.

References to natural riverine floodplain systems often focus on large tropical rivers, as if floodplain rivers no longer existed in North America. In fact, several of the most natural unregulated medium-size rivers remaining in the U.S.A. are those with broad floodplains (Benke 1990). These systems are found primarily in the southeastern U.S.A. and appear to possess many of the same fundamental properties as the larger systems.

My colleagues and I have studied two of these medium-sized low gradient systems, the Satilla and Ogeechee rivers, in eastern Georgia. These rivers are much larger (i.e., mean annual discharge >50 m^3/s) than most streams studied by lotic ecologists (<1 m^3/s), but are still substantially smaller than the largest rivers in the U.S.A. (>1000 m^3/s). Both rivers flow primarily across the Atlantic Coastal Plain (see Meyer 1992 for general comparison). Drainage into the Satilla is entirely from the lower Coastal Plain, with the water having a naturally low pH (4-6) and alkalinity (<10 mg $CaCO_3$/L). . The "blackwater" appearance of the Satilla is due to a high concentration of total organic carbon (15-25 mg C/L), most of which is dissolved. The Ogeechee, two river basins north of the Satilla, flows mostly across the Coastal Plain, but originates in the Piedmont. The Ogeechee is rarely as black in appearance as the Satilla, with a consistently higher pH (6-7), higher alkalinity (10-40 mg $CaCO_3$/L) and lower total organic carbon (6-12 mg C/L) (Meyer 1992).

Coastal Plain blackwater rivers such as the Satilla and Ogeechee deviate substantially from the stream ecosystem paradigm described above (Benke and Meyer 1988, Meyer 1990, 1992) by possessing the following characteristics: (1) broad forested floodplain swamps adjoin the meandering river along most of its length (unless altered by human interference), (2) benthic habitats are represented by sandy/silty bottoms rather than rocky substrata such as cobbles, (3) the unstable nature of the shifting sandy bottom prevents the establishment of extensive attached algae and macrophytes, and aquatic primary production does not reach the high levels for a river of this size as predicted by the RCC, (4) woody substrata (snags), which also occur in high-gradient systems, represent the major stabilizing feature of Coastal Plain systems, including their utilization as habitat by animals, (5) flooding of the swamps usually occurs for several weeks or months during most years, resulting in important exchanges of nutrients, organic matter and organisms between channel and swamp, (6) dissolved organic matter (DOM), fine particular organic matter (FPOM) and microbes are released from these swamps to form riverine seston, and (7) the system is heterotrophic throughout its length, rather than becoming autotrophic in middle orders, as predicted by the RCC.

DEVIATIONS OF COASTAL PLAIN RIVER INVERTEBRATES FROM THE PARADIGM

In addition to the major ecosystem properties of Coastal Plain rivers described above, we have shown that the dynamics of their invertebrate communities also differ greatly from the many generalizations derived from working on small streams. These differences can be divided into at least five major categories: (1) the relative significance of habitat types, (2) the significance of flooding and floodplains, (3) the distribution of secondary production among functional groups and habitats, (4) the trophic basis of invertebrate production, and (5) invertebrate drift dynamics.

Habitats of sand, mud, and wood

The habitats of the Satilla and Ogeechee rivers are quite unlike our typical image of rocky bottom streams (Fig. 1). The main channel consists mostly of relatively clean shifting sand, and backwater areas (sloughs) possess organic deposition and lentic conditions. Each habitat has its own distinctive community that is quite unlike that found in a typical stream riffle. In addition, wood accumulates in the channel along the banks, primarily from the undercutting of trees which fall into the river. These snags can remain in a slowly decomposing state for decades, providing the only stable substratum for invertebrate animals (Wallace and Benke 1984, Benke and Wallace 1990).

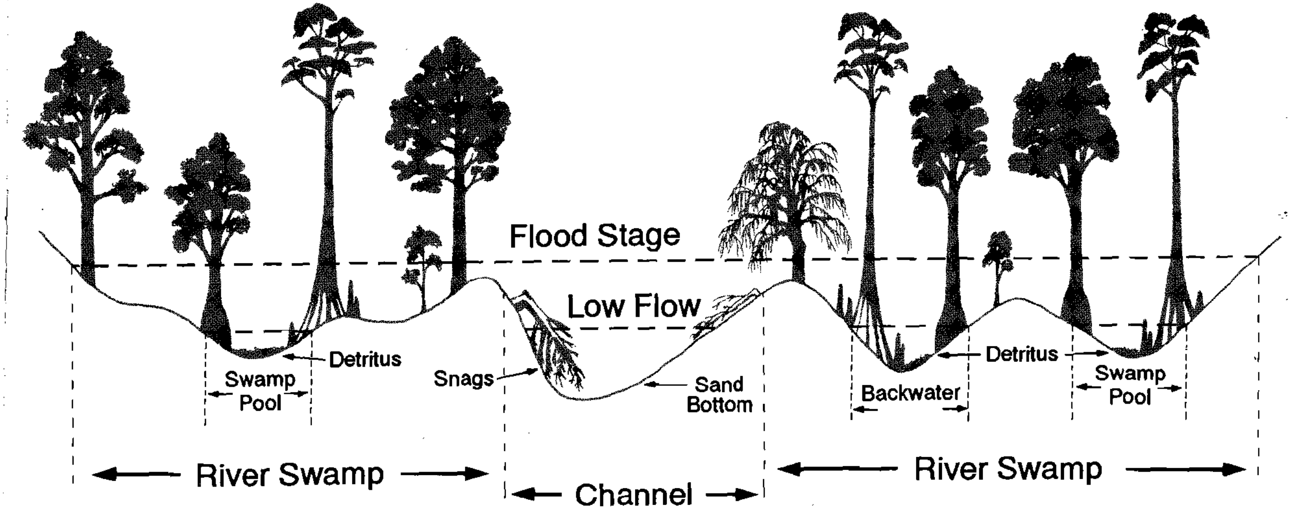

Figure 1. Cross section of a Coastal Plain river and its floodplain swamp, with vertical distances exaggerated, to illustrate invertebrate habitats of main channel (sand, snags), backwaters (mud and detritus), and swamp floor (sand, detritus accumulations, tree trunks, etc.). In the Ogeechee River, the floodplain swamp is about 40 times wider than the river channel (30-40 m).

The shifting sand of the main channel has historically been considered to be a harsh environment with little life (Hynes 1970), a view that has survived to the present (e.g., Junk *et al.* 1989). However, recent studies of the sandy benthos of various rivers, including the Satilla and Ogeechee, suggest that this view is incorrect. Although the benthic fauna of sandy habitats are primarily limited to chironomids, oligochaetes and molluscs, densities of small animals can be very high. In the Satilla River, we found high densities (annual mean $>40,000/m^2$) of a small midge, *Rheosmittia* (originally called *Parakieferiella*), in addition to other chironomids and oligochaetes (Benke *et al.* 1984). In the Ogeechee River, midges also occurred, but enchytraeid oligochaetes had the highest density (annual mean $>47,000/m^2$), and molluscs (mostly the filter-feeding Asiatic clam, *Corbicula fluminea*) had the highest biomass (Stites 1986, 1987).

Backwater habitats are abundant along these meandering rivers and typically contain an entirely different fauna than the sandy main channel. The organic deposition and low flow results in larger, but less abundant midges and oligochaetes in the Satilla (Benke *et al.* 1984). In the Ogeechee, backwaters were also the location of the largest size classes of *Corbicula fluminea* (Stites 1986).

Wood in small streams is usually associated with debris dams (e.g., Harmon *et al.* 1986), but in the Satilla and Ogeechee, snags are the only stable substratum (Benke *et al.* 1984, Wallace and Benke 1984). Tagging experiments demonstrated that snags in the main channel moved very little over a two-year study period (Benke and Wallace 1990). Snags are the habitat that is typically removed for navigation purposes by agencies such as the Corps of Engineers. In the Satilla River, snags were estimated to comprise only about 5% as much surface area as the river bottom (Benke *et al.* 1984). However, the Ogeechee apparently sustained much less snag removal and snag abundance was roughly five times that found in the Satilla (Wallace and Benke 1984).

The snag community is very diverse biologically and is high in density, biomass and production (e.g., Benke *et al.* 1984, Wallace and Benke 1984, Jacobi and Benke 1991). In the Satilla River, the snag habitat is dominated by filtering collectors such as black flies and hydropsychid caddisflies (Benke *et al.* 1984). Ogeechee river snags also have a major filter-feeder component (Wallace and Benke 1984), but the gathering collectors are also highly diverse and productive. For example, snags from the Ogeechee are the home for more than a dozen species of mayflies, a number that is high for all habitats in most streams (Jacobi and Benke 1991, Benke and Jacobi, unpublished) . That snag invertebrates are an important fraction of the total river biomass and production is documented by the fact that the majority of drifting invertebrates originate from snags (Benke *et al.* 1986, Benke *et al.* 1991), and snag invertebrates are the major food source for the insectivorous fishes (Benke *et al.* 1985).

Floods go up and out

Most discussions of stream flooding treat floods as disturbances of the biotic components, including the invertebrates (e.g., Resh *et al.* 1988, Poff 1992). Flooding in Coastal Plain rivers like the Satilla and Ogeechee requires an entirely different perspective for invertebrates. Rather than being a disturbance, flooding in such rivers greatly expands the habitat areas in two dimensions. Average stream velocity increases (up to 0.6 m/s) with increasing discharge only when most of the flow is within the channel. Once the swamp is completely inundated and a substantial portion of the discharge flows through it, velocity declines substantially (Roberts *et al.* 1985, Benke and Wallace 1991).

In the vertical dimension, a rising water level inundates increasing amounts of wood in the main channel, providing greater snag surface areas. Many components of the snag fauna have short developmental times and high drift rates, and are thus highly adapted to take advantage of newly created snag surfaces. The major instability of the habitat is that when water height declines, the upper portions of snags become desiccated. Animals must either take their chances in the drift or make their way, by crawling or lowering themselves on a silk lifeline, to wetted portions of the wood. In estimating abundance and production of snag-dwelling invertebrates in the Ogeechee, we quantified the snag habitat, and were able to estimate the amount of wood surface inundated as a function of discharge (Wallace and Benke 1984).

In the horizontal dimension, floods expand the benthic surface area by about 40 times as flood waters sweep into the floodplain swamp covering the organic soils and creating new, but temporary benthic habitats. The flood waters rise slowly, perhaps no more than 10 cm per day, and once into the floodplain, they may remain for weeks or months at a time. Since the basic stream paradigm does not consider flooding of floodplain forests, it also does not recognize that an enormous floodplain fauna exists, especially during high water. The floodplain swamp consists of a mosaic of invertebrate habitats, including benthic areas that are either sandy or heavy with organic debris, tree trunks, small bushes, floodplain snags, and debris dams (Fig. 1). Many of these habitats are extremely difficult to sample quantitatively or even identify under the black waters.

Many types of animals can thrive in the swamp, and even after discharge declines and flow through the swamp ceases, water may still cover substantial portions. During the driest periods of the summer, there are still small pools present. Lentic assemblages of organisms associated with leaf litter are present during all discharge stages throughout the swamp. These include isopod (*Lirceus* and *Asellus*) and amphipod (*Hyalella*) crustaceans as the major shredder organisms, as well as chironomids, oligochaetes, and microcrustaceans (cladocerans, copepods, and ostracods) (Cuffney and Wallace 1987; Benke, unpublished data). Invertebrates not only colonize benthic habitats, but solid surfaces as well, such as moss-covered tree trunks. During flood stage, lotic assemblages invade the swamp as tree-trunks and low branches are colonized by a diverse macrofauna, similar to main-channel snags, with midges, mayflies, caddisflies and stoneflies.

Invertebrate production is high in large natural rivers

Invertebrate production is defined as the formation of population biomass through time, and is usually presented as g dry mass (DM) $m^{-2}yr^{-1}$. It is a reflection of energy flow and is a function of density, biomass and individual growth rate (Benke 1993). Production analysis is a means of quantifying the activity of a population and its utilization of space and food. Several studies of mostly small natural systems suggest that streams tend to have community invertebrate production values ranging from 4 to 25 g DM $m^{-2}yr^{-1}$ with annual production/biomass ratios (P/B) less than 12 for most populations and for the community as a whole (Waters 1977, Benke 1993).

In both the Satilla and Ogeechee rivers, we estimated taxon-specific and functional group production as has been done in other studies (Benke 1993). However, because of the special importance of snags, in contrast to typical benthic habitats, we could not employ standard benthic sampling techniques. We estimated production first on a habitat surface area basis, and then, through our quantification of the snag habitat, we also estimated production on a river bottom basis. Production analyses for the Satilla River have been completed (Benke *et al.* 1984, 1985). Analyses for the Ogeechee River include floodplain as well as channel habitats, but this work is only partially done (Stites 1986, 1987; Benke and Parsons 1990; Benke 1993; Benke and Jacobi, unpublished).

Among the three major habitats (sand, mud, snags) in the Satilla River, the highest production per habitat surface area was on the snag habitat (Table 1). Filtering collectors, particularly black flies and hydropsychid caddisflies, contributed the most to snag production. Gathering collectors, primarily midges with high turnover rates, also contributed a substantial amount to production. Invertebrate biomass in the sandy habitat was relatively low, but with high biomass turnover rates for the small midges, production was relatively high (Table 1), in contrast to early notions of low production in such habitats. In the muddy habitat of backwaters, biomass was higher and dominated by midges and oligochaetes, with production about the same as in the sand (Table 1). Benthic production in the Ogeechee was approximately the same as in the Satilla, with oligochaetes and midges contributing about 16 g DM $m^{-2}yr^{-1}$ and *Corbicula fluminea* about 1.7 g DM $m^{-2}yr^{-1}$ (Stites 1986, 1987).

TABLE 1. Annual invertebrate production within habitats in the Satilla River according to functional feeding group (from Benke *et al.* 1984). All production values are in units of g dry mass $m^{-2}yr^{-1}$. River bottom estimates are adjusted for relative abundance of habitats.

Site/Habitat	Filterers	Gatherers	Predators	Total
Upper Site				
Snag (g/m^2 snag)	57.29	7.04	7.91	72.24
Sand (g/m^2)	0.00	24.45	3.91	28.36
Mud (g/m^2)	0.16	7.06	14.74	21.96
River bottom (g/m^2)	3.85	24.07	5.56	33.52
Lower Site				
Snag (g/m^2 snag)	41.38	9.01	7.03	57.42
Sand (g/m^2)	0.00	11.32	2.37	13.69
Mud (g/m^2)	0.13	10.11	3.67	13.91
River bottom (g/m^2)	1.99	11.86	2.98	16.84

Even after habitat surface areas are taken into account, with snags contributing only 4-6% of total surface area, the invertebrate biomass was still higher on snags than in benthic habitats of the Satilla River (Table 2). However, due to higher biomass turnover (annual production/biomass = P/B) in the benthic habitats, total river production was dominated by the gathering collectors of the benthic habitats (Table 1). This relationship may be somewhat different in the Ogeechee River, however, when snag production analyses are completed. Here snags contribute more than 5 times as much surface area as found in the Satilla. Production of both gathering and filtering collectors per habitat surface appears even higher on snags from the Ogeechee than the Satilla, but the relative contributions of all functional groups from the Ogeechee snags are uncertain at this time.

TABLE 2. Comparison of percentage of standing stock biomass and production occurring in each of three main-channel habitats (snag, sand, mud), after adjusting for relative abundance of habitats, with the habitat origin of drift biomass in the Satilla River (from Benke *et al.* 1986).

	Fauna on substratum		Fauna in Drift
Site/Habitat	% Biomass	% Production	% Biomass
Upper Site			
Snag	53.7	14.7	82.3
Sand	32.3	79.5	9.0
Mud	13.9	6.0	8.7
Lower Site			
Snag	60.4	16.2	78.0
Sand	17.5	69.6	10.5
Mud	22.1	14.2	11.5

One of the notable aspects of our study on the Satilla River was that P/B values were estimated to be extremely high for black flies and midges (>100 for the latter), substantially higher than most previous estimates for benthic populations. Since our estimates from the Satilla were based on a combination of field observations and laboratory-derived growth rates from the literature (Benke *et al.* 1984), subsequent studies on the Ogeechee incorporated growth studies of midges, black flies, and mayflies in mesocosms simulating natural conditions. For several taxa, we developed equations predicting growth rate as a function of temperature (e.g., Fig. 2). The high rates predicted by the black fly equations generated black fly P/B values of 37-48 in the Ogeechee, and 55-85 (after re-analysis) in the Satilla (Benke and Parsons 1990), consistent with original estimates of 71-79 in the Satilla (Benke *et al.* 1984). Similarly, annual P/B for various mayflies in the Ogeechee have been estimated from 12 to 68 (Benke 1993). The high growth rates found for chironomids (e.g., Fig. 2, Stites and Benke 1989, Hauer and Benke 1991) indicate that annual P/B for this group will undoubtedly be well over 100, consistent with our original assumptions for similar populations in the Satilla.

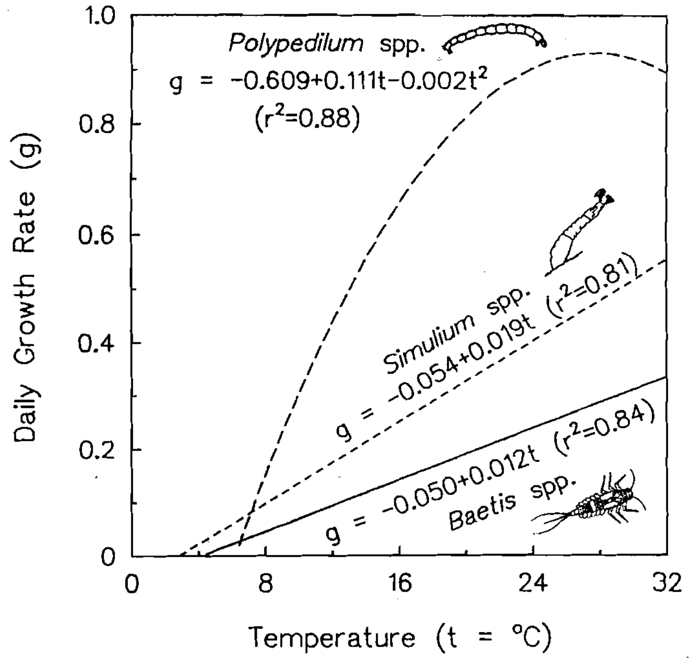

Figure 2. Daily biomass growth rates (g, in units of mg $mg^{-1}d^{-1}$) as a function of temperature for the midge *Polypedilum* spp. (Hauer and Benke 1991), the black fly *Simulium* spp. (Hauer and Benke 1987), and the mayfly *Baetis* spp. (Benke *et al.* 1992). These snag-dwelling insects were reared in stream-side artificial streams simulating natural conditions. From Benke (1993).

The Satilla and Ogeechee rivers are the largest natural rivers for which invertebrate community production estimates have been made, and the magnitude of production is among the highest reported. This leads to the obvious question of the relationship between stream size and production. The RCC predicts shifts in invertebrate functional groups as streams increase in size, but does not address the question of production. Most tests of the RCC have used numbers of individuals within each functional group. In order to address production trends along the continuum, I summarized literature values for functional-group production in natural streams of various sizes (Fig. 3, Benke 1993). There was clearly a significant increase in invertebrate production with increase in stream size. Furthermore, functional group patterns of production were reasonably consistent with RCC predictions, with notable clarifications or exceptions. Production of shredders was highest in small streams, and declined with stream size, as predicted by the RCC. Production of scrapers tended to be highest in mid-order streams (as predicted by the RCC), but was not nearly as high as the production of collectors at any point along the continuum. Both gathering and filtering collectors had the highest production all along the continuum, but especially in the larger streams. Filtering collectors dominated on solid substrata of the largest rivers (including the Satilla). Clearly, there is room for additional analysis of production in rivers larger than the Satilla and Ogeechee. An important aspect of such studies will be the incorporation of floodplain production, which I have also addressed in my research, but for which data are not yet available.

The high annual P/B values found in the Satilla and Ogeechee rivers (> 50) at first glance indicated significant departures from previous findings that P/B values for invertebrate populations rarely exceed 10-12 (Waters 1977). Whether there are consistent trends of P/B with stream size remains to be seen. In the case of the Satilla and Ogeechee rivers, it must be acknowledged that these subtropical rivers are much warmer than the smaller north-temperate streams in which most production studies have been done. It should be recognized that the highest P/B values are found among the gathering and filtering collectors (Benke 1993). Since there is an abundance of collectors in streams of all sizes (Fig. 3), the potential exists for relatively high P/B in small streams (unless extremely cold or low in food). For example, relatively high growth rates have been found for chironomids in a cool Appalachian stream (Huryn and Wallace 1986), and P/B values for chironomids and mayflies in a small warm desert stream were comparable to values in the Satilla and Ogeechee (Fisher and Gray 1983, Jackson and Fisher 1986).

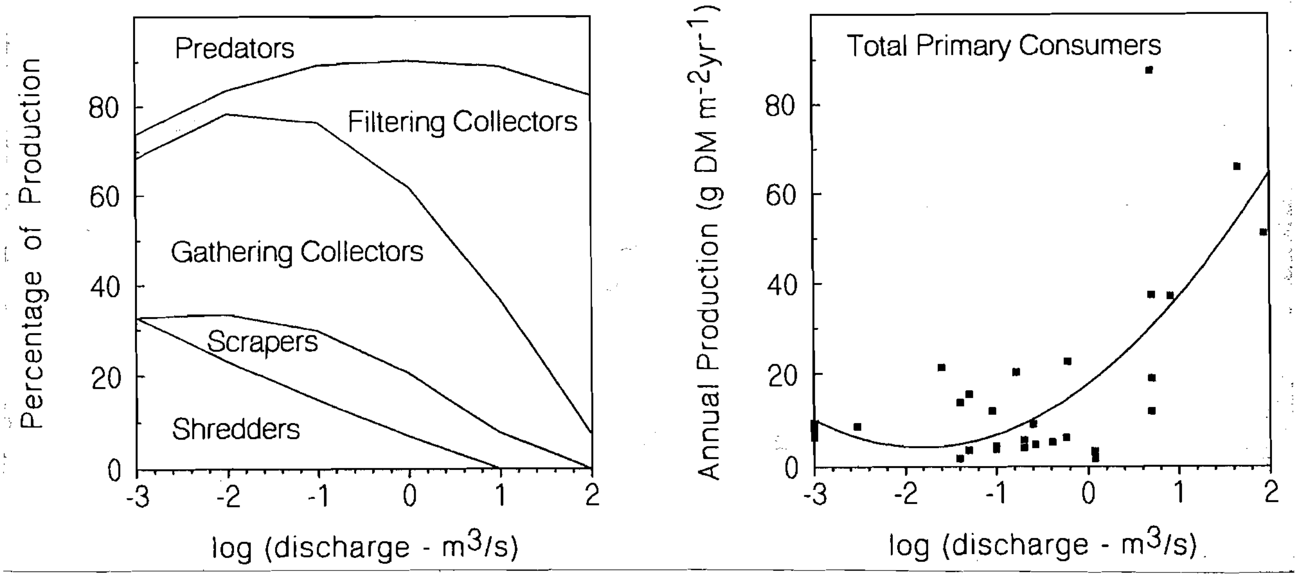

Figure 3. Trends in invertebrate production and in the contribution of functional groups to invertebrate production with river discharge, using data from 19 streams and 31 separate community estimates. Modified from Benke (1993).

Large rivers appear capable of having high production under natural conditions, but human activities can have a strong influence. As a relatively undisturbed river, the Satilla has one of the highest invertebrate production estimates to date. The Ogeechee River, also relatively undisturbed, promises to be even higher when snags are fully taken into account. However, streams of various sizes have shown high production of pollution-tolerant species when enriched by organic effluents (Benke 1993). Other types of degradation, such as on the large connecting channels of the Great Lakes (the largest rivers on which invertebrate community production has been measured) probably result in reduced production (Edwards *et al.* 1989).

Food from DOM, FPOM, microbes

The high production of invertebrates from the Satilla River, particularly from the snag habitat, raises the issue of its trophic basis. What is the quantity, quality and source of organic matter used by invertebrates in Coastal Plain rivers that results in such high production? This was the underlying question in our ecosystem-level study on the Ogeechee River where we addressed biological production at multiple trophic levels (e.g., Meyer 1990). Early in our study on the Ogeechee, we carefully looked at the gut contents of a wide array of invertebrates (Wallace *et al.* 1987). Regardless of where the invertebrates were found, by far the highest proportion of material in the guts of primary consumers was amorphous detritus, with small fractions of diatoms. The composition of gut contents was very similar to the composition of seston. Parallel studies by Judy Meyer and her students have revealed that much of this amorphous material originated from floodplain soils in the form of DOM, FPOM, and microbes (e.g., Meyer 1990, Wainright *et al.* 1992). The organic matter is delivered as seston to various habitats where it is either filtered by invertebrates or where it flocculates and aggregates on surfaces for consumption by gathering collectors. In experiments designed to determine the relative importance of food quantity and quality, we grew mayfly gathering collectors (*Stenonema* spp.) under conditions of complete darkness (no algal growth) and in river water filtered of all but the finest particles (< 1 um) (Benke *et al.* 1992). Even under these conditions, mayfly growth was little affected. Thus, unlike the stream paradigm, collectors, rather than algal scrapers, are the most important type of consumer in the main channel of this 6th order river.

Drift is high, long and far

When benthic animals are swept into the current by either active or passive means, their presence in the moving water is known as drift. Drift has fascinated aquatic entomologists and ecologists for decades, particularly due to the fact that there is usually a strong diel pattern, with nocturnal densities much higher than diurnal densities. As with most stream studies, drift has been examined most commonly in small streams. The stream paradigm suggests that only a very small fraction of benthic animals generally drift at one time, remaining in the drift for only a short distance and amount of time (Table 3, Waters 1972).

Drift studies in the Satilla and Ogeechee present quite a different scenario from the findings in small streams (Benke *et al.* 1986, 1991). Organisms display a strong nocturnal pattern as would be predicted, but more than 3/4 of the drift numbers and biomass originate from snags, rather than benthic habitats, providing independent verification of the importance of snags to river production (Table 2). Although drift density in the Satilla was toward the high range of most other drift studies, densities in the Ogeechee were about 5 times higher than this (Table 3), corresponding to the approximately 5-times greater amount of wood in the Ogeechee (Wallace and Benke 1984). Thus, Ogeechee River drift densities were substantially higher than the usual range (Table 3).

TABLE 3. Comparison of drift parameters between Ogeechee and Satilla Rivers with small-stream paradigm.

	Satilla River	Ogeechee River	Small Stream
Density (no./m^3)	3.2	21	0.5-5.0
Biomass (mg DM/m^3)	0.4	2.4	0.2-1.0
Drift Distance (m)	>1000	>1000	<10
Drift Time (min.)	>60	>60	<1
% in Drift	0.1-1.0	0.1-1.0	<0.01

Once invertebrates on snags are swept out into the current, they cannot simply swim to the bottom to re-attach, as with most small streams, but they must wait until the current brings them into close proximity to another snag. This results in drift distance and times being much longer than formerly shown (Table 3). In addition, a substantially higher fraction of the invertebrate population (from snags) must be involved in drift than has been estimated previously for benthic populations. With 0.1 to 1.0% of animals in the nocturnal drift at a moment in time (Table 3), this means that between 1 and 10% of the population probably drifts nightly, resulting in a net displacement of the average snag invertebrate 180 m downstream (Benke *et al.* 1991).

While these high drift rates suggest their significance as a means of recolonizing newly inundated snags, drift has a distinct trophic function as well. Net-spinning caddisflies (macro-filtering collectors) on snags in the Ogeechee River obtain most of the nutrition responsible for their high production by capturing drifting animals (Wallace *et al.* 1987). Much of the snag fauna consumed by insectivorous fishes in the Satilla also may be obtained from the drift (Benke *et al.* 1985).

Although the major biomass component of drift originates from snags in the form of aquatic insects, substantial numbers of microcrustaceans are also found. During low discharge, drifting crustaceans appear to represent "leakage" from slackwater habitats where they reside as shallow-water zooplankton (i.e., in backwaters and in small low-velocity pockets along the main channel). At high discharge they are most likely flushed from the pools found deep within the floodplain swamp.

CONCLUSIONS

Low-gradient rivers with broad floodplains clearly function in a different manner than our views based on the stream paradigm. As a result, the invertebrate communities in these systems function in correspondingly different ways as well (Table 4). To what extent our results from medium-size rivers of the Atlantic Coastal Plain can be extrapolated to larger rivers in general is uncertain. However, issues of habitat origin, the role of flooding and floodplains, distribution of invertebrate production among habitats and functional groups, feeding pathways, and drift must all be considered. I expect that efforts to discover the lost characteristics and functions of regulated rivers will benefit from studies of these natural medium-size systems in combination with analyses of the less-perturbed reaches of the larger rivers. Both approaches will hopefully lead to river management strategies that contribute to a restoration of ecological integrity.

TABLE 4. Summary of selected ecosystem and invertebrate community characteristics for the stream paradigm (small-to-medium size) and for Coastal Plain floodplain rivers (medium-size).

	Stream Paradigm	Floodplain Rivers
Riparian Zone	Narrow	Broad floodplain swamps
Channel habitats	rocky (gravel to bedrock)	sand, snags
Slackwater habitats	pools	backwaters (sloughs)
System Metabolism	heterotrophic to autotrophic	heterotrophic
Effects of floods	catastrophic, brief	beneficial, prolonged
Floodplain fauna (aquatic)	none on surface	extensive, year-round
Functional groups (aquatic)		
channel	shredders, scrapers	gathering and filtering collectors
floodplain		shredders, gathering collectors
Invertebrate Production	low-to-moderate (4-25 g DM $m^{-2}yr^{-1}$)	moderate-to-high (>25 g DM $m^{-2}yr^{-1}$)
Invertebrate Drift	short distances and times origin from benthic habitats	long distances and times origin from snags
Invertebrate food	Riparian litterfall, periphyton	Swamp-derived DOM, FPOM, microbes

Much remains unknown about the natural function of floodplain rivers, but it is clear that many past management practices have had devastating impacts on natural ecosystem function. Future conservation of the few remaining natural floodplain rivers cannot be accomplished if snags are removed and channels are deepened, if broad floodplain forests are destroyed, or if natural flooding regimes are greatly altered by upstream dams or water diversions. All these characteristics are essential for a highly diverse and productive riverine ecosystem. Similarly, attempts to restore some of these same characteristics in the future management of previously altered rivers should help return them to a more natural state.

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FROM LOCAL HABITAT PATCHES TO LANDSCAPES IN STREAM FISH ECOLOGY

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ABSTRACT. Spatial habitat heterogeneity in lotic ecosystems exists within a hierarchical framework of physical units, ranging from microhabitats to drainage basins. Interactions between physical habitats, as mediated by the controlling influence of the ecotones between them, has potentially dramatic effects on organic matter supply, structural complexity of the environment, and movement of individual organisms. Stream fish exhibit complex life cycles and habitat use patterns associated with the spatial and temporal heterogeneity of lotic environments. Numerous studies have revealed differences among fish species and life history stages in their use of physical habitats and the influence of key life cycle events on fish distribution. Lotic ecologists, however, have largely left unexplored the influence of large-scale spatial habitat relationships on the critical rate-dependent processes regulating fish population dynamics. Large-scale habitat relationships that are likely to be important include habitat complementation, habitat supplementation, source vs. sink interactions, and neighborhood effects. Current data in the fish ecology literature suggests all four of these spatial habitat relationships are likely to be important in determining fish population dynamics. Quantitative descriptive and experimental studies directly elucidating the role these spatial habitat relationships play in regulating the distribution and abundance of fish will, however, be essential if a rigorous landscape perspective for lotic fish ecology is to be developed.

INTRODUCTION

The River Continuum Concept depicts the stream as an upstream-downstream gradient of gradually changing physical conditions and associated adjustments in energetic processes and functional attributes of the biota (Cummins 1975, Vannote *et al.* 1980). Associated theoretical constructs, like the organic spiralling concept (Elwood *et al.* 1981, 1983), further emphasize longitudinal linkages along the continuum, with ecosystem processes in downstream areas linked to those in upstream areas by the unidirectional flow of water, nutrients, and organic matter. The River Continuum and spiralling concepts have been useful in forcing stream ecologists to examine linkages between the terrestrial drainage basin and stream energetics and between upstream and downstream areas (Naiman *et al.* 1988a, Gregory *et al.* 1991).

When viewed at finer spatial scales, it is also apparent that streams and rivers frequently do not exhibit the gradual transition in physical and biological characteristics emphasized in the River Continuum Concept (Huet 1959, Hawkins 1985, Frissell *et al.* 1986, Naiman *et al.* 1988a). Rather, distinct habitats types are frequently observed in streams, with well defined boundaries or ecotones between the habitats (Naiman *et al.* 1988a). To incorporate these added complexities stream ecologists are increasingly emphasizing the importance of viewing streams as a collection of habitat patches, which interact with each other across well defined ecotones (Naiman *et al.* 1988a, Pringle *et al.* 1988).

The objectives of this paper are to: (1) illustrate the key role habitat and ecotone interactions play in regulating spatial heterogeneity and energetic processes in natural headwater streams and rivers, (2) outline the basic life cycle of lotic fish and the nature of their habitat use, and (3) examine the potential impact large-scale spatial relationships among habitat units and boundaries can have on the critical rate-dependent processes influencing population dynamics of lotic fish.

THE HIERARCHICAL AND PATCHY NATURE OF LOTIC ECOSYSTEMS

Lotic ecosystems can be best viewed as hierarchically organized physical environments that incorporate, at successively lower levels of organization, the drainage basin, subbasin, stream segment, stream reach, habitat, and microhabitat (Fig. 1, Frissell *et al.* 1986). Development and persistence of each of these environments is controlled by processes that function at particular temporal and spatial scales. Furthermore, the hierarchy is spatially nested in that the physical units at any given level form the physical units at the next higher level of organization (Frisell *et al.* 1986). In turn, because streams are hierarchical in nature, spatial habitat heterogeneity can be defined at a variety of scales, ranging from the microhabitat to the subbasin. In an ecological context, however, the appropriate scale will be defined by the ecological processes being considered, which in the case of stream fish is strongly influenced by the size, mobility, and life history characteristics of the particular species being examined. In this paper I primarily concentrate on spatial habitat heterogeneity at the stream reach or segment level.

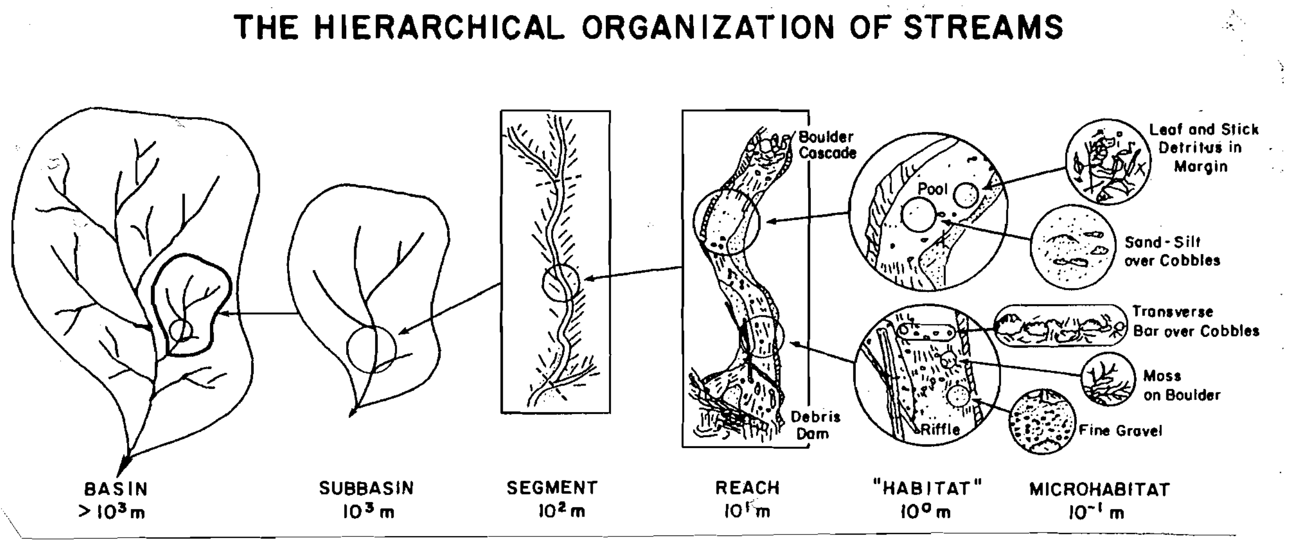

Figure 1. Hierarchical organization of physical units in stream ecosystems (Adapted from Frissell *et al.* 1986).

The key physical factors controlling habitat heterogeneity at the reach or segment level are the expenditure of kinetic energy associated with the downhill transport of water and sediment, obstructions in the channel, and the extent of channel meandering (Keller and Swanson

1979, Richards 1982). The interaction between the energy flux and channel obstructions creates substantial longitudinal and lateral heterogeneity in lotic ecosystems (Frissell *et al.* 1986, Ward and Stanford 1989). Longitudinal habitat heterogeneity is primarily associated with differences in depth, substrate, and current velocity related to pool-riffle development (Yang 1971). Lateral habitat heterogeneity is primarily associated with the proximity of the habitat to the main stream channel, nature of the interaction between the terrestrial and aquatic environment, and the extent of channel meandering. In small streams, these lateral habitats include stream margins, backwaters, and isolated pools (Moore and Gregory 1988a,b; Gregory *et al.* 1991). In large rivers, an extensive network of side channels normally connects the main river channel with outer areas of the floodplain, which in turn possesses a tremendous diversity of permanent or semipermanent habitats, including sloughs, oxbow lakes, meander scroll depressions, and backwater swamps (Ellis *et al.* 1979, Welcomme 1985, Junk *et al.* 1989).

In addition to physical processes, animal activity also has potentially strong effects on spatial heterogeneity in lotic ecosystems, especially in headwater streams. Beaver (*Castor canadensis*) activity, in particular, creates well defined habitats (Naiman *et al.* 1988a, Pringle *et al.* 1988). The building of dams by beavers alters the hydrologic regime and kinetic energy of the stream, resulting in pond formation and sediment and organic matter deposition (Naiman *et al.* 1986). Foraging by beavers on riparian vegetation is also highly selective, causing changes in both the amount and composition of allochthonous inputs by the riparian vegetation (Naiman *et al.* 1988b). Consequently, beaver activity creates considerable habitat heterogeneity, along with ecotonal boundaries coinciding with spatial discontinuities in soil, water and/or vegetation properties (Johnston and Naiman 1987). Longitudinal habitat boundaries include those between the upstream area and beaver pond and between the dam and downstream area, while lateral boundaries occur between the pond and riparian zone.

THE INFLUENCE OF HABITAT BOUNDARIES ON ENERGY FLOW IN STREAMS AND RIVERS

Interactions between different habitats, as mediated by the controlling influence of the ecotones between them, has potentially dramatic effects on energetic processes in streams and rivers (Gregory *et al.* 1991). A comparison of stream segments in Quebec, Canada with and without beaver dams and ponds, for example, indicates how beaver-induced channel modifications and increased boundary complexity result in dramatic changes in carbon inputs, standing stock, and outputs in small streams (Naiman *et al.* 1986, 1988b). Stream segments without beaver ponds received a total annual input of organic carbon of 220.5 $g/m^2/yr^{-1}$, while beaver ponds had an input of 65.1. Yet the standing stock of organic matter in the pond was 2.7 times that in the unponded segment and total carbon output was 2.4 times as high in the ponded than unponded section. Furthermore, since the ponded section was approximately seven times as wide as the unponded section (Naiman *et al.* 1986), if these values were put on a unit length basis, total carbon input in the unponded section was 48% of the ponded section, standing stock was 5%, and total carbon output was only 6% (Naiman *et al.* 1988b). Presence of beaver dams also had dramatic effects on the ability of the stream to retain and process organic material. Both the carbon turnover length and rate of downstream movement by the carbon were

80-90% lower in the segment with ponds. Together, these results indicate the occurrence of a critical ecotone in a small stream ecosystem, in this case a beaver dam, has dramatic effects on both the structural heterogeneity of the physical environment and the patterns of energy flow.

Similarly, in natural unconstrained rivers with extensive floodplains, energy sources derived from lateral interactions between the river and adjacent habitats in the floodplain appear to be more important than upstream inputs in regulating energetic processes (Welcomme 1979, Winterbourn *et al.* 1981, Minshall *et al.* 1985, Statzner and Higler 1985, Cuffney 1988, Junk *et al.* 1989, Sedell *et al.* 1989). Since most of the "terrestrial" resource patches adjacent to floodplain rivers exhibit higher plant productivity than the river itself, they are a major source of nutrients and organic material for the river (Welcomme 1979, Junk *et al.* 1989, Sedell *et al.* 1989). Pulses of discharge associated with prolonged flooding allow the river to transgress patch boundaries and interact with the complex array of "terrestrial" resource patches. Both the surface area for exchange between the river and floodplain (Sedell *et al.* 1989) and the rate water moves on and off the floodplain are important in determining the amount and type of exchange (Junk *et al.* 1989). Consequently, lateral interactions between the river and resource patches in the floodplain are thought to be primary determinants of overall productivity in large floodplain rivers (Welcomme 1979, Edwards and Meyer 1987, Junk *et al.* 1989, Sedell *et al.* 1989, Meyer and Edwards 1990).

LIFE CYCLES AND MOVEMENT PATTERNS OF LOTIC FISH

Associated with the spatial heterogeneity in physical habitats and food resources that exists in lotic ecosystems, fish exhibit complex life cycles and habitat use patterns (Fig. 2). Life begins at spawning, after which there is an incubation period lasting anywhere from a few days to several months. Hatched fish usually then move to feeding habitats where most growth and development occurs. These feeding habitats normally consist of a mosaic (Fig. 2) of several habitat types (e.g., pools, riffles, stream margins etc.), all of which can potentially be used by fish during the growing season and serve as nursery and rearing habitats for larval stages and juveniles. Depending on the life cycle of the fish and local climatic conditions, the fish then go through several seasonally favorable (growth) and seasonally unfavorable (reduced growth) periods until sexual maturity is reached (Fig. 2). In north-temperate areas, favorable and unfavorable periods primarily involve movement between summer feeding habitats and winter refugia (Cunjak 1988). In tropical streams, favorable and unfavorable periods usually involve movement between wet season feeding habitats and dry season refugia. Once sexual maturity is reached, the fish then undergo spawning movements to appropriate spawning sites for egg deposition and reinitiation of the cycle.

Although this depiction of fish life cycles in lotic environments is relatively basic and simple (Fig. 2), it has three important implications for understanding the impact of habitat heterogeneity and landscape attributes on stream fish. First, because various life stages of fish require different physical habitats, spatial heterogeneity and the connectivity of habitat patches will be critical for the completion of their life cycles (Bisson *et al.* 1982, Schiemer and Spindler

1989). Second, since the life cycle of stream fish can potentially extend over long temporal and large spatial scales, lotic fish ecologists need to increasingly examine the influence of large spatial and long temporal attributes of environmental heterogeneity on fish population dynamics. Third, natural or anthropogenic factors disrupting this heterogeneity over space or time will have potentially profound effects on fish population dynamics.

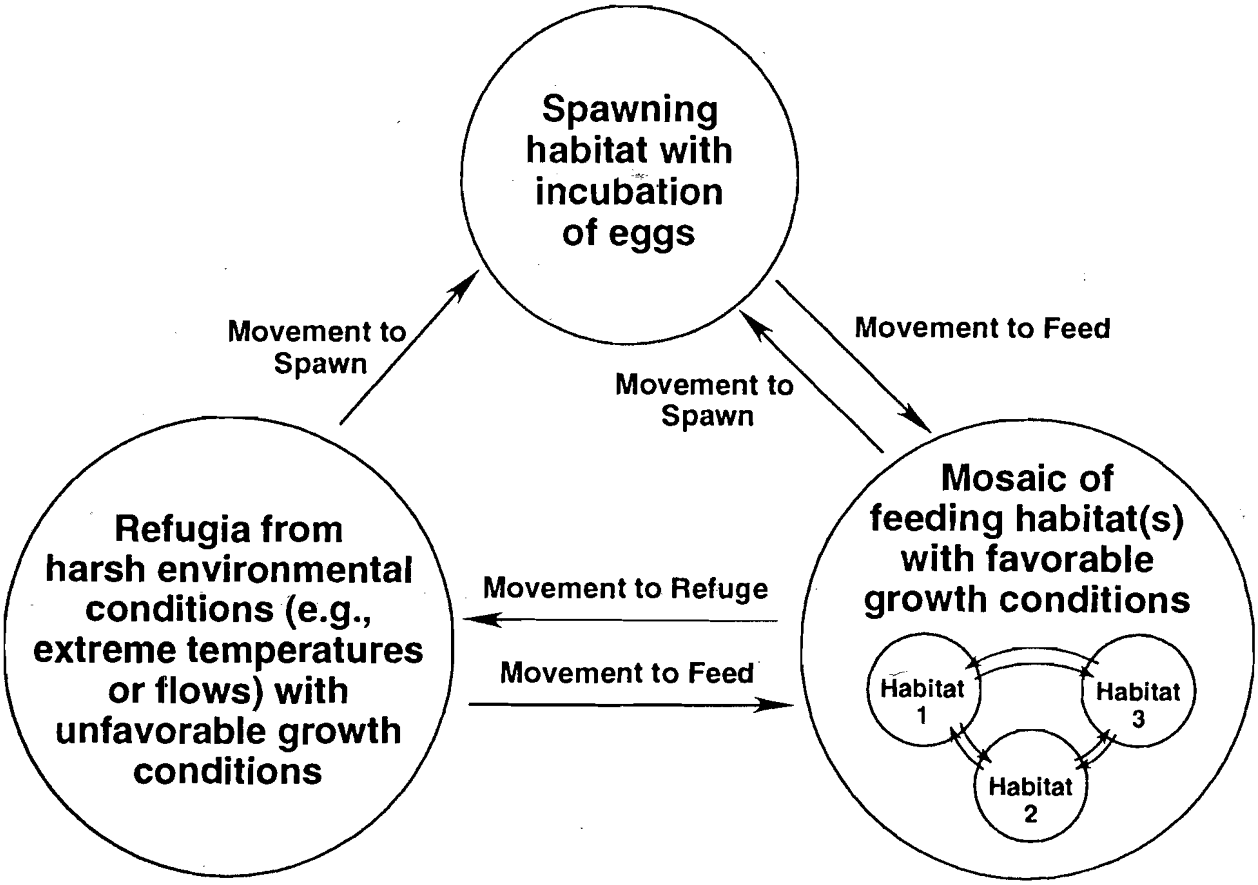

Figure 2. The basic life cycle of stream fish with emphasis on patterns of habitat use and movement (Based on Jones 1968, Northcote 1978, Schlosser 1991).

THE PATCHY AND TEMPORALLY DYNAMIC DISTRIBUTION OF LOTIC FISH

Numerous studies of fish in headwater streams and large rivers have, in turn, revealed associations between the structural characteristics of the environment and the occurrence of fish species or size classes. Studies of fish communities conducted along longitudinal and lateral dimensions indicate many fish species exhibit well defined zonation, suggesting adaptation to habitat conditions associated with upstream versus downstream (Huet 1959) or floodplain versus midchannel habitats (Welcomme 1985). The distribution of stream fish along both axes is, however, highly dynamic, with much of the movement involving reproductive activities during which adult fish move into shallow, upstream or floodplain habitats to spawn and juvenile fish move out of these areas once a sufficient size is reached (Northcote 1978, Lowe-McConnell 1987, Schlosser 1987, Copp 1989). In conjunction with these spawning migrations, considerable complementarity occurs in the distribution of large and small fish along longitudinal and lateral axes, with small fish being found predominantly in shallow upstream or lateral habitats (Welcomme 1985, Power 1987, Schlosser 1987, Moore and Gregory 1988ab) and large fish being more abundant in deeper downstream or midchannel habitats (Welcomme 1985, Schlosser 1987).

Studies on small spatial scales, within stream reaches or within specific types of habitat, also reveal differences in habitat use by various species and life history stages of fish. In either upstream reaches (Fig. 3) or large rivers, spawning habitats normally differ from juvenile rearing habitats, juvenile habitats differ from adult habitats, and habitat use by adults and juveniles vary between species (Bisson *et al.* 1982, Copp 1989, Schiemer and Spindler 1989, Lobb and Orth 1991). Furthermore, as on large spatial scales, habitat use on small spatial scales is dynamic and strongly influenced by the sequence of events in the life cycle of the fish (Bisson *et al.* 1982, Lowe-McConnell 1987, Schiemer and Spindler 1989).

CONSEQUENCES OF SPATIAL HABITAT RELATIONSHIPS FOR FISH POPULATION DYNAMICS

While numerous studies have revealed associations between physical habitats and the occurrence of fish species or size classes, few studies by lotic fish ecologists have addressed the more important question of how large-scale spatial habitat relationships influences the rate-dependent processes regulating population dynamics. Four large-scale spatial habitat relationships are likely to be important: habitat complementation, habitat supplementation, source vs. sink interactions, and neighborhood effects (Dunning *et al.* 1992).

Habitat complementation. Habitat complementation refers to the spatial proximity of different nonsubstitutable resources or habitat types required by a particular species (Dunning *et al.* 1992). For example, if a stream consists of two habitat types and each habitat contains a different "resource" required by a particular species, stream segments can differ in the spatial proximity or complementation of the habitats (Fig. 4.1). Furthermore, since these "resources" are found in different habitats, the organism must travel between the habitats to be successful. For stream fish these "resources" might be spawning vs. feeding habitats, feeding vs. refugia habitats, etc. (Fig. 2).

Portions of the landscape where different habitat types are in close proximity (Fig. 4.1A) will supposedly support higher populations of fish than portions of the landscape where they are farther apart (Fig. 4.1B; Dunning *et al.* 1992). The mechanism(s) by which habitat complementation increases fish population size is due to its effect on the rate-dependent processes regulating population dynamics. In particular, habitat complementation would potentially: (1) decrease the energetic costs of migration between different habitat types, with an ensuing increase in growth and survival rates and (2) decrease the travel time between habitat patches, with an ensuing decrease in their exposure to predation or other risks of mortality during transition periods.

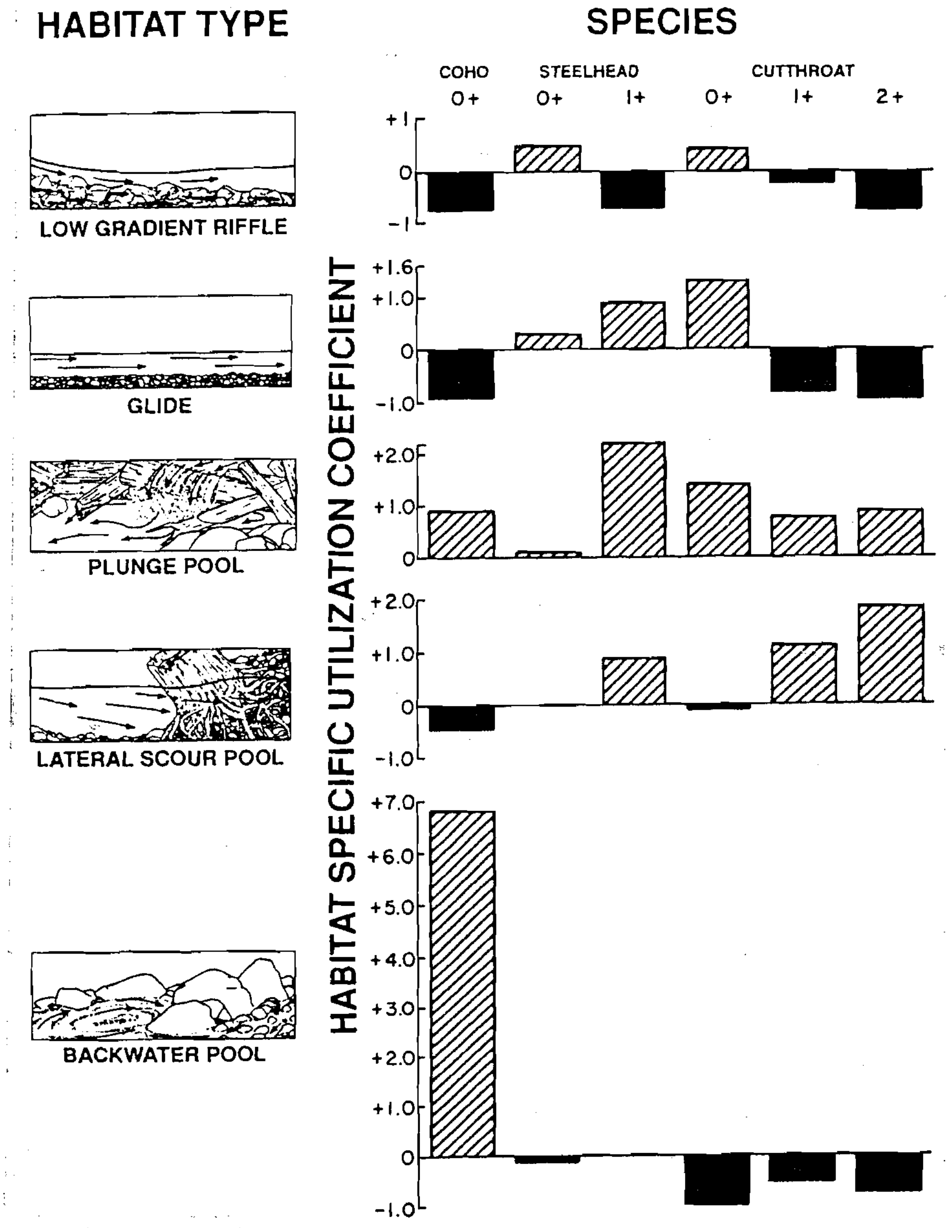

Figure 3. Habitat utilization by different age classes of coho salmon (*Oncorhynchus kisutch*), steelhead trout (*Salmo gairdneri* Richardson), and cutthroat trout (*Salmo clarki* Richardson) in headwater streams of western Washington (From Schlosser 1991 as adapted from Bisson *et al.* 1982). Habitat utilization (HU) calculated as the difference between habitat specific density (HSD; the average density of fish in a particular habitat type) and average total density (ATD; average density of fish over all habitat types combined) divided by ATD. HU theoretically varies from minus one, indicating total non-use of the habitat type, to positive infinity as a greater proportion of the population resides in the habitat type of interest.

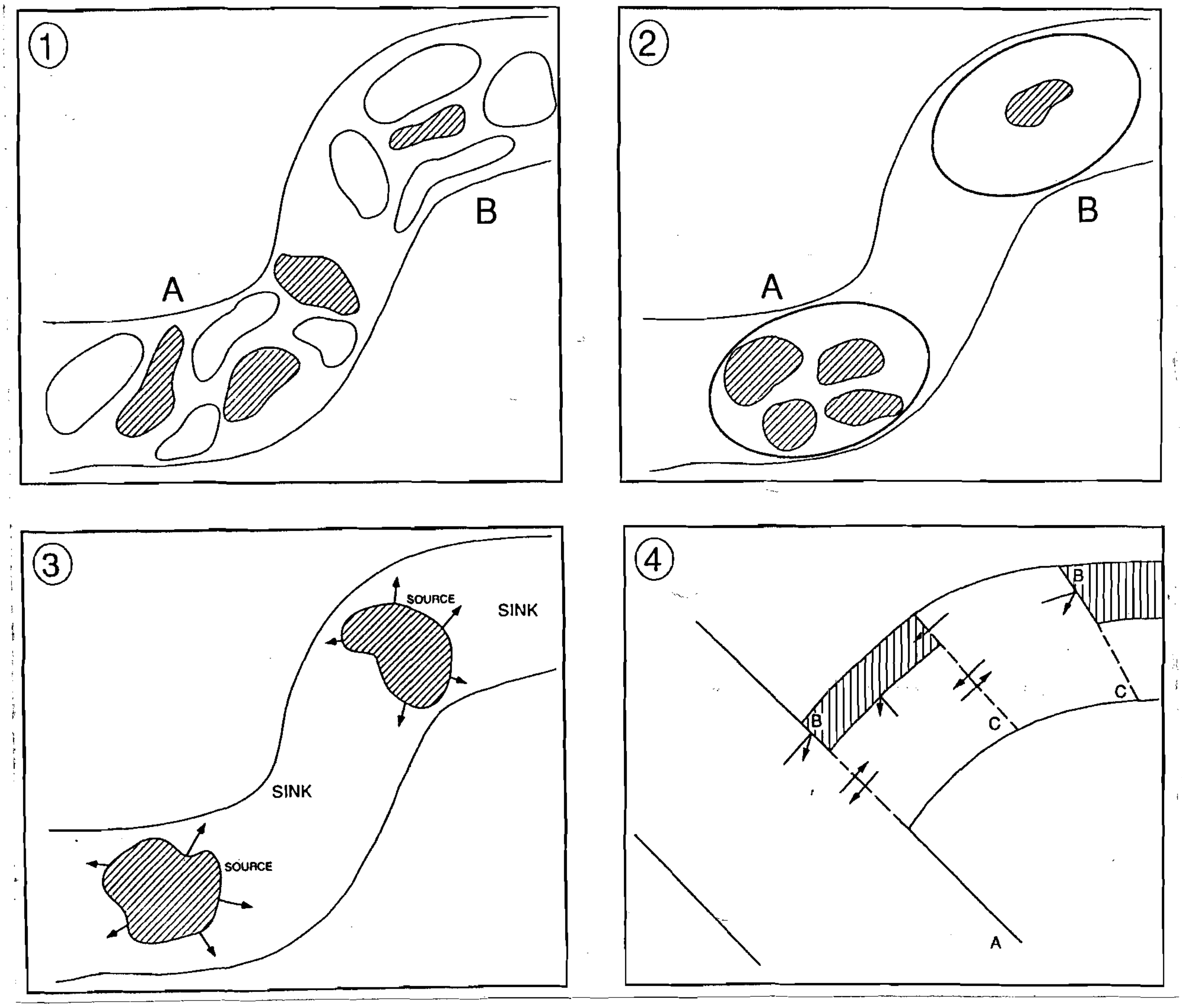

Figure 4. Four large-scale spatial habitat relationships potentially influencing the population dynamics of stream fish: (1) habitat complementation: a species requires non-substitutable resources found in two different habitats (cross-hatched and open), (2) habitat supplementation: a species requires substitutable resources found in the cross-hatched habitat patches and all patches within the ovals are accessible, (3) source vs. sink relationships: a species occupies two habitat types, with one (sources: shaded area) producing excess individuals or dispersers (arrows) and the other (sink: open areas) not producing enough individuals to maintain a local population, (4) neighborhood effects: dispersers (arrows) are more likely to move into adjacent than distant habitat patches and habitat patches with permeable (dotted lines) versus impermeable (solid lines) boundaries (From Schlosser 1993 as adapted from Dunning *et al.* 1992).

If the spatial arrangement among habitats is temporally stable, increased habitat complementation can also result in increased stability or persistence of populations (Dunning *et al.* 1992). Complementation will increase persistence of populations by increasing the probability fish will find an appropriate habitat during critical transition or migratory periods (e.g., from summer feeding habitats to overwintering habitats), which enhances their survival and persistence in that region of the landscape. If, however, the spatial arrangement of habitats is temporally unstable, then the stability of the fish population becomes a more complex function of both the temporal and spatial persistence of habitats and the ability of fish to find those habitats.

Recent studies in large rivers and headwater streams suggest habitat complementation is likely to be a critical factor determining population size and persistence of fish. For example, based on detailed studies of habitat use and recruitment by fish in the Danube River, Schiemer *et al.* (1991) concluded that a fundamental factor influencing juvenile recruitment and population size was not just the presence of both spawning and larval feeding habitats but also the spatial proximity of the two areas. Similarly, in headwater streams in the central United States, Schlosser (1987) concluded that spatial proximity of deep pool refugia to shallow juvenile rearing habitats was a fundamental factor determining the temporal persistence of juvenile fish, particularly during harsh winter periods.

Habitat supplementation. In contrast to habitat complementation, habitat supplementation occurs when "resources" are substitutable and these "resources" can be either food or physical habitat. Since fish in headwater streams frequently exhibit flexible foraging behavior (Angermeier 1982, 1987), they can expand or supplement their "resource" supply by using different resources in the same habitat or the same resource in different habitats, particularly when local densities are high. Population size will supposedly be higher in regions of the landscape where supplementation occurs (Fig. 4.2A) than where it does not occur (Fig. 4.2B) because it: (1) allows individuals to increase their food intake and subsequently their growth, survival, and fecundity rates and/or (2) increases the range of feeding habitats available for use by the organism that are within range of suitable refugia from predation (Dunning *et al.* 1992). The end result is that supplementation will allow a stock of fish to increase and dampen density-dependent mortality rates following high levels of recruitment.

I know of no studies explicitly testing the effect of habitat supplementation on recruitment dynamics or the population size of stream fish. Recent studies, however, have demonstrated that habitat supplementation does affect critical rate-dependent processes influencing fish population dynamics. For example, Power and her colleagues (Power 1984a,b; Power *et al.* 1989) assessed the response of armored catfish (Loricariidae) to spatial heterogeneity in food resources and predation intensity. They documented that: (1) periphyton productivity in the stream was patchily distributed, with the highest rates in shallow, open sunny reaches and the lowest rates in deep, densely shaded areas, (2) individual loricariids continually redistributed themselves in response to changes in food availability in pool habitats, to the extent that fish in sunny crowded pools had food intake and growth rates similar to fish in dark, sparsely populated pools, and (3) although periphyton resources were most abundant in shallow habitats, they were largely unexploited by loricariids because fish in these areas experienced higher mortality rates from terrestrial predators. These results strongly suggest individual fish in streams supplement resource intake by using a number of different habitat patches, that the selection of these habitat patches is finely balanced by its influence on the food intake and growth rate of individual fish, and that predators place major constraints on the ability of fish to engage in habitat shifts for the purpose of resource supplementation.

Source vs. sink relationships. In contrast to habitat complementation and habitat supplementation, which deals with the spatial distribution of nonsubstitutable or substitutable resources for individual organisms, source vs. sink relationships deal with spatial variation in the production of juveniles (Pulliam 1988). Sources are defined as those areas that for a variety of reasons (e.g., high organic matter supply and low piscivory) exhibit high juvenile recruitment. These source areas in turn provide immigrants to less productive habitats on the landscape, which are termed sinks (Fig. 4.3). Since local recruitment in sinks is not sufficient to maintain the population, immigration from source habitats is the primary rate-dependent process determining population dynamics in sinks (Fig. 4.3). Similarly, since individuals in sinks do not exhibit strong recruitment, the relative amount of source/sink habitat on the landscape can have strong effects on overall recruitment in the population (Pulliam 1988).

Do source vs. sink relationships play a critical role in determining the population dynamics of stream fish? I know of no study in the current literature that directly addresses this question. This is partly due to the difficulty in collecting the appropriate data to document such a relationship, which would include measurements of reproductive success, dispersal, and persistence of dispersers in adjacent habitats (Dunning *et al.* 1992). However, data recently collected in beaver ponds and associated stream reaches suggest source vs. sink relationships play a critical role in determining the population dynamics of fish in these areas (I.J. Schlosser, unpublished data). Specifically, new beaver ponds are organically rich relative to lotic environments (Naiman *et al.* 1988b), juvenile fish recruitment tends to be higher in ponds than associated lotic habitats, and pond species disperse along streams in search of new pond habitats with lower fish densities but usually they do not reproduce successfully in intervening lotic reaches. Consequently, immigration from pond (source) habitats is a primary factor maintaining many of the pond species in associated lotic (sink) habitats.

Neighborhood effects. Since movement between different habitats is a fundamental part of the life cycle of stream fish (Fig. 2), the abundance of a species in a particular patch of habitat can be strongly influenced by the type of adjoining habitats and the nature of the boundaries between them (Dunning *et al.* 1992). For example, since species are more likely to disperse by chance into adjoining rather than distant habitat patches, the species composition and temporal dynamics of fish would probably be very different in the two, type C habitats in Fig. 4.4 because of differences in their spatial proximity to the type A habitat. Similarly, the ability of fish to disperse into a neighboring habitat depends on the size and permeability of the boundary between them (Fig. 4.4).

Is there any evidence that spatial proximity of different habitat patches influences immigration processes and, consequently, the population and community dynamics of stream fish? Osborne and Wiley (1992) examined the influence of stream channel position within the drainage network on species richness in the midwestern United States. They observed that the proximity of the tributary sampling location to the downstream main channel was more important than local habitat structure in determining species richness in tributary streams. Osborne and Wiley (1992) concluded that dispersal-mediated interchanges between the main channel and tributary were more critical than local biological interactions, such as habitat mediated competition, in determining species richness in these areas. Gorman (1986) reached a similar conclusion regarding the importance of the spatial proximity of large rivers to tributary sites in determining fish species richness in tributaries.

The permeability of habitat boundaries also appears to be important in some natural streams. In many mountain streams, for example, natural geological barriers such as waterfalls strongly influence species colonization (Gilliam *et al.* 1993). Species composition across these barriers depends on the height of the barrier, stream discharge, and the colonizing ability of different species.

CONCLUSIONS

Lotic ecosystems exhibit considerable physical heterogeneity, with boundaries between the physical habitats playing critical roles in regulating structural habitat complexity, energetic processes, and the movement of individual organisms. Since physical units in streams are hierarchically organized from microhabitats to drainage basins, habitat heterogeneity can be defined at a variety of spatial scales. The most relevant spatial scale for study will depend on the ecological question being considered and the life history characteristics of the particular species being examined. Historically, however, stream ecologists have primarily studied the influence of habitat heterogeneity on the population and community ecology of fish at relatively small spatial scales (Matthews and Heins 1987 and references therein). Lotic ecologists need to increasingly examine the influence of habitat heterogeneity on fish at larger spatial scales. Studies directly assessing the influence of habitat complementation, habitat supplementation, source vs. sink interactions, and boundary effects on rate-dependent processes influencing fish population dynamics are especially needed if we are going to develop a suitable landscape perspective for lotic fish ecology.

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CONTRIBUTED PAPERS

SESSION I: AQUATIC BIOLOGY AND ZOOLOGY

Saturday, March 6, 1993

Moderated by:

Cindy Taylor
Department of Biology
Austin Peay State University

BEST MANAGEMENT PRACTICES FOR IMPROVING WATER QUALITY IN THE WEST SANDY CREEK WATERSHED, HENRY COUNTY, TENNESSEE

Mack T. Finley, Steven W. Hamilton[1], and James A. Gore[2]

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ABSTRACT. Numerous Best Management Practices (BMPs) are being applied throughout the West Sandy Creek Watershed for erosion control and water quality improvement. A variety of BMPs are being installed to reduce soil erosion and animal waste contamination from agricultural activities. Also, instream modification structures are being used to trap silt and organic particulates. Natural wetlands are being enhanced by managing existing beaver ponds to increase silt removal, and to improve fish and waterfowl habitat. Biological monitoring will be done prior to and after the installation of BMPs in the upper tributaries of all major streams in the West Sandy Creek Watershed. Water chemistry analyses and aquatic macroinvertebrate determinations will be used to monitor effects of BMPs on water quality. This 5-year research project is a cooperative effort between several state, federal, and private agencies with the overall objective of reducing nonpoint sources of pollution in the West Sandy Creek Watershed.

WEST SANDY WETLAND AND EMBAYMENT RECOVERY PROJECT KENTUCKY RESERVOIR, HENRY COUNTY, TENNESSEE

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G. A. UPHAM AND J. W. WILSON

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ABSTRACT. The Nonpoint Source staff of The Tennessee Department of Environment and Conservation, Division of Water Pollution Control conducted a reconnaissance survey of the West Sandy embayment of Kentucky Lake, during July 1992, in order to further document oxygen sinks associated with organic loading and toxic levels of manganese sediments. Low dissolved oxygen levels, < 2.5 ppm at 2.0 m depth, have been documented in the West Sandy Embayment of Kentucky Lake, Henry County, Tennessee, especially in the summer and fall. Also caged animal and juvenile mussel bioassays have been conducted in areas of suspended manganese toxicity resulting from upland eroded soils. The West Sandy Creek and embayment is a 8,500 acre watershed of which 4,000 acres is hardwood wetland. The target watershed project objectives are to reduce sediment loading from agricultural sources and reconstruct wetland/riverine habitat. Two Hydrolab DataSonde 3 internal logging samplers were deployed by buoys in the West Sandy embayment (one downstream of the dewatering dike and the other upstream from the mouth) for two 24 hour periods. Dissolved oxygen, pH, temperature and conductivity readings were gathered at 15 minute intervals. Along with the buoy samples, five cross section transects were logged near the mouth of West Sandy continuing east to near the dewatering dike of the West Sandy embayment, collecting dissolved oxygen, temperature and conductivity. Dissolved oxygen levels near the mouth of the embayment were found for the most part, to be below the water quality standard (X = 3.8 ppm) of 5 ppm during the study period. The levels near the dewatering dike averaged higher when the TVA pumps were operating (X = 7.5 ppm), but dropped rapidly after they were turned off to levels similar to those recorded at the mouth of the embayment indicating high deposition of organics and sediment during storm events. The soils have been cultivated extensively and runoff during storm events can deposit greater than 2,000 tons of sediment into the organically rich bottomland wetlands. There have been 48 agricultural best management practices, BMPs, implemented to reduce sedimentation or establish cover crops; another 72 are planned for the next three years. In addition, 24 instream structures are planned for riverine habitat improvement and 2000 acres of drained wetland habitat will be reclaimed.

PRELIMINARY RESULTS OF A SURVEY OF MACROINVERTEBRATES FROM SOME SPRINGS IN LAND BETWEEN THE LAKES, KENTUCKY AND TENNESSEE

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ABSTRACT. The aquatic macroinvertebrate fauna of North American springs is poorly documented. With increasing concerns over loss of biological diversity and contamination of groundwater, interest in springs and spring biota has increased substantially in recent years. Frequently springs have unique and endemic faunas that are threatened by various perturbations of the groundwater sources. These perturbations may include lowering of the water table due to increased surface runoff or pumping of water for irrigation and domestic needs. These sources are also threatened by groundwater contamination from infiltration of pesticides and various other toxic materials. In LBL springs, springbrooks, and the streams into which they flow into are the only perennial lotic habitats. These habitats provide a stable environment for an interesting but limited macroinvertebrate fauna. During the drought summer of 1988, we located 28 permanent springs throughout Land Between The Lakes. Two of the larger springs, Lost Creek and Pryor Creek springs, were investigated in depth. Reports on these springs have been presented at earlier Symposia and elsewhere. Eight lower volume springs were selected for a less intensive quarterly macroinvertebrate faunal survey. Two other springs were added to the survey after the project had begun. These ten springs are the topic of this presentation. Temperature, pH, and dissolved oxygen were measured at the groundwater resurgence. Discharge of the springs were approximated using the "cork float" method. Observation about substrate composition, canopy cover, vegetation and air temperature were also noted. Qualitative macroinvertebrate samples were collected using a kick net and by hand picking specimens off rocks, branches, leaves and other substrates. Kick samples were placed in a white plastic pan and hand picked at the sites. No effort was made to quantify the samples. From these samples the mayflies, odonates, stoneflies, megalopterans, caddisflies, beetles, dipterans, amphipods and isopods have been identified to the lowest practical taxon, always to genus and often to species. Taxa richness from these springs ranged from 16 taxa at "Little Demumbers Creek Spring" to 52 at the "Telegraph Trail Spring." The most taxonomically diverse macroinvertebrate group is the dipterans, the majority being from the family Chironomidae. Arlt Spring had 25 dipteran taxa, 19 of which were chironomid genera. Trichoptera were a distant second in regards to taxa richness with a maximum of ten taxa at "Turkey Creek Spring #2." The amphipod *Crangonyx* was collected in abundance at eight of the springs and *Gammarus psuedolimnaeus* was collected in one spring. *Lirceus fontinalis*, an isopod, was abundant in three springs and *Caecidotea* sp. was collected from three springs. Oddly, no amphipods or isopods were collected at Arlt Spring. An examination of the cumulative taxa collected during subsequent quarterly samples suggests that, on the average, greater than 95% of the taxa occurring in these springs were collected as of the fourth quarterly sample. Further collecting effort would likely reveal, on the average, only one or two more taxa per spring. Jaccard's Coefficient of Community Similarity for spring pairs were correlated with the linear

distances between these pairs using Spearman's Rank Order Correlation. Spearman's R was -0.43, significant at $p < 0.01$, indicating the shorter the distance between springs the greater the community similarity. This may suggest some faunistic exchange between nearer springs, or it may reflect some aspect of hydrologic or geologic similarity between nearer springs.

UTILIZATION OF A GEOGRAPHIC INFORMATION SYSTEM TO STUDY NONPOINT SOURCE POLLUTION POTENTIAL IN A PORTION OF THE KENTUCKY LAKE DRAINAGE BASIN

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ABSTRACT. Nonpoint source pollution contributes a major portion of the pollution that reaches the world's surface and groundwater supplies. Because of the importance of the Kentucky Lake reservoir to the surrounding areas, an attempt was made to determine which areas in the Kentucky Lake drainage basin have the potential to produce above average amounts of nonpoint source pollution. A system to incorporate land use, soils, and nutrient and chemical loadings was developed using the data available in the Kentucky Lake Geographic Information System. Results showed that 41 of the 174 basins in the study area have an above average pollution potential.

THE INFLUENCE OF TRIBUTARY STREAMS ON KENTUCKY LAKE EMBAYMENTS: WATER CHEMISTRY AND PRODUCTIVITY

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ABSTRACT. The Center for Reservoir Research Long-Term Monitoring Program collects physical, chemical, and biological data at 17 sites in Kentucky Lake every 16 days. Five of the sites form a depth gradient in Ledbetter embayment from the tributary stream to the interface with the mainstem. An additional site is located on Ledbetter Creek approximately 1.2 km upstream from the embayment. Comparisons of chemical and biological cycles at the six sites and at one site on the mainstem were made over a 14 month period. Patterns for P, N, chlorophyll *a*, Si, and Cl were similar for sites within the embayment but differed from patterns in the tributary stream and mainstem sites indicating possible physical differences among the three water bodies: hydraulic retention time of the embayment is on the order of months to years compared with days to weeks for the stream and the mainstem which may increase productivity; current patterns within the embayment tend to focus productivity toward the middle of the embayment; the effects of tributary inputs on most parameters appear to be minimal except following heavy rains. Reservoirs traditionally are viewed as having three zones: riverine, transitional, and lacustrine. Based on physical, chemical, and biological data, we propose that embayments may be viewed as having five functional zones: tributary (riverine), transitional, embayment (lacustrine), transitional, and mainstem (lacustrine).

THE KENTUCKY LAKE GEOGRAPHIC INFORMATION SYSTEM

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ABSTRACT. The Kentucky Lake Geographic Information System (KLGIS), housed at the Mid-America Remote Sensing Center (MARC), contains a wide variety of information related to the lower reaches of Kentucky Lake and its drainage basin, extending from the Scott Fitshugh Bridge near Paris Landing, Tennessee on the south to Kentucky Dam on the north. KLGIS was implemented as part of an effort by the Center for Reservoir Research (CRR) to assess, monitor, and analyze land/water interactions. Software packages utilized for input and analysis include ERDAS, ELAS, and PC ARC/INFO. Most of the hardware used for construction of KLGIS was IBM PC-based. dBASE III PLUS is interfaced with KLGIS to allow for the utilization of water quality monitoring data which has been collected every sixteen days for nearly four years. The 16-day cycle coincides with Landsat satellite overpasses. Thirteen information layers with associated attribute files reside in KLGIS and include archeological sites, bathymetry, cultural features, elevation, drainage basins, geology, ground water, hydrography, land cover, soils, terrain, water quality, and wetlands. Examples of KLGIS implementations include land cover change detection, potential erosion analysis, land-use planning and water quality modeling. KLGIS output products include maps, graphs, statistical data, and photographic products.

MOVEMENTS OF NATIVE AND INTRODUCED ALLIGATOR SNAPPING TURTLES, *MACROCLEMYS TEMMINCKII*, IN KENTUCKY LAKE

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ABSTRACT. Movements of seven Alligator Snapping Turtles (two natives and five aliens) were monitored in an 8-km stretch of Kentucky Lake (river miles 54 to 59) during July, August, and September 1992. Study animals were relocated by radio telemetry an average of 14.3 times each (range 5 to 23) over periods ranging from 3 to 69 days per individual. The average time between relocations was 1.9 days (range 0.6 to 32). Means and ranges (in parentheses) of the averages of selected measures of movement (all straight-line distances) for all seven individuals follow: 1) distance between successive relocation points, 236.4 m (62 to 401); 2) distance between extreme relocation points, 2120.0 m (400 to 4910); 3) distance from relocation points to shore, 7.6 m (2 to 22); and 4) depth at relocation sites, 2.3 m (1.5 to 4.2). Comparisons of pooled data for native versus alien individuals revealed significant differences ($P < 0.05$) between distances measured from relocation points to shore and depths of relocation points. Native turtles were generally found farther from shore and in deeper water than aliens. No significant differences were detected between distances traveled or habitats frequented by the two groups. A typical habitat was one near shore in shallow water with a substrate of mixed rocks, gravel, and silt, and some type of underwater cover (e.g. tree trunks, tops of fallen trees, entrances to bank burrows of muskrats or beavers, and patches of aquatic plants).

WATERFOWL USAGE OF CROSS CREEKS NATIONAL WILDLIFE REFUGE: THE FIRST THIRTY YEARS

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ABSTRACT. Cross Creeks National Wildlife Refuge (CCNWR), created in 1962, is located east of Dover, Tennessee, in Stewart County. The refuge, comprising 3586 ha of Cumberland River floodplain and adjacent, mostly wooded uplands, is primaryily intended to provide feeding and resting habitat for overwintering waterfowl. The refuge was established to mitigate the loss of parts of Kentucky Woodlands National Wildlife Refuge that were flooded when Lake Barkley was created. Various management practices, such as controlling water levels in the refuge's 16 water impoundments to promote the growth of moist-soil plants, and the raising of such crops as corn, wheat, and milo, have been used by the refuge's managers to provide suitable habitat for wintering waterfowl. The purpose of this study was to assess waterfowl usage of the refuge, as reflected by data collected weekly during the waterfowl season by refuge personnel during the first thirty years of the refuge's existence. Thirty-three of the 48 species of waterfowl recorded from North America have been documented on the refuge since 1962. Nine of these (Mute Swan, Atlantic Brant, Barnacle Goose, Ross' Goose, Cinnamon Teal, Fulvous Tree Duck, Greater Scaup, Oldsquaw, and White-winged Scoter), each recorded but once or twice, are considered accidentals. The Tundra Swan and Eurasian Wigeon have been observed at the refuge more than twice, but also should probably be considered as accidentals. The duck population at CCNWR for the period 1962 through 1991 was inversely correlated with winter temperatures on their breeding grounds (R = .534). No similar correlation was apparent in the data for goose populations. Peak weekly duck populations ranged from 1,000 (1962/63) to 111,000 (1964/65), and occurred in December. The size of the duck population in recent years, although erratic, appears to have generally declined. Peak weekly goose populations ranged from 40 (1962/63) to 74,000 (1989/90), and occurred in January. Goose populations in recent years show a general upward trend. A typical mid-winter duck population at CCNWR is dominated by Mallards (74%) and American Black Ducks (15%). American Wigeons, Ring-necked Ducks, Northern Pintails, and Gadwalls collectively make up 8%. Canada Geese comprise 99.9% of the goose population using the refuge during the winter.

WATER QUALITY FROM LANDSAT TM FOR WEST POINT LAKE, GEORGIA

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ABSTRACT. This paper documents work performed by MARC for WES Environmental Laboratory involving mapping water parameters for West Point Lake using LANDSAT TM data and providing Geographic Information System (GIS) layers to WES. Water parameter maps were produced for two TM scenes from 1991: June 8 and September 28. The water quality parameters mapped included: turbidity, Secchi depth, chlorophyll a, and temperature. Regressions of the TM data values with the measured parameter at approximately 50 sample points were used to derive the water parameters maps. Outlier analyses were used to eliminate some of the sample points from the regressions, while some points were eliminated because of large standard deviations in TM data values, obvious land values, and bridges near the sample points. Relationships were generally very good and are documented in this presentation. The June chlorophyll a/TM data value relationship was very poor and deemed unusable; however, an interpolation technique is being developed which should at least provide a map of chlorophyll a for the June date. Digital Line Graph data were acquired from USGS for the West Point Lake area. These data are shown in map form in this presentation and are being made available to WES. A general landcover classification of the drainage area is being performed using both dates of TM data (multi-temporal classification) using aerial photography of the LaGrange 1:24,000 topographic map area for ground truth verification. Landcover distributions for watersheds draining into different portions of the reservoir and the associated GIS layers will be made available to WES by the end of March, 1993.

ANALYSIS OF PLECOPTERA ASSEMBLAGES ALONG AN ALTITUDINAL GRADIENT IN THE GREAT SMOKY MOUNTAINS, TENNESSEE

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ABSTRACT. Plecoptera immatures were qualitatively sampled from the Little Pigeon River and its tributaries, Ramsay Prong, Middle Prong, and Porter's Creek in the Great Smoky Mountains, Tennessee. The samples were collected from twelve sites along an 864-m altitudinal gradient from September 1977 to August 1978. Relative taxa abundance of Plecoptera along the altitudinal profile is examined. Sites and taxa were classified by cluster analysis and ordinated by correspondence analysis and related to physio-chemical parameters and food.

POPULATION DYNAMICS OF *DAPHNIA LUMHOLTZI*, A ZOOPLANKTER NEW TO KENTUCKY LAKE

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ABSTRACT. *Daphnia lumholtzi* is a cladoceran native to Australia, southern Asia, and eastern Africa with some populations in South America. The species was first collected in North America in 1990 and 1991 in reservoirs from Texas to Missouri eastward to the Carolinas. Zooplankton have been monitored in Kentucky Lake since August 1988 through the Center for Reservoir Research Long-Term Monitoring Program. *D. lumholtzi* was first observed in low densities in Kentucky Lake in August 1990. Initial distribution was confined to the main channel. By 1992 *D. lumholtzi* was widely distributed throughout the main channel and the embayments reaching peak abundances of 8.5 L^{-1}, similar to densities of native caldocerans. *D. lumholtzi* exhibits a single peak in August corresponding with maximum lake temperatures and the decline of *Daphnia retrocurva*. The density peak overlaps those of *Diaphanosoma* and some copepods and has been followed in September by a dinoflagellate bloom (200 mg C m^3 hr^{-1}). *D. lumholtzi* is distinguished by its comparatively long caudal and apical spines which may act as a deterrent to predation. The effects that *D. lumholtzi* may have on water quality, fish populations, and naturally occurring plankton remain to be studied.

INITIAL OBSERVATIONS OF WATER QUALITY MONITORING IN WEST SANDY CREEK, HENRY COUNTY, TENNESSEE.

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ABSTRACT. Water quality in West Sandy Bay and Big Sandy Bay of Kentucky Lake Reservoir has become a concern to various Tennessee state agencies (e.g., Tennessee Department of Environment and Conservation - Water Pollution Control, Tennessee Wildlife Resources Agency) and to commercial and private fishermen in recent years. Fishermen and mussel divers have reported a decline in fin and mussel fisheries in these bays. Previous monitoring in West Sandy Bay by The Center for Field Biology, TDEC-WPC, and Memphis State University has indicated that during the summer months water quality severely deteriorates, particularly in terms of the low dissolved oxygen levels. West Sandy Creek at Elkhorn Road is the channel receiving flow from the West Sandy watershed that drains much of eastern Henry County including the city of Paris. The stream is separated from the bay by a dike which has a pumping station on it that regulates flow from the stream into the bay. Water from the West Sandy Creek watershed is held back in the winter to flood the West Sandy Wildlife Area for migratory waterfowl and in the spring the pumps dewater the area to prevent drowning of green timber. In an attempt to understand how the flow from West Sandy Creek might be contributing to the water quality problems in West Sandy Bay, macroinvertebrate sampling using Hester-Dendy artificial substrates was begun in West Sandy Creek at Elkhorn Road in 1989 and has continued. In the fall of 1991 physico-chemical and bacteriological sampling were added to the monitoring strategy for the creek. In addition to the Hester-Dendys, Ponar dredge and bank/root mass sweep samples were added for sampling the macroinvertebrates. The data reviewed will be from the first three six-week sampling periods of the sampling year September 1991 to September 1992. Initial observations suggest a degraded habitat and community in West Sandy Creek.

THE INFLUENCE OF TRIBUTARY STREAMS ON KENTUCKY LAKE EMBAYMENTS: ORGANIC MATTER AND FEEDING OF BENTHIC INVERTEBRATES

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ABSTRACT. Organic matter content and tubificid oligochaete feeding rates were examined in sediments collected along a depth gradient from the mouth of Ledbetter Creek through Ledbetter embayment to the interface of the embayment with the mainstem of Kentucky Lake. The natural distribution of invertebrates also was examined along this gradient. Feeding rates (measured as sediment marker layer burial rates) were determined in laboratory microcosms utilizing a non-destructive radiotracer technique. Feeding rates initially were highest in sediments from sites nearest the mainstem but decreased after 200 hr. Feeding rates were more constant in sediments from sites nearest the tributary and were generally higher after 200 hr than from sediments toward the mainstem. Total organic matter was lowest in sediments nearest the tributary decreasing with distance toward the main stem. It is hypothesized that, while the potential food supply becomes greater with distance from the tributary, this matter is older and more recalcitrant resulting in a reduced bacterial component, the probable food resource of tubificids. This hypothesis is supported by 1) greater final mean oligochaete weight in microcosms containing sediments from nearest the tributary and 2) significantly higher densities of benthic invertebrates, particularly tubificids, found in sediments nearest the tributary input.

SUBSTRATE PREFERENCE IN JUVENILE ALLIGATOR SNAPPING TURTLES, *MACROCLEMYS TEMMINCKII*: RESULTS OF LABORATORY TESTS

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ABSTRACT: Juvenile Alligator Snapping Turtles, *Macroclemys temminckii*, were tested in the laboratory to determine 1) if they would choose equally or unequally from among a variety of substrates, and 2) whether the addition of cover would alter their initial choice of substrates. To answer the first question, 18 second-year individuals were placed, one at time, in the center of a circular arena containing equal areas of mud, sand, fine gravel, and coarse gravel. At the end of a 10-minute acclimation period and every 5 minutes thereafter for 20 minutes, the substrate supporting the turtle was noted. This procedure was performed four times. To answer the second question, the first experiment was repeated (using 16 of the original 18 turtles) with artificial cover (a small, green, plastic flower pot) present on a different substrate throughout each trial. Chi square analyses of the results indicate that, under controlled laboratory conditions, juvenile *M. temminckii* 1) exhibit a significantly disproportionate ($P < 0.05$) affinity for the substrates tested (with coarse gravel topping the list), and 2) that the presence of cover significantly alters their choice, except in the case of fine gravel, the substrate they prefer least.

THE HERPETOFAUNA OF FORT CAMPBELL MILITARY RESERVATION, KENTUCKY AND TENNESSEE: A PRELIMINARY REPORT

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ABSTRACT: Fort Campbell is a 42,686-hectare military reservation on the northwestern Highland Rim in southern Kentucky and northern Tennessee. In May 1992, a herpetological survey of the fort (excluding firing ranges, munitions impact areas, and cantonment areas) was begun. All major habitats are being sampled each season using standard collecting techniques. As of 1 February 1993, 42 taxa (23 amphibians and 19 reptiles) have been encountered. Frequently encountered species include: *Ambystoma maculatum*, *Desmognathus fuscus*, *Eurycea longicauda*, *Plethodon dorsalis*, *Bufo americanus*, *Bufo woodhousii*, *Hyla chrysoscelis*, *Pseudacris crucifer*, *Pseudacris feriarum*, *Rana catesbeiana*, *Rana sphenocephala*, *Terrepene carolina*, *Agkistrodon contortrix*, *Coluber constrictor*, *Elaphe obsoleta*, and *Nerodia sipedon*. Evidence of intergradation exists within several species (e.g. *Notophthalmus viridescens*, *Agkistrodon contortrix*, and *Diadophis punctatus*). Unusual finds include records of *Hyla gratiosa* from one site and *Ambystoma talpoideum* at three sites. Final results will augment existing knowledge of the amphibians and reptiles in the lower Cumberland Basin and provide baseline data useful in long-term trend analysis of environmental changes on the fort.

CONTRIBUTED PAPERS

SESSION II: BOTANY AND MICROBIOLOGY

Saturday, March 6, 1993

Moderated by:

William Ellis
Department of Biology
Austin Peay State University

SEED GERMINATION ECOLOGY OF *LEPTOCHLOA PANICOIDES*, A C_4 SUMMER ANNUAL GRASS OF SEASONALLY-DEWATERED MUDFLATS

CAROL C. BASKIN[1,3], JERRY M. BASKIN[1,3] AND EDWARD W. CHESTER[2]

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ABSTRACT. *Leptochloa panicoides* is one of many summer annuals that grows on mudflats that form when water levels in Lake Barkley, an impoundment on the Cumberland River in western Middle Tennessee and west-central Kentucky, USA, are lowered in summer. Seeds were dormant at maturity in autumn, and they afterripened (lost dormancy) over a range of temperatures (5, 15/6, 20/10, 25/15 and 30/15°C). However, they afterripened much faster at high than at low temperatures. Seeds buried in flooded and nonflooded soil in October and exposed to natural seasonal temperature changes became nondormant by the following June. Some afterripening occurred during winter, but the remainder took place as temperatures increased from February through May. Nondormant seeds required light for germination. After the initial (primary) dormancy was broken, flooded and nonflooded seeds did not re-enter (secondary) dormancy during burial for an additional 12 and 20 months, respectively. Throughout these periods, exhumed seeds germinated to 80-100% at 35/20°C and to 45-100% at 30/15°C, while germination at 25/15°C reached a maximum (20-100%) in summer and a minimum (0%) in winter. The high temperatures required for germination of nondormant seeds overlap with habitat temperatures from mid-May to mid- to late September. Thus, seeds of *L. panicoides* are capable of germinating at the latitude of the Lake Barkley mudflats only in summer. However, since seeds remain nondormant, they can germinate at any time during summer, whenever water levels drop and the mud is exposed.

[3]JMB and CCB are Senior Research Fellows with The Center for Field Biology, Austin Peay State University.

SEED DORMANCY IN THE RARE ENDEMIC PLANT SPECIES, *ILIAMNA COREI* (MALVACEAE)

JERRY M. BASKIN, CAROL C. BASKIN, ANTHONY HAYS,
GREGORY ALLEN, AND JOHN WILSON

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ABSTRACT. *Iliamna corei* (Sherff) Sherff [=*Phymosia remota* (Green) Britton; *Iliamna remota* Greene, in part; *Iliamna remota* Greene var. *corei* Sherff], Peters Mountain Mallow, is an herbaceous, self-incompatible, polycarpic perennial known only from a single (present and historical) locality near The Narrows in Giles County, Virginia (Ridge and Valley Physiographic Province) at an elevation of *ca* 800 m a.s.l. on the NW-facing slope of Peters Mountain. Here, it grows in an open mixed deciduous-pine woodland in shallow soil of the Clinch sandstone (Williams, C. E, T. F. Wieboldt, and D. M. Porter. 1992. Recovery of the endangered Peters Mountain Mallow, Iliamna corei. Nat. Areas J. 12:106-107).

Iliamna corei was listed as a federal-endangered species on 11 June 1986 [FR 51 (91): 1743-1746]. Since its discovery in 1927 by Dr. Earl L. Core (Strausbaugh, P. D. and E. L. Core. 1932. *Phymosia remota*. Rhodora 34: 142-146), the population has declined from about 50 individuals (clumps) to just four. However, a sizeable seed bank is present at the population site (Jacobs, J. 1990. Recovery plan for Peters Mountain Mallow [*Iliamna corei* (Sherff) Sherff]. Unpubl. Tech. Draft, U.S. Fish & Wildlife Service, Region 5. 23 p.). As part of an effort being conducted by us and by personnel of The Nature Conservancy, the Virginia Division of Natural Heritage, and Virginia Polytechnic Institute and State University to learn more about the biology and management of this rare endemic, we have been investigating ways to break dormancy of its seeds.

Seed dormancy is due only to a water-impermeable (*i.e.*, "hard") seed coat. Intact seeds do not imbibe water, and the embryo is nondormant. Under laboratory conditions, dormancy was broken in a high percentage of the seeds by mechanical scarification (*i.e.*, cutting a hole in the seed coat), dipping the seeds in boiling water for a few seconds, and heating the seeds for 15 to 60 minutes in a drying oven at constant temperatures of 70 to 110°C. Nondormant seeds germinated to high percentages in both light (14 h daily photoperiod of *ca.* 20 μmoles m^{-2} s^{-1}, 400-700 nm) and constant darkness at 20 (day)/10 (night), 25/15, and 30/15°C; a lower percentage of the seeds germinated at 15/6 and at 35/20°C.

Compared with results obtained with other hardseeded species, soaking seeds of *I. corei* in concentrated sulfuric acid was only moderately effective in breaking dormancy. The highest germination percentage obtained using this method was 43.3, after soaking seeds for 9 h.

Neither shifting seeds of *I. corei* from lower to higher temperatures in a series (5 → 15/6, 20/10, ... 50/20°C; 15/6 → 20/10, 25/15, ... 50/20°C; ... 40/25 → 50/20°C; or from 5, 15/6, ... 35/20 → 50/20°C) after 14 w of incubation on moist sand prior to the shift; freezing and thawing daily for 30 days [-10°C (8 h)/5°C (16 h)]; nor soaking in absolute ethanol caused breakdown of the hard seed coat. All of these treatments have been shown to break dormancy in seeds of some other hardseeded species.

In a nonheated greenhouse study, fire was effective in breaking dormancy of seeds of *I. corei* sown on the soil surface in metal flats, but not in those buried 3 cm below the surface. In one experiment, 1989 seeds planted in November 1989, covered with leaves and wheat straw, and burned in June 1990, 1991, and 1992 had germinated to the following percentages by 31 December 1992: buried, nonburned - 1.7% (8/450); nonburied, nonburned - 3.1% (14/450); buried, burned - 2.0% (9/450); and nonburied, burned - 20.4% (92/450). Fire stimulated some seeds to germinate after each of the three burns. Interestingly, even after the third burn (1992), 37 seeds germinated in the nonburied, burned treatment, demonstrating that seeds can remain ungerminated and viable on the soil surface for a least 2.5 yr. In a second burning experiment, 1991 seeds planted in metal greenhouse flats on and 3 cm below the soil surface in March 1992 and subjected to fire (treatment) or not (control) in June 1992 had germinated to the following percentages by 31 December 1992: buried, nonburned - 0.1% (1/900); nonburied, nonburned - 1.4% (13/900); buried, burned - 2.1% (19/900); and nonburied, burned - 12.7% (114/900).

In nature, fire probably is the primary factor that breaks dormancy in *I. corei* seeds, as appears to be the case in the closely-related *I. remota* Greene (the Kankakee Mallow) (Schwegman, J. 1990. Preliminary results of a program to monitor plant species for management purposes. Pp. 113-116 in R. S. Mitchell, C. J. Sheviak, and D. J. Leopold (editors) 1990. Ecosystem management: Rare species and significant habitats. Proc. 15th Ann. Nat. Areas Conf. New York State Mus. Bull. No. 471.), and *I. rivularis* (Dougl. ex Hook.) Greene, a postfire successional species of coniferous forests in the western United States (Steele, R. and K. Geier-Hayes. 1989. The Douglas-fir/ninebark habitat type in Central Idaho: Succession and management. USDA For. Serv. Gen. Tech. Rep. INT - 252). In 1992, a controlled burn conducted in the habitat of *I. corei* on Peters Mountain by personnel from The Nature Conservancy and the Virginia Division of Natural Heritage stimulated some seeds in the seed bank of this rare endemic to germinate. Thus, use of fire as a management tool appears to be a key element in the recovery of *I. corei*. In addition to promoting recruitment from the seed bank, fire also opens up the canopy and thus allows vigorous growth and reproduction of this relatively shade-intolerant species (Buttrick, S. C. 1992. Habitat management: A decision-making process. Rhodora 94: 258-286).

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CHARACTERIZATION OF SOME REMNANT BOTTOMLAND FORESTS OF THE LOWER CUMBERLAND RIVER IN TENNESSEE AND KENTUCKY: 1. INTRODUCTION AND THE CROSS CREEKS SITE IN STEWART COUNTY, TENNESSEE

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ABSTRACT. The extensive bottomland forests that once occurred on the floodplains and terraces of the lower Cumberland River in Tennessee and Kentucky are represented only by a few remnant stands today. We have ongoing floristic and vegetational studies on some of these remnants south of Barkley Dam that are designed to (1) characterize present conditions, (2) provide insight into original conditions, and (3) establish baseline data for future studies, especially for stands in protected sites. This paper introduces these studies and gives a characterization of one forest, a 15-ha stand in Stewart County, Tennessee. In that forest, nested plot studies yielded a sample of 998 stems representing 31 species (dbh equal to or greater than 2.54 cm). Analyses showed that the overstory of this forest is dominated (dbh equal to or exceeding 10.15 cm) by *Carya ovata, Fagus grandifolia, Liquidambar styraciflua, Quercus michauxii, Q. shumardii*, and *Ulmus rubra*, with significant contributions by *Acer saccharum, Celtis laevigata, Fraxinus pennsylvanica*, and *Quercus pagoda*. The sapling and small tree stratum (dbh of 2.54 - 10.14 cm) is dominated by *Celtis laevigata*, with significant contributions by *Acer saccharum, Asimina triloba, Carpinus caroliniana, Celtis occidentalis, Fagus grandifolia, Ostrya virginiana, Ilex decidua*, and *Ulmus* spp. Most abundant in the shrubs and woody seedlings layer (dbh less than 2.54 cm) are *Arundinaria tecta, Asimina triloba, Carya* spp., *Celtis* spp., *Fraxinus* spp., and *Quercus* spp.

INTRODUCTION

Extensive wetlands occur along rivers and streams throughout much of the United States but especially in the east and southeast. Those that are forested and occasionally flooded by the adjacent bodies of water but are otherwise dry for varying portions of the growing season are referred to as bottomland hardwood forests. Since the major United States coverage is in the southeast, the term "bottomland hardwood forest" historically has been used to describe such stands in Coastal Plain and Piedmont floodplains. However, the term now applies to floodplain forests throughout the eastern and central United States as well (Mitsch and Gosselink 1986), and "bottomland hardwoods" is the term generally used to describe forest species of floodplains (Turner *et al.* 1981). Such forests are notable because of the large areas covered and because of their importance for timber, wildlife, flood storage, recreation, and for providing habitat for plants and animals.

Bottomland hardwood forests show significant vegetational and floristic variation between physiographic regions and between riverine systems within regions. Even within a stand, there is variation along gradients of flooding frequency, microtopography, relief, soils, and soil-moisture regimes. Yet all are characterized by (1) periodic inundation or saturation of the soil by surface or groundwater, (2) soils that are periodically saturated throughout the rooting zone and that may become anaerobic for various periods, and (3) dominant species that have the ability to survive, mature, and reproduce under these conditions.

In Tennessee, about 80% of the bottomland hardwood forests occur west of the Tennessee River on the fertile alluvium of the Mississippi River Basin and in belts along the tributary waterways of the Mississippi River, especially the Hatchie, Wolf, Obion, and Forked Deer. Construction of a network of reservoirs in the Tennessee and Cumberland valleys has considerably reduced the type acreage eastward. In early 1950s, Tennessee had about 0.922 million acres of bottomland hardwood forests (Sternitzke 1955); this had been reduced to 0.72 million acres in 1970 (Turner et al. 1981), and is no doubt even lower today. Overall, the selective loss of United States forested wetlands was five times higher than that of non-wetland forests between 1940 and 1980 (Abernethy and Turner 1987).

A considerable forested floodplain once occurred along the lower Cumberland River in Tennessee and Kentucky. Killebrew, in 1874, referred to "The heavy forests on the Cumberland, that now sigh in loneliness and uselessness to the touch of the breeze." Yet most of these forests had been removed by the late 1800s and the rich lands converted to agriculture (Sudworth 1897). Barkley Dam, at River Mile 30.6 south of the confluence with the Ohio River, was closed in 1966, inundating most of the lower Cumberland River floodplains southward through Kentucky and into Tennessee. Thus today, except for a few remnant stands, all of this forest type has disappeared (Smalley 1980).

We presently have vegetational and floristic studies underway that are designed to characterize some remnant bottomland hardwood forests along the lower Cumberland River south of Barkley Dam. While land utilization has been so complete that it will be impossible to determine limits and characteristics of the original forests, data from existing remnants will provide insight into original conditions. Also, some of the tracts are in protected ownership and these baseline data can be used for comparisons as maturity occurs in the absence of anthropogenic influences. This report provides introductory material and characterization of one bottomland hardwood forest in Stewart County, Tennessee.

LITERATURE REVIEW

A prodigious literature on wetlands has been developed over the last decade as their importance has been realized. Even a cursory review is beyond the scope of this paper, but some important major works are the overviews of Mitsch and Gosselink (1986) and Hook *et al.* (1988). Some major compendia on bottomland hardwood forests are those of Clark and Benforado (1981), Hook and Lea (1988), and Wharton *et al.* (1982). Such features as management options, research priorities, and methods of preservation were pointed out by Neal and Haskins (1986).

Vegetational studies including Northwest Highland Rim bottomlands are those of Carpenter and Chester (1988), Chester and Ellis (1989), Dodson (1973), Duncan and Ellis (1969), Fralish and Crooks (1988, 1989), Jensen (1972), Jensen *et al.* (1973), and Schibig (1972). A classification and/or evaluation of forest sites was presented by Scott *et al.* (1980), Smalley (1980), and the Tennessee Department of Conservation (1983).

DESCRIPTION OF THE REGION AND STUDY SITE

The Region

The lower Cumberland River (south of Barkley Dam and west-northwest of Cheatham Dam) flows through the Western Highland Rim Subsection, Highland Rim Section, Interior Low Plateaus Physiographic Province. This subsection consists of a dissected upland plateau between the Central Basin Section on the east, the Costal Plain Province on the west, the Southern Highland Rim Subsection on the south, and the Pennyroyal Plain Subsection on the north. The upland is developed primarily on limestones of Mississippian age. Karst features are present and there are numerous caverns and springs (Smalley 1980). Elevations range from about 108 to 185 m. The vegetation is transitional between more mesic forest types eastward (Mixed Mesophytic) and more xeric types westward (Oak-Hickory) and is referred to as the Western Mesophytic Forest by Braun (1950). Deciduous hardwoods predominate, with taxa of *Acer*, *Carya*, *Quercus*, and *Ulmus* of most importance (Chester and Ellis 1989, Schibig *et al.* 1990).

The Study Site

This study site is a 15-ha tract at Cumberland River Mile 93 within the Cross Creeks National Wildlife Refuge. It is between the 360 and 370-foot contour lines on the Dover, Tennessee, U.S.G.S. Topographic quadrangle (1950, photorevised 1971), on the south side of the reservoir. Normal summer pool elevation of the reservoir is 359 feet. The woods have been in federal ownership since the 3650-ha National Refuge was established in 1962 to provide feeding and resting habitat for migrating waterfowl. Prior to the closing of Barkley Dam in 1966, the bottomlands were flooded one or more times yearly, often for several days each time, by overflow and backwater. Flood control measures at the dam now limit flooding of the site to occasional; in recent years the forest floor was covered by at least two feet of water for several days during the winter-early spring of 1984, 1989, 1990, and 1991. Soils of the forest are Arrington-Lindell-Egam-Armour; these are well-drained and moderately well-drained, silty, loamy, and clayey soils of Cumberland River bottomlands (Springer and Elder 1989). On first bottoms near the stream channels (such as in this case), dark, well-drained silty Arrington and brown, moderately well-drained loamy Lindell soils predominate. The parent material is alluvium; phosphate levels are normally high but decrease northward due to the strong influence of local parent materials from soils of the cherty uplands.

This forest is nearly level but one depressed area of about 0.1 ha holds water for extended periods. Water was present during July of 1989 but had dried by September. A little-used hiking trail passes through the area, as does a road providing access for Refuge personnel.

In addition, the forest is divided by a small field that is often planted in annual crops for waterfowl food. However, the forest has not been disturbed by pasturing or tree removal for at least 30 years (since purchase) and the lack of stumps indicates little disturbance for several years prior to that. The owner (for many years) prior to governmental purchase is deceased, so historical usage cannot be documented. However, the common practice prior to 1962 was to plant corn in those bottomlands dry enough for tilth. There was little pasturing and fire was very rare. The few remnant forests remaining today are mostly on sites that were too wet for tillage, and some tree removal has occurred in all of these. Certainly this forest is secondary, but nevertheless one of the better remnants remaining in the area.

METHODS

Twenty, 0.04 ha (0.1 acre) circular plots were established in a systematic method to insure that all parts of the woodland were surveyed. Plots were permanently marked with plastic pipe, compass bearings, and witness trees. Within each plot, all trees with a diameter breast height (dbh, ca. 4.5 feet above ground) of 2.5 cm (1 inch) were recorded by species. These data were used to calculate density (number/ha), dominance (square dm/ha), and frequency (percent of plots with the species). Relative values of density, dominance, and frequency also were determined and the three relative values summed to give an importance value (300).

At the center of each plot, a smaller, circular plot of 0.004 ha (0.01 acre) was nested. Shrubs and tree seedlings (dbh less than 2.5 cm) were counted to obtain density and frequency (absolute and relative) data for that group.

All quantitative data were taken on 14-15 July 1989. In addition, the scant herbaceous layer and woody vines were qualitatively surveyed on 14-15 July and 10 and 15 October 1989, 7 April 1990, and 10 July 1991. Taxonomic determinations and nomenclature generally follow Fernald (1950), who gives authority for each taxon.

RESULTS AND DISCUSSION

Size-Class Distribution

A total of 998 stems with diameters of 2.54 cm and above were measured. The 31 species represented are listed alphabetically, with the number of each species, average diameter per species, and size-class distribution, in Appendix 1. The majority of these 998 stems (548 or 55 percent) are in the 2.54-10.14 cm (1-3.9 inch) dbh size class. The 450 stems with dbh of 10.15 cm and above make up 45 percent of stems. The average diameter of all stems is 14.76 cm (5.81 inch); for stems greater than 10.14 cm, the average is 26.89 (10.59 inch). However, average diameters are higher for dominant species, *e.g.*, 38.43-53.37 for four species of *Quercus*, 23.50-47.88 for three species of *Carya*, 25.44 for *Platanus*, and 32.22 for *Liquidambar*.

Canopy Species

Twenty-five species with dbh exceeding 10.14 cm (4 inches and above) were found. Appendix 2 provides data on the 450 stems sampled, including ranking by IV and percent of total IV. The data indicate a forest with dominance shared by at least six species, *i.e.*, *Liquidambar styraciflua*, *Ulmus rubra*, *Fagus grandifolia*, *Carya ovata*, *Quercus michauxii*, and *Q. shumardii*. Contributions are made also by *Celtis laevigata*, *Q. pagoda*, *Fraxinus pennsylvanica*, and *Acer saccharum*. Also represented are some species more typically found in the understory, including *Carpinus caroliniana*, *Cercis canadensis*, *Morus rubra*, and *Ostrya virginiana*. Some genera are represented by more than one species, including *Quercus* (4 species, 23.08% of total IV), *Carya* (3, 12.87%), *Ulmus* (2, 12.24%), *Celtis* (2, 7.24%), *Acer* (3, 6.05%), and *Fraxinus* (2, 6.03%). No other canopy species were observed in the stand that did not appear in sampling data.

Saplings and Small Trees

As shown in Appendix 3, this stratum (dbh 2.54-10.14 cm), based on 548 sampled stems, is dominated by *Celtis laevigata* (20.88% of the IV). An additional 60% of the IV is made up by *Acer saccharum*, *Asimina triloba*, *Carpinus caroliniana*, *Celtis occidentalis*, *Fagus grandifolia*, *Ilex decidua*, *Ostrya virginiana*, and *Ulmus rubra* (probably including some *U. alata* and possibly *U. americana*). Five of the 25 species represented (*Asimina triloba*, *Cornus florida*, *Crataegus viridis*, *Ilex decidua*, *Lindera benzoin*) did not exceed 10.14 cm dbh and hence are not represented in the canopy stratum. Five canopy species (*Carya cordiformis*, *Gleditsia triacanthos*, *Juglans nigra*, *Prunus serotina*, *Quercus alba*) did not appear in this stratum. Two species (*Diospyros virginiana* and *Staphylea trifolia*) were observed but did not appear in plots.

Shrubs and Woody Seedlings

Shrubs and woody seedlings data are given in Appendix 4. This stratum, based on counts in nested quadrats and general observations, is not dense. It is dominated by *Arundinaria tecta*, which is scattered throughout and sometimes occurs in dense stands. Other common taxa generally found in this stratum include *Asimina triloba*, *Euonymus americana*, *Ilex decidua*, and *Lindera benzoin*. Also, seedlings of most dominants occur; identification was only at the generic level for the ashes (*Fraxinus*), elms (*Ulmus*), hickories (*Carya*), hackberries (*Celtis*), and oaks (*Quercus*). The oaks were separated into "white" and "red-black" groups.

Woody Vines

Lianas were not quantitatively sampled except for grapes (*Vitis* spp.), which were counted in the shrub and woody seedling layer. Large grapevine stems occur throughout. Other common woody vines include crossvine (*Bignonia capreolata*), greenbriars (*Smilax* spp.), poison ivy (*Rhus radicans*), and Virginia creeper (*Parthenocissus quinquefolia*). Trumpet creeper (*Campsis radicans*) was infrequent.

Herbaceous Flora

The herbaceous flora (including ferns) is not diverse, probably due to frequent flooding. Large expanses of the forest floor remain almost bare of herbs during the entire growing season. No unexpected or rare taxa were encountered, based on lists of expected taxa given by Carpenter and Chester (1988).

Comparisons

We have little information on the original bottomland forests of the lower Cumberland River Valley. Neither Braun (1950) nor Gordon (1930) provided information on them. However, Sudworth (1897) provides some insight into the original bottomland forests of Middle Tennessee by describing remnants existing in the latter half of the 19th century:

> The remnant old forest-trees in rich, moist bottoms are usually large, and consist principally of tuliptree, white, red, green, and blue ashes, white oak, chestnut oak, bur oak, cow oak, overcup oak, chinquapin oak, red, yellow, and Texas oaks, together with red, black, sugar, and ash-leaved maples. The white linden, or basswood, which is the peculiar *Tilia* of southern forests, is a large timber tree throughout Middle Tennessee, scattered in single or groups of a few individuals along the streams or here and there over the dry, rocky hills. One sees an occasional silverleaf maple, black willow, water and honey locust, box-elder, winged and American elms, and also the adaptive Southern hackberry, occupying the low clayey spots.

This historical description included all of Middle Tennessee and provides little basis for comparison with the lower Cumberland valley. Several studies, previously cited in the literature review, provide meaningful, contemporary data on area forests and will be summarized in our future papers.

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Appendix 1. Number of stems, average dbh in cm, and size class distribution for all stems sampled (998) with a dbh of 2.54 cm and above.

			Size Classes[1] & Number of Stems				
Taxa	No.	Avg. dbh	1	2	3	4	5
Acer negundo	4	8.51	2	2	-	-	-
Acer rubrum	6	20.24	1	2	2	1	-
Acer saccharum	31	14.27	15	7	7	1	1
Asimina triloba	53	3.09	53	-	-	-	-
Carpinus caroliniana	80	6.63	64	15	1	-	-
Carya cordiformis	2	47.88	-	-	-	1	1
Carya laciniosa	10	20.47	2	4	1	2	1
Carya ovata	53	27.70	5	8	14	19	7
Celtis laevigata	173	6.58	148	16	7	1	1
Celtis occidentalis	61	7.91	47	10	1	3	-
Cercis canadensis	3	10.24	2	1	-	-	-
Cornus florida	3	3.39	3	-	-	-	-
Crataegus viridis	8	5.08	8	-	-	-	-
Fagus grandifolia	132	14.01	60	45	16	6	5
Fraxinus americana	13	13.09	5	6	2	-	-
Fraxinus pennsylvanica	24	21.37	5	6	8	2	3
Gleditsia triacanthos	2	23.12	-	1	1	-	-
Ilex decidua	47	3.85	47	-	-	-	-
Juglans nigra	3	33.44	-	-	1	2	-
Lindera benzoin	2	2.54	2	-	-	-	-
Liquidambar styraciflua	75	27.54	13	5	17	30	10
Morus rubra	5	17.63	2	1	1	1	-
Ostrya virginiana	30	4.78	29	1	-	-	-
Platanus occidentalis	8	23.27	1	4	-	2	1
Prunus serotina	1	16.00	-	1	-	-	-
Quercus alba	3	48.26	-	-	-	-	3
Quercus michauxii	33	35.60	6	2	4	5	16
Quercus pagoda	23	25.46	9	4	2	2	6
Quercus shumardii	23	42.82	5	1	1	3	13
Ulmus alata	5	20.52	-	3	2	-	-
Ulmus rubra[2]	82	19.59	14	35	21	10	2
TOTALS	998	14.76	548	180	110	91	70

1. Size Classes: 1. 2.54 - 10.14 cm
   2. 10.15 - 20.31 cm
   3. 20.32 - 30.47 cm
   4. 30.48 - 40.63 cm
   5. 40.64 and higher.
2. Possibly including some *Ulmus americana*.

Appendix 2. Trees 10.15 cm dbh and above (450 stems), ranked by importance value.

Taxa	No.[1]	Dens.[2]	Domin.[3]	Pl.[4]	IV[5]	%IV[6]
Liquidambar styraciflua	62	76.57	672.02	14	38.14	12.71
Fagus grandifolia	72	88.92	371.51	19	35.48	11.83
Ulmus rubra[7]	68	83.64	386.62	19	32.97	10.99
Carya ovata	48	59.28	451.19	16	30.55	10.18
Quercus michauxii	27	33.35	527.57	14	26.73	8.91
Quercus shumardii	18	22.23	554.38	13	24.86	8.29
Celtis laevigata	25	30.88	101.00	11	13.97	4.66
Quercus pagoda	14	17.29	249.68	8	13.66	4.55
Fraxinus pennsylvanica	19	23.47	140.40	11	13.62	4.54
Acer saccharum	16	19.76	85.00	10	12.11	4.04
Carpinus caroliniana	16	19.76	28.86	10	9.63	3.21
Celtis occidentalis	14	17.29	56.82	6	7.75	2.58
Carya laciniosa	8	9.88	57.47	5	5.89	1.96
Platanus occidentalis	7	8.65	53.83	4	5.05	1.69
Fraxinus americana	8	9.88	22.18	4	4.48	1.49
Acer rubrum	5	6.18	26.84	5	4.45	1.48
Quercus alba	3	3.71	68.99	3	4.00	1.33
Ulmus alata	5	6.18	21.54	4	3.75	1.25
Juglans nigra	3	3.71	33.25	2	2.57	0.86
Morus rubra	3	3.71	22.78	2	2.31	0.77
Carya cordiformis	2	2.47	48.22	1	2.18	0.73
Gleditsia triacanthos	2	2.47	10.75	2	1.78	0.59
Acer negundo	2	2.47	3.61	2	1.60	0.53
Cercis canadensis	1	1.24	3.13	1	0.83	0.28
Prunus serotina	1	1.24	2.47	1	0.81	0.27
Ostrya virginiana	1	1.24	1.76	1	0.79	0.26

1. Number of stems.
2. Density in number/ha.
3. Dominance in sq. dm./ha.
4. Number of plots with this species.
5. Importance value (300).
6. Percentage of total importance value.
7. Possibly including some *Ulmus americana*.

Appendix 3. Saplings and small trees, 2.54-10.14 cm dbh (548 stems), ranked by importance value.

Taxa	No.[1]	Dens.[2]	Domin.[3]	Pl.[4]	IV[5]	%IV[6]
Celtis laevigata	148	182.78	34.30	19	62.65	20.88
Fagus grandifolia	60	74.10	24.42	15	37.27	12.42
Carpinus caroliniana	64	79.04	18.17	19	36.28	12.09
Celtis occidentalis	47	58.05	12.10	13	25.18	8.39
Ilex decidua	47	58.05	7.48	12	21.38	7.13
Asminia triloba	53	65.46	5.21	12	20.92	6.97
Ostrya virginiana	29	35.82	6.99	6	13.92	4.64
Acer saccharum	15	18.53	6.41	9	12.89	4.30
Ulmus rubra[7]	14	17.29	5.61	9	12.16	4.05
Liquidambar styraciflua	13	16.06	4.07	3	7.07	2.36
Crataegus viridis	8	9.88	2.27	6	6.86	2.29
Carya ovata	5	6.18	3.41	5	6.45	2.15
Quercus pagoda	9	11.12	2.69	4	6.04	2.01
Fraxinus americana	5	6.18	3.36	3	5.13	1.71
Fraxinus pennsylvanica	5	6.18	2.18	4	4.96	1.65
Quercus michauxii	6	7.41	1.86	3	4.28	1.43
Quercus shumardii	5	6.18	1.30	1	2.44	0.81
Cercis canadensis	2	2.47	0.78	2	2.19	0.73
Cornus florida	3	3.71	0.34	2	2.07	0.69
Carya laciniosa	2	2.47	1.35	1	1.93	0.64
Morus rubra	2	2.47	0.31	2	1.86	0.62
Acer negundo	2	2.47	0.24	2	1.81	0.60
Lindera benzoin	2	2.47	0.06	2	1.73	0.58
Acer rubrum	1	1.24	0.63	1	1.25	0.42
Platanus occidentalis	1	1.24	0.64	1	1.25	0.42

1. Number of stems
2. Density in number/ha.
3. Dominance in sq. dm./ha.
4. Number of plots with this species.
5. Importance value (300).
6. Percentage of total importance value.
7. Probably including some *Ulmus alata* and possibly some *Ulmus americana*.

Appendix 4. Plot data for shrubs and woody seedlings with dbh less than 2.54 cm.

Taxa	No.[1]	Dens.[2]	RD[3]	Pl.[4]	RF[5]	IV[6]	%IV[7]
Arundinaria tecta	413	5100.6	42.88	11	7.28	50.16	25.08
Asimina triloba	145	1790.8	15.06	13	8.61	23.67	11.84
Carya spp.	98	1210.3	10.18	16	10.60	20.78	10.39
Celtis spp.	37	457.0	3.84	12	7.95	11.79	5.90
Quercus (reds)	34	419.9	3.53	11	7.28	10.81	5.41
Quercus (whites)	36	444.6	3.74	8	5.30	9.04	4.52
Fraxinus spp.	34	419.9	3.53	7	4.64	8.17	4.09
Ilex decidua	12	148.2	1.25	10	6.62	7.87	3.94
Acer saccharum	16	197.6	1.66	8	5.30	6.96	3.48
Euonymus americana	21	259.4	2.18	5	3.31	5.49	2.75
Morus rubra	9	111.2	0.94	6	3.97	4.91	2.46
Vitis spp.	19	234.7	1.97	4	2.65	4.62	2.31
Lindera benzoin	12	148.2	1.25	5	3.31	4.56	2.28
Sambucus canadensis	17	210.0	1.77	4	2.65	4.42	2.21
Symphoricarpos orbiculatus	20	247.0	2.08	3	1.99	4.07	2.04
Acer rubrum	5	61.8	0.52	4	2.65	3.17	1.59
Crataegus viridis	4	49.6	0.42	4	2.65	3.07	1.54
Fagus grandifolia	7	86.5	0.73	3	1.99	2.72	1.36
Ulmus spp.	5	61.8	0.52	3	1.99	2.51	1.26
Acer negundo	4	49.6	0.42	3	1.99	2.41	1.21
Carpinus caroliniana	4	49.6	0.42	2	1.32	1.74	0.87
Gleditsia triacanthos	4	49.6	0.42	2	1.32	1.74	0.87
Acer saccharinum	2	24.7	0.21	2	1.32	1.53	0.77
Cornus florida	1	12.4	0.10	1	0.66	0.76	0.38
Liquidambar styraciflua	1	12.4	0.10	1	0.66	0.76	0.38
Ostrya virginiana	1	12.4	0.10	1	0.66	0.76	0.38
Carya cordiformis	1	12.4	0.10	1	0.66	0.76	0.38
Bumelia lycioides	1	12.4	0.10	1	0.66	0.76	0.38

1. Number of stems.
2. Density in number/ha.
3. Relative density.
4. Number of plots with this species.
5. Relative frequency.
6. Importance value (200).
7. Percentage of total importance value.

THE BIOLOGY OF *PENSTEMON TENUIFLORUS* PENNELL (SCROPHULARIACEAE SECTION *GRACILES*).

I. TAXONOMY AND GEOGRAPHIC ECOLOGY

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ABSTRACT. A taxonomic study of *Penstemon tenuiflorus* and the closely-related species *Penstemon hirsutus* (L.) Willd. used information from herbarium specimens, field and greenhouse observations, and the literature. The geographic distribution of both species was established from herbarium records and literature reports, and county dot distribution maps were prepared. The geographic ecology of *P. tenuiflorus* was described from field observations and the use of topographic, geologic, and physiographic maps; county soil surveys; literature and herbarium specimen data; and climatic records.

A total of 701 herbarium sheets initially labelled and/or annotated as *Penstemon tenuiflorus* or *P. hirsutus* were examined and annotated; 207 of them were determined to be other species of *Penstemon* within Section *Graciles*. Closing of the corolla orifice by the lower corolla lobes separates *P. tenuiflorus* and *P. hirsutus* from other taxa which exhibit either a non-pleated and inflated distal corolla tube with flaring lobes or a strongly-pleated tube and forward-projecting lower corolla lobes. Leaves of *P. tenuiflorus* are distinctly pubescent on both surfaces. This character readily separates the species from *P. hirsutus*, whose leaves have sparse pubescence on the lower surface when young but become glabrous with age. This character is consistent for plants in the field, on herbarium sheets, and on those grown from seeds under identical conditions in the greenhouse. Flowers of *P. tenuiflorus* are pure creamy-white (very rarely with faint purple nectar guides), while those of *P. hirsutus* have purple-violet corolla tubes with white lobes. However, this character is extremely difficult to detect in dried specimens because flowers of *P. hirsutus* nearly always fade to white when dried. The literature suggests that the ratio of sepal length to capsule length can be used to distinguish between these species, but this character is so variable that it is essentially useless. *Penstemon tenuiflorus* and *P. hirsutus* also appear to differ in habitat requirements; even though their ranges overlap I have not observed them growing together in the field.

A. Koelling suggested (unpublished Ph.D. dissertation, University of Illinois, 1964) that *Penstemon tenuiflorus* may be a variety or subspecies of *P. hirsutus*, because they produce fertile hybrids of intermediate characteristics when artificially crossed. However, there has been no attempt to merge these taxa, and the relevant literature and technical manuals published since *P. tenuiflorus* was described in 1919 maintain them as separate species. Based on the apparently stable taxonomic characters of flower color and leaf pubescence, and on distinct habitat preferences and geographic ranges, these two taxa are accepted as separate species.

***Penstemon tenuiflorus* ranges from southwest central Kentucky south through Middle Tennessee to northern Alabama and east-central Mississippi. With the exception of seven counties west of the Tennessee River in Tennessee and a few counties in the Black Belt, its range is in the Interior Low Plateaus Physiographic Province. Within the Interior Low Plateaus, *P. tenuiflorus* occurs in the Shawnee Hills Section (Ohio River Hills and Lowlands Subsection, Mammoth Cave Plateau Subsection); the Highland Rim Section (Pennyroyal Plain, Western Highland Rim, Southwestern Highland Rim, Southern Highland Rim, and Moulton Valley subsections); and all**

subsections of the Central Basin Section (Cumberland River Basin, Harpeth River Basin, Duck River Basin, and Elk River Basin). Outside of the Interior Low Plateaus, *P. tenuiflorus* occurs in the Coastal Plain Province (Black Belt Section) of Mississippi and Alabama.

This species grows primarily at the edges of cedar glades, with some plants occuring in the adjacent open woodlands. In Land Between The Lakes, *P. tenuiflorus* occurs on open limestone bluffs above Kentucky Lake (Tennessee River) and is common along the (disturbed) shoulders of the Trace. In the Black Belt of Mississippi, *P. tenuiflorus* occurs on disturbed sites including "prairie patches."

Penstemon tenuiflorus grows on soils derived primarily from calcareous bedrock: Mississippian limestones in the Shawnee Hills and on the Highland Rim, Ordovician limestone in the Central Basin, and Cretaceous chalk in the Black Belt. Soils are generally shallow, rocky silt loams, with some populations occurring on silty clay and clay soils. Soil reaction varies from strongly acid (pH 5.1-5.5) to moderately alkaline (pH 7.9-8.4); most soils are in the medium to slightly acid range.

Mean annual precipitation throughout the range of *Penstemon tenuiflorus* exceeds 1100 mm, and is generally well distributed during the year. Mean annual temperatures range from 13.6°C in southwest central Kentucky to 16.9°C in the Black Belt of Mississippi. The frost-free season averages about 190 days in the northern part of the range and about 225 days in the southern part. The range of *P. tenuiflorus* falls within U.S.D.A. Hardiness Zones 6a (-20.6 to -23.3°C) in the north to 7b (-12.3 to -15.0°C) in the south.

J. Baskin and C. Baskin (Distribution and geographical/evolutionary relationships of cedar glade endemics in southeastern United States. *Bull. Assoc. Southeastern Biologists* 33:138-154, 1986; Cedar glade endemics in Tennessee, and a review of their autecology. *J. Tenn. Acad. Sci.* 64:63-74, 1989) listed *Penstemon tenuiflorus* as an endemic of the cedar glades of the southeastern United States. Although the primary native habitats of the species are cedar glades and glade-like areas, it also grows on limestone cliffs and in Black Belt prairies. Thus, in the strict sense, *Penstemon tenuiflorus* is not a cedar glade endemic.

THE BIOLOGY OF *PENSTEMON TENUIFLORUS* PENNELL (SCROPHULARIACEAE SECTION *GRACILES*).
II. ECOLOGICAL LIFE HISTORY

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ABSTRACT. ***Penstemon tenuiflorus*** **is a C_3 herbaceous perennial hemicryptophyte apparently without vegetative reproduction. The inflorescence is an indeterminate panicle of two to five verticels. Flowering progresses upward from the base of the inflorescence, with the oldest buds of a verticel opening first. Two pairs of anthers and the stigma are located on the dorsal surface and the bearded staminode on the ventral surface. Flowers are protandrous. At the beginning of anthesis, the distal pair of stamens dehisce, but the stigma is not receptive. By the third day, the proximal pair of anthers has dehisced and the stigma has become receptive. Flowers are insect pollinated. To effect pollination, an insect must land on the lower lip of the flower, which causes the corolla orifice to open. The pollinator's head and thorax are dusted with pollen, which is rubbed against the stigma when the insect visits another flower. The primary pollinators are bumblebees (*Bombus* spp., Apidae), but small solitary bees (Megachilidae) also pollinate the flowers. Pollinators do not systematically work individual inflorescences, but randomly visit flowers of different plants in the immediate vicinity. Carpenter bees (*Xylocopa* sp., Apidae) slit the base of the floral tube and rob nectar from the flower. Honeybees (*Apis mellifera*, Apidae) and a small wasp (Vespidae, Eumeninae) visit these slits. Bee flies (Bombyliidae) and hawk moths (Sphingidae) visit the flowers for nectar, but they do not assist in pollination.**

Penstemon tenuiflorus **is a facultative outcrosser; a small number of seeds are produced agamospermously. In a field experiment, significantly more seeds were produced by cross-pollinated flowers (mean = 783.9 per treatment) than by self-pollinated flowers (mean = 141.2 per treatment) (PLSD = 295.66, $p < 0.05$). Seed production in *P. tenuiflorus* was not pollinator-limited. The mean number of seeds produced was not significantly different between pollinator-assisted flowers (mean = 817.1 seeds per treatment) and non-assisted flowers (mean = 717.8 seeds per treatment) (PLSD = 295.66, n.s.). A small number of (apparently) asexual seeds were produced (mean = 6.0 per treatment). Weight per seed was significantly higher in sexually- than in asexually-produced seeds (mean = 119.5 μg vs 18.9 μg, PLSD = 88.5 μg, $p < 0.05$), as was seed viability (mean = 62.3% vs 17.3%, PLSD = 16.9%, $p < 0.005$). However, there was no significant difference in seed weight (mean = 134.3 μg vs 109.6 μg, PLSD = 88.5 μg, n.s.) or viability (65.8% vs 58.8%, PLSD = 16.9%, n.s.) between outcrossed and selfed seeds.**

Penstemon tenuiflorus **produces a septicidal capsule that matures in late August. Lepidopteran larvae consume the seeds in some of the capsules. Seed dispersal begins in late August or September and continues throughout winter. Seeds have no specialized dispersal structures. They are shaken from the capsules by wind, and perhaps rain, and fall near the base of the plant.**

About 90% of freshly-matured seeds are dormant and 10% conditionally dormant. About 10% of seeds sown on soil in flats in an unheated greenhouse germinated in fall and 40% germinated in early spring. Cold stratification broke dormancy, and nondormant seeds germinated over a wide range of temperatures in light. Seeds buried in pots of soil in a nonheated greenhouse did not survive for more than one year, and no seedlings germinated in soil samples collected in the field

after the spring germination season. Thus, *P. tenuiflorus* does not appear to produce a persistent seed bank.

Most seeds do not germinate. Of those that do only a small percentage of seedlings become established. Survival rates were higher in fall-germinated than in spring-germinated seedlings. Seedlings marked in spring 1991 had formed only small rosettes (<2.5 cm diameter) by the end of their first growing season, and they were less than 5 cm in diameter at the end of their second year. Thus, plants do not reach reproductive maturity until the third year or later. Reproductive plants bolt and flower in spring; rosettes must be vernalized to flower. Bolting begins in March and flowering occurs in April and May. Timing of flowering is controlled by temperature and not by photoperiod. Most reproductive plants produce offshoot rosettes from early summer (after flowering) until fall. Larger non-reproductive rosettes may produce offshoot rosettes from the woody caudex throughout the growing season. In a cedar glade population in Cedars of Lebanon State Park, Tennessee, and in a population in a glade-like area in Mammoth Cave National Park, Kentucky, the total number of rosettes has remained nearly constant during the first two years of a study on the autecology and population biology of *Penstemon tenuiflorus*.

BARRENS AND GLADES OF THE SOUTHERN RIDGE AND VALLEY

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ABSTRACT. Sixty-nine sites representing barrens, glades, and related vegetation were studied floristically and by the plot method in the Ridge and Valley of southwestern Virginia, East Tennessee, northwest Georgia, and northeast Alabama. Most sites were on Chickamauga limestone. Native taxa totaled 803; regional intraneous, local intraneous, and southern percentages approximated those of the barren floras. The percentage of northern taxa was similar to that of the barrens of the cooler Cumberland Plateau. The western taxa occurred chiefly on sites in southern East Tennessee and adjacent Georgia and Alabama. Taxa considered rare in any of the four states totaled 45; restricted range and edge-of-range phenomena contributed to rarity. Plot sampling of glades revealed high rock and gravel cover, and plant cover percentages similar to those in Middle Tennessee. Barren samples had high perennial grass cover.

INTRODUCTION

The barrens and glades of the Ridge and Valley Physiographic Province occur widely in the Province and are related to other vegetation on carbonate bedrocks. The glades resemble small versions of the extensive cedar glades of Middle Tennessee, and have less than 50 percent perennial grass cover. The barrens resemble grassy openings (prairie) of Middle and West Tennessee and of the middle-western United States, and have more than 50 percent perennial grass cover. However, intensive land use and valley position may have modified vegetation of these sites in the past.

The term barrens was used by early travelers, *e.g.* Michaux (1793-1796), and was used subsequently for grassy vegetation and also adjacent low density woodland, thicket, and savanna vegetation (Safford 1869, Killebrew *et al.* 1874, Dicken 1935, DeSelm and Murdock in press). Previous area studies of these vegetation types include those of DeSelm *et al.* (1969), DeSelm (1989b), Carr (1965), Van Horn (1980, 1981a, 1981b), and Finn (1968). This paper lists the flora of the glades and barrens and describes certain characteristics. It also describes the vegetation of typical glades and barrens.

THE STUDY AREA

The Ridge and Valley Physiographic Province extends from the Hudson River Valley of New York to central Alabama, where it touches the Coastal Plain (Fenneman 1938). The portion studied here lies between the Cumberland Plateaus and Mountains to the west and the Blue Ridge to the east (Fig. 1). Reported sites lie between southwestern Virginia and St. Clair County, Alabama--further descriptions apply chiefly to that portion.

The Ridge and Valley is underlain by Paleozoic limestones, dolomites, shales, and sandstones, which are extensively faulted and folded. Most dip at shallow to steep angles, exposing various strata to surface weathering forces. The resulting landscape exhibits parallel knobby mountain ridges of the more resistant sediments and intervening valleys of softer limestones and shales, all extending in a northeast to southwest direction (Rodgers 1953, Hardeman 1966, Calver *et al.* 1963, Butts and Guildersleeve 1948, Szabo *et al.* 1988). Elevations vary from about 800 feet in the south to 1500 feet in Lee County, Virginia. Sites generally occupy valley bottoms or side slope positions and slope angles are slight (1-10 percent) except for the cliff site where the slope exceeds 100 percent.

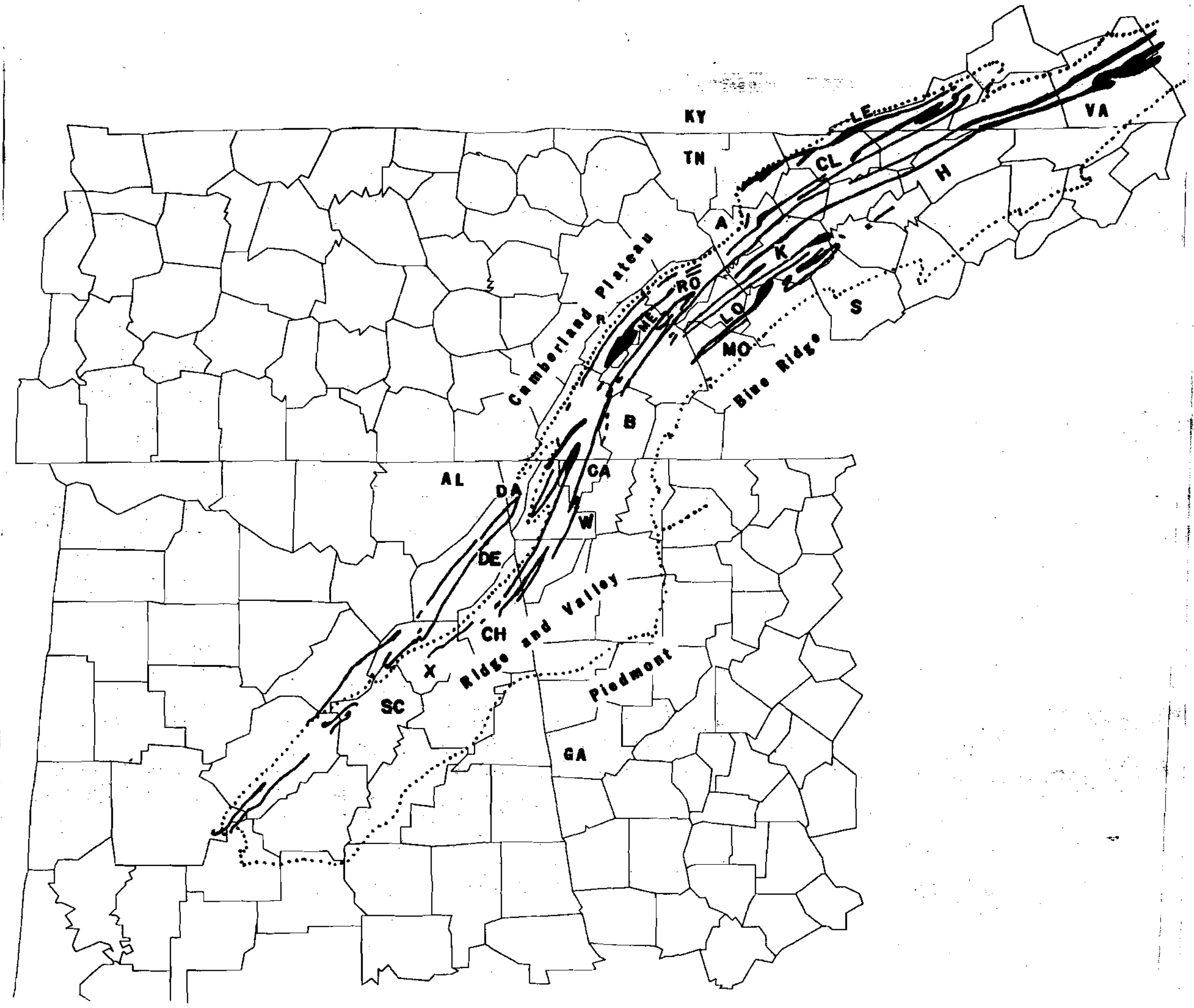

Figure 1. County outline map of the study area. The Ridge and Valley lies within the dotted line. The blackened areas are Chickamauga limestone exposures. The X in AL locates Gadsden, from which northeast and southwest the Conasauga Formation is extensively exposed. Study sites by state and county (number per county) are: VA: LE - Lee (1); TN: CL - Claiborne (5), H - Hawkins (1), A - Anderson (9), K - Knox (10), S - Sevier (1), LO - Loudon (2), RO - Roane (7), ME - Meigs (10), R -Rhea (5), MO - Monroe (1), B - Bradley (1); GA: CA - Catoosa (9), DA - Dade (1), W - Walker (2); AL: DE - DeKalb (1), CH - Cherokee (1), SC - St. Clair (2).

Soils of the glade and barren sites are mapped nationally (U.S. Soil Cons. Service 1970) as Udults: Paleudults, Hapludults, and Rhodoudults. At the state soil association level, Talbott, (Conasauga Series), appears most frequently; others, including Colbert and Rock Outcrop, appear with lower frequency (U.S. Soil Cons. Service 1979, Elder and Springer 1978, Perkins and Shaffer 1977, U.S. Soil Cons. Service 1974). Generally soils are shallow, stony, and clayey. In glades and cedar stands, pH exceeds 7.0 in the A horizon and ranges from 6.6 to over 7.0 in the B/C (McGinnis 1958, Finn 1968).

Thornthwaite (1948) places the study area in the Humid B_3 and B_2, mesothermal B'_3 and B'_2 climate with "no" water deficiency. Average temperatures range from 40 to 45°F in December to 70-80°F in July (Baldwin 1973). Annual average precipitation ranges from 44 to 52 inches (Baldwin 1973, Dickson 1960). The growing season averages 180-220 days (Baldwin 1973). In the East Tennessee meteorological district, 10.9 percent of the months between May and August had moderate, severe or extreme drought. Between 1952 and 1956, there were 48 consecutive months of meteorological (Palmer Index) drought (Vaiksnoras and Palmer 1973). At Chattanooga, the probability of a seven-day one inch (average water holding capacity) drought varies from 11 to 25 percent in the June through September months. At Knoxville, the probability is 9 to 30 percent. Probabilities increase for periods shorter than seven days and decrease for droughts of 2-7 inch average water holding capacity loss (Safley and Parks 1974).

The size of the flora of this part of the Ridge and Valley is not known although the flora of the adjacent southern Blue Ridge is 2391 (2051 native) vascular taxa (Wofford 1989). Studies of local areas, such as the Oak Ridge Reservation (Mann *et al.* 1985) and Chickamauga and Chattanooga National Military Park (Van Horn 1981b), and atlases (Virginia: Harvill *et al.* 1992; Georgia: Jones and Coile 1988) suggest that it is 1800-2000 taxa. Various floristic elements are noted by Carr (1965) and Harvill *et al.* (1977). Glades and barrens are reported in West Virginia (Bartgis 1992).

The vegetation ecology has not been described in detail but was summarized by Braun (1950) and DeSelm (1984). Braun places the study area in the Ridge and Valley section of the Oak-Chestnut Forest Region and the southern half in the Gulf Slope section of the Oak-Pine Forest Region of the Deciduous Forest. Both authors note forests of calcareous soils and further, DeSelm (1984) notes the barrens and glades scattered in them.

Graham (1964) summarizes certain knowledge on the occurrence of families and genera in eastern United States in the Cretaceous and Tertiary Eras. Many modern families evolved/immigrated here during those periods of fluctuating climate (Graham 1964, Wolfe 1978). The Pleistocene of the past 1-2 million years has been characterized as a time of alternating warm and cool climates; Emeliani (1966) postulates eight cool periods in the past 425,000 years alone. The Sangamon may have been warm (King and Saunders 1986). The last full glacial is best known and extensive spruce-pine forests are suggested by pollen profiles in the study area (Watts 1970, 1975, Delcourt *et al.* 1983, Delcourt & Delcourt 1985) as far south as 34°N (just south of Centre, Cherokee County, Alabama).

Late Pleistocene and Holocene warming brought about the return of deciduous/southern and Appalachian softwood vegetation to the area (Delcourt & Delcourt 1979, 1985, Delcourt *et al.* 1983). The warmer/drier interval, the Hypsithermal, is inferred at about 5000 years BP (Delcourt 1979), between 8500 and 4000 BP (Delcourt & Delcourt 1985) and a time of "greater evapotranspiration stress" is inferred at Cahaba Pond, AL, at 10000-8400 BP (Delcourt *et al.* 1983). The Hypsithermal is the period of prairie expansion in the Middle West (Webb *et al.* 1983). At Anderson Pond on the eastern Highland Rim (87 miles west of Knoxville), "A mid-Holocene warming and drying trend is inferred for Middle Tennessee from 8000 to 5000 yr. BP . . ." (Delcourt 1979).

Pleistocene animal remains have been found in bog and cave deposits near the study area; included species now extinct locally. Both deposit types indicate cool climatic episodes of the Pleistocene. Some cave deposits include southern animals well out of their current range, suggesting that some assemblages are heterochronic (Ray *et al.* 1967, Greer 1964, Corgan 1976, Bogan *et al.* 1980, Parmalee *et al.* 1976, Ray 1967, Whetmore 1967, Holman 1967, Robison 1981).

Parts of the study area were occupied by Native American cultures at least 10000 years BP (Archaic culture); these were preceded by Paleoindian hunters. Woodland and Mississippian cultures evolved subsequently; most settlements were along major streams while uplands were used mostly for hunting and gathering. By the time of European settlement, up to 80 villages of the Cherokee Nation and those of the Creek Nation controlled most of the area; Yuchi and Kaskinampo tribes were also present. The use of fire, especially in hunting areas, may be an important factor in the occurrence of barrens as seen by early travelers, and also in the widespread occurrence of disturbance species such as *Pinus* spp., *Juniperus virginiana*, and in many barrens species (Lewis and Kneberg 1958, Swanton, 1946, DeSelm *et al.* 1969, Delcourt *et al.* 1986).

Various parts of the area were opened to settlement by Europeans between about 1790 and 1835 (Folmsbee *et al.* 1969, Abernethy 1922). Clearing and row-crop cultivation of valleys and lower slopes, and logging and pasturing of upper slopes (and lower slopes as they eroded) were common practices. Because of non-cropland grazing, burning the woods was common until the 1930s. Usually, abandoned land eventually grew up to stands of *Juniperus*, *Pinus* spp., or *Liriodendron* if not heavily grazed (Folmsbee *et al.* 1969, Killebrew *et al.* 1874, Minckler 1946, Smith 1968, McCalley 1897). Some vegetation of study sites only persists today because of mowing, bushhogging, or burning regimes. Some may have been fields in the past.

Early explorers and settlers saw the matrix xeric vegetation in the study area and sometimes noted the contained openings. DeSelm *et al.* (1969) mentioned some, and others include, for example, grasslands in the John Adair section of Knox County (Hicks 1968), the "grassy valley" along the Tennessee River in west Knox County (Creekmore 1988) (both seen by early settlers), and the "poor, broken, badly watered, Grassey Barrans . . ." in eastern Knox County seen by T. Lenoir in 1806 (Patton 1958). Other examples include the barrens seen by Colonel Donelson in 1789 in Campbell County (Ridenour 1941), and the Wautauga old fields

(Hyder 1903). Glades were noted by McCalley (1897), including, on shale, "many glady places" in St. Clair County, "naked cedar glades" in Cherokee County, and "a natural cedar glade" in Jefferson County, Alabama. Teeple and Smith (1887) noted that "cedar covers the ridges, knolls and glades" in Jefferson County, Alabama. Place names on modern maps suggest the nature of the vegetation: VA, The Cedars, Cedarville, Glade Spring, Meadowview; TN, Long Savannah, Savannah Creek, Strawberry Plains, Glade Springs, Grassy Valley, Barren Creek (over 90 topographic map place names begin with "cedar," U.S. Geological Survey 1980): GA, Cedar Grove, Cedar Town; AL, Cedar Bluff, Grassland, Cedar Grove (two sites), and Cross Plains.

METHODS

General

Locating and examining Ridge and Valley barrens and glades began in autumn 1956, and except for the short-term intensive study on the Oak Ridge area (DeSelm *et al.* 1969), it was occasional until 1973 when reconnaissance began again and continued through 1989. It was particularly intensive 1988-9, when all Tennessee Chickamauga limestone valleys were road reconnaissanced. When a site was located and its boundaries determined, a cumulative floristic list was compiled. Usually several visits were made in the various seasons, sometimes over a several-year period. In 1977, records from the Herbarium of the University of Tennessee were added for three sites. Included in this paper are records not previously published from Oak Ridge sites (DeSelm *et al.* 1969). The location of about nine sites was learned from other researchers. Specimens are at TENN or EKY.

Plot sampling was carried out in 1985, 1987, and 1989. Plots were placed at one- to two-meter intervals on a straight line through the center of a large opening. Plot size at Mascot (Finn 1968) was one square foot. Plots in 1985 were one fourth square meter in size; other years plot size was one half square meter. Plot number varied from 10 to 40 (average 25) but depended somewhat on size of the opening. Cover was estimated for each vascular species on each plot. Cover by bedrock, gravel, soil, tree leaf litter, bryophytes, lichens, and algae was also estimated. Slope angle was measured and aspect determined.

Species frequency, relative frequency, mean cover, relative cover, and importance value-200 (sum of relative cover and relative frequency) was calculated. Using floristic lists (both total and plot sampled floras), Jaccard's coefficient of community (Muller-Dombois and Ellenberg 1974) was calculated in some cases.

Species ranges were taken from Fernald (1950), Little (1971, 1977), Pennell (1935), Cronquist (1980), and Isley (1990). Nomenclature follows chiefly Gleason and Cronquist (1991) except for composites (Cronquist 1980) and legumes (Isley 1990). Eighty-six sites were studied but results from 69 are included here; 52 from Tennessee, 12 from Georgia, four from Alabama and one from Virginia. Sites were located on appropriate topographic and geologic maps (Calver *et al.* 1963, Rodgers 1953, Milici *et al.* 1973, Butts and Gildersleeve 1948, Szabo *et* *al.* 1988). USGS topographic quadrangles for specific sites are given (in brackets) as part of the site descriptions. Usually larger scale geologic and soils maps were available to locate and characterize sites more specifically but they are not cited in the site descriptions below. Most sites (62) occur on Chickamauga limestone, six occur on calcareous shales (Ottossee Shale and the Conasauga Formation) and one occurs on the Knox Group (dolomite). Sites 2-14 (below) were used by DeSelm *et al.* (1969).

Site Numbers and Locations

1. Norris Area, chiefly University of Tennessee Herbarium records, collections of Arthur Cole and A. J. Sharp, Anderson County, TN. On Chickamauga ls.

2. Oak Ridge Hospital Site Barren - small barren in city of Oak Ridge, Anderson County, TN - later developed [Windrock, Tenn., 1952]. On Chickamauga ls.

3-6. Oak Ridge Girl Scout Camp Barren near Oak Ridge, Anderson County, TN. [Windrock, Tenn., 1952]. On Chickamauga ls.

7. Bus Terminal Road Barren in Oak Ridge, Anderson County, TN. [Windrock, Tenn., 1952]. On Chickamauga ls.

9. Fairbanks Road Barren near junction with Emory Valley Road, Anderson County, TN. [Windrock, Tenn., 1952]. AKA Oak Ridge Barren, Junior High School Barren. On Chickamauga ls.

13. Scarlett/Karns Library Barren. Old field on Rt. 62 west of Knoxville, Knox County, TN. [Lovell, Tenn., 1953]. On Conasauga Formation.

14. Cedar Thicket. Rt. 95, 3.9 miles from Oak Ridge, Roane County, TN. [Bethel Valley, Tenn., 1952]. On Chickamauga ls.

16. Mascot-Cedar-Pine Glade. Glade, cedar stand, and oak forest, Knox Co., TN. [Mascot, Tenn., 1986, revised]. One mile on the Mascot road west from the Holston River bridge. Chickamauga ls. (cf. Finn 1968, Daubenmire 1968, fig. 91).

17. Cedar Bluff - open woods and fields on Cedar Bluff Road all within one mile north of I40 exit at Cedar Bluff, Knox Co., TN. [Bearden, Tenn., 1966]. On Chickamauga ls.

18. Keller Bend Area - open woods and road edge, Knox Co., TN. [Louisville, Tenn., 1953]. Southern Keller Bend Road from Northshore Drive (Rt. 332) ca. one mile, along Ft. Loudon Lake. Chickamauga ls.

18. Keller Bluff Cliff - with adjacent open and closed woods in cedar, pine and oak, overlooking Fort Loudon Lake, Knox Co., TN. [Louisville, Tenn., 1953]. On Keller Bend 1.2 miles SSW of Bluegrass on various units of Chickamauga ls.

19. John Sevier Highway at Asbury Pike - northeast corner in Knox Co., TN. [Shooks Gap, Tenn., 1966]. An old pasture grown up to cedar (barn in middle, dumping here and there). In 1990 the site was bushhogged and disked in prepation for use as a quarry. On Chickamauga ls.

20. John Sevier Highway at Burnett Creek Road, Knox Co., TN. [Shooks Gap., Tenn., 1966]. An open area along road, partly mowed, partly successional to pine and cedar. Ottossee Shale.

21. Burnett Ck. Glade and old field and forest, on Burnett Ck. Rd. 0.6 mile from Island Home Pike, Knox Co., TN. [Shooks Gap, Tenn., 1966]. Chickamauga ls. (cf. Baskin *et al.* 1986).

22. Raccoon Valley, Knox Co., TN. [Big Ridge, Tenn., 1952, and Powell, Tenn., 1952]. On road edges, cuts, fields, and forest borders from the Union County line south to I75 along Raccoon Valley Road, on Chickamauga ls.

26. Bat Creek Knobs roadedge and adjacent open oak forest, Monroe County, TN. [Madisonville, Tenn., 1940]. On the road (2509) south one mile from Rockville. Chickamauga ls.

27. Paint Rock Creek Barren, Roane Co., TN. [Pattie Gap, Tenn., 1952]. Both sides of Rt. 322 about a mile south of Paint Rock on Chickamauga ls. Forest border and one mown road edge.

28. Lawnville Barren, Roane Co., TN. [Elverton, Tenn., 1968]. West side of Lawnville Road just north of Patterson Branch. Chickamauga ls. Glady opening, cedar-pine barren border and adjacent oak forest.

29. Spiers Trailer Barren, Roane Co., TN. [Bacon Gap, Tenn., 1952]. On a dead-end road east from Rt. 58 near Barnardville. Chickamauga ls. Road and field edge and cedar-hardwood forest border.

31. Ten-Mile Church Barren, Meigs Co., TN. [Ten Mile, Tenn., 1952]. Road edge and successional area around church just east of Rt. 58 on Ten-Mile Road. Chickamauga ls.

32. Hurricane Ck. Barren, Meigs Co., TN. [Ten Mile, Tenn., 1952]. Chickamauga ls. Mown road edge on the road south from Ten Mile about one mile.

33. Fezzel Barren and Glade, Meigs Co., TN. [Tranquility, Tenn., 1942]. Chickamauga ls. Successional barren growing up to cedar and pine with adjacent rocky glade. East on Fezzell Road (or Little Hickory Flat Road) from Rt. 58 (about two miles south of its junction with Rt. 68).

35. Ferguson Old Field, Meigs Co., TN. [Goodfield, Tenn., 1942]. On Conasauga Shale in Price Creek Valley east from Rt 58 on the road from Goodfield. Grassy old field, thickets, open forest.

36. Allen Open Cedar, Meigs Co., TN. [Goodfield, Tenn., 1942]. Open cedar thicket south of Allen residence on Rt. 58. Chickamauga ls.

38. Quarry-Fence, Meigs Co., TN. [Birchwood, Tenn., 1942]. Fence row and edge of quarry on Rt. 58 at "Texas 2-779" topographic map notation. Chickamauga ls.

39. East View School area, Meigs Co., TN. [Birchwood, Tenn., 1942]. Road edge, electric line right-of-way, and thickets on north-south road at East View School just north of intersection at school. Chickamauga ls. Site noted by Baskin *et al.* (1986) and Baskin and Baskin (1982).

40. Gunstocker Creek Area, Meigs Co., TN. [Birchwood, Tenn., 1942]. Glady pastures, thickets, and open cedar-pine-hardwood stands on road between Texas and Georgetown east of Rt. 58 on Chickamauga ls.

41. Gilliland Glade and Forest, Bradley Co., TN. [East Cleveland, Tenn., 1965]. On U.S. Rt. 64, 2.6 miles east of the U.S. Rt. 11 junction and behind the Gilliland Fruit Farm Stand, cedar-pine glade and associated forest with stream. On Knox Group (flat lying here).

78. Old Tazewell Barren, Claiborne Co., TN. [Tazewell, Tenn., 1943, revised 1971]. West-facing slope of Blue Top Road at former school site just south of Rt 33; eroded grassy, rocky slope with cedar-hardwood thickets on Chickamauga ls.

79. New Tazewell Barren, Claiborne Co., TN. [Tazewell, Tenn., 1943, revised 1971]. Rocky open and thicket areas around an old quarry near Old Cedar Fort. Chickamauga ls.

80. Gap Creek Glade, Claiborne Co., TN. [Middlesboro South, Tenn.-Kent.-Virginia, 1959]. Rocky open cedar-pine thickets on sinkhole border on Bug Hollow Road off Rt. 63 west of Arthur on Chickamauga ls.

89-90. Strickland Branch, Walker Co., GA. [Kensington, Georgia, 1946, revised 1969]. On Rt. 341 at Strickland Branch crossing 0.7 miles north of Tennessee-Alabama-Georgia RR. Old road, road edge, thickets, and adjacent forest border on Chickamauga ls.

91. US Rt. 27 at Chickamauga Creek, Walker Co., GA. [Fort Oglethorpe, Georgia, 1969]. Rocky slope, roadedge and brushy open forest at northeast corner of junction on Chickamauga ls.

92. Rt. 138 Barren. On local road 138 south of Fort Oglethorpe, Catoosa Co., GA. [Fort Oglethorpe, Georgia, 1969]. Mainly a grass-covered opening on the Chickamauga ls.

93. Route 2 at junction of Chickamauga Creek, Catoosa Co., GA. [Fort Oglethorpe, Georgia, 1969]. Rocky open forest and forest border at east edge of Fort Oglethorpe. On Chickamauga ls. Site has been developed.

94. Centre, Alabama, Cherokee County, AL. [Weisner Mt., Alabama, 1967]. On Rt. 9 about five miles south of Centre, roadedge, open forest, and old field, on Conasauga Shale.

95. Lee County, VA. [Hubbard Springs, Virginia, 1946, revised 1969]. In "The Cedars" west of Jonesville along U.S. Rt. 58, Rts. 662, 679 and cross roads between them in open woods, rock outcrops, pastures. On middle Ordovician ls.

97. Crowder Cemetery Barren Roane Co., TN. [Elverton, Tenn., 1953]. Formerly on ORNL, now Boehing Co. land and consists of open forest, thickets, and rocky barrens on Chickamauga ls. (cf. Patrick and DeSelm 1985 and Pounds *et al.* 1989).

103. Julian Lane Logged Hill, Knox Co., TN. [Shooks Gap, Tenn., 1966]. On Chickamauga ls. A hilltop and southfacing slope with cedar-hardwood, recently logged, with several rock outcrops.

116. Loudon Barren, Loudon County, TN. [Philadelphia, Tenn., 1952]. On Chickamauga ls on U.S. Rt. 11 ca. 4.4 miles south of the south edge of Watts Bar Lake. Barren species persisting around rock outcrops along the highway and under powerlines in former fescue pasture. This is probably the "prairie relict" of A. J. Sharp of 1932 and 1952 (DeSelm *et al.* 1969).

117. GA Rt. 218 at Rt. 146 Barren. Catoosa Co., GA. [East Ridge, Georgia, 1969]. Thickets and barrens on Chickamauga ls. Site subsequently developed into housing.

118. GA Rt. 218 at Rt. 146 Glade, Catoosa Co., GA. [East Ridge, Georgia, 1969]. Thickets and glades on Chickamauga ls.

119. GA, Fort Oglethorpe High School, Catoosa Co., GA. [East Ridge Georgia, 1969]. Barrens, thickets, open forest on a gentle south-facing slope behind the high school (which is on Rt. 2). On Chickamauga ls.

120. Rt. 58 at Rt. 60 Barren, Meigs Co., TN. [Birchwood, Tenn., 1942]. On Chickamauga ls. just north of junction of Rt. 58. Rock outcrops, barrens, thickets, open forest, bushhogged forest understory.

121. Newly Bulldozed Glade Meigs/Bradley Co., TN. [Birchwood, Tenn., 1942]. On Gunstocker Ck. north of Georgetown on Chickamauga ls. Rocky thicket with phone line and newly opened strip of understory.

128. GA Rt. 218 Under Power Line. Catoosa Co., GA. [East Ridge, Georgia, 1969]. Barren under high tension line probably bushhogged annually. About 0.4 mile north of Rt. 146 junction. On Chickamauga ls.

129. Across From Elementary School, Catoosa Co., GA. [East Ridge, Georgia, 1969]. On Rt. 2 near Chickamauga Creek (across Rt. 2 from school); barrens, glades, thickets on Chickamauga ls.

130-1. Viniard-Alexander Road Barren and Glade, Catoosa Co., GA. [East Ridge, Georgia, 1969]. On Viniard-Alexander Rd. south of Fort Oglethorpe off US Rt. 27. Barren, glade and open forest on Chickamauga ls.

142. Raccoon Creek Barren, Roane Co., TN. [Bethel Valley, Tenn., 1953]. On flat land and steep south-facing slope over Watts Bar Lake of Clinch River at ORNL. Old field, thickets, forest, rock outcrops, and barrens. On Chickamauga ls.

145. New Salem Baptist Church Barren, Anderson Co., TN. [Clinton, Tenn., 1952]. A flat corner of annually mown roadside barren and roadedge on Rt. 61 south of Clinton across the road from the church. On Chickamauga ls.

146. Yeary Barren, Claiborne Co., TN. [Coleman Gap, Tenn., 1946]. Gently south-sloping barren under an electric line on Rt. 345 0.7 mile north of the Powell River in the north-east corner of the county. On Chickamauga ls, partly barren, partly pasture and probably all originally forested and opened for pasturage.

148. Eidson Barren, Hawkin Co., TN. [Kyle's Ford, Tenn., 1947]. Steep south and southeast facing probably former pasture, on War Creek north of Eidson. On Chickamauga ls.

149. New Hope Barren, Roane Co., TN. [Rockwood, Tenn., 1952]. Barren (former pasture?) on south-facing slope on Chickamauga ls. about two miles southeast of New Hope Church.

150. Strong Mailbox Barren. Knox Co., TN. [Boyds Creek, Tenn., 1953]. Mown or bushhogged roadside on Will Merritt Drive at Will Brooks Lane on Chickamauga ls.

151. Rt. 139 near I40 Barren. Sevier Co., TN. [Boyds Creek, Tenn., 1953]. On Rt. 139 just north of I40 on Chickamauga ls. It is old field, thickets, barren and roadcut.

152. Blue Water Trail, Rhea Co., TN. [Ten Mile, Tenn., 1952]. About one mile east of Euchee Chapel Road on Chickamauga ls. This site is a bushhogged road edge (under an electric line) and roadcut.

153. Glover (Glover - Groover) Road open cedar stand, Rhea Co., TN. [Ten Mile, Tenn., 1952]. On Chickamauga ls., about one mile east of Euchee Chapel Road; this is an open rocky cedar stand.

154. Exxon Barren, Rhea Co., TN. [Decatur, Tenn., 1942]. On Chickamauga ls. About one mile east of Rt. 302 on Bogle's Chapel Road. A rocky, glady barren and thickets.

155. Garland Porter Barren, Rhea Co., TN. [Decatur, Tenn., 1942]. On both sides of Rt. 302 at Garland Porter mailbox on Chickamauga ls.; mown barren, old field and cedar thicket.

156. Henry Harris Glade, Rhea Co., TN. [Evensville, Tenn., 1942]. On the Cottonport Loop Road from Old Washington about 0.1 mile east from Rt. 302. Grassy, rocky glade on Chickamauga ls.

159. Cedar Knob, Claiborne Co., TN. [Coleman Gap, Tenn., 1946]. On Rt. 63 about a mile north of the Rt. 345 junction. Road edges, roadcut, cedar-hardwood thickets on Chickamauga ls.

160. Cloyd Creek/Centerville Glade, Loudon Co., TN. [Meadow, Tenn., 1952]. Cedar glade and open cedar-hardwood forest west of Centerville 0.6 miles on Cloyd Ck. Rd. Chickamauga ls.

161. Rt. 151 at Little Chickamauga Ck., Catoosa Co., GA. [Nickajack Gap, Georgia, 1969]. Mown rocky roadedge. Bedrock is Chickamauga ls.

162. Collinsville Exit of I59, DeKalb Co., AL. [Portersville, Alabama, 1946]. Roadcut and rocky thickets on Chickamauga ls.

163. South of Ashville, AL, St. Clair Co., AL. [Ashville, Alabama, 1958]. On Route 231 south of the Ashville Elementary School this is roadedge barren, thicket, and forest border on the Conasauga Formation (cf. Kral 1982).

164. Near Steele Exit, AL, St. Clair Co., AL. [Hyatt Gap, Alabama, 1958]. Along I59 on west side 2.5 miles north of the U.S. Rt. 231 exit. Mown right-of-way and adjacent open (burned) forest. On the Conasauga Formation.

165. South of Trenton, GA, Dade Co., GA. [Trenton, Georgia-Alabama, 1972]. Roadside along U.S. Rt. 11 just south of Trenton, grassy roadside and adjacent forest border on Chickamauga ls.

RESULTS

General

The taxa found in this study total 917; 114 (12.3 percent) are introduced; 154 (16.7 percent) are woody. The largest share (58.9 percent) of the 803 native taxa are intraneous--certainly the similar bedrocks and soils of the Ridge and Valley provide suitable migration routes facilitating spread at least to and from the north and south. Other floristic elements are: southern (22.6), northern (11.8), western (4.7), and local intraneous (2.0). Similar percentages were calculated for West Tennessee (DeSelm 1989a), the western Highland Rim (DeSelm 1988), the Central Basin (DeSelm 1991b), the eastern Rim (DeSelm 1990), and the Cumberland Plateau (DeSelm 1991a) of Tennessee. Among these, the 58.9 percent intraneous element is intermediate in the series (range 54.1-70.5), as is the southern (range 14.2-30.2), western (range 1.6-8.8) and local intraneous (range 1.1-4.3). The northern percentage of 11.8, compared to the range of 3.8 to 12.8, is high and approaches that from the Cumberland Plateau with its higher elevation and continuity of habitats northward. The Ridge and Valley has the continuity but scarcely the elevation of the Plateau. Shanks (1958) found that high mountain (Blue Ridge), Cumberland Plateau, and broader ranging Appalachian species occur in the Ridge and Valley to some extent. Certainly the Pleistocene cooling previously discussed provided impetus for migration of northern taxa into this area. Total taxa are distributed among the four substrates as follows: Chickamauga limestone (61 sites, 844 taxa); Conasauga Formation and Ottossee Shale (6 sites, 337 taxa); Knox Group (1 site, 214 taxa); and Chickamauga Cliff (1 site, 163 taxa). Coefficients of community between bedrock types are related largely to size of floras and vary from 0.304 to 0.512.

The listed absence of *Leavenworthia exigua* var. *lutea*, which occurs in the southern end of the valley (Kral 1983), and *Trifolium calcaricum* from Lee County, Virginia (Collins and Wiebolt 1992), indicates that this study incompletely sampled the vegetation. Serpentine comparisons indicate that 77 to 81 percent of taxa listed by Tyndall (1992b) and Tyndall and Farr (1990) also occur on the list in this paper.

Local Taxa

Fourteen local intraneous (endemic?) taxa occur on the study sites (see list). Among these are mesophytic or cliff taxa: *Liatris scariosa* var. *scariosa*, *Philadelphus hirsutus* (see Hu 1954-56), *Thaspium pinnatifidum,* and *Trillium luteum.* Five cedar glade endemics occur: *Leavenworthia* (3 species), *Dalea gattingeri*, and *Pediomelum subacaulis.* Three midwestern-central southeastern taxa occur: *Hypericum dolabriforme, Baptisia australis,* and *Viola egglestonii.* One central south-eastern taxon, *Penstemon brevisepalus,* occurs, as does one southern taxon, *Marshallia mohrii.* The number of state occurrences among these taxa is: Alabama, 4; Georgia, 10; and Tennessee, 9; but the numbers of study sites used was 4, 12 and 52, respectively. The numbers of Georgia and Alabama occurrences far exceed their proportion relative to the number of study sites there. The reasons for this will be explored in a later paper.

Rare Plants

Based on state lists of rare taxa, *i.e.*, Alabama (Freeman *et al.* 1979), Georgia (Georgia Freshwater Wetlands and Heritage Inventory 1991), Tennessee (Somers *et al.* 1989), and Virginia (Ludwig 1991), there are 45 rare taxa on glades and barrens of the study area. This number exceeds that in other barrens studies (cf. DeSelm 1990) because of the inclusion of glades in addition to barrens and the comparatively larger geographic area included. Several floristic elements occur among these plants, *e.g.* intraneous *(Carex meadii)*, northern (*Houstonia canadensis)*, southern (*Arenaria patula*), western (*Aster pratensis*), and local intraneous, as previously discussed. About 29 percent of these rare taxa are western extraneous, versus 5.7 percent of the whole flora; 20 percent are local intraneous, versus 2.0 percent of the whole flora. Restricted range and edge-of-range phenomena contribute heavily to rarity. Other factors include a myriad of physiological/structural features which influence survival and spread; many have been examined by Baskin and Baskin (1985, 1988).

In the following list of rare plants, floristic elements are abbreviated as I: (intraneous), L (local intraneous), N (northern), S (southern), and W (western); designations precede taxa names. Abbreviations following taxa names are: A - Alabama, F - Federal, G - Georgia, T - Tennessee, V - Virginia; e - endangered, sc - special concern, t - threatened, ru - rare and unusual, 3c - rarity examined but not currently supported, c2 - rarity being studied. Georgia: s1 - critically imperiled, s2 - imperiled, s3 - rare or uncommon, su - status uncertain. Virginia: s1 - extremely rare, s2 - very rare.

S	*Arenaria patula* - V (s1)
W	*Aster pratensis* - T (c)
W	*Baptisia australis* - G (s2?)
W	*Bouteloua curtipendula* - G (s1)
S	*Buchnera americana* - G (s1)
I	*Carex meadii* - V (s1)
I	*Chamaecrista fasciculata* - G (e)
I	*Commandra umbellata* - A (sc)
S	*Coreopsis X delphinifolia* (C. major var. linearis) - T (e)
W	*Dalea candida* - T (e)
L	*D. gattingeri* - G (s1), F (3c)
S	*Delphinium exaltatum* - T (e)
W	*D. virescens* - G (s1)
S	*Dodecatheon meadia* - G (s2)
I	*Echinacea purpurea* - A (sc)
I	*Eleocharis compressa* - G (s1)
S	*Euphorbia mercurialiana* - G (s2)
W	*Fraxinus quadrangulata* - V (s2)
I	*Gentiana villosa* - A (c)
N	*Houstonia canadensis* - V (s1)
L	*Hypericum dolabriforme* - G (s2), A (t), F (c2)
W	*Isoetes butleri* - A (sc)
L	*Leavenworthia exigua* - G (s1), F (c2) L
L	*L. torulosa* - T (s), F (3c)
W	*Liatris cylindracea* - T (e)
I	*Linum sulcatum* - G (s3?)
S	*Manfreda virginica* - V (s1)
L	*Marshallia mohrii* - A (e)
L	*Penstemon brevisepalus* - G (s3?)
L	*Pediomelum subacaulis* - T (s), G (s1), F (3c)
I	*Scutellaria leonardii* - G (su)
S	*Schoenolirion croceum* - A (sc)
W	*Sedum pulchellum* - G (s2?)
I	*Sisyrinchium albidum* - V (s2)
I	*Silphium pinnatifidum* - T (t)
W	*S. terebinthenaceum* - G (s1?)
W	*Solidago ptarmicoides* - T (e)
S	*Spiranthes ovalis* - G (s2?)
I	*Sporobolus asper* - V (s1)
W	*S. heterolepis* - G (S1?)
I	*S. neglectus* - V (s2)
L	*Thaspium pinnatifidum* - G (s1)
W	*Tomanthera auriculata* - T (e), F (c2)
I	*Triosteum augustifolium* - G (s1?)
L	*Viola egglestonii* - G (s1), F (3c)

Communities - Glades

Results from plot sampling on nine cedar-pine glades revealed high frequency (64-100 percent), and cover (33-75 percent) of bedrock and/or gravel surface. Bryophytes present on six sites had 10-40 percent frequency and 1-69 percent cover. Lichen cover, present on one site, had frequency and cover of 8 percent. An especially arid rocky central area at Mascot was sampled separately; an alga (*Nostoc*), a lichen (*Verucaria*), and bryophytes had frequencies of 47.1, 70.6 and 58.8 percent, and covers of 10.1, 20.9 and 15.6; herb cover there was only 2.4 percent (Finn 1968).

The herbaceous layer (which included a few woody plants) on the nine glades ranged from 15 to 50 vascular taxa per sample set. Much of the variation in richness was due to size of area sampled. Areas totaling about 4.5 square meters averaged 23 taxa; areas totaling 11.25 square meters averaged 39 taxa. Floristic elements previously discussed were present. Both introduced and native weeds also occurred.

Sums of importance values for species groups in nine glades are: annual grasses (range = 0.097 - 1.129, median = 0.258); perennial grasses (range = 0.000 - 0.738, median = 0.297); legumes (range = 0.063 - 0.940, median = 0.124), and composites (range = 0.206 - 0.901, median = 0.410). Thus, it is apparent that annual and perennial grass importances are about equal, though not high, that legumes are less important, and that composite percentages are highest of these groups. This is in keeping with the concept of glades as communities with high forb importance (Quarterman 1950). Five glades may be in fact degraded barrens; four of them occurred with adjacent sampled barrens. Their mean richness was 24.5 taxa; in the four glades which are apparently not degraded barrens, the mean richness was 32.8 taxa.

Three representative glades have been selected for illustration (Appendix 1). They are: Burnett Creek Glade, H. Harris Glade, and the GA Route 218 at Rt. 146 Glade. The sites may be periodically disturbed. Regarding physical factors and species richness, they fall in the middle to upper end of the ranges for characteristics already cited. The sizable numbers of weedy taxa (24 taxa, 26 percent cover) illustrate the open nature of glades and their susceptibility to invasion with disturbance. Much the same can be said for woody taxa; some, such as *Juniperus* and *Quercus muhlenbergii*, are normal for such sites; some, like *Lonicera*, are edge invaders. Many spring taxa, such as *Arenaria patula*, were overlooked in September sampling.

The list (Appendix 1), when compared with the most frequent taxa in the seven Middle Tennessee glade types (Somers *et al.* 1986), has community coefficients that range from 22.6 to 29.0. Specific community comparisons are at the same level. The site at GA Route 218 at Rt. 146 compares with type 4 (*Dalea gattingeri*) and type 5 (*Sporobolus vaginiflorus*) at 26.6 percent. The H. Harris site compares with type 5 at 29.2 percent and with type 7 (*Panicum flexile - Pleurochete - Sporobolus vaginiflorus*) at 21.3 percent. Clearly these are only modestly related, although 88 percent of the common vascular taxa from the Middle Tennessee glades occur in the flora of this study.

In the three sample sites (Appendix 1), various forbs and woody plants were important, but only *Hypericum dolabriforme* was important on two sites. Among perennial grasses only *Danthonia spicata* was important on two sites. The annual grasses *Sporobolus vaginiflorus* (one site), *S. neglectus* (one site), and *S.* annual spp. (the two above and/or *S. ozarkanus*) were important on all three sites. Thus it is difficult to assign dominance to these communities' leading species. Most sites have a preponderance of species with cover of about one percent (Appendix 1).

Communities - Barrens

The results of sampling 16 sites (Tennessee, 10; Georgia, 5; Alabama, 1) are summarized in Table 1. Percentage presence, range of frequencies (where present), and range of average covers (where present) are given for various environmental characteristics and clearly show the severe aridity of these sites.

Table 1. Site characteristics for 16 sampled sites.

Site Characteristic	P%	F Range	C Range
Bedrock exposed	75	3-74	8.3-36
Gravel exposed	31	36-100	9.7-53
Soil exposed	50	7-52	7.0-26
Tree litter	31	12-48	1.0-50
Bryophytes	50	5-48	1.5-50
Lichens	31	5-16	1.0-5
Algae	13	4-8	1.0

Results of summing importance values for species groups are shown in Table 2, along with percentage presence, range of importance values where present, and median importance value. Clearly, perennial grasses and composites are the most important parts of the vegetation; annual grasses and legumes are about a tenth as important.

Species numbers range from 21 to 54 (median 34). Sample area (quadrat number X size) must account for some of this range; sites with sampled areas of 5-7.5 square meters average 28 taxa, while sites with sampled areas of 10-12.5 square meters average about 34 taxa. Floristic elements seen previously are present in these barren samples.

Comparison of barrens-sampled species number per meter square with site aridity (X = approximated by sum of frequency and cover of bedrock and gravel) indicates a linear relationship, with numbers of taxa falling from about 5 when the index is low to about 1.5 at

Table 2. **Summary of importance values at 16 sampled sites.**

Taxa Group	P%	IV Range	Median IV
Annual grasses	63	0.027 - 0.147	0.034
Perennial grasses	100	0.628 - 1.25	0.838
Legumes	94	0.019 - 0.397	0.116
Composites	100	0.105 - 0.589	0.332

the maximum index. The equation is: Y(Avg. No. taxa/m^2) = 5 - 0.016X. $R^2 = 0.497$; slope is significantly different from zero ($P = 0.0023$). Sites which might have been used recently as fields (pastures) average 29.8; taxa sites not believed to be so used recently average 36 taxa (but all may have been pastured at some time in the past).

Three sites illustrating barrens (Appendix 2) exhibit great ranges of frequency and cover. Crowder and the Elementary School are rocky and have some bryophyte cover. The site near Centre showed no exposed rock cover but a few plots had exposed soil. A weed flora (12 taxa, 15.2 percent), as in glades, suggests the open nature of this community. Woody taxa present also suggests this; some are native plants of shallow limestone soils and others are introduced invaders. Thirteen known taxa have importance values at 0.100 (5 percent) or more. Of these, eight are perennial grasses whose importance values total 0.759 to 1.164. Here, as seen above, perennial grasses are very important.

SUMMARY AND CONCLUSIONS

Variable climates of the Tertiary, Pleistocene, and Holocene provided impetus for the invasion of heliophytic xerophytes and meso-xerophytes in the Ridge and Valley of southwestern Virginia, East Tennessee, northwest Georgia, and north Alabama. Landscape disturbances caused by Native Americans, over and above such natural disturbances as lightning-caused fires, helped maintain necessary openings. European man pastured and burned these xeric sites and perhaps increased their area by plowing that resulted in soil loss. Cessation of widespread burning of open range resulted in loss of many sites to succession except where very rocky or where grazed or mowed/bushhogged. Loss due to succession has been seen in Ohio (Annala *et al.* 1983) and Maryland (Tyndall 1992a). Periodic modern drought also helped maintain these areas on shallow soils.

Sixty-nine sites representing barrens, glades, and related vegetation were studied floristically. Most sites occurred on shallow soil over Chickamauga limestone; a few occurred on calcareous shales and one occurred on the Knox Group (dolomite). Native taxa totaled 803, including 45 which are rare in one or more of the states; restricted range and edge of range phenomena contributed to rarity. Regional intraneous, local intraneous, western, and southern percentages were within the ranges of those from similar studies elsewhere. The percentage of northern taxa (11.8) was similar to that of barrens on the cooler Cumberland Plateau of Tennessee. The western taxa occurred chiefly on southern East Tennessee, adjacent Georgia, and Alabama sites, but the reasons for this are not known. Too few sites from such areas as cliffs, successional fields, and thickets were sampled floristically to generalize about their flora.

Nine cedar-pine glades were sampled (three are reported here). High gravel and rock cover indicated site aridity. Importance values of composites, perennial and annual grasses, and legumes were in keeping with, *e.g.*, cover values known in Middle Tennessee.

Sixteen barrens were sampled (three are reported here). Again, cover of rock, gravel, and soil exposure is high. The sum of importance values of perennial grasses exceeded the total for annual grasses, composites, and legumes.

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Appendix 1. **Frequency, mean cover and Importance Value 200 of species of three glade sample areas. Also shown is frequency and mean cover of bedrock, gravel, soil, bryophytes, algae, and tree litter.**

	Burnett	**H. Harris**	**GA Rt. 218 at 146**
Plot number/plot size (m^2)	20/1/4	25/1/2	2
		Frequency - Mean Cover	
Bedrock		44-13.5	
Gravel	95-75.0	84-71.7	83-43.1
Soil	4-20.0	6- 7.5	
Algae	4- 1.0		
Bryophytes	10- 1.0	20-15.7	
Tree Litter		24-30.8	26- 6.0
		Frequency - Mean Cover - Importance Value 200	
Allium cernuum			14- 2.8-.037
A. vineale	5- 1.0-.025		
Ambrosia artemisiifolia		24- 1.2-.022	3- 1.0-.009
Andropogon virginicus	4- 2.0-.013		
Aster dumosus			77- 4.10.155
A. oblongifolius	95- 6.0-.311		
A. patens		16- 1.5-.019	
A. pilosus			9- 1.0-.020
Belamcanda chinensis			3- 2.0-.013
Berchemia scandens			3- 1.0-.009
Bouteloua curtipendula			3-50.0-.217
Centrosema virginianum	10- 1.0-.037		
Chamaecrista nictitans		64- 1.4-.050	
Chrysanthemum leucanthemum	10- 1.0-.037	8- 1.0-.010	
Coreopsis tinctoria			3- 1.0-.009
Croton monanthogynous	35- 1.0-.100	48- 2.0-.042	60- 1.0-.112
Crotonopsis elliptica			6- 2.0-.019
Dalea gattingeri			26-17.0-.119
Danthonia spicata	10-28.0-.367	16-35.0-.188	
Daucus carota		28- 1.0-.024	3- 1.0-.009
Desmodium ciliare		20- 1.0-.018	
Erigeron strigosus			17- 6.0-.056
Euphorbia corollata	20- 1.0-.062	24- 1.8-.025	
E. preslii		36- 1.2-.030	
Festuca elatior			3-10.0-.047
Fragaria virginiana		4- 2.0-.013	

Appendix 1 (cont.)

	Frequency - Mean Cover - Importance Value 200		
Fraxinus americana		4- 2.0-.013	
Galactia volubilis	10- 1.0-.037	60- 1.2-.046	
Gaura filipes		76- 1.5-.071	
Gerardia tenuifolia	10- 1.0-.037		
Gramineae, unknown			9- 1.0-.020
Helianthus hirsutus	10- 1.0-.037		11- 2.0-.028
Heliotropium tenellum		16- 1.0-.016	9- 1.0-.020
Houstonia purpurea var. *calycosa*	5- 1.0-.013		
H. nigricans		72- 1.3-.055	
Hypericum denticulatum			3- 1.0-.009
H. dolabriforme	25-10.0-.185		31-46.5-.253
H. sphaerocarpon		60- 1.6-.048	
Ipomea pandurata		4- 1.0-.008	
Isanthus brachiatus		16- 1.3-.018	11- 1.0-.026
Kuhnia eupatorioides		16- 1.0-.016	
Juniperus virginiana		32-51.9-.283	
Leavenworthia uniflora	5- 1.0-.025		
Lespedeza procumbens		42- 1.2-.034	
L. stipulacea		20- 1.8-.022	17- 1.3-.037
L. virginica		4- 1.0-.008	
Liatris cylindracea			6- 5.5-.034
Linum medium		12- 1.0-.013	
Lithospermum canescens		12- 1.3-.015	6- 1.0-.015
Lobelia spicata		40- 1.5-.035	
Lonicera japonica			3- 1.0-.009
Manfreda virginica		24- 1.0-.021	
Medicago lupulina	15- 1.0-.050		
Monarda fistulosa	5- 1.0-.025		
Opuntia compressa		4- 1.0-.008	
Panicum capillare	5- 1.0-.025		
P. commutatum	10- 1.0-.037		
P. depauperatum		16- 3.8-.030	
P. flexile	50- 1.0-.137	44- 9.3-.076	
P. lanuginosum	5- 1.0-.025		
P. sp.	5- 1.0-.025	4- 1.0-.008	3- 1.0-.009
Penstemon brevisepalus		8- 2.5-.018	
Physostegia virginiana		16- 1.0-.160	
Plantago aristata			9- 1.0-.020
P. lanceolata		16- 1.0-.016	
P. virginica			9- 1.0-.020
Polygala verticillata		40- 1.0-.032	
Potentilla simplex		24- 2.5-.029	6- 1.0-.015
Prunella vulgaris var. *lanceolata*		4- 1.0-.008	
Quercus muhlenbergii		8- 1.5-.013	
Q. shumardii	5-15.0-.196		
Rhamnus caroliniana		4- 1.0-.008	

Appendix 1 (cont.)

	Frequency - Mean Cover - Importance Value 200		
Rosa carolina			3- 1.0-.009
Rudbeckia fulgida			6-20.5-.098
Ruellia humilis		68- 1.4-.052	29- 3.2-.066
Sabatia angularis			14- 1.0-.029
Salvia lyrata	5- 1.0-.025	40- 2.5-.040	
Schizachyrium scoparium		40-21.0-.133	3- 1.0-.009
Senecio anonymus		28- 1.3-.024	14- 1.0-.029
Setaria geniculata			3- 1.0-.009
Sida elliottii			3- 1.0-.009
Sisyrinchium albidum	20- 1.0-.062	40- 1.1-.033	
Smilax bona-nox		4- 1.0-.008	
Solidago canadensis var. *scabra*		4- 1.0-.008	
S. nemoralis		88- 1.9-.069	
S. ptarmicoides		68- 1.5-.053	3- 1.0-.009
S. rigida	5- 1.0-.025		
Sporobolus asper	10- 1.0-.037		3- 1.0-.009
S. neglectus		76-10.3-.103	
S. annual spp.			94-31.5-.303
S. vaginiflorus	45- 1.0-.125		
Symporicarpos orbiculatus			3- 4.0-.022
Unknown forb	5- 1.0-.025	32- 1.3-.029	3- 1.1-.010
Verbena simplex			9- 1.0-.009
Viola pedata			3- 1.0-.009
V. sp.	16- 1.5-.019		

Appendix 2. Frequency, mean cover and Importance Value 200 of species of three barrens sample areas. Also shown is frequency and mean cover of bedrock/gravel, soil, bryophytes/algae, lichens and tree litter.

	Crowder Cemetery, TN	**Elementary School, GA**	**Centre, AL**
Plot number/plot size (m²)	30 1/4	20 1/2	20 1/4
		Frequency - Mean Cover	
Bedrock/Gravel	35-16.0	9-45.0	
Soil	35-16.0	3-15.0	20- 7.0
Bryophytes/Algae	15- 3.0	6-30.0	
Lichens	5- 1.0		
Tree Litter		2-10.0	
		Frequency - Mean Cover - Importance Value 200	
Acerates viridiflora		5- 1.0-.011	
Allium cernuum		20- 1.0-.036	
Andropogon gerardii	50-35.0-.485	20-30.3-.129	
A. gyrans			5- 1.0-.016
Anemone virginica	5-1.0-.022		
Anisostichus capreolata		5- 1.0-.011	
Aristida longispica			10- 1.0-.027
A. purpurescens			75-29.0-.341
Aster dumosus		40- 2.0-.072	5- 1.0-.016
A. laevis	38-2.0-.115		
A. lateriflorus			5- 1.0-.016
A. pilosus			5- 1.0-.016
A. undulatus			5- 1.0-.016
Bouteloua curtipendula		40-41.4-.202	
Ceanothus americanus	15-2.0-.058		
Composite, unknown			5- 5.0-.042
Croton capitatus		15- 1.0-.028	
C. monanthogynous		15- 1.0-.028	
Crotonopsis elliptica		5- 1.0-.011	
Dalea gattingeri		10- 1.0-.019	
Daucus carota		5- 1.0-.011	
Dicot, unknown		10- 1.0-.019	
Diodia teres		20- 1.0-.036	5- 1.0-.016
Erigeron strigosus		5- 1.0-.011	
Euphorbia corallata		15- 1.0-.028	
Fimbristylis puberula		10- 2.0-.019	
Fragaria virginica	5- 1.0-.022		

Appendix 2 (cont.)

	Frequency - Mean Cover - Importance Value 200		
Galium pilosum	5- 1.0-.022		
Gaura filipes		5- 1.0-.011	
Gymnopogon brevifolius			5- 1.0-.016
Helianthus hirsutus	10- 1.0-.034		
H. occidentalis	18- 2.0-.066	40- 1.1-.069	
Heliotropium tenellum		5- 1.0-.011	
Houstonia longifolia		25- 1.0-.044	
H. nigricans	5- 1.0-.022		
H. purpurea var. *calycosa*			20- 1.0-.047
Hypericum dolabriforme	20- 5.0-.102	50-12.0-.121	15- 1.0-.037
Juniperus virginiana		5- 1.0-.011	10- 1.0-.027
Lespedeza procumbens	30- 1.0-.084		
Liatris cylindracea	19- 6.0-.109	10- 1.0-.019	
Lithospermum canescens	5- 1.0-.022		
Lobelia spicata		10- 1.0-.019	
Lonicera japonica		10- 5.5-.033	
Lythrum alatum	5- 1.0-.016		
Manfreda virginica	10- 1.0-.034	5- 1.0-.011	
Mecardonia acuminata			15- 1.0-.037
Monarda fistulosa	5- 1.0-.022		
Muhlenbergia capillaris			20-20.0-.169
Panicum anceps			15-20.0-.159
P. commutatum		5- 1.0-.011	5- 1.0-.016
P. lanuginosum		10- 1.0-.019	
P. sp.			5- 1.0-.016
P. virgatum		15-63.3-.226	15-16.0-.134
Paspalum floridanum			5- 1.0-.016
P. laeve			5- 1.0-.016
Physostegia virginiana			5- 1.0-.016
Pinus virginiana			5- 1.0-.016
Potentilla simplex		5- 1.0-.011	
Prunella vulgaris var. *lanceolata*	5-1.0-.022		
Pycnanthemum tenuifolium	20-1.0-.060		
Ratibida pinnata	5-1.0-.022	15- 1.0-.028	
Rosa carolina		15-10.7-.059	10- 2.0-.034
Rubus "dewberry"			5- 1.0-.016
Rudbeckia fulgida		30- 2.7-.059	
R. hirta		5- 1.0-.011	
Ruellia humilis		60- 1.0-.102	
Salvia lyrata		5- 1.0-.011	
Schizachyrium scoparium	23-21.0-.274	55-37.7-.211	60-37.0-.361
Schoenolirium wrightii			60- 5.0-.137
Senecio anonymus	10- 1.0-.034	5- 1.0-.011	
Setaria geniculata		5-10.0-.040	
Silphium pinnatifidum		5- 1.0-.011	

	Frequency - Mean Cover - Importance Value 200		
S. terebinthinaceum	11- 6.0-.089		
S. trifoliatum			25- 1.0-.058
Solidago nemoralis	5- 1.0-.022		
S. ptarmicoides	35- 1.0-.097	35- 1.0-.061	
S. rigida	25- 1.0-.070		
Sporobolus asper		10- 7.5-.040	
S. heterolepis		10-55.0-.191	
S. neglectus/vaginiflorus		10- 5.5-.034	
Tragia cordata			5- 1.0-.016
Unknown forb	19- 1.0-.057	50- 3.0-.122	
Zizia aptera	10- 1.0-.034		

APPENDIX 3.

FLORA OF BARRENS AND GLADES OF THE SOUTHERN RIDGE AND VALLEY[1]

PTERIDOPHYTA

Aspidiaceae
Dryopteris marginalis (L.) Gray - **I**; 95
Polystichum acrostichoides (Michx.) Schott - **I**; 5, 16, 33, 79, 95, 156
Woodsia obtusa (Sprengel) Torrey - **I**; 95

Aspleniaceae
Asplenium platyneuron (L.) Oaks - **I**; 9, 14, 16, 18, 33, 35, 40, 79, 93, 95, 120, 142, 149, 152, 153
A. ruta-muraria L. - **I**; 18, 80, 95

Isoetaceae
Isoetes butleri Engelm. - **W**; 94

Ophioglossaceae
Botrychium virginianum (L.) Swartz - **I**; 16, 21, 27, 40, 41, 79, 95, 103, 142, 151, 153, 160
Ophioglossum engelmannii Prantl - **S**; 16, 21, 30, 119, 120, 121, 142, 149, 154

Polypodiaceae
Polypodium polypodioides (L.) Watt.- **I**; 14, 16, 18, 28, 31, 40, 41, 90, 129, 130, 142, 149, 162

Pteridaceae
Cheilanthes alabamensis (Buck.) Kunze - **S**; 18
C. lanosa (Michx.) D. C. Eaton - **I**; 18
Pellaea atropurpurea (L.) Link - **I**; 16, 18, 40, 79, 80, 95, 120, 130, 142, 149, 162
Pteridium aquilinum (L.) Kuhn - **N**; 163

Selaginaceae
Selaginella apoda (L.) Spring - **I**; 41

GYMNOSPERMAE

Cupressaceae
Juniperus virginiana L. - **I**; 2, 3, 7, 9, 13, 14, 16, 17, 18, 19, 20, 21, 22, 26, 27, 28, 29, 30, 31, 32, 33, 35, 36, 38, 39, 40, 41, 78, 79, 80, 89, 92, 93, 94, 103, 116, 117, 118, 119, 120, 128, 129, 130, 131, 142, 145, 146, 148, 149, 150, 151, 152, 153, 154, 155, 156, 159, 160, 161, 162, 163, 164, 165

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[1] **Site numbers follow Methods. Location abbreviations are:** (I) regional intraneous,(L) local intraneous, (N) northern, (S) southern, (W) western, (X) introduced.

Pinaceae
Pinus echinata Mill. - **S**; 3, 7, 16, 19, 22, 26, 27, 28, 29, 33, 35, 40, 103, 119, 120, 129, 146, 148, 149, 151, 152, 153
P. strobus L. - **N**; 29, 97, 142, 152, 153, 156
P. taeda L. - **S**; 35, 39, 40, 41, 92, 93, 94, 97, 117, 119, 120, 128, 129, 130, 162, 163, 164
P. virginiana Mill. - **I**; 2, 3, 7, 9, 13, 14, 16, 20, 22, 26, 27, 28, 29, 33, 35, 36, 39, 92, 94, 95, 97, 119, 121, 142, 145, 149, 150, 151, 152, 153, 154, 155, 156, 162

ANGIOSPERMAE

Acanthaceae
Ruellia caroliniensis (Walt.) Steud. - **I**; 16, 18, 19, 20, 21, 22, 33, 80, 92, 128, 159
R. humilis Nutt. **I**; 2, 7, 9, 14, 16, 19, 22, 26, 27, 29, 30, 31, 32, 36, 38, 39, 40, 41, 79, 91, 93, 94, 95, 97, 116, 118, 119, 120, 128, 129, 130, 131, 142, 145, 146, 148, 149, 150, 151, 153, 154, 155, 156, 161, 162, 165
R. strepens L. - **I**; 21, 22

Aceraceae
Acer negundo L. - **I**; 3, 21, 33, 95, 150
A. nigrum Michx. f. - **N**; 95
A. rubrum L. - **I**; 3, 9, 27, 40, 97, 142, 152, 153
A. saccharum Marshall - **I**; 16, 18, 19, 20, 21, 40, 41, 80, 94, 95, 103, 120, 129, 142, 151

Alismataceae
Alisma subcordatum Raf. - **I**; 3, 94

Amaryllidaceae
Manfreda virginica (L.) Salisburg - **S**; 2, 7, 9, 13, 14, 16, 17, 20, 21, 22, 26, 28, 29, 30, 31, 33, 35, 36, 38, 39, 40, 41, 78, 79, 80, 91, 95, 97, 103, 116, 117, 118, 119, 120, 121, 128, 129, 130, 131, 142, 146, 149, 152, 153, 154, 155, 156, 159, 160, 161, 162, 163
Hypoxis hirsuta (L.) Cov. - **I**; 16, 21, 41, 95, 117, 118, 119, 129, 130, 146

Anacardiaceae
Rhus aromatica Aiton - **I**; 19, 21, 22, 78, 79, 80, 92, 93, 95, 97, 103, 117, 118, 119, 120, 128, 129, 130, 131, 135, 146, 154, 156, 159, 162, 165
R. copallina L. - **I**; 2, 3, 7, 9, 13, 14, 16, 17, 20, 21, 22, 29, 31, 32, 33, 35, 36, 38, 39, 40, 41, 78, 80, 92, 95, 97, 103, 116, 119, 120, 128, 142, 148, 149, 150, 151, 152, 154, 156, 159, 163, 164
R. glabra - **I**; 3, 7, 9, 14, 16, 18, 19, 20, 21, 22, 27, 31, 32, 33, 35, 39, 40, 41, 78, 79, 80, 95, 97, 103, 116, 117, 118, 120, 128, 151, 153, 154, 159, 165
R. radicans L. - **I**; 9, 16, 19, 21, 27, 29, 31, 32, 33, 35, 36, 39, 40, 78, 79, 92, 95, 103, 116, 117, 120, 128, 131, 142, 145, 146, 148, 149, 150, 151, 152, 153, 154, 155, 156, 159, 163, 164, 165
R. toxicodendron L. - **S**; 2, 3, 7, 9, 14, 20, 21, 22, 28, 31, 38, 40, 41, 80, 92, 95, 103, 104, 118, 119, 120, 145, 148

Annonaceae
Asimina triloba (L.) Dunal - **I**; 16, 95

Apiaceae
Angelica venenosa (Greenway) Fern. - **I**; 16, 27, 33, 35, 80, 95
Bupleurum rotundifolium L. - **X**; 19, 21
Chaerophyllum tainturieri Hook. - **S**; 18, 21, 38, 40, 116, 118, 119, 120, 152

Cicuta maculata L. - **I**; 3
Cryptotaenia canadensis (L.) DC. - **I**; 21, 29, 80
Daucus carota L. - **X**; 3, 7, 9, 14, 16, 18, 19, 20, 21, 22, 26, 27, 28, 29, 31, 32, 33, 35, 36, 38, 39, 40, 41, 78, 79, 80, 92, 94, 95, 97, 103, 116, 117, 118, 119, 120, 128, 129, 130, 131, 142, 145, 146, 148, 149, 150, 151, 152, 153, 154, 155, 156, 159, 162, 165
Eryngium yuccifolium Michx. - **I**; 7, 29, 30, 91, 92, 93, 128
Ligusticum canadense (L.) Britt. - **I**; 162
Oxypolis rigidior (L.) C. and R. - **I**; 94
Sanicula canadensis L. - **I**; 2, 9, 16, 21, 26, 27, 28, 31, 36, 40, 41, 79, 92, 93, 95, 97, 103, 119, 120, 142, 149, 152, 153, 154
S. gregaria Bickn. - **I**; 21, 80, 95
S. smallii Bickn. - **S**; 41
Thaspium barbinode (Michx.) Nutt. - **N**; 80
T. pinnatifidum (Buckl.) Gray - **LSA**; 93, 94, 130
T. trifoliatum (L.) Gray - **I**; 33, 41, 80
Torilis arvensis (Huds.) Link - **X**; 19, 40, 78, 89
Zizia aptera (Gray) Fern. - **I**; 7, 16, 27, 29, 30, 41, 91, 93, 97, 128, 142, 146, 152, 159, 162, 163
Z. aurea (L.) Koch. - **I**; 91, 120

Apocynaceae
Amsonia tabernaemontana Walter - **I**; 90, 93
Apocynum cannabinum L. - **I**; 3, 7, 9, 16, 19, 20, 21, 22, 27, 31, 32, 79, 80, 91, 92, 93, 94, 95, 97, 103, 116, 117, 119, 120, 128, 129, 142, 146, 150, 151, 153, 154, 155, 159, 164

Aquifoliaceae
Ilex decidua Walt. - **S**; 21
I. opaca Ait. - **I**; 152, 153

Araceae
Arisaema triphyllum (L.) Schott. - **I**; 95

Aristolochiaceae
Aristolochia serpentaria L. - **S**; 93, 148
Hexastylis arifolia (Michx.) Small var. *ruthii* (Ashe) Small - **S**; 16

Asclepiadaceae
Ampelamus albidus (Nutt.) Britt. - **S**; 18, 19
Asclepias amplexicaulis Small - **I**; 9
A. exaltata L. - **N**; 152, 154
A. hirtella (Pennell) Wood. - **W**; 94
A. quadrifolia - **N**; 80
A. syriaca L. - **N**; 19, 20, 80
A. tuberosa L. - **I**; 7, 9, 16, 19, 20, 21, 22, 27, 29, 30, 32, 33, 38, 39, 40, 41, 78, 80, 89, 94, 95, 97, 103, 116, 117, 119, 120, 128, 142, 145, 146, 148, 150, 151, 154, 155, 159
A. variegata L. - **I**; 91, 93, 95, 128, 154
A. verticillata L. - **I**; 1, 2, 9, 14, 16, 19, 20, 21, 22, 28, 29, 31, 32, 33, 35, 36, 39, 40, 41, 78, 79, 80, 91, 92, 94, 95, 97, 116, 117, 118, 119, 120, 121, 128, 129, 130, 131, 142, 145, 146, 148, 149, 150, 151, 152, 153, 154, 155, 156, 161, 162, 163
A. viridiflora Raf. - **I**; 2, 7, 9, 13, 19, 20, 21, 22, 27, 28, 29, 32, 40, 78, 89, 92, 93, 94, 97, 116, 117, 118, 119, 120, 128, 129, 142, 145, 146, 151, 154, 155
A. viridis (Walt.) Gray - **W**; 40, 92, 119, 128, 154, 155

Matelea decipiens (Alex.) Woods. - **S**; 120
M. gonocarpa (Walt.) Shinners - **S**; 93, 142
M. obliqua (Jaeq.) Woods. - **I**; 16, 21, 26, 27, 40, 120

Asteraceae

Achillea millifolium L. - **X**; 2, 3, 19, 22, 27, 32, 33, 39, 40, 78, 80, 95, 97, 103, 116, 120, 121, 129, 142, 145, 146, 148, 150, 151, 152, 153, 154, 155, 156
Ambrosia artimisiifolia L. - **I**; 7, 9, 13, 14, 16, 18, 19, 20, 21, 22, 27, 28, 29, 32, 33, 36, 38, 40, 41, 78, 79, 80, 92, 94, 95, 97, 103, 116, 117, 118, 119, 120, 121, 128, 129, 130, 131, 142, 145, 148, 149, 150, 151, 156, 162, 164, 165
A. bidentata Michx. - **S**; 92, 93, 119, 128, 161
A. trifida L. - **I**; 3, 9, 22, 29, 40, 79, 97, 121, 148
Antennaria plantaginifolia (L.) Hook. - **I**; 16, 22, 26, 27, 33, 40, 41, 79, 80, 93, 95, 97, 102, 119, 120, 128, 130, 131, 132, 146, 152
A. solitaria Rydb. - **S**; 80
Arctium minus (Hill) Berah, - **X**; 32
Artemisia annua L. - **X**; 95
Aster concolor L. - **S**; 164
A. cordifolius L. - **I**; 21, 103
A. divaricatus L. - **I**; 95
A. dumosus L. - **I**; 2, 14, 20, 28, 29, 30, 33, 35, 36, 39, 89, 91, 92, 93, 94, 97, 116, 117, 118, 119, 120, 128, 129, 130, 131, 142, 145, 146, 149, 151, 154, 155, 156, 161, 163, 164, 165
A. hemisphericus E. J. Alex. - **S**; 91, 92, 93, 94, 119, 128, 163, 164
A. infirmus Michx. - **N**; 16
A. laevis L. - **I**; 27, 29, 93, 97, 142, 162
A. lateriflorus (L.) Britton - **N**; 3, 16, 18, 22, 28, 79, 94, 95, 97, 120, 142, 145, 148, 151, 163
A. novae angliae L. - **N**; 3, 22, 28, 128, 142
A. oblongifolius Nutt. var. *angustatus* Shinners - **I**; 16, 18, 19, 21, 95, 103, 142, 146, 159
A. ontarionis Wieg. - **N**; 41, 156
A. patens Ait. - **I**; 16, 27, 29, 30, 35, 36, 39, 41, 78, 80, 91, 95, 117, 120, 128, 142, 146, 149, 150, 151, 152, 153, 156, 159
A. paternus Cronquist - **I**; 94, 95, 128
A. pilosus Willd. - **N**; 2, 3, 9, 13, 14, 16, 17, 18, 21, 22, 26, 27, 28, 32, 33, 35, 36, 38, 39, 40, 41, 78, 94, 97, 103, 117, 118, 120, 128, 142, 145, 149, 150, 151, 152, 162, 164, 165
A. prenanthoides Muhl. - **N**; 7
A. pratensis Raf. - **W**; 29, 30, 45, 59, 85, 107, 137, 144
A. saggitifolius Willd. - **N**; 16, 19, 27, 28, 30, 33, 95, 97, 103, 120, 130, 142, 145, 162
A. shortii Lindl. - **N**; 18, 21, 79, 120
A. simplex Willd. - **N**; 18, 22, 28, 41, 93, 94, 97, 142, 155, 162
A. solidagineus Michx. - **I**; 41, 91, 94, 128, 129, 163, 164
A. surculosus Michx. - **S**; 2, 7, 9, 94
A. umbellatus Mill. - **N**; 146
A. undulatus L. - **I**; 16, 18, 19, 21, 22, 26, 27, 28, 29, 30, 40, 41, 80, 94, 95, 97, 103, 119, 120, 130, 145, 146, 148, 149, 150, 151, 152, 153, 155, 156, 159, 163, 165
Astranthium integrifolium (Michx.) Nutt. - **W**; 91, 130
Bidens bipinnata L. - **I**; 3, 14, 26, 29, 41, 95
B. frondosa L. - **I**; 21, 41, 95, 163
B. polylepis Blake - **W**; 9, 27, 93, 95
B. tripartita L. - **X**; 22
Cacalia atriplicifolia L. - **I**; 9, 18, 21, 40, 97, 152, 159
Centaurea maculosa Lam. - **X**; 80

Chrysanthemum leucanthemum L. - **X**; 7, 9, 14, 16, 18, 19, 20, 21, 22, 26, 28, 29, 31, 32, 33, 35, 36, 38, 39, 40, 78, 79, 80, 92, 95, 103, 116, 120, 128, 130, 131, 142, 145, 146, 148, 149, 150, 151, 152, 153, 154, 155, 156

Chrysopsis camporum Greene - **W**; 9, 14, 20, 94, 103, 121, 150, 151, 155

C. mariana (L.) Ell. - **S**; 27, 33, 35, 36, 128, 164

Cichorium intybus L. - **X**; 78, 79, 145, 151

Circium carolinianum (Walt.) Fern. and Schub. - **S**; 26, 29, 31, 32, 33, 35, 40, 92, 93, 95, 117

C. discolor (Muhl.) Spreng. - **N**; 3, 7, 9, 13, 14, 22, 29, 78, 97, 142

Coreopsis auriculata L. - **S**; 16, 103

C. X delphinifolia Lam. - **S**; 41, 118

C. major Walt. - **S**; 7, 16, 35, 41, 80, 95, 117, 119, 120, 128, 130, 146, 152, 153, 163, 164

C. pubescens Ell. - **S**; 93, 94, 117

C. tinctoria Nutt. - **X**; 93, 117, 118, 119, 124, 128

C. tripteris L. - **I**; 16, 35, 94, 95, 150, 159, 164

Crepis pulchra L. - **X**; 38, 95

Echinacea purpurea (L.) Moench. - **I**; 1, 20, 22, 27, 28, 93, 150, 162

Elephantopus carolinianus Willd. - **I**; 95, 159

E. tomentosus L. - **S**; 41, 156

Erechtites hieracifolia (L.) Raf. - **I**; 33, 40

Erigeron annuus (L.) Pers. - **I**; 18, 21, 29, 31, 32, 38, 39, 40, 78, 79, 95, 97, 116, 119, 120

E. canadensis L. - **I**; 9, 16, 18, 20, 26, 32, 40, 79, 95, 124

E. philadelphicus L. - **I**; 2, 20, 21, 33, 41, 78, 121

E. pulchellus Michx. - **I**; 21, 78, 80, 95, 103, 117, 120, 146, 148, 152, 153

E. strigosus Muhl. - **N**; 2, 3, 7, 9, 13, 16, 18, 19, 20, 21, 22, 26, 27, 28, 29, 31, 32, 33, 35, 38, 39, 40, 41, 78, 79, 80, 93, 94, 95, 97, 103, 116, 117, 118, 119, 120, 128, 129, 130, 142, 145, 146, 148, 149, 150, 151, 152, 153, 155, 163, 165

Eupatorium album L. - **S**; 159

E. altissimum L. - **I**; 2, 7, 9, 13, 19, 20, 21, 22, 28, 29, 31, 32, 38, 40, 78, 80, 93, 94, 95, 97, 117, 119, 120, 121, 128, 142, 150, 151, 154, 165

E. aromaticum L. - **I**; 18, 35, 40, 94, 153, 156

E. coelestinum L. - **S**; 3, 22, 119

E. fistulosum Barratt - **I**; 3, 142

E. hyssopifolium L. - **S**; 27, 29, 35, 40, 41, 90, 94, 120, 142, 151, 154, 156, 161

E. incarnatum Walt. - **S**; 18, 19, 21, 26, 30, 40, 79, 89, 120, 121, 148

E. perfoliatum L. - **I**; 21, 35, 41, 94, 163

E. rotundifolium L. - **S**; 94

E. rugosum Houtt. - **I**; 16, 79, 95

E. serotinum Michx. - **S**; 3, 18, 22, 29, 32, 39, 41, 79, 93, 119, 121, 152, 159

E. sessilifolium L. - **N**; 16, 22, 95, 103, 124, 152, 159

Gnaphalium obtusifolium L. - **I**; 3, 14, 16, 21, 26, 27, 29, 30, 31, 32, 33, 35, 40, 41, 79, 94, 95, 119, 120, 121, 128, 142, 146

Helenium amarum (Raf.) Rock - **I**; 40

H. autumnale L. - **N**; 3, 94, 120, 163

Helianthus angustifolius L. - **S**; 33, 35

H. atrorubens L. - **S**; 9, 21, 27, 97

H. decapetalus L. - **N**; 95

H. hirsutus Raf. - **I**; 7, 9, 16, 20, 21, 22, 26, 27, 28, 29, 30, 33, 35, 38, 39, 40, 41, 78, 92, 93, 95, 97, 103, 116, 117, 118, 119, 120, 128, 129, 130, 131, 145, 146, 148, 150, 151, 152, 159, 161, 162, 163, 164, 165

H. lateriflorus Pers. - **N**; 95

Helianthus microcephalus T. and G. - **I**; 7, 16, 22, 26, 27, 28, 35, 39, 41, 89, 95, 103, 120, 146, 151, 152, 159

H. mollis Lam. - **I**; 39, 119, 128

H. occidentalis Riddell - **W**; 3, 7, 9, 21, 30, 97, 117, 119, 129

H. strumosus L. - **I**; 40, 95

H. tuberosus L. - **I**; 21

Heliopsis helianthoides (L.) Sweet - **I**; 95

Hieracium gronovii L. - **I**; 2, 14, 35, 94, 148

H. pratense Tausch. - **X**; 148

Iva annua L. - **W**; 29

Krigia biflora (Walt.) Blake - **S**; 41

Kuhnia eupatorioides L. - **I**; 2, 7, 9, 13, 14, 16, 20, 21, 22, 26, 27, 28, 29, 30, 31, 32, 33, 39, 40, 78, 79, 93, 94, 95, 103, 117, 120, 121, 142, 146, 148, 149, 150, 151, 152, 153, 154, 156, 159, 161, 162, 165

Lactuca canadensis L. - **N**; 13, 18, 19, 20, 21, 22, 26, 27, 29, 31, 32, 33, 78, 79, 80, 93, 95, 97, 103, 117, 146, 151, 152, 156

L. floridana (L.) Gaertn. - **I**; 21, 93, 95

L. saligna L. - **X**; 31, 32, 95, 103, 150

L. scariola L. - **X**; 38, 40

Liatris aspera Michx. - **S**; 2, 3, 21, 27, 29, 30, 37, 116, 119, 120, 162

L. cylindracea Michx. - **W**; 33, 97, 117, 118, 129, 152

L. graminifolia Willd. - **S**; 94, 163

L. microcephala (Small) K. Schum. - **S**; 94

L. scariosa (L.) Willd. - **L**; 93, 117, 128

L. spicata (L.) Willd. - **I**; 9, 28, 29, 92

L. squarrosa (L.) Michx. - **S**; 9, 13, 20, 28, 29, 33, 35, 92, 93, 97, 116, 119, 128, 152, 164

L. squarrulosa Michx. - **S**; 91, 93, 94, 117

Marshallia Mohrii Beadle and Boynton - **L**; 94

Parthenium integrifolium L. - **I**; 13, 21, 30, 31, 93, 94, 118, 120, 152

P. integrifolium var. *auriculatum* (Britton) Cornelius ex Cronquist - **S**; 16, 91, 119

P. integrifolium var. *Henryanum* Meers - **S**; 94, 164

P. integrifolium var. *hispidum* (Raf.) Mears - **W**; 117, 128

Pluchea camphorata (L.) DC. - **S**; 41

Polymnia canadensis L. - **I**; 16, 80, 95

P. uvedalia L. - **I**; 16, 80

Prenanthes barbata (T. and G.) Milstead - **S**; 94

P. serpentaria Pursh - **I**; 22, 27, 36, 40, 93, 120

P. trifoliata (Cass.) Fern. - **N**; 152

Pyrrhopappus carolinianus (Walt.) DC. - **S**; 29, 31, 33, 38, 39, 40, 93, 116

Ratibida pinnata (Vent.) Barnh. - **N**; 3, 9, 18, 22, 27, 33, 38, 39, 40, 89, 91, 92, 94, 97, 116, 117, 118, 119, 120, 128, 129, 130, 131, 142, 155, 160, 162, 165

Rudbeckia fulgida Ait. - **N**; 2, 3, 7, 9, 14, 16, 20, 21, 22, 26, 27, 28, 29, 30, 31, 32, 33, 36, 38, 39, 40, 41, 78, 79, 92, 93, 94, 95, 97, 116, 118, 119, 120, 121, 128, 129, 130, 131, 142, 145, 146, 150, 151, 152, 153, 154, 155, 160, 161, 162, 163, 164

R. hirta L. var. *pulcherrima* Farw. - **W**; 3, 14, 16, 22, 27, 29, 32, 33, 36, 40, 41, 94, 95, 118, 119, 129, 151, 155, 163

R. triloba L. - **I**; 21, 40, 80

Senecio anonymus A. Wood - **S**; 2, 3, 7, 9, 13, 14, 16, 18, 19, 20, 21, 22, 26, 27, 28, 29, 31, 32, 33, 35, 36, 38, 39, 40, 41, 78, 79, 80, 89, 92, 95, 97, 103, 116, 117, 118, 119, 120, 128, 129, 131, 142, 145, 146, 148, 149, 150, 151, 152, 153, 154, 155, 156, 159, 160

S. obovatus Muhl. - **I**; 18, 22

Silphium radula Nutt. - **W**; 91, 92, 93, 94, 128
S. asteriscus L. - **S**; 2, 20, 22, 26, 29, 117, 128, 142, 145, 148, 150, 161
S. asteriscus L. var. *scabrum* Nutt. - **S**; 91, 93, 94
S. compositum Michx. - **S**; 93
S. dentatum Ell. - **S**; 22, 29, 93
S. pinnatifidum Ell. - **I**; 92, 93, 117, 118, 119, 120, 128, 129
S. terebinthenaceum Jacq. - **W**; 2, 9, 17, 20, 22, 28, 29, 31, 32, 33, 38, 39, 40, 78, 97, 116, 120, 150, 151, 161, 162, 163, 164
Silphium trifoliatum L. (incl. var. *latifolium A.* Gray) - **N**; 7, 14, 21, 22, 26, 27, 28, 29, 39, 40, 78, 89, 93, 94, 97, 116, 117, 120, 142, 145, 151, 152, 154, 155, 156, 159, 162, 163, 164
Solidago arguta Ait. spp. *caroliniana* (Gray) G. Morton - **S**; 94
S. bicolor L. - **N**; 94, 95
S. caesia L. - **I**; 80
S. canadensis L. var. *scabra* (Muhl.) T. and G. - **I**; 2, 3, 7, 9, 14, 16, 18, 19, 21, 22, 29, 32, 35, 36, 38, 39, 40, 78, 79, 80, 94, 95, 97, 103, 117, 120, 128, 141, 142, 145, 146, 148, 151, 153, 154, 156, 159, 161, 163, 164, 165
S. erecta Pursh - **I**; 80, 94, 142, 163
S. flaccidifolia Small - **S**; 18
S. gigantea Ait. - **I**; 3, 7, 33, 35, 89
S. hispida Muhl. - **N**; 152
S. juncea Ait. - **N**; 21, 26, 89, 95, 117, 119, 128, 162
S. missouriensis Nutt. var. *fasciculata* Holz. - **W**; 93
S. nemoralis Ait. - **I**; 2, 3, 7, 9, 14, 16, 20, 21, 22, 26, 27, 28, 29, 30, 31, 32, 33, 35, 36, 39, 40, 41, 78, 79, 80, 89, 92, 93, 94, 95, 97, 103, 120, 128, 131, 142, 145, 146, 148, 149, 150, 151, 153, 154, 155, 156, 159, 161, 163, 164
S. odora Ait. - **I**; 94
S. ptarmicoides (Nees) Boivin. - **W**; 9, 28, 91, 92, 93, 97, 117, 118, 119, 128, 129, 154, 155, 156
S. puberula Nutt. - **I**; 16
S. rigida L. - **I**; 21, 27, 28, 29, 33, 39, 92, 93, 97, 116, 120, 128, 150, 154, 155, 162
S. rigida L. var. *glabrata* E. L. Braun - **S**; 30
S. rugosa Miller ssp. aspera (Ait.) Cron. - **I**; 16, 89, 93, 119, 120, 142, 145, 164
S. speciosa Nutt. - **I**; 27, 33, 35, 120, 164
S. speciosa Nutt. var. *rigidiscula* T. and G. - **W**; 16, 30
S. sphacelata Raf. - **S**; 21, 80
S. ulmifolia Muhl. - **N**; 16, 18, 21, 27, 31, 40, 89, 91, 93, 119, 152, 162
Sonchus asper (L.) Hill - **X**; 93
Taraxicum officinale L. - **X**; 16, 18, 21, 29, 31, 39, 78, 79, 80, 95, 97, 103, 121, 145, 148, 149, 151, 155
Tragopogon pretensis L. - **X**; 116, 121
Verbesina occidentalis (L.) Walt. - **S**; 14, 16, 19, 21, 79, 95, 97, 142, 148
V. virginica L. - **S**; 3, 16, 18, 19, 20, 21, 22, 26, 28, 29, 30, 38, 89, 91, 93, 116, 120, 121, 129, 130, 142, 145, 146, 153, 154, 162
Vernonia flaccidifolia Small - **S**; 163
V. gigantea (Walt.) Trel. - **S**; 1, 2, 3, 7, 9, 19, 21, 22, 32, 33, 35, 36, 39, 80, 89, 90, 91, 93, 94, 95, 117, 121, 128, 131, 142, 145, 149, 151, 152, 154, 156, 162, 163, 164, 165

Berberidaceae
Podophyllum peltatum L. - **I**; 16, 79

Betulaceae
Alnus serrulata (Ait.) Willd. - **I**; 3

Carpinus caroliniana Walter - **S**; 18, 27, 146, 159
Ostrya virginiana (Mill.) K. Koch. - **N**; 16, 18, 33, 80, 89, 94, 95, 97, 103, 128, 142, 146, 148, 156, 159, 162

Bignoniaceae
Anisostichus capreolata (L.) Bureau - **S**; 16, 18, 20, 21, 22, 29, 31, 32, 33, 35, 36, 38, 40, 80, 89, 95, 103, 120, 129, 142, 146, 148, 164
Campsis radicans (L.) Seem. - **S**; 3, 9, 14, 16, 18, 19, 20, 21, 26, 27, 29, 31, 32, 33, 35, 38, 40, 41, 91, 92, 97, 103, 116, 120, 128, 130, 142, 145, 146, 151, 159, 163, 164, 165
Catalpa bignonioides Walt. - **S**; 151

Boraginaceae
Cynoglossum virginianum L. - **I**; 16, 21, 41, 93, 103
Heliotropium tenellum Torr. - **W**; 92, 93, 118, 119, 128, 129, 130, 131, 154, 155, 156
Lithospermum arvense L. - **X**; 19, 28, 38
L. canescens (Michx.) Lehm. - **I**; 1, 7, 9, 14, 16, 20, 21, 22, 28, 30, 33, 39, 40, 79, 80, 92, 93, 95, 97, 103, 118, 119, 120, 128, 129, 130, 131, 142, 146, 149, 150, 151, 152, 153, 154, 155, 156, 162
L. tuberosum Rugel - **S**; 16, 103, 117, 119
Mertensia virginica (L.) Pers. - **N**; 93
Myosotis macrosperma Engelm. - **S**; 16, 95
M. verna Nutt. - **I**; 40
Onosmodium molle Michx. ssp. occidentale (Mack.) Cochrane - **I**; 21, 39, 40

Cactaceae
Opuntia humifusa Raf. - **I**; 16, 17, 19, 21, 31, 38, 39, 40, 93, 95, 97, 117, 118, 119, 120, 130, 131, 142, 148, 154, 156, 160

Campanulaceae
Campanula americana L. - **I**; 21, 95
Triodanis biflora (R. and P.) Greene - **S**; 41
T. perfoliata (L.) Nieawl. - **I**; 121

Caprifoliaceae
Lonicera fragrantissima Lindley and Pax - **X**; 19, 21
L. japonica Thunb. - **X**; 3, 7, 9, 13, 14, 16, 19, 21, 22, 26, 27, 28, 29, 31, 32, 33, 35, 36, 38, 39, 40, 41, 78, 79, 80, 92, 95, 97, 103, 117, 118, 119, 120, 128, 129, 130, 131, 142, 145, 148, 150, 151, 152, 153, 154, 155, 159, 162, 164, 165
L. mackii - **X**; 9, 18, 21
L. sempervirens - **I**; 27, 40, 94
Sambucus canadensis L. - **N**; 3, 95
Symphoricarpos orbiculatus Moench - **I**; 9, 22, 29, 40, 80, 89, 91, 92, 93, 94, 95, 116, 117, 118, 119, 120, 128, 129, 130, 148, 154, 159
Triosteum angustifolium L. - **I**; 16, 21, 41, 91, 93, 97
T. perfoliatum L. - **N**; 91, 95, 119
T. perfoliatum L. var. *aurantiacum* (Bichn.) Wieg. - **N**; 93, 120, 165
Viburnum dentatum L. - **I**; 159
V. prunifolium L. - **I**; 18, 28, 79, 80, 94
V. rhytidophyllum Hemsl. - **X**; 9
V. rufidulum Raf. - **S**; 7, 9, 16, 18, 21, 22, 26, 27, 29, 36, 40, 78, 80, 89, 91, 93, 94, 95, 97, 103, 120, 142, 145, 146, 148, 149, 150, 151, 153, 155, 156, 162, 164

Caryophyllaceae
Arenaria patula Michx. - **S**; 16, 19, 21, 30, 38, 40, 41, 78, 79, 91, 95, 103, 119, 120, 130, 131, 140, 146, 159, 160
A. serpyllifolia L. - **X**; 18, 19, 21, 95, 148
Cardamine parviflora - **N**; 40
Cerastium brachypetalum Persoon - **X**; 38
C. glomeratum Thuillier - **X**; 21, 32, 41, 94, 95, 120, 121
C. nutans Raf. var. *brachypodum* Engelm. - **I**; 95
C. semidecandrum L. - **X**; 121, 148
C. vulgatum - **X**; 97
Dianthus armaria L. - **X**; 29, 36, 38, 95, 97, 152
Holosteum umbellatum L. - **X**; 16, 17, 19, 21, 38, 79, 95
Paronychia canadensis (L.) Wood - **N**; 95
Silene antirrhina L. - **I**; 124
S. virginica L. - **I**; 16, 21, 29, 79, 80
Stellaria media (L.) Cyrillo - **X**; 38, 41, 79, 95, 97, 152, 154

Celastraceae
Celastrus scandens L. - **I**; 16, 18, 19, 95, 97, 103, 146, 148, 159
Euonymus americanus L. - **I**; 3, 21, 22, 27, 41, 80, 93, 94, 95, 142

Clusiaceae
Hypericum densiflorum Pursh - **I**; 142
H. denticulatum Walt. - **S**; 118, 128
H. dolabriforme Vent. - **L**; 1, 7, 9, 16, 19, 20, 21, 28, 30, 38, 40, 78, 91, 92, 93, 94, 97, 103, 117, 118, 119, 120, 128, 129, 130, 131, 142, 160, 161, 165
H. drummondii (Grev. and Hook.) T. and G. - **S**; 94
H. frondosum Michx. - **S**; 80
H. gentianoides (L.) B.S.P. - **I**; 13, 35, 36
H. hypericoides (L.) Crantz - **S**; 89, 152, 164
H. mutilum L. - **I**; 3, 93, 94
H. perforatum L. - **X**; 95, 150, 151
H. prolificum L. - **N**; 41, 93, 95, 129, 148, 159
H. punctatum Lam. - **I**; 3, 13, 16, 19, 27, 29, 31, 32, 35, 36, 78, 79, 80, 92, 93, 94, 95, 97, 120, 128, 130, 142, 146, 148, 150, 152, 163
H. sphaerocarpon Michx. - **I**; 16, 94, 117, 118, 119, 129, 130, 131,149, 154, 155, 156
H. stans (Michx.) P. Adams and Robson - **I**; 35, 41
H. stragalum P. Adams and Robson - **I**; 9, 16, 29, 32, 35, 36, 41, 78, 79, 95, 119, 120, 130, 146, 152, 164

Commelinaceae
Commelina communis L. - **X**; 3
C. erecta L. - **I**; 16

Convolvulaceae
Calystegia spithamaeus (L.) Pursh - **N**; 16, 21, 95
Convolvulus sepium L. - **I**; 120, 128, 149
Cuscuta campestris Yunker - **I**; 28
C. compacta Juss. - **I**; 29, 91
C. coryli Engelm. - **N**; 16
C. pentagona Engelm. - **I**; 9

Ipomea hederaceae (L.) Jacq. - **X**; 32, 41
I. lacunosa L. - **S**; 14
I. pandurata (L.) G. F. W. Mey. - **I**; 2, 9, 13, 16, 18, 19, 20, 21, 22, 26, 27, 29, 32, 33, 35, 41, 79, 80, 92, 93, 94, 95, 97, 103, 116, 117, 119, 120, 128, 130, 142, 145, 148, 149, 151, 152, 153, 154, 156, 162

Cornaceae
Cornus amomum Mill. - **N**; 30, 42
C. florida L. - **I**; 7, 9, 13, 16, 18, 19, 21, 22, 26, 27, 28, 29, 31, 33, 35, 36, 39, 40, 41, 80, 95, 97, 103, 119, 120, 121, 128, 131, 142, 146, 148, 149, 151, 153, 154, 155, 156, 159
C. foemina Mill. - **S**; 3, 27, 41, 94

Crassulaceae
Sedum pulchellum Michx. - **W**; 30, 38, 41, 95, 103, 119, 121, 130, 131, 160
S. ternatum Michx. - **N**; 79, 80, 95

Cruciferae
Arabis laevigata (Muhl.) Poir. - **I**; 16, 18, 21, 78, 79, 80, 95, 97, 103, 119, 120, 129, 142, 146, 151
Brassica napus L. - **X**; 18, 41
Capsella bursa-pastoris (L.) Medic - **X**; 19, 21, 94
Cardamine douglassii (Torr.) Britt. - **N**; 18, 80
C. hirsuta L. - **X**; 19, 22, 38, 41, 94, 95, 97, 103, 142, 152, 154
C. parviflora (L.) var. *arenicola* (Britt.) Schulz - **I**; 93, 104
C. pensylvanica Muhl. - **I**; 38, 119
Dentaria laciniata Muhl. - **I**; 18, 21
Draba brachycarpa Nutt. - **S**; 21
D. verna L. - **X**; 16, 19, 21, 22, 94, 95, 160
Leavenworthia exigua Rollins - **L**; 92, 118, 119, 128, 129, 130, 131
L. torulosa Gray - **L**; 41, 121
L. uniflora (Michx.) Britt. - **L**; 16, 21, 30, 38, 40, 94, 103, 120, 121
Lepidium campestre (L.) R. Br. - **X**; 16, 18, 19, 21, 32, 38, 79, 80, 95, 103, 116, 148, 150
L. virginicum L. - **X**; 19, 78, 79, 93, 103, 120, 154
Nasturtium officinale R. Br. - **X**; 21, 22
Thlaspi perfoliatum L. - **X**; 79, 95, 160

Cyperaceae
Carex amphibola Steud. - **I**; 16, 18, 21, 40, 93, 95
C. annectens Bichn. - **I**; 21
C. artitecta Mackenz. - **N**; 18, 146, 154
C. blanda Dew. - **I**; 16, 18, 19, 21, 27, 28, 29, 31, 33, 41, 103, 116, 117, 151, 153
C. caroliniana Schw. - **I**; 79, 94, 103
C. cephalophora Muhl. - **I**; 16, 18, 19, 40, 80, 120
C. cherokeensis Schwein. - **S**; 41, 89, 92, 93, 94, 117, 118, 119, 120, 121, 128, 129, 130
C. complanata Torr. and Hook. - **S**; 3, 29, 33, 41, 39, 80, 93
C. crawei Dew. - **N**; 91, 92, 93
C. digitalis Willd. - **I**; 94
C. eburnea Boott. - **I**; 80
C. festucaceae Schk. - **I**; 21
C. floccosperma Dew. - **I**; 41, 91, 93, 118, 128, 130, 148, 151, 156
C. frankii Kunth - **I**; 18, 21, 93, 97, 121, 128, 129
C. gracilescens Steud. - **I**; 3

Carex granularis Muhl. - **I**; 16, 21, 22, 40, 41, 89, 93, 95, 97, 103, 148, 151
C. grisea Wahl. - **I**; 21, 93
C. hirsutella Mackenz. - **I**; 2, 9, 13, 16, 20, 21, 22, 27, 28, 29, 31, 33, 39, 40, 41, 78, 79, 80, 89, 92, 93, 94, 95, 97, 103, 116, 117, 120, 121, 128, 129, 130, 142, 145, 146, 148, 149, 150, 151, 152, 153, 154, 155
C. leavenworthii Dew. - **I**; 97
C. lupulina Muhl. - **I**; 163
C. meadii Dew. - **I**; 21, 27, 28, 29, 41, 91, 92, 93, 94, 95, 117, 118, 119, 128
C. muhlenbergii Schk. - **I**; 97, 150
C. nigromarginata Schwein. - **I**; 148, 152, 155
C. normalis Mack. - **N**; 128
C. oligocarpa Schk. - **I**; 21
C. pensylvanica Lam. - **N**; 97, 142, 152
C. retroflexa Muhl. - **I**; 16, 97, 120
C. squarrosa L. - **N**; 3
C. striatula Michx. - **I**; 91
C. swanii (Fern.) Mackenz. - **N**; 33
C. texensis (Torr.) Bailey - **S**; 16
C. umbellata Schk. - **I**; 40
C. vulpinoidea Michx. - **I**; 3, 21, 120, 128, 129
Cyperus aristatus Rottb. - **I**; 94
C. filiculmis Vahl. - **I**; 93
C. flavescens L. - **I**; 9, 21, 22, 93, 94, 95
C. pseudovegetus Steud. - **I**; 163
C. retrofractus (L.) Torr. - **S**; 3
C. strigosus L. - **I**; 22
Eleocharis acicularis (L.) R. and S. - **I**; 40, 80
E. compressa Sulliv. - **I**; 41, 92, 93, 94, 117, 118, 119, 120, 128, 129, 130
E. obtusa (Willd.) Schultes - **I**; 7, 41, 94
E. tenuis (Willd.) Schultes - **N**; 3, 94, 121
E. tenuis (Willd.) Schultes var. *pseudoptera* (Weath.) Svenson - **N**; 41
Frimbristylis autumnalis (L.) R. and S. - **I**; 22, 94
F. puberula (Michx.) Vahl. - **I**; 94, 117, 119, 129
Rhynchospora caduca Ell. - **S**; 163
R. globularis (Chapm.) Small - **S**; 94
Scirpus atrovirens Willd. - **N**; 3, 9, 21, 40, 41, 89, 93, 120, 128, 153
S. lineatus Michx. - **I**; 3, 16, 21, 28, 41, 94, 95, 97, 103, 120, 121
Scleria oligantha Michx. - **S**; 16, 18, 21, 29, 41, 92, 93, 94, 95, 97, 103, 119, 128, 130, 142, 146, 150, 151, 153
S. pauciflora Muhl. - **S**; 13, 29, 33, 94
S. triglomerata Michx. - **I**; 41, 91, 93, 95, 103, 119

Dioscoreaceae
Dioscorea batatas Dcne. - **X**; 80
D. quaternata (Walt.) J. F. Gmel. - **S**; 80, 93, 97
D. villosa L. - **I**; 95

Ebenaceae
Diospyros virginiana L. [incl. var. *pubescens* (Pursh) Dippel] - **I**; 3, 7, 9, 14, 17, 18, 19, 20, 21, 22, 26, 27, 29, 31, 32, 33, 35, 38, 39, 40, 41, 79, 80, 92, 95, 97, 103, 117, 118, 119, 120, 128, 129, 131, 142, 146, 148, 150, 151, 152, 155, 163, 164, 165

Ericaceae
Oxydendron arboreum (L.) DC. - **S**; 9, 27, 31, 35, 152, 164
Vaccinium arboreum Marsh - **S**; 35
V. stamineum L. [incl. var. *interius* (Ashe) Palmer and Steyerm.] - **I**; 13, 16, 27, 95, 149
V. vacillans Torr. - **N**; 80

Euphorbiaceae
Acalypha graciliens Gray - **I**; 21, 31, 33, 40, 41, 79, 95, 97, 117, 119
A. rhomboidea Raf. - **I**; 18, 41, 95
A. virginica L. - **I**; 93, 97, 146, 159
Croton capitatus Michx. - **S**; 91, 92, 93, 117, 118, 119, 128, 129, 130, 131, 161
C. glandulosus L. - **I**; 95
C. monanthogynum Michx. - **S**; 9, 16, 17, 18, 19, 21, 22, 39, 89, 91, 92, 93, 116, 117, 118, 119, 120, 121, 128, 129, 130, 131, 146, 150, 151, 155, 156, 160, 161, 162, 165
Crotonopsis elliptica Willd. - **I**; 21, 22, 38, 39, 40, 94, 118, 119, 129, 130, 131
Euphorbia chamaecyche L. - **S**; 19
E. commutata Engelm. - **I**; 18
E. corollata L. - **I**; 2, 7, 9, 13, 14, 16, 19, 20, 21, 22, 26, 27, 28, 29, 33, 35, 36, 38, 39, 40, 41, 78, 79, 80, 92, 94, 95, 97, 103, 117, 118, 119, 120, 128, 130, 131, 142, 146, 149, 151, 152, 153, 154, 155, 159, 162
E. dentata Michx. - **I**; 2, 16, 18, 19, 21, 38, 39, 40, 91, 95, 97, 119, 120, 121, 146, 151
E. maculata L. (including *E. preslii* Guss.) - **I**; 3, 7, 9, 14, 16, 18, 19, 20, 21, 22, 26, 27, 29, 32, 38, 40, 41, 78, 79, 80, 89, 92, 93, 94, 97, 119, 120, 121, 130, 131, 142, 145, 146, 148, 149, 150, 152, 153, 154, 156, 159, 162, 165
E. mercurialina Michx. - **S**; 18, 40, 89, 92, 94
Tragia cordata Michx. - **S**; 91, 92, 93, 94, 118, 119, 120, 128, 129, 130, 131, 163, 164

Fabaceae
Albizia julibrissin Durazzini - **X**; 9, 22, 151
Amorpha fruticosa L. - **I**; 31, 33, 93, 120, 142, 163
Amphicarpa bracteata (L.) Fern. [including var. *comosa* (L.) Fern.] - **I**; 3, 16, 18, 21, 22, 27, 29, 32, 33, 36, 38, 40, 80, 93, 97, 142, 146, 148, 155
Apios americana Medic. - **I**; 3, 27, 38
Astragalus canadensis L. - **I**; 18, 97, 142
Baptisia australis (L.) R. Br. - **L**; 91, 92, 93, 117, 119, 128, 130, 131
Chamaecrista fasciculata (Michx.) Greene - **I**; 3, 9, 13, 16, 18, 19, 20, 21, 22, 26, 27, 28, 29, 30, 31, 33, 35, 36, 38, 39, 40, 94, 95, 97, 117, 120, 128, 142, 150, 151, 154, 161, 162, 163, 164, 165
C. nictitans (L.) Moench - **I**; 3, 7, 9, 14, 18, 19, 20, 21, 22, 26, 27, 28, 29, 31, 33, 35, 36, 40, 41, 80, 94, 95, 97, 103, 118, 120, 128, 131, 142, 146, 152, 153, 154, 156, 162
Centrosema virginianum (L.) Benth. - **S**; 21, 30, 31, 33, 38, 40, 97, 120, 142, 150, 151, 152, 153, 156
Cercis canadensis L. - **I**; 9, 13, 16, 17, 18, 20, 21, 22, 26, 27, 28, 29, 31, 33, 40, 41, 78, 79, 80, 92, 94, 95, 97, 103, 117, 118, 119, 120, 128, 129, 130, 142, 145, 146, 148, 149, 150, 151, 152, 153, 154, 156, 159, 161, 165
Clitoria mariana L. - **I**; 26, 31, 32, 38, 40, 93, 113, 120, 121, 130
Crotalaria sagittalis L. - **I**; 35, 128
Dalea candida Michx. ex Willdenow. - **W**; 39, 94
D. gattingeri (Heller) Barneby - **L**; 38, 39, 40, 91, 92, 93, 94, 117, 118, 119, 120, 128, 129, 130, 131
Desmanthus illinoensis (Michx.) MacMill. - **W**; 9, 21, 39, 91, 92, 93, 94, 117, 118, 119, 120, 128
Desmodium canescens (L.) DC. - **I**; 2, 3, 18, 21, 27, 31, 95, 145

Desmodium ciliare (Muhl.) DC. - **I**; 7, 9, 13, 14, 16, 20, 22, 27, 28, 29, 30, 31, 32, 33, 36, 39, 78, 79, 80, 89, 93, 94, 95, 97, 103, 120, 128, 142, 146, 149, 150, 151, 153, 154, 155, 156, 159, 165

D. cuspidatum (Muhl.) Loud. - **I**; 18, 40, 93

D. laevigatum (Nutt.) DC. - **I**; 27, 142, 152, 154

D. marilandicum (L.) DC. - **I**; 2, 9, 22, 27, 28, 29, 31, 32, 33, 35, 36, 40, 79, 94, 103, 120, 124, 142, 149, 153, 163, 164

D. nudiflorum (L.) DC. - **I**; 16, 95

D. nuttallii (Schindl.) Schub. - **I**; 16, 20, 21, 27, 32, 94, 148, 150

D. obtusum (Muhl. ex. Willd.) DC. - **I**; 32, 33, 39, 93, 116, 120, 121, 142, 146, 165

D. paniculatum (L.) DC. - **I**; 3, 7, 16, 18, 19, 20, 21, 22, 27, 28, 29, 31, 35, 89, 94, 95, 97, 103, 117, 119, 120, 142, 146, 148, 152, 156, 165

D. pauciflorum (Nutt.) DC. - **I**; 28, 97, 151

D. rotundifolium DC. - **I**; 16, 18, 21, 27, 29, 36, 79, 80, 95, 97, 103, 120, 142, 146, 152, 153, 154, 159, 162

D. sessilifolium (Torr.) T. and G. - **I**; 117

D. viridiflorum (L.) DC. - **I**; 3, 27, 31, 41, 142, 150

Galactia volubilis (L.) Britt. - **S**; 2, 3, 7, 9, 13, 16, 18, 19, 20, 21, 22, 26, 29, 30, 31, 32, 33, 35, 36, 38, 39, 40, 41, 78, 79, 80, 89, 91, 92, 93, 94, 95, 97, 103, 116, 117, 118, 119, 120, 128, 129, 130, 142, 145, 146, 148, 149, 150, 151, 152, 153, 154, 155, 156, 159, 162, 163, 164, 165

Gleditsia triacanthos L. - **W**; 9, 21, 95, 165

Lespedeza bicolor Turcz. - **X**; 9

L. capitata Michx. - **I**; 16, 27, 39

L. cuneata (Dumot) G. Don - **X**; 13, 14, 16, 18, 27, 32, 33, 40, 78, 79, 95, 97, 117, 128, 142, 145, 146, 151, 152, 153, 155, 162, 164, 165

L. hirta (L.) Hornem - **I**; 35

L. intermedia (S. Wats.) Britt. - **I**; 2, 3, 9, 14, 18, 27, 29, 32, 35, 38, 39, 78, 79, 80, 97, 116, 120, 142, 145, 148, 154, 155, 159

L. procumbens Michx. - **I**; 2, 3, 7, 9, 14, 16, 19, 20, 21, 22, 26, 27, 28, 29, 30, 31, 32, 33, 35, 38, 39, 40, 78, 79, 80, 92, 94, 95, 97, 103, 117, 119, 120, 128, 130, 142, 145, 146, 148, 149, 150, 151, 153, 154, 155, 156, 159, 161, 165

L. repens (L.) Bart. - **I**; 3, 9, 16, 22, 26, 29, 31, 32, 33, 35, 36, 38, 40, 41, 79, 80, 94, 95, 97, 119, 128, 145, 148, 149, 152, 159, 164

L. stipulacea Maxim. - **X**; 7, 9, 13, 14, 19, 20, 29, 33, 38, 39, 40, 41, 79, 89, 93, 94, 95, 117, 118, 119, 120, 142, 148, 149, 151, 154, 156

L. striata (Thunb.) H. and A. - **X**; 3, 9, 13, 27, 28, 33, 40, 78, 91, 94

L. violacea (L.) Pers. - **I**; 3, 9, 18, 19, 80, 89, 95

L. virginiaca (L.) Britt. - **I**; 2, 7, 9, 14, 16, 19, 20, 27, 28, 29, 31, 32, 33, 35, 36, 38, 39, 78, 80, 91, 95, 119, 120, 129, 131, 142, 146, 150, 151, 153, 155, 156, 159, 162, 163

Medicago lupulina L. - **X**; 19, 20, 21, 22, 40, 78, 79, 89, 95, 97, 103, 116, 118, 119, 120, 142, 148, 150, 151, 152, 155

Medicago sativa L. - **X**; 18, 22, 32

Melilotus alba Desr. - **X**; 2, 7, 9, 13, 14, 18, 19, 20, 21, 22, 26, 27, 28, 29, 32, 33, 35, 36, 39, 40, 41, 78, 80, 97, 103, 116, 117, 118, 128, 142, 145, 146, 150, 151, 152, 153, 155, 163

M. officinalis (L.) Lam. - **X**; 9, 16, 18, 19, 20, 21, 22, 39, 40, 78, 95, 97, 117, 120, 128, 148, 149

Orbexilum onobrychis (Nutt.) Rydb. - **I**; 20, 21, 40, 97, 116

O. pedunculatum (Miller) Rydb.- **S**; 16, 21, 27, 33, 35, 93, 116, 119, 120, 128, 130, 158

Pediomelum subacaule (T. and G.) Rydberg - **L**; 93, 118, 119, 120, 128, 129, 130

Phaseolus polystachios (L.) B.S.P. - **I**; 30, 94

Rhynchosia tomentosa (L.) H. and A. - **S**; 3, 9, 27, 30, 89, 91, 92, 94, 97, 103, 119, 120, 128, 130, 154, 163, 164

Robinia pseudoacacia L. - **I**; 18, 26, 29, 40, 120, 142, 148, 153

Schrankia microphylla (Drylander) Macbr. - **S**; 94, 117, 119, 128, 164
Senna hebecarpa (Fern.) Irwin and Barneby - **N**; 19, 22
S. marilandica (L.) Link. - **I**; 1, 16, 19, 21, 38, 93, 95, 97, 116, 142, 148
S. obtusifolia (L.) Irwin and Barneby - **I**; 1, 18, 80, 94
Strophostyles helvula (L.) Ell. - **I**; 33
S. umbellata (Muhl.) Britt. - **I**; 2, 3, 9, 30, 39, 78, 94, 97, 146, 154, 156, 159
Stylosanthes biflora (L.) B.S.P. - **I**; 16, 41, 94, 120, 128, 130, 146
Tephrosia spicata (Walt.) T. and G. - **S**; 7, 35, 131
T. virginiana (L.) Pers. - **I**; 2, 7, 16, 41, 94, 119, 120, 128, 164
Trifolium campestre Schreb. - **X**; 16, 19, 20, 22, 32, 33, 35, 38, 40, 89, 94, 95, 116, 118, 120, 148, 150
T. pretense L. - **X**; 9, 18, 19, 22, 28, 29, 31, 33, 35, 36, 38, 40, 78, 95, 97, 116, 120, 145, 148, 150, 151
T. repens L. - **X**; 19, 22, 80, 95, 97, 146, 148
Vicia sativa L. spp. *nigra* (L.) Ehrhart - **X**; 20, 31, 117, 118, 120, 150
V. caroliniana Walt. - **I**; 41, 91, 93, 95, 120
V. grandiflora Scop. - **X**; 41

Fagaceae
Fagus grandifolia Ehrh. - **I**; 16, 18, 27, 31, 41, 95, 97, 142, 151
Quercus alba L. - **I**; 3, 7, 9, 16, 17, 31, 35, 40, 41, 95, 97, 103, 142, 151, 152, 153
Q. falcata Michx. - **S**; 7, 13, 16, 26, 27, 35, 39, 40, 41, 79, 95, 97, 117, 119, 128, 129, 130, 142, 146, 149, 151, 152, 153, 154
Q. imbricaria Michx. - **N**; 41
Q. laurifolia Michx. - **S**; 91, 93, 94
Q. marilandica Muenchh. - **S**; 2, 13, 16, 29, 39, 95, 103, 117, 119, 120, 128, 129, 153, 154, 155, 163, 164
Q. muehlenbergii Engelm. - **W**; 9, 16, 17, 18, 19, 20, 21, 22, 26, 27, 28, 29, 31, 33, 38, 39, 40, 41, 78, 79, 80, 95, 97, 103, 117, 119, 120, 121, 129, 130, 142, 145, 146, 149, 151, 152, 153, 154, 155, 156, 159, 162, 165
Q. nigra L. - **S**; 94, 119, 163
Q. phellos L. - **S**; 41, 92, 117, 119, 128, 163, 164
Q. prinoides Willd. - **N**; 16, 95, 97
Q. rubra L. - **I**; 16, 26, 27, 95, 103
Q. shumardii Buckl. - **S**; 7, 16, 17, 18, 20, 21, 22, 26, 28, 29, 31, 38, 39, 40, 41, 78, 79, 80, 95, 97, 103, 119, 120, 129, 130, 131, 142, 145, 146, 149, 151, 152, 153, 154, 155, 159, 160, 162, 165
Q. stellata Wang. - **I**; 2, 7, 16, 17, 18, 19, 20, 21, 26, 27, 28, 31, 38, 39, 41, 78, 79, 80, 95, 97, 103, 116, 117, 118, 119, 120, 121, 128, 129, 130, 142, 146, 149, 150, 151, 153, 154, 155, 163, 164
Q. velutina Lam. - **I**; 9, 17, 41, 94, 95, 97, 119, 121, 129, 142, 149, 153, 164

Fumariaceae
Corydalis flavula (Raf.) DC. - **I**; 18

Gentianaceae
Frasera caroliniensis Walt. - **S**; 120, 153, 155, 156
Gentiana quinquefolia L. - **I**; 21, 97, 153, 159
G. villosa L. - **I**; 16, 94, 155, 163
Obolaria virginica L. - **I**; 16
Sabattia angularis (L.) Pursh - **I**; 3, 7, 9, 13, 16, 22, 27, 29, 31, 33, 36, 40, 79, 89, 92, 93, 94, 95, 117, 118, 119, 120, 130, 142, 151, 152

Sabbattia capitata (Raf.) Blake - **S**; 94, 163

Geraniaceae
Geranium carolinianum L. - **I**; 19, 31, 33, 38, 41, 94, 95, 97, 117, 118, 119, 120, 128
G. columbianum L. - **X**; 148
G. maculatum L. - **N**; 7, 16, 18, 27, 28, 40, 95, 154, 155
G. molle L. - **X**; 79

Hamamelidaceae
Hammamelis virginiana L. - **N**; 80
Liquidambar styraciflua L. - **I**; 3, 9, 18, 19, 27, 35, 41, 94, 97, 142, 163, 164

Hippocastanaceae
Aesculus sylvatica Bartr. - **S**; 21

Hydrophyllaceae
Phacelia dubia - **I**; 21

Iridaceae
Belamcanda chinensis (L.) DC. - **I**; 14, 16, 17, 18, 19, 31, 40, 95, 103, 116, 117, 118, 153
Iris cristata Ait. - **S**; 27, 80
Sisyrinchium albidum Raf. - **I**; 2, 7, 9, 16, 18, 21, 22, 26, 27, 28, 29, 30, 31, 32, 33, 39, 40, 41, 78, 79, 80, 89, 91, 92, 93, 94, 95, 97, 103, 116, 117, 118, 119, 120, 128, 129, 130, 131, 145, 146, 148, 149, 150, 151, 153, 154, 155, 156, 159, 162, 165
S. angustifolium Mill. - **I**; 22, 33, 97, 142
S. atlanticum Bickn. - **I**; 41, 93, 94, 128
S. graminoides Bickn. - **I**; 18, 19, 20, 21, 41, 80, 94, 117, 151

Juglandaceae
Carya cordiformis (Wang.) K. Koch - **I**; 16, 80
C. glabra (Mill.) Sw. - **I**; 16, 95
C. ovalis (Wang.) Sarg. - **N**; 29
C. ovata (Mill.) K. Koch - **I**; 20, 21, 41, 95
C. ovata (Mill.) K. Koch var. *australis* (Ashe) Little - **S**; 16, 19, 20, 21, 26, 27, 29, 38, 39, 40, 41, 95, 103, 118, 119, 120, 162
C. tomentosa Nutt. - **I**; 7, 16, 26, 31, 35
Juglans nigra L. - **I**; 14, 16, 18, 19, 21, 22, 26, 27, 28, 29, 33, 39, 40, 41, 79, 80, 95, 97, 103, 120, 130, 142, 145, 146, 149, 159

Juncaceae
Juncus acuminatus Michx. - **I**; 3, 7, 41, 94, 120
J. biflorus Ell. - **I**; 3, 29, 80, 94
J. brachycarpus Engelm. - **I**; 2, 3, 41, 94
J. coriaceus Mackenz. - **S**; 3, 41, 163
J. dichotomus Ell. - **I**; 21
J. dudleyi Wieg. - **N**; 21, 22, 40, 94, 120, 128, 129
J. effusus L. var. *solutus* Fern. and Wieg. - **I**; 3, 40
J. filipendulus Buckl. - **S**; 93, 94, 119
J. interior Wieg. - **N**; 41
J. marginatus Rostk. - **I**; 40, 41, 93, 94, 119, 130
J. scirpoides Lam. - **I**; 94

Juncus tenuis Willd. - **I**; 3, 28, 29, 41, 93, 94, 95, 153
Luzula bulbosa (Wood) Rydb. - **I**; 32
L. campestris (L.) DC. - **X**; 41
L. multiflora (Retz.) Lejeune - **I**; 121, 152

Lamiaceae
Agastache nepetoides (L.) Kuntze - **N**; 95
Blephilia ciliata (L.) Benth. - **I**; 16, 22, 130, 162
Hedeoma pulegioides (L.) Pers. - **I**; 33, 41, 79, 93, 95, 97
Isanthus brachiatus (L.) B.S.P. - **I**; 2, 7, 9, 14, 16, 17, 18, 19, 21, 22, 26, 28, 31, 32, 33, 36, 38, 39, 40, 41, 78, 79, 89, 91, 92, 93, 94, 95, 97, 103, 116, 117, 118, 119, 120, 128, 129, 130, 131, 142, 145, 148, 149, 150, 151, 153, 154, 155, 156, 159, 160, 162
Lamium amplexicaule L. - **X**; 38, 79
L. purpureum L. - **X**; 19
Lycopus americanus Muhl. - **I**; 2, 3, 9
Monarda citriodora Cev. - **W**; 40, 91
M. fistulosa L. - **I**; 2, 7, 9, 16, 18, 20, 21, 22, 26, 27, 29, 33, 36, 38, 40, 41, 78, 79, 80, 89, 92, 93, 94, 95, 97, 103, 117, 119, 120, 128, 142, 145, 146, 148, 150, 151, 152, 153, 155, 156, 159, 160, 161, 162, 164, 165
Mosla dianthera (Buch.) Maxim. - **X**; 119
Physostegia virginiana (L.) Benth. [including ssp. *praemorsa* (Shinners) Cantino] - **N**; 2, 16, 21, 22, 28, 41, 78, 92, 94, 95, 117, 119, 142, 146, 152, 154, 155, 156, 159
Prunella vulgaris L. var. *lanceolata* (Bart.) Fern. - **I**; 1, 2, 3, 7, 9, 13, 16, 19, 20, 21, 22, 26, 27, 28, 29, 31, 32, 33, 35, 36, 39, 40, 41, 78, 79, 80, 92, 94, 95, 97, 103, 116, 117, 118, 119, 120, 128, 129, 130, 142, 145, 146, 148, 149, 150, 151, 152, 153, 154, 155, 156, 158, 159, 161, 163
Pycnanthemum incanum (L.) Michx. - **N**; 13, 16, 22, 27, 35, 40, 41, 89, 93, 94, 120, 151
P. muticum (Michx.) Pers. - **I**; 16, 18, 22, 27, 151
P. pilosum Nutt. - **W**; 2, 7, 9, 153
P. pycnanthemoides (Leavenw.) Fern. **I**; 27, 80, 93, 95, 128, 151, 152, 159
P. tenuifolium Schrad. - **I**; 2, 3, 7, 9, 16, 21, 27, 28, 32, 33, 35, 41, 91, 92, 93, 94, 97, 117, 118, 119, 120, 128, 146, 150, 151, 156, 161, 162, 163, 164
P. verticillatum (Michx.) Pers. - **N**; 124
P. virginianum (L.) Durand and Jackson - **N**; 2, 105
Salvia azurea Lam. - **W**; 163
S. lyrata L. - **I**; 2, 3, 9, 16, 18, 19, 20, 21, 22, 26, 27, 28, 29, 30, 31, 33, 35, 40, 78, 79, 92, 94, 95, 97, 103, 116, 117, 118, 119, 120, 128, 129, 130, 131, 142, 145, 146, 148, 149, 150, 151, 152, 153, 154, 155, 156, 162, 165
S. urticaefolia L. - **S**; 7, 16, 21, 30, 41, 78, 79, 80, 89, 92, 93, 95, 103, 116, 117, 119, 120, 124, 128, 129, 130, 131, 152, 153, 154, 156, 162
Satureja calamintha (L.) Scheele - **X**; 19, 79, 116
S. vulgaris L. var. *neogaea* Fern. - **N**; 28, 40, 95, 97, 142, 148, 151
Scutellaria australis Epl. - **S**; 19, 21, 30, 40, 41, 80, 94, 103
S. elliptica Muhl. - **I**; 3, 7, 18, 40, 79, 80, 91, 93, 94, 95, 103, 119, 128, 129, 152
S. incana Biehler - **N**; 27, 80, 97
S. integrifolia L. - **I**; 35, 94, 124
S. lateriflora L. - **S**; 41
S. nervosa Pursh - **I**; 21, 27
S. ovata Hill - **S**; 120
S. leonardi Epl. - **I**; 1, 2, 7, 9, 13, 16, 22, 27, 28, 29, 31, 32, 36, 39, 40, 41, 78, 79, 80, 91, 95, 97, 103, 119, 120, 129, 130, 142, 149, 153, 154
Trichostema dichotomum L. - **S**; 21, 41, 97, 142

Trichostema lineare Walt. - **I**; 35, 38

Lauraceae
Sassafras albidum (Nutt.) Nees - **I**; 9, 13, 16, 18, 20, 22, 27, 31, 33, 35, 38, 95, 97, 103, 119, 146, 151, 152, 153

Liliaceae
Allium canadense L. - **I**; 16, 93, 94, 117, 118, 119, 120, 128, 142
A. cernuum Roth - **I**; 22, 30, 80, 91, 92, 93, 94, 95, 97, 118, 119, 120, 128, 129, 130, 131
A. vinale L. - **X**; 19, 20, 21, 22, 26, 28, 29, 31, 32, 33, 38, 39, 40, 41, 78, 91, 94, 95, 116, 117, 118, 120, 128, 142, 145, 148, 149, 150, 151, 155, 162
Asparagus officinale L. - **X**; 9, 20, 22, 78, 128, 151, 155
Camassia scilloides (Raf.) Cory - **I**; 117
Nothoscordum bivalve (L.) Britt. - **S**; 19, 33, 39, 40, 41, 93, 94, 116, 118, 119, 120, 128, 129, 130, 131, 162
Polygonatum canaliculatum (Muhl.) Pursh - **N**; 16, 18, 21, 27, 41, 79, 80, 91, 93, 95, 103, 146, 152, 159, 162
Schoenolirion croceum (Michx.) Gray - **S**; 94
Smilacina racemosa (L.) Desf. - **I**; 16, 79, 80, 95, 97, 103
Smilax bona-nox L. - **S**; 2, 16, 19, 20, 21, 22, 26, 29, 31, 32, 33, 40, 79, 80, 92, 94, 95, 97, 103, 117, 118, 119, 120, 128, 129, 130, 142, 146, 149, 151, 152, 153, 154, 156, 159, 162, 163, 164, 165
S. glauca Walt. - **S**; 7, 9, 16, 18, 27, 35, 40, 79, 80, 94, 95, 120, 142, 148, 149, 154, 158, 163
S. hispida Muhl. - **I**; 95
S. rotundifolia L. - **I**; 16, 18, 19, 21, 22, 27, 35, 38, 39, 40, 41, 78, 95, 103, 117, 119, 152, 155, 159
Trillium luteum (Muhl.) Harbison - **LSA**; 16, 18, 40, 89, 120
Uvularia perfoliata L. - **I**; 16, 27, 28, 41, 93, 95, 146, 152
U. sessilifolia L. - **I**; 18
Yucca filamentosa L. - **I**; 16, 27, 80, 94, 95, 117, 119, 142

Linaceae
Linum medium (Planch.) Britt. - **I**; 13, 16, 27, 80, 94, 119, 120, 128, 129, 149, 156, 163
L. sulcatum Riddell - **I**; 2, 9, 16, 29, 32, 39, 40, 78, 92, 93, 97, 117, 119, 120, 129, 130, 131, 146, 149, 154, 155
L. virginianum L. - **I**; 41, 95

Lobeliaceae
Lobelia inflata L. - **I**; 3, 7, 16, 27, 29, 79, 95, 97
L. puberula Michx. - **S**; 94, 120, 128, 163, 164
L. siphilitica L. - **I**; 3, 35, 142
L. spicata Lam. - **N**; 2, 7, 9, 14, 16, 19, 21, 22, 26, 27, 28, 29, 30, 31, 32, 33, 35, 36, 39, 40, 41, 78, 79, 80, 91, 92, 94, 95, 97, 103, 117, 118, 119, 120, 128, 129, 130, 131, 142, 145, 146, 148, 149, 150, 151, 152, 153, 154, 155, 156, 159, 162

Loganiaceae
Cynoctonum mitreole (L.) Britt. - **S**; 41, 94, 119
Gelsemium sempervirens (L.) Ait. - **S**; 94, 117
Spigelia marilandica L. - **S**; 16, 18, 21, 40, 41, 95, 117, 120, 153

Lythraceae
Cuphea petiolata (L.) Koehne - **I**; 21, 79, 80, 93, 95
Lythrum alatum Pursh - **I**; 41, 93, 94, 95

Magnoliaceae
Liriodendron tulipifera L. - **I**; 3, 9, 16, 22, 35, 80, 97, 146, 149, 152, 153

Malvaceae
Hibiscus moscheutos L. - **S**; 128
Sida elliottii T. and G. - **S**; 38, 40, 117, 118, 119, 130, 131
S. spinosa L. - **S**; 18, 29, 31, 40, 79, 94, 117

Melastomataceae
Rhexia mariana L. - **I**; 3

Menispermaceae
Cocculus carolinus (L.) DC. - **S**; 9, 16, 17, 18, 19, 36, 38, 94, 116, 118, 119, 120, 142, 145, 164, 165
Menispermum canadense L. - **I**; 21

Moraceae
Maclura pomifera (Raf.) Schneid. - **N**; 19, 31, 95, 162
Morus rubra L. - **I**; 16, 17, 18, 19, 21, 22, 26, 27, 28, 31, 32, 38, 39, 40, 41, 79, 89, 91, 94, 95, 97, 103, 116, 117, 119, 120, 128, 142, 151, 154, 165

Nyssaceae
Nyssa sylvatica Marsh. - **I**; 16, 26, 27, 33, 35, 36, 40, 92, 95, 97, 146, 152, 163

Oleaceae
Chionanthus virginicus L. - **S**; 94
Fraxinus americana L. - **I**; 3, 7, 9, 16, 18, 21, 22, 26, 27, 28, 29, 31, 36, 38, 39, 40, 41, 78, 79, 92, 94, 95, 97, 103, 117, 118, 120, 121, 128, 129, 130, 131, 142, 146, 149, 152, 153, 156, 159, 162, 163, 164
F. pensylvanica Marsh. - **I**; 3
F. quadrangulata Michx. - **W**; 16, 18, 95, 159
Ligustrum vulgare L. - **X**; 9, 14, 18, 19, 20, 21, 22, 27, 40, 41, 80, 92, 97, 117, 118, 119, 128, 129, 130, 131, 145, 148, 149, 156

Onagraceae
Epilobium coloratum Biehler - **N**; 3
Gaura biennis L. - **N**; 7, 9, 14, 19, 21, 22, 78, 79, 80, 97, 142, 150, 151
G. filipes Spach - **S**; 27, 29, 30, 31, 33, 39, 40, 91, 92, 93, 94, 119, 120, 128, 129, 155, 156, 163
Ludwigia alternifolia L. - **I**; 3, 41, 93
L. microcarpa Michx. - **S**; 94, 119
L. palustris (L.) Ell. - **I**; 3, 22
Oenothera biennis L. - **I**; 4, 14, 16, 18, 20, 21, 22, 33, 119, 146, 151
O. fruticosa L. - **I**; 16, 41, 94, 119
O. laciniata Hill - **I**; 79
O. speciosa Nutt. - **W**; 89, 93, 94, 128
O. triboba Nutt. - **S**; 19, 21, 22

Orchidaceae

Goodyera pubescens (Willd.) R. Br. - **I**; 95, 142
Hexalectris spicata (Walt.) Barnh. - **S**; 16
Spiranthes gracilis (Bigel.) Beck - **I**; 2, 3, 13, 29, 79, 92, 95, 116, 119, 151, 155, 164
S. ovalis Lindl. - **S**; 119
S. tuberosa Raf. - **S**; 93, 94
S. vernalis Engelm. and Gray - **S**; 150
Tipularia discolor (Pursh) Nutt. - **I**; 27, 31, 95

Orobanchaceae

Conopholis americana (L.) Wallr. - **I**; 16

Oxalidaceae

Oxalis dillenii Jacq. - **I**; 97, 148
O. stricta L. - **I**; 3, 16, 19, 21, 22, 29, 31, 32, 38, 40, 79, 89, 93, 94, 95, 97, 116, 118, 119, 120, 128, 130, 142, 145, 146, 148, 159
O. violacea L. - **I**; 16, 18, 19, 21, 33, 40, 41, 79, 95, 103, 118, 119, 120, 142, 154

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Passiflora incarnata L. - **S**; 19, 97, 120, 128, 130
P. lutea L. - **S**; 16, 21, 26, 95, 120, 142, 159

Phrymaceae

Phryma leptostachya L. - **I**; 16, 95, 103, 120

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Phytolacca americana L. - **I**; 97

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P. lanceolata L. - **X**; 9, 19, 22, 29, 32, 38, 39, 40, 78, 79, 103, 116, 118, 119, 120, 142, 145, 148, 150, 151, 153, 154, 155, 156
P. major L. - **X**; 9, 18, 19, 22, 28, 29, 78, 95, 97, 103, 142, 148, 153
P. virginica L. - **I**; 21, 26, 29, 31, 32, 33, 38, 39, 40, 41, 79, 89, 91, 94, 95, 117, 118, 119, 120, 128, 129, 130, 148, 153

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Platanus occidentalis L. - **I**; 3, 9, 41, 97, 130, 146, 151

Poaceae

Agrostis hyemalis (Walt.) B.S.P. - **I**; 33, 94
A. perennans (Walt.) Tuckerm. - **I**; 13, 36, 95, 164
A. stolonifera L. - **X**; 3, 13, 19, 22, 27, 28, 33, 35, 39, 92, 95, 117, 119, 120
Alopecurus carolinianus Walt. - **I**; 94
Andropogon gerardii Vitman - **I**; 2, 3, 7, 9, 14, 16, 20, 22, 27, 28, 29, 32, 33, 35, 39, 78, 80, 92, 95, 119, 124, 128, 129, 130, 145, 146, 149, 150, 152, 154, 155, 156, 162, 164
A. glomeratus (Walt.) B.S.P. - **S**; 163
A. gyrans Ashe - **I**; 16, 94, 95, 103, 117, 119, 120, 128, 129, 131, 163, 164
A. ternarius Michx. - **S**; 9, 14, 22, 26, 29, 31, 33, 35, 124, 128, 131, 152

Andropogon virginicus L. - **I**; 2, 7, 9, 13, 16, 17, 18, 19, 20, 21, 22, 26, 27, 28, 29, 32, 33, 35, 36, 38, 39, 40, 79, 94, 95, 103, 117, 118, 119, 120, 121, 124, 128, 131, 145, 148, 151, 152, 153, 155, 156, 159, 160, 161, 162, 163, 164, 165
Aristida curtisii (Gray) Nash - **I**; 40, 94
A. dichotoma Michx. - **I**; 13, 29, 33, 35
A. longespica Poir - **I**; 29, 33, 35, 92, 94, 117, 119, 120, 121
A. oligantha Michx. - **I**; 9, 16, 19, 28, 29, 31, 33, 40, 94, 119, 120, 121, 124, 161, 163
A. purpurescens Poir. - **I**; 21, 27, 31, 32, 33, 35, 94, 95, 117, 119, 128, 129, 131, 142, 146, 164
Arthraxon hispidus (Thunb.) Makino - **X**; 9, 40, 41, 95, 119
Arundinaria gigantea (Walt.) Chapm. - **S**; 120, 148
Bothriochloa saccharoides (Swartz) Rydb. var. *Torreyana* (Steud.) Gould - **X**; 117, 118
Bouteloua curtipendula (Michx.) Torr. - **W**; 1, 22, 78, 79, 80, 91, 92, 95, 103, 117, 118, 119, 120, 128, 129, 130, 131, 142, 146, 162
Bromus commutatus Schrad. - **X**; 118, 152
B. japonicus Thunb. - **X**; 2, 13, 16, 17, 18, 19, 20, 21, 22, 29, 31, 33, 38, 39, 79, 95, 120
B. pubescens L. - **I**; 16, 18, 40, 79, 80, 89, 93, 95, 103, 118, 146, 148
B. racemosus L. - **X**; 21, 22, 79, 93, 94, 95, 116, 120, 150, 151, 155
B. sterilis L. - **X**; 116
B. tectorum L. - **X**; 21
Chasmanthium latifolium (Michx.) H. O. Yates - **S**; 39, 89, 93, 119, 120, 128, 130, 142, 163
C. laxum (L.) H. O. Yates - **S**; 41, 94
C. sessilifolium (Poir) H. O. Yates - **S**; 89, 94
Coelorachis cylindrica (Michx.) Nash - **S**; 94
Cynodon dactylon (L.) Pers. - **X**; 9, 94, 164
Dactylis glomerata L. - **X**; 22, 118, 120, 148
Danthonia compressa Aust. - **N**; 129
D. spicata (L.) Beauv. - **I**; 2, 7, 9, 13, 16, 19, 20, 21, 22, 25, 27, 28, 29, 31, 33, 35, 38, 39, 40, 41, 78, 79, 80, 92, 93, 94, 95, 97, 103, 116, 117, 118, 119, 120, 128, 129, 130, 131, 138, 142, 145, 146, 148, 149, 150, 151, 152, 153, 154, 155, 156, 159, 162, 163, 165
Digitaria filiformis (L.) Koel. - **I**; 13, 16, 28, 35, 95, 153
D. ichaemum (Schreb.) Muhl. - **X**; 18, 22, 26, 29, 93, 97
D. sanguinalis (L.) Scop. - **X**; 3, 9, 38, 94
Echinochloa colonum (L.) Link. - **X**; 9, 94
E. crusgalli (L.) Beav. - **X**; 9, 18, 41, 90, 93, 95, 124
Elymus villosus Muhl. - **I**; 16, 80
E. virginicus L. - **I**; 3, 9, 78, 94, 95
E. virginicus L. var. *glabriflorus* (Vasey) Bush - **I**; 3, 9, 16, 18, 20, 21, 22, 28, 29, 31, 33, 35, 36, 38, 39, 80, 93, 94, 95, 103, 117, 118, 119, 128, 130, 142, 161, 163, 164
Eragrostis capillaris (L.) Nees. - **I**; 16, 41, 94
E. frankii C. A. Mey. - **I**; 9, 16, 21, 22, 28, 41, 79, 91, 93, 94, 95, 97, 120, 158
E. pectinacea (Michx.) Nees. - **I**; 19
E. spectabilis (Push) Steud. - **I**; 3, 13, 14, 16, 19, 22, 28, 29, 30, 31, 32, 33, 35, 36, 38, 40, 41, 79, 89, 91, 92, 93, 94, 95, 97, 119, 120, 128, 129, 131, 142, 145, 146, 149, 152, 153, 155, 160, 161, 163, 164
Erianthus alopecuroides (L.) Ell. - **S**; 21, 22, 27, 36, 39, 94, 97, 103, 120, 142, 152, 153
Festuca pretensis Huds. - **X**; 9, 18, 19, 20, 22, 28, 29, 31, 32, 33, 36, 38, 39, 40, 41, 78, 80, 92, 94, 95, 97, 116, 117, 118, 119, 120, 128, 129, 142, 145, 146, 148, 150, 151, 152, 155, 156, 159, 162, 165
F. obtusa Biehler - **I**; 40
F. paradoxa Desv. - **I**; 128
Glyceria striata (Lam.) Hitchc. - **I**; 21, 41, 93, 119

Gymnopogon ambiguus (Michx.) B.S.P. - **S**; 163
G. brevifolius Trin. - **S**; 94, 164
Hordeum pusillum Nutt. - **I**; 19, 21, 41, 117
Hystrix patula Moench. - **N**; 16, 22, 29, 32, 41, 80, 91, 92, 95
Leersia virginica Willd. - **I**; 3, 95, 120
Lolium perenne L. - **X**; 38
Melica mutica Walt. - **S**; 16, 18, 21, 93, 94, 103, 118, 120, 128, 129, 130, 142
Microstegium vimineum (Trin.) A. Camus - **X**; 3, 18, 26, 27, 29, 35, 36, 40, 41, 95, 97, 130, 142, 152, 153, 156
Muhlenbergia capillaris (Lam.) Trin. - **I**; 16, 94, 128, 142, 146, 163
M. schreberi J. F. Gmel. - **X**; 16, 79, 95, 97, 142
M. sobolifera (Muhl.) Trin. - **I**; 80, 95
M. tenuiflora (Willd.) B.S.P. - **N**; 95
Panicum anceps Michx. [including var. *rhizomatum* (Hitchc. and Chase) Fern.] - **S**; 3, 7, 9, 13, 14, 16, 18, 19, 20, 21, 22, 25, 27, 28, 29, 30, 31, 32, 33, 35, 36, 39, 41, 79, 92, 93, 94, 95, 97, 103, 119, 120, 124, 128, 130, 142, 145, 148, 150, 151, 154, 155, 156, 161, 163, 164
P. angustifolium Ell. - **S**; 94, 128, 164
P. annulum Ashe - **I**; 16, 128, 163, 164
P. bicknellii Nash - **N**; 89, 118, 120
P. boscii Poir. - **I**; 16, 18, 20, 21, 22, 27, 29, 36, 40, 41, 79, 91, 93, 94, 95, 103, 117, 119, 120, 142, 145, 146, 152, 154, 156, 159, 162, 165
P. capillare L. - **I**; 9, 18, 19, 21, 28, 38, 41, 78, 117, 119, 146, 154
P. clandestinum L. - **I**; 3, 9, 14, 117
P. commutatum Schult. [including var. *ashei* (Pearson) Fern.] - **I**; 16, 18, 20, 21, 22, 26, 27, 30, 36, 40, 41, 80, 89, 91, 93, 94, 95, 97, 103, 116, 119, 120, 128, 129, 142, 145, 146, 149, 150, 151, 152, 153, 154, 159, 163, 165
P. depauperatum Muhl. - **I**; 13, 16, 21, 22, 27, 29, 30, 33, 35, 36, 39, 40, 78, 79, 80, 89, 91, 92, 93, 94, 95, 103, 118, 119, 120, 129, 151, 153, 154, 155, 156
P. dichotomiflorum Michx. - **I**; 22, 41, 93
P. dichotomum L. - **I**; 30, 80
P. flexile (Gatt.) Scribner - **I**; 1, 2, 7, 9, 14, 16, 17, 18, 19, 20, 21, 22, 26, 27, 28, 29, 31, 32, 33, 36, 38, 39, 40, 41, 79, 80, 91, 92, 93, 94, 95, 97, 103, 117, 118, 119, 120, 128, 129, 130, 131, 142, 145, 146, 148, 149, 150, 151, 153, 154, 155, 156, 159, 160, 161, 162, 163, 165
P. hians L. - **S**; 163
P. lanuginosum Ell. - **I**; 2, 3, 7, 9, 13, 16, 19, 21, 22, 26, 27, 28, 29, 31, 32, 33, 35, 36, 38, 39, 40, 41, 78, 79, 80, 92, 93, 95, 97, 103, 117, 118, 119, 120, 128, 129, 130, 142, 148, 149, 151, 153, 154, 155, 156
P. latifolium L. - **N**; 16
P. laxiflorum Lam. - **S**; 16, 19, 40, 41, 93, 94, 95, 117, 120, 130, 131, 142, 165
P. leucothrix Nash - **S**; 129
P. lindheimeri Nash - **I**; 19, 33
P. linearifolium Scribn. - **I**; 22, 80
P. meridionale Ashe - **N**; 16
P. microcarpon Muhl. - **I**; 13, 14, 29, 33, 40, 41, 92, 93, 94, 95, 117, 119, 128, 152, 164
P. nitidum Lam. - **S**; 130
P. oligosanthes Schultes [including var. *Scribnerianum* (Nash) Fern.] - **I**; 2, 9, 16, 19, 21, 22, 27, 29, 33, 36, 41, 92, 93, 95, 103, 116, 118, 119, 120, 128, 129, 145
P. philadelphicum Bernh. - **I**; 16, 19, 22, 35, 78, 79, 94, 95
P. philadelphicum Bernh. ssp. campestre D. F. Fairbr. - **N**; 21, 38, 95
P. polyanthes Schultes - **I**; 27, 35, 128
P. scoparium Lam. - **I**; 35

Panicum sphaerocarpon Ell. - **I**; 13, 16, 19, 27, 31, 33, 35, 36, 40, 41, 79, 92, 93, 94, 95, 118, 119, 120, 128, 129, 130, 142
P. stipitatum Nash - **I**; 3, 163
P. villosissimum Nash - **I**; 41, 92, 95, 97, 148, 151, 153
P. virgatum L. (including var. *cubense* Griseb.) - **I**; 9, 92, 94, 117, 118, 119, 128, 129, 156, 164
Paspalum dilatatum Poir - **X**; 41, 93, 94, 128, 163
P. floridanum Michx. - **S**; 39, 93, 94, 161, 163
P. laeve Michx. [including var. *circulare* (Nash) Fern. and var. *pilosum* Scribn.] - **S**; 13, 14, 19, 22, 31, 32, 36, 38, 92, 93, 94, 116, 119, 129, 130
P. pubiflorum Rupr. ex Fourn. var. *glabrum* Vasey ex Scribn. - **S**; 9, 18, 22, 45, 95, 118, 124, 145, 152, 163
P. setaceum Michx. var. *ciliatifolium* (Michx.) Vasey - **S**; 31, 47, 94, 120, 130, 148, 153
P. setaceum Michx. var. *Muhlenbergii* (Nash) D. Banks - **I**; 9, 13, 16, 29, 38, 45, 79, 94, 95, 97, 113, 141
P. setaceum Michx. var. *stramineum* (Nash) D. Banks - **W**; 45, 110
Phleum pretense L. - **X**; 19, 21, 32, 78, 79, 95, 97, 103, 145, 155, 163
Poa annua L. - **X**; 41
P. chapmaniana Scribn. - **X**; 94
P. compressa L. - **X**; 3, 9, 18, 19, 20, 21, 22, 26, 28, 29, 33, 38, 78, 80, 92, 95, 97, 116, 120, 121, 142, 145, 148, 149, 150, 151, 152, 154, 156
P. cuspidata Nutt. - **I**; 80
P. pratensis L. - **X**; 2, 3, 16, 18, 19, 20, 27, 28, 29, 31, 38, 78, 80, 89, 95, 97, 116, 118, 120, 128, 129, 130, 145, 148, 149, 150, 151, 155
P. sylvestris Gray - **I**; 95, 97
Schizachyrium scoparium (Michx.) Nash. - **I**; 2, 3, 7, 9, 16, 20, 21, 22, 27, 28, 29, 31, 32, 33, 35, 39, 40, 41, 78, 79, 80, 92, 94, 95, 97, 116, 117, 118, 119, 120, 128, 129, 130, 131, 142, 145, 146, 148, 149, 150, 151, 152, 153, 154, 155, 156, 161, 162, 163, 164
Setaria geniculata (Lam.) Beauv. - **S**; 3, 9, 22, 41, 89, 92, 93, 94, 97, 117, 118, 119, 120, 128, 129, 130, 131, 142, 145, 146, 150, 151, 158, 161, 163, 164
S. glauca (L.) Beauv. - **X**; 16, 21, 26, 31, 32, 33, 35, 38, 79, 92, 94, 95, 148
S. viridis (L.) Beauv. - **X**; 19, 33, 38, 79, 80
Sorghastrum elliottii (Mohr) Nash - **S**; 9
S. nutans (L.) Nash - **I**; 2, 9, 19, 28, 29, 32, 35, 79, 92, 94, 95, 117, 118, 119, 120, 128, 129, 130, 131, 142, 146, 150, 153, 154, 156, 161, 163, 164
Sorghum halepense (L.) Pers. - **X**; 9, 38, 39, 80, 128
Sphenopholis nitida (Biehler) Scribn. - **I**; 16, 18, 21, 22, 27, 28, 29, 30, 40, 41, 79, 89, 91, 92, 93, 95, 97, 103, 119, 120, 130, 142, 146, 150, 152, 153, 154, 155, 160
S. obtusata (Michx.) Scribn. - **I**; 97, 129
S. obtusata (Michx.) Scribn. var. *major* (Torr.) K. S. Erdm. - **I**; 40, 95, 151
S. x pallens (Biehler) Scribn. - **?**; 141
Sporobolus asper (Michx.) Kunth - **I**; 3, 13, 16, 19, 20, 21, 22, 26, 29, 31, 32, 36, 38, 39, 41, 79, 80, 89, 91, 92, 94, 95, 103, 118, 119, 120, 128, 129, 130, 142, 145, 151, 154, 155, 156, 160, 161, 163, 164, 165
S. asper (Michx.) Kunth var. *drummondii* (Trin.) Vasey - **W**; 9, 40, 85, 97, 124, 148
S. clandestinus (Biehler) Hitchc. - **I**; 16, 19, 21, 27, 30, 92, 93, 94, 95, 97, 103, 117, 118, 119, 120, 129, 130, 131, 142, 145, 146, 148, 153, 154, 155, 156, 159, 162, 163, 164
S. heterolepis Gray - **W**; 117, 119, 128, 129
S. junceus (Michx.) Kunth - **S**; 94
S. neglectus Nash - **I**; 2, 7, 9, 13, 21, 22, 26, 29, 32, 33, 39, 40, 78, 79, 80, 92, 94, 95, 97, 117, 120, 130, 145, 146, 149, 150, 151, 153, 154, 155, 156, 162, 163, 165

Sporobolus ozarkanus Fern. - **W**; 16, 19, 20, 21, 22, 26, 27, 28, 30, 31, 39, 40, 41, 47, 80, 89, 92, 93, 94, 95, 97, 116, 117, 119, 120, 131, 149, 152, 153, 159
S. vaginiflorus (Torr.) Wood - **I**; 19, 32, 40, 94, 117, 120, 128, 129, 142, 146, 151, 154, 156, 161
Stipa avenacea L. - **I**; 41, 93, 119, 130
Tridens flavus (L.) Hitchc. - **I**; 3, 7, 9, 13, 14, 16, 18, 19, 20, 21, 22, 26, 27, 28, 29, 30, 31, 32, 33, 35, 36, 39, 40, 41, 79, 80, 92, 94, 95, 97, 103, 118, 119, 120, 121, 124, 128, 129, 130, 131, 142, 145, 146, 148, 150, 151, 152, 153, 154, 155, 156, 161, 162, 163, 164, 165
T. strictus (Nutt.) Nash - **S**; 94, 119
Tripsacum dactyloides L. - **I**; 119
Vulpia octoflora Walt. - **I**; 21, 29, 33, 97, 121, 150

Polemoniaceae
Phlox amoena Sims - **S**; 27, 28, 29, 41, 93, 94, 118, 119, 120, 128, 129, 130, 131, 152
P. divaricata L. - **I**; 16
P. pilosa L. - **I**; 28, 94, 97

Polygalaceae
Polygala ambigua Nutt. - **I**; 13, 16, 19, 21, 33, 35, 36, 39, 79, 89, 93, 94, 95, 129, 149, 151
P. boykinii - **S**; 94, 164
P. sanguinea L. - **I**; 35
P. senega L. - **N**; 16, 80, 95, 103
P. verticillata L. - **I**; 119, 146, 151, 153, 154, 156

Polygonaceae
Polygonum hydropiperoides Michx. - **I**; 95
P. sagittatum L. - **I**; 3
P. tenue Michx. - **I**; 103
Rumex crispus L. - **X**; 94, 128

Portulaccaceae
Claytonia virginica L. - **I**; 130
Portulaca oleracea L. - **X**; 16, 19, 94

Primulaceae
Anagalis arvensis L. - **X**; 95, 119
Dodecatheon meadii L. - **S**; 93, 117, 118, 119
Lysimachia quadrifolia L. - **I**; 21
Samolus parviflorus Raf. - **I**; 41, 119, 130
Steironema lanceolata Walt. - **I**; 27, 29, 41, 89, 91, 92, 93, 94, 95, 97, 103, 120, 128

Pyrolaceae
Chimaphila maculata (L.) Pursh - **I**; 1, 16, 18, 22, 27, 31, 80, 95, 97, 142, 152, 153, 154

Ranunculaceae
Anemone virginica L. - **N**; 2, 5, 7, 9, 14, 16, 19, 20, 21, 26, 27, 28, 29, 30, 31, 32, 33, 36, 39, 40, 41, 78, 79, 80, 92, 94, 95, 97, 103, 116, 119, 120, 128, 130, 142, 145, 146, 148, 149, 150, 151, 152, 153, 154, 155, 156, 159, 160, 161, 162, 163, 165
Anemonella thalictroides (L.) Spach. - **I**; 18, 22, 41, 80, 92, 93, 118, 119, 128, 130, 131
Aquilegia canadensis L. - **N**; 16, 18, 80, 95, 119, 159
Clematis versicolor Small - **W**; 97
C. viorna L. - **I**; 79

Clematis virginiana L. - **I**; 16, 20, 95, 159
Delphinium exaltatum Ait. - **S**; 1, 97
D. tricorne Michx. - **I**; 16, 18, 20, 21, 40
D. virescens Nutt. - **W**; 30, 40, 91, 93, 119, 120, 130, 131
Ranunculus abortivus L. - **I**; 19, 22, 40, 151
R. bulbosus L. - **X**; 119, 121, 148, 150
R. fascicularis Muhl. - **I**; 30, 41, 80, 93, 95, 118, 119, 120, 128, 130, 152
R. hispidus Michx. - **N**; 93, 94
R. recurvatus Poir. - **I**; 16, 18, 21, 29, 32, 33, 40, 41
R. sardous Crantz - **X**; 94, 128
Thalictrum dioicum L. - **N**; 40
T. revolutum DC. - **I**; 2, 3, 7, 16, 20, 27, 28, 29, 78, 79, 94, 95, 97, 103, 163

Rhamnaceae
Berchemia scandens (Hill) K. Koch - **S**; 41, 92, 93, 94, 117, 118, 119, 128, 129, 153, 154, 155, 156, 164
Ceanothus americanus L. - **I**; 7, 9, 14, 16, 20, 21, 27, 28, 29, 30, 33, 35, 36, 41, 95, 97, 120, 128, 131, 146, 150, 151, 152, 153, 154, 155, 159, 161, 163, 164
Rhamnus caroliniana Walt. - **S**; 1, 2, 3, 7, 9, 14, 16, 17, 18, 19, 21, 22, 26, 28, 29, 31, 36, 38, 39, 40, 41, 78, 79, 80, 92, 95, 103, 116, 117, 119, 120, 129, 149, 151, 159, 162, 165

Rosaceae
Agrimonia microcarpa Wallr. - **S**; 91, 120, 128, 154
A. parviflora Ait. - **I**; 97
A. pubescens Wallr. - **I**; 16, 18, 21, 26, 27, 28, 29, 31, 40, 41, 79, 80, 93, 95, 97, 119, 128, 146, 148
A. rostellata Wallr. - **I**; 93, 95, 97, 142, 152
Amelanchier arborea (Michx. f.) Fern. - **I**; 7, 27, 28, 31, 35, 80, 97, 103, 159
Crataegus crus-galli L. - **I**; 128, 163, 164
C. marshallii Eggl. - **S**; 128, 142, 153, 163, 164
C. uniflora Muenchh. - **I**; 16, 19, 21, 22, 91, 92, 95, 103, 120, 163, 164
Duchesnea indica (Andr.) Focke - **X**; 18, 21
Fragaria virginiana Duchesne - **N**; 3, 7, 9, 14, 16, 18, 19, 21, 22, 27, 28, 29, 31, 32, 33, 40, 41, 78, 79, 80, 94, 95, 97, 103, 119, 120, 128, 129, 130, 131, 142, 145, 146, 148, 149, 150, 151, 152, 153, 154, 155, 156, 159, 160, 165
Geum canadensis Jacq. - **N**; 3, 21, 41, 80
G. vernum - **N**; 40, 79, 93, 95
G. virginianum L. - **N**; 16, 18, 19, 27, 29, 79, 93, 95, 97, 119, 120, 128, 142, 148, 155, 156
Gillenia stipulacea (Muhl.) Baill. - **I**; 18
Potentilla canadensis L. - **N**; 9, 16, 20, 28, 29, 31, 32, 40, 41, 95, 97, 142, 150, 155
P. recta L. - **X**; 16, 19, 21, 29, 31, 32, 38, 40, 79, 95, 116, 118, 145, 148, 151
P. simplex Michx. - **N**; 2, 3, 7, 9, 13, 14, 16, 19, 20, 22, 27, 28, 29, 32, 33, 35, 36, 38, 39, 40, 41, 78, 79, 80, 92, 94, 95, 97, 103, 116, 117, 118, 119, 120, 128, 129, 130, 131, 142, 145, 146, 148, 149, 150, 151, 152, 153, 154, 155, 156, 158, 159, 161
Prunus americana Marsh. - **I**; 3, 7, 9, 16, 18, 20, 21, 27, 33, 78, 95, 103, 116, 120, 128, 150, 151
P. angustifolia Marsh. - **S**; 22, 31, 32, 35, 151
P. mahaleb L. - **X**; 95, 103
P. persica (L.) Batsch. - **X**; 14, 16
P. serotina Ehrh. - **I**; 2, 3, 7, 9, 13, 14, 16, 18, 19, 27, 28, 29, 31, 33, 35, 36, 40, 41, 78, 79, 80, 95, 97, 103, 116, 120, 129, 130, 131, 142, 145, 148, 149, 151, 152, 153, 154, 156, 159, 162
Pyrus angustifolia Ait. - **S**; 164

Rosa carolina L. - **I**; 9, 16, 20, 21, 22, 27, 28, 29, 31, 32, 33, 35, 36, 38, 39, 40, 41, 78, 79, 80, 89, 91, 92, 94, 95, 97, 103, 116, 117, 118, 119, 120, 128, 129, 130, 142, 146, 148, 150, 151, 156, 159, 162, 164
R. multiflora Thunb. - **X**; 95, 97, 118, 146, 152, 159
R. palustris - **I**; 2, 3
R. setigera Michx. - **I**; 3, 9, 16, 18, 19, 20, 21, 22, 28, 39, 40, 92, 97, 103, 119, 120, 130, 142, 148, 163
Rubus spp. (dewberry) - **I**; 18, 32, 33, 35, 38, 78, 128, 129, 131, 145, 148, 150, 151
R. spp. (erect) - **I**; 9, 19, 29, 31, 33, 35, 41, 80, 120, 128, 146, 148, 150, 152, 164
R. phoenicolasius Maxim. - **X**; 156

Rubiaceae
Cephalanthus occidentalis L. - **I**; 3, 92, 94
Diodia teres Walt. - **I**; 9, 14, 16, 19, 35, 40, 41, 79, 93, 117, 119, 129, 130, 131, 151
D. virginiana L. - **S**; 3, 93, 94, 117
Galium aparine L. - **I**; 3, 18, 19, 38, 40, 41, 79, 95, 97, 103, 118, 119, 120, 146, 150
G. ciraezans Michx. - **I**; 16, 18, 27, 31, 36, 40, 41, 80, 91, 92, 93, 95, 97, 103, 119, 142, 148, 149, 150, 151, 152, 153, 154, 155, 156, 159
G. pedimontanum All. - **X**; 94, 95
G. pilosum Ait. - **I**; 13, 16, 18, 20, 21, 22, 26, 27, 28, 29, 31, 33, 35, 36, 38, 39, 40, 41, 78, 79, 80, 89, 92, 93, 94, 95, 97, 103, 120, 128, 130, 142, 163, 164, 165
G. tinctorium L. - **I**; 2, 3
G. triflorum Michx. var. *asprelliforme* Fern. - **I**; 95, 97
Houstonia caerulea L. - **I**; 1, 22, 41, 93, 94, 95, 103, 118, 124, 131, 152
H. canadensis Willd. - **N**; 2, 7, 9, 22, 78, 79, 80, 95, 97, 119, 142, 145, 146, 159, 161
H. longifolia Gaertn. - **I**; 22, 26, 27, 29, 31, 32, 33, 40, 89, 91, 92, 93, 97, 103, 116, 117, 118, 119, 128, 129, 130, 131, 142, 145, 149, 152, 153, 154, 155
H. nigricans (Lam.) Fern. - **I**; 33, 97, 119, 152, 153, 154, 155, 156
H. purpurea L. - **I**; 80
H. purpurea L. var. *calycosa* Gray - **I**; 13, 16, 18, 19, 20, 21, 22, 26, 28, 38, 39, 40, 41, 89, 93, 94, 103, 120, 129, 150, 151, 152, 155, 156, 165

Salicaceae
Salix humilis Marsh. - **I**; 1, 2, 7, 26, 27, 28, 29, 33, 152
S. nigra Marsh. - **I**; 3, 35, 41
S. tristis Ait. - **I**; 2, 7, 27, 28, 31, 95

Santalaceae
Comandra umbellata (L.) Nutt. - **I**; 94, 95, 117, 118, 128, 130, 150

Sapotaceae
Bumelia lycioides (L.) Gaertn. f. - **S**; 91, 93, 94, 142, 162

Saxifragaceae
Heuchera americana L. - **N**; 16, 38, 80, 95, 120
Penthorum sedoides L. - **I**; 7
Philadelphus hirsutus Nutt. - **L**; 18

Scrophulariaceae
Aureolaria virginica (L.) Pennell - **I**; 16, 18, 91, 93, 94, 120, 152
Buchnera americana L. - **S**; 119

Dasistoma macrophylla (Nutt.) Raf. - **I**; 95
Gerardia flava L. - **I**; 146, 159
G. purpurea L. - **I**; 94, 128, 129, 163
G. tenuifolia Vahl - **I**; 1, 9, 16, 21, 22, 28, 29, 41, 95, 97, 117, 128, 146, 151, 162, 164
Gratiola neglecta Torr. - **I**; 41
Leucospora multifida (Michx.) Nutt. - **I**; 21, 41, 93, 94, 119, 120
Mecardonia acuminata (Walt.) Small - **S**; 33, 40, 93, 94, 119, 120, 129, 135, 154
Mimulus ringens L. - **I**; 4
Pedicularis canadensis L. - **I**; 18, 93, 94
Penstemon brevisepalus Pennell - **L**; 16, 21, 22, 27, 29, 30, 33, 35, 41, 79, 80, 93, 95, 103, 118, 120, 128, 130, 142, 146, 151, 152, 154, 155, 156, 159
P. canescens (Britt.) Britt. - **I**; 89, 103
P. laevigatus Ait. - **S**; 1, 2, 3, 7, 9, 14, 16, 18, 19, 20, 21, 22, 28, 29, 33, 36, 39, 40, 41, 78, 89, 91, 93, 94, 95, 97, 118, 120, 142, 145, 148, 154, 155, 162
P. tubaeflorus Nutt. - **I**; 16
Tomanthera auriculata (Michx.) Raf. - **W**; 97
Verbascum blattaria L. - **X**; 16, 18, 78, 79, 116, 148
V. thapsus L. - **X**; 18, 40, 79, 95, 103, 146, 148, 149
Veronica arvensis L. - **X**; 16, 19, 21, 40, 41, 79, 80, 95, 148, 150
V. officinalis L. - **N**; 28, 79, 80, 95, 142, 148
V. peregrina L. - **I**; 94
V. serpyllifolia L. - **X**; 128
Veronicastrum virginicum (L.) Farw. - **I**; 7, 16, 95

Solanaceae
Physalis heterophylla Nees - **I**; 18, 19, 21, 22, 40, 148, 149, 151, 156
P. longifolia Nutt. - **W**; 22, 116, 154, 159
Solanum caroliniensis L. - **I**; 2, 3, 9, 14, 18, 22, 30, 31, 41, 78, 79, 80, 92, 97, 103, 116, 117, 119, 120, 128, 129, 142, 145, 148, 151
S. nigrum L. - **X**; 79
S. rostratum Dunal - **X**; 19

Typhaceae
Typha latifolia L. - **I**; 3, 21

Ulmaceae
Celtis laevigata Willd. - **S**; 16, 17, 19, 21, 22, 27, 32, 40, 80, 95, 97, 103, 116, 118, 119, 129, 130, 131, 142, 145, 162
C. occidentalis L. - **W**; 9, 18, 20, 21, 22, 26, 29, 32, 36, 38, 39, 40, 41, 79, 92, 94, 95, 97, 103, 116, 117, 118, 119, 120, 129, 142, 145, 146, 151, 159, 162, 165
C. tenuifolia Nutt. - **S**; 7, 9, 16, 19, 21, 26, 29, 40, 78, 79, 80, 95, 103, 117, 120, 142, 148, 162, 164
Ulmus alata Michx. - **S**; 3, 7, 9, 13, 16, 18, 20, 21, 22, 26, 27, 28, 31, 32, 33, 36, 38, 39, 40, 41, 94, 95, 97, 103, 117, 118, 119, 120, 128, 129, 130, 131, 142, 145, 146, 148, 150, 151, 152, 154, 159, 162, 163, 164, 165
U. americana L. - **I**; 3, 9, 79, 94
U. rubra Muhl. - **I**; 9, 16, 18, 19, 21, 26, 27, 28, 29, 31, 32, 38, 40, 41, 80, 94, 95, 97, 103, 116, 118, 142, 146, 148, 151, 152, 162

Urticaceae

Boehmeria cylindrica (L.) Sw. - **I**; 3

Parietaria pensylvanica Muhl. - **I**; 95

Valerianaceae

Valerianella radiata (L.) Dufr. - **I**; 19, 32, 33, 38, 39, 40, 41, 92, 93, 94, 117, 119, 120, 128, 130, 150, 162

Verbenaceae

Callicarpa americana L. - **S**; 18

Lippia lanceolata Michx. - **I**; 3, 93, 120

Verbena simplex Lehm. - **I**; 2, 7, 9, 16, 17, 18, 19, 20, 21, 22, 28, 29, 32, 33, 38, 39, 40, 41, 78, 79, 80, 92, 93, 94, 95, 97, 103, 116, 117, 118, 119, 120, 128, 130, 142, 148, 149, 150, 153, 154, 155, 156, 159, 160, 162, 165

V. urticaefolia L. - **I**; 3, 18, 19, 20, 22, 28, 79, 95, 142

Violaceae

Viola cuculata Ait. - **N**; 18, 19, 21, 22, 89, 92, 93, 94, 119, 120

V. egglestonii Brainerd - **L**; 30, 38, 40, 92, 93, 118, 119, 128, 130, 131

V. hirsutula Brainerd - **I**; 16, 27

V. pedata L. var. *lineariloba* DC. - **I**; 16, 21, 27, 40, 89, 118, 119, 120, 128, 129, 131

V. rafinesquii Greene - **X**; 17, 19, 38, 94, 95, 118

V. sagittata Ait. - **I**; 13, 41

V. sororia Willd. - **N**; 16, 18, 19, 21, 29, 40, 79, 89, 91, 92, 93, 94, 95, 97, 120, 153, 154, 156, 160

V. sororia Willd. var. *missouriensis* (Greene) - **W**; 146, 148, 160

V. triloba Schwein. - **I**; 1, 7, 16, 21, 26, 27, 29, 31, 36, 38, 39, 40, 41, 93, 103, 119, 153, 165

Vitaceae

Ampelopsis cordata Michx. - **S**; 3, 9, 20, 21

Parthenocissus quinquefolia (L.) Planch. - **I**; 16, 18, 21, 25, 26, 28, 31, 38, 40, 41, 78, 79, 80, 92, 95, 97, 103, 117, 120, 142, 148, 149, 151, 152, 154, 159

Vitis aestivalis Michx. - **I**; 7, 9, 16, 32, 36, 79, 92

V. cinerea Engelm. - **I**; 19, 95, 149

V. riparia Michx. - **I**; 20, 21, 27, 31, 39, 103

V. rotundifolia Michx. - **I**; 3, 18, 29, 31, 38, 40, 41, 80, 95, 97, 142, 149, 153, 154, 155

V. vulpina L. - **I**; 21, 26, 32, 78, 80, 93, 120, 150, 151

FURTHER STUDIES ON THE BARRENS OF THE NORTHERN AND WESTERN HIGHLAND RIMS OF TENNESSEE

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ABSTRACT. Data were combined from (1) five recently-studied sites and (2) several previously-studied areas that now are mostly in tilth to determine the flora and vegetational features of northern Highland Rim barrens in Tennessee. These barrens, mostly in Montgomery, Robertson, and Stewart counties, are chiefly on flat to gently sloping sites with soils developed from loess. The native flora contains at least 364 taxa; the adjacent western Rim barrens have a native flora of 400 taxa. The floras (i.e., those of western and northern Rim barrens) are related at nearly 60% (Sorensen's coefficient). Floristic element percentages are similar, but the percentage of northern taxa is higher and southern taxa lower on the northern Rim. The plot-sampled vegetation is grass-forb dominated; the most important grass is *Schizachyrium scoparium*, as has been the case in most other Tennessee barrens studied.

INTRODUCTION

Early explorers, surveyors, and settlers in central-western Tennessee and Kentucky saw grassy and shrubby-grassy openings in the prevailingly forest vegetation and called the openings barrens. An extensive area in central Kentucky, the "Kentucky Meadows" or "Big Barrens," extended slightly into Tennessee on the northern Highland Rim, with outliers on the eastern and western rims (Transeau 1935, Haywood 1823, Filson 1784, Dicken 1935, Chester 1988, DeSelm 1988, 1990). These and other Tennessee barrens, today mostly represented by scattered remnants, are part of a large southeastern barrens system (DeSelm 1981, 1986; DeSelm and Murdock in press).

Studies of Tennessee Highland Rim barrens include those of DeSelm (1990), who presented the results of quadrat sampling and a floristic list for the eastern Rim, and DeSelm (1988), who characterized western Rim barrens based on quadrat sampling but did not list the flora. Chester (1988) described northern Rim barrens from a historical perspective but sampling data were not available and only a limited floristic list was included. This paper will provide additional information on the flora and vegetation of Highland Rim barrens. We will (1) further characterize northern Rim barrens, based on recent sampling data and floristic studies dating from the 1930s to the present, (2) list the vascular plants known from western and northern Rim barrens, and (3) compare the barrens floras from the two areas.

THE STUDY AREAS

Barrens of the western and northern Highland Rim are on flat to gently rolling landscapes and on soils derived from loess or cherty Mississippian limestones. DeSelm (1988) also found some western Rim barrens on shallow soils derived from Devonian and Silurian limestones. Details of the geology, soils, climate, paleoecology and human history of these areas have been reviewed by Chester (1988, northern Rim) and DeSelm (1988, western Rim). Both studies discussed presettlement grassland communities with a moderate percent of the flora characteristic of the midwestern U.S. prairie center described by Weaver (1954).

METHODS

Locations and methods for pre-1988 western Rim sites were detailed by DeSelm (1988). Floristic studies began on the northern Rim (mostly Montgomery, Robertson, and Stewart counties) in the late 1930s by Alfred Clebsch and his sons and associates, Royal Shanks, A. J. Sharp, and later by others, and continues to the present by the second author. Voucher specimens are curated at APSC with many duplicates at TENN and elsewhere.

Three northern Rim barrens were quadrat-sampled. Twenty to 40, 0.5 m^2 plots were placed at one m intervals on a straight line through the long axis of one or more openings at each site. Cover of each vascular plant taxon was estimated in each quadrat and frequency, relative frequency, mean cover, relative cover, and Importance Value 200 (IV = sum of relative frequency and relative cover) calculated. Also, each site was surveyed floristically on numerous visits.

Species ranges were categorized, based on data in Little (1971, 1977), Fernald (1950), Gleason and Cronquist (1991), Pennell (1935), Cronquist (1980) and Isley (1990). Nomenclature chiefly follows Cronquist (1980) for composites, Isley (1990) for legumes and Gleason and Cronquist (1991) for others. Calculation of Sorensen's coefficient of community similarity follows Mueller-Dumbois and Ellenburg (1974).

Study Sites

Six northern Rim sites were studied; for continuity, these are numbered beyond the 18 listed by DeSelm (1988) for the western Rim:

19. Tennessee Ridge Barren, Houston County (quadrat sampled 8 August 1990, studied floristically eight times 1989-present). This sloping site is on Highway 147, 0.4 miles southwest of the old railroad bed in Tennessee Ridge (Stewart, TN, USGS 7.5' quad, 1950, photorevised 1973). Soils are Dickson silt loam and Mountview silt loam (Wildermuth et al. 1958); bedrocks are Warsaw and St. Louis limestones (Wilson and Finlayson 1984). The site is in an area known as the "Coalings" and has been cut and burned repeatedly since the discovery of iron ore in the region in the early 1800s (cf. Ash undated).

20. St. Paul Barren, Stewart County (quadrat sampled 24 August 1990, studied floristically six times 1989-present). This flattish site is on the east side of St. Paul Road, 1.9 miles north of the junction with Cumberland City Road (Needmore, TN, USGS 7.5' quad, 1957). Soils are Dickson silt loam, rolling phase (Austin et al. 1953);

bedrock is St. Louis limestone which is very cherty here (Stearns et al. 1968). The area is also in the "Coalings."

21. Oakwood Barren, Montgomery County (quadrat sampled 18 August 1988, floristically studied 12 times 1988-present). This flat site is on Route 79, 1.3 miles west of Palmyra Road (Gate 11) of Fort Campbell Military Reservation (Woodlawn, TN, USGS 7.5' quad, 1957). Soils are Dickson silt loam (Lampley et al. 1975) and bedrock is Ste. Genevieve Limestone (Wilson 1986). This area is bushhogged periodically but where not so treated, is heavily invaded by *Rhus copallina*.

22. Warfield Barren, Montgomery County (flora studied 14 times 1981-present and also seen numerous times by Alfred Clebsch and his associates, 1930-1960). This mostly depressional site is between the L & N Railroad and U.S. Route 41, centering 1.5 miles southeast of Guthrie, Kentucky (Guthrie, KY-TN, USGS 7.5'quad, 1957). Soils are Guthrie, Pembroke and Taft silt loams with a small area of Dickson silt loam (Lampley et al. 1975). Bedrock is the Ste. Genevieve Limestone (Klemic 1966).

23. Ridgetop Barren, Davidson County (floristic studies on six visits since 1984). This site is adjacent to the Robertson County line at the north end of and above the railroad tunnel, 0.7 miles southeast of Ridgetop Cemetery (Greenbrier, TN, USGS 7.5' quad, 1961). This south-facing, upper slope has Bodine-Sulphura complex soils with 20-50% slopes (North et al. 1981). It is underlain by Warsaw Limestone and Fort Payne Formation (Wilson and Lounsbury 1976) and believed to be held open by railroad fires and soil slump. A brief description is included in Smith et al. (1983) and the site was examined as a station for *Polytaenia nuttallii* by Chester and Wofford (1992).

24. The herbaria at APSC and TENN were searched for specimens from northern Rim barrens, especially from sites known to Clebsch, Shanks, and Sharp that are now in tilth or have been modified otherwise. These taxa, where not present on sites 19-23, have been included in the list as number 24.

RESULTS AND DISCUSSION

Floras

Vascular taxa (593) known from northern and western Rim barrens are given in the Appendix. The northern Rim flora includes 389 taxa (5.9% non-native) while the western Rim flora includes 425 taxa, also with 5.9% non-native. Woody taxa are 14.9%, compared with 20.3% from the more disturbed and generally smaller western Rim sites. The floras are similar in that both have many composites (21.9% for northern Rim, 21% for western Rim), grasses (14.4% and 13.5%), legumes (7.2% and 6.0%), and sedges (6.7% and 4.5%).

The northern and western Rim barrens floras are related at 59.5%, using Sorensen's coefficient of community similarity. This number exceeds by about 10% similar numbers calculated between eastern Rim barrens and barrens in other areas, and between West Tennessee barrens and those in other areas (DeSelm 1989, 1990). The northern Rim barrens list, when compared with Kentucky barrens lists (Bryant 1977, 1981; Baskin and Baskin 1981) exhibits coefficients ranging from 11.9 to 32.2. However, the percentage of species in these three Kentucky lists that occur on our northern Rim barrens range from 55.3 to 76.6.

Floristic element percentages for native plants on northern Rim barrens are (for comparison, data from western Rim (WR) sites are given in parentheses): regional intraneous 59.3% (WR = 62.6% for loess sites, 60.2% for limestone sites); southern 24.7% (WR = 30.3% for loess sites, 27.9% for limestone sites); northern 10.2% (WR = 3.8% for loess sites, 7.1% for limestone sites); western 3.9% (WR = 3.8% for loess sites, 1.6% for limestone sites); and local intraneous 1.7% (WR = 1.9% for loess sites, 3.2% for limestone sites).

Regional intraneous and western percentages are quite similar for the two areas. The lower southern and higher northern percentages for the northern Rim flora probably result from the slightly more northern geographic location. The smaller local intraneous element on the northern Rim is probably due to the paucity of limestone outcrop habitats on barrens sites.

Rare Plants

Nine state-listed taxa were found on the western Rim (DeSelm 1988) and 10 on the northern; only *Salvia azurea* is in common. In the following list of northern Rim rare taxa, S is special concern and T is threatened (Somers et al. 1989). *Prenanthes barbata* will be listed on subsequent revisions of the state list, but its status has not been determined at present (Paul Somers, personal communication, 1991).

Asclepias hirtella - S
Echinacea pallida - T
Lilium michiganense - T
Muhlenbergia glabriflora - S
Polytaenia nuttallii - T
Platanthera peramoena - T
Prenanthes barbata - ?
Rudbeckia subtomentosa - T
Salvia azurea - S
Silphium laciniatum - T

Community Sampling

Based on quadrat data, the three sites sampled are rather similar; coefficients of community similarity range from 48.6 to 51.5. They are dominated (Appendix 1) by graminoids (IV totals range from 77.8 to 80.5) and forbs (IV totals from 76.3 to 93.4). The dominant grass, *Schizachyrium scoparium,* is also the dominant on barrens of the western Rim and elsewhere in Tennessee (DeSelm 1988, 1989). This taxon is not only drought tolerant (Weaver 1954), but most of its leaf area occurs at the base of the culm and it is thus able to withstand some grazing and mowing/bushhogging.

With respect to available moisture, the intermediate, xero-mesic nature of northern Rim sites is suggested by the relative absence of hydro/mesophytes and xerophytes characterizing western Rim sites (DeSelm 1988). Present, for example, are *Acer rubrum, Boltonia, Helianthus augustifolius, Liquidambar,* and *Nyssa,* all considered previously as hydro/mesophytes, but 19 other mesophytic taxa are missing in the samples. Xerophytes present are *Linum medium,* and *Pinus virginiana*--the 20 other more extreme xerophytes are missing.

CONCLUSIONS AND SUMMARY

Descriptions of Kentucky and Tennessee barrens are found in 18th and 19th-century travel and scientific literature. The time of origin of these forest openings is not known; Transeau (1935) believed that the Kentucky Barrens were part of the Hypsithermal age (8000-5000 YBP) Prairie Peninsula but Wilkins (1988) did not find an increase in Poaceae pollen at Jackson Pond on the edge of the Kentucky Barrens until about 2000 years ago. This suggests that these openings may be in part a Native American fire-use phenomena. Their rapid return to forest after settlement (Chester 1988, DeSelm 1989) also suggests this.

Northern and western Rim barrens occur on upland, loess-derived soils which are winter wet and summer dry. Some western Rim barrens also occur on shallow limestone-derived soils. The sloping barren at Ridgetop may represent a third community type but more study is required to fully characterize that site.

The combined vascular flora of 593 taxa includes 389 taxa on the northern and 425 on the western Rim. Ten state-listed rare taxa are known from northern Rim barrens and nine from the western Rim; only one species is in common. Floristic element percentages of native taxa that are regional intraneous, local intraneous, and western are similar. The northern Rim has a lower percentage of southern taxa and a higher percentage of northern taxa than the western Rim (which had most sample sites in the southern half of its area). The virtual absence of hydro/mesophytes and xerophytes used to characterize the western Rim flora suggests that the northern Rim barrens flora is xero-mesic in nature.

The three sites quadrat sampled supported a grass-forb dominated vegetation. The most important grass was *Schizachyrium scoparium,* as had been seen in other Tennessee barrens. In two sites *Smilax glauca* was second; *Pycnanthemum tenuifolium, Aster dumosus, Aster solidagineus,* and *Stylosanthes biflorus* had the highest forb importance.

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Appendix 1. **Frequency, mean cover (each rounded) and Importance Value (200) for vascular plants on three northern Rim barrens.**

Taxa	TN Ridge #19	St. Paul #20	Oakwood #21
Acer rubrum	25- 1- 3.5		30- 3- 5.7
Achillea millefolium	3- 1- 1.0		
Ambrosia bidentata		5- 1- 1.2	
Andropogon gyrans	18- 2- 3.3	25- 6- 6.1	15- 4- 4.6
Aristida purpurascens		10- 2- 2.2	
Aster dumosus	45- 1- 5.8	60-10-12.3	40- 1- 5.3
A. hemisphericus	20- 1- 2.9		
Aster solidagineus	55- 1- 6.9	10- 1- 1.7	30- 5- 7.0
Boltonia diffusa			10- 1- 1.2
Buchnera americana		10- 1- 1.7	
Carex hirsutella	20- 1- 2.9		
C. sp.		5- 2- 1.7	
Cassia (Senna) nictitans	5- 1- 1.2	30- 1- 4.0	
Clitoria mariana	3- 1- 1.0		
Coreopsis major	8- 1- 1.5	55- 2- 7.3	
C. tripteris	20- 3- 4.0		
Danthonia spicata	28- 8- 7.8		
Desmodium ciliare		25- 5- 5.5	
D. marilandicum	10- 1- 1.8	5- 2- 2.0	
Diodia teres	5- 2- 1.8	10- 1- 1.7	10- 1- 1.9
Diospyros virginiana		5- 5- 3.3	20-23-18.1
Eragrostis spectabilis		5- 2- 1.7	5- 1- 1.3
Eupatorium hyssopifolium		15- 1- 2.3	20- 1- 3.2
E. rotundifolium	5- 1- 1.2		40- 2- 6.0
Euphorbia corollata	3- 1- 1.0		
Galactia volubilis	25- 1- 3.5		
Galium obtusum	8- 1- 1.5		
Gerardia tenuifolia	3- 1- 1.0	15- 1- 2.3	15- 1- 2.4
Gymnopogon ambiguus		5- 5- 3.3	
Helianthus angustifolius			65- 2- 8.6
H. atrorubens		40- 8- 8.9	
H. silphioides	5- 1- 1.2		
Hieracium gronovii	3- 1- 1.0		
Juncus brachycarpus			5- 1- 1.3
Juniperus virginiana	5- 1- 1.2		
Lespedeza procumbens	10- 1- 1.8	5- 5- 3.3	
L. repens	3- 1- 1.0		
L. striata		5- 1- 1.2	
L. virginica	23- 2- 3.9	55- 4- 8.4	55- 2- 7.5
Linum medium	3- 1- 1.0		5- 1- 1.3
Liquidambar styraciflua	13- 1- 2.1		
Lobelia puberula	18- 1- 2.7		5- 1- 1.3

Appendix 1 (cont.).

Taxa	TN Ridge #19	St. Paul #20	Oakwood #21
Lonicera japonica	10- 4- 3.5		
L. sempervirens	8- 1- 1.5		
Nyssa sylvatica	3- 1- 1.0		
Panicum commutatum			30- 1- 4.2
P. lanuginosum			20- 1- 3.0
P. laxiflorum	16- 1- 3.1	10- 3- 2.7	
P. longiligulatum			5- 1- 1.3
P. microcarpon		30- 1- 4.0	
P. polyanthes	5- 3- 2.3		
Pinus virginiana	3- 3- 2.1		
Polygala ambigua	3- 1- 1.0		15- 1- 2.4
P. sanguinea			10- 1- 1.9
Potentilla simplex	30- 1- 4.1	10- 2- 2.2	
Prunus serotina	5- 1- 1.2		
Pycnanthemum tenuifolium	15- 1- 2.3	50- 2- 6.8	75- 9-14.7
Rhus copallina	13- 5- 4.4	30-10- 8.9	10- 2- 2.6
Rosa carolina	5- 2- 1.8	30- 2- 4.5	
R. multiflora	5- 3- 2.3		
Rubus flagellaris	8- 2- 3.1		
Sabatia angularis		10- 1- 1.7	
Schizachyrium scoparium	100-74-54.3	100-76-52.8	100-58-50.7
Schrankia microphylla	3- 1- 1.0		
Scleria pauciflora	40- 2- 5.8	35- 1- 4.6	15- 1- 2.4
Scutellaria elliptica		10- 1- 1.7	
Setaria geniculata	3- 1- 1.0		
Silphium integrifolium	10- 3- 1.9		
Smilax glauca	85- 8-14.4	75- 5-11.2	50- 2- 7.0
Solidago erecta	18- 1- 2.7		
S. juncea	15- 2- 2.9	20- 5- 5.0	65- 2- 9.1
S. nemoralis	5- 1- 1.2	5- 2- 1.7	20- 1- 3.2
S. rugosa	3- 6- 3.9		5- 1- 1.3
Sorghastrum nutans			30- 8- 9.0
Spiranthes cernua			5- 1- 1.3
Strophostyles umbellata	13- 1- 2.1	30- 4- 5.6	5- 1- 1.3
Stylosanthes biflora	50- 2- 7.0	45- 2- 6.2	
Tephrosia virginiana		5- 2- 1.7	
Unknown forb	3- 1- 1.0		
Vernonia gigantea			30- 4- 6.4

Appendix 2. Vascular Flora of Western and Northern Rim Barrens, Tennessee[1,2]

PTERIDOPHYTA

Adiantaceae
Cheilanthes lanosa (Michx.) Eaton - **S**; 23

Aspidiaceae
Woodsia obtusa (Spreng.) Torr. - **I**; 13

Aspleniaceae
Asplenium platyneuron (L.) Oakes - **I**; 13
Onoclea sensibilis L. - **I**; 22

Equisetaceae
Equisetum arvense L. - **I**; 24

Ophioglossaceae
Ophioglossum engelmannii Prantl - **I**; 13

Polypodiaceae
Polypodium polypodioides (L.) Watt. - **S**; 17

Pteridaceae
Pellaea atropurpurea (L.) Link - **I**; 13, 23

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[1] Floristic element abbreviations are:

I - intraneous (regional)
S - southern
W - western
N - northern
L - intraneous (local)
X - introduced

[2] Sites are (1-18 are Western Rim, 19-24 are Northern Rim):

1 - Ethridge
2 - South of Lawrenceburg
3 - Between Dickson and Centerville
4 - Pickadilly (including Mashburn site)
5 - Rt. 114 at Bobs Landing Road
6 - Parnassia site
7 - Decatur No. 5
8 - Swallow Bluff Road
9 - Mt. Carmel Church
10- Big Barren
11- Mt. Lebanon Church
12- Gravel Road Barren near Long Point
13 - Cub Creek
14 - Carol Cabin Road
15 - Decatur County No. 4
16 - Long Point
17 - Hill Barren (above Swallow Bluff Rd.)
18 - Clifton Cliff
19 - Tennessee Ridge
20 - St. Paul
21 - Oakwood
22 - Warfield
23 - Ridgetop
24 - Composite, NR Barrens

SPERMATOPHYTA: GYMNOSPERMAE

Cupressaceae
Juniperus virginiana L. - **I**; 4, 5, 6, 8, 10, 12, 13, 14, 18, 19, 21, 22, 23

Pinaceae
Pinus echinata Mill. - **S**; 15
P. taeda L. - **S**; 10, 14, 21
P. virginiana Mill. - **S**; 9, 15, 18, 19, 23

SPERMATOPHYTA: ANGIOSPERMAE

Acanthaceae
Ruellia caroliniensis (Walt.) Steud. - **S**; 15, 18, 24
R. humilis Nutt. - **S**; 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 23

Aceraceae
Acer rubrum L. - **I**; 1, 3, 4, 19, 20, 21, 22, 24
A. saccharum Marsh. - **N**; 5, 9, 10, 11, 13, 15, 16, 21

Amaryllidaceae
Hymenocallis occidentalis (LeConte) Kunth - **S**; 21
Manfreda virginica (L.) Salisb. - **S**; 1, 2, 3, 4, 5, 7, 8, 10, 11, 12, 13, 14, 15, 16, 17, 19, 20, 23
Hypoxis hirsuta (L.) Coville - **I**; 10, 14, 15, 19, 24

Anacardiaceae
Rhus aromatica Aiton - **I**; 5, 10, 11, 12, 15, 16
R. copallina L. - **I**; 2, 3, 4, 8, 10, 11, 12, 14, 16, 19, 20, 21, 22, 23
R. glabra Britt. - **I**; 1, 11, 13, 19, 22
R. radicans L. - **I**; 5, 11, 21, 23
R. toxicodendron L. - **I**, 13

Apiaceae
Angelica venenosa (Greenway) Fern. - **I**, 19, 24
Chaerophyllum tainturieri Hook. - **S**; 13, 22
Cicuta maculata L. - **I**; 21, 22, 24
Daucus carota L. - **X**; 8, 10, 11, 13, 15, 19, 22
Eryngium yuccifolium Michx. - **I**; 4, 14, 15, 24
Polytaenia nuttallii DC. - **W**; 23
Sanicula canadensis L. - **I**; 5, 8, 11, 13
Thaspium pinnatifidum (Buckl.) Gray - **L**; 15
T. trifoliatum (L.) Gray - **I**; 6, 15
Zizia aurea (L.) Koch - **I**; 24

Apocynaceae
Apocynum cannabinum L. - **I**; 10, 11, 14, 15, 16, 22

Asclepiadaceae
Asclepias amplexicaulis Sm. - **I**; 4, 21
A. exaltata L. - **N**; 13
A. hirtella (Pennell) Woodson - **W**; 22
A. incarnata L. - **I**; 22
A. syriaca L. - **N**; 22
A. tuberosa L. - **I**; 5, 13, 22, 23

Asclepias variegata L. - **I**; 16, 21
A. verticillata L. - **I**; 7, 8, 9, 10, 11, 15, 16, 17, 23, 24
A. viridiflora Raf. - **W**; 8, 10, 11, 15, 16, 22

Asteraceae
Achillea millifolium L. - **X**, 3, 11, 19, 21, 22
Ambrosia artemisiifolia L. - **I**; 1, 8, 11, 13, 15, 16, 20, 22, 23
A. bidentata Michx. - **I**; 14, 20
Antennaria plantaginifolia (L.) Hook. - **I**; 3, 4, 10, 13, 15, 16, 19, 20, 21, 23
Aster concolor L. - **I**; 4
A. dumosus L. - **S**; 1, 4, 10, 12, 19, 20, 21, 24
A. hemisphericus E. J. Alex. - **S**; 1, 2, 3, 12, 16, 19
A. laevis L. - **I**; 15
A. linearifolius L. - **I**; 2, 4
A. novae-angliae L. - **I**; 4, 24
A. oblongifolius Nutt. - **I**; 15, 23
A. patens Ait. - **I**; 1, 2, 3, 4, 10, 11, 12, 14, 15, 16, 19, 20
A. pilosus Willd. - **I**; 1, 4, 13, 16
A. sagittifolius Willd. - **N**; 24
A. sericeus Vent. - **I**; 14, 15
A. solidagineus Michx. - **I**; 1, 3, 4, 14, 19, 20, 21, 24
A. undulatus L. - **I**; 4, 10, 11, 15
Bidens bipinnata L. - **I**; 13, 19, 22
B. frondosa L. - **I**; 22
Boltonia diffusa Ell. - **S**; 1, 4, 20, 21, 24
Carduus nutans L. - **X**; 23
Chrysanthemum leucanthemum L. - **X**; 19, 22
Chrysopsis camporum Greene - **X**; 24
C. mariana (L.) Ell. - **S**; 4
Cirsium carolinianus (Walt.) Fern. & Schub. - **S**; 15
C. discolor (Muhl.) Spreng. - **N**; 24
Coreopsis major Walt. - **S**; 2, 3, 4, 10, 11, 14, 15, 16, 19, 20, 21
C. pubescens Ell. - **S**; 11, 12, 16
C. tripteris L. - **N**; 1, 3, 5, 14, 16, 19, 20, 21, 22, 24
Echinacea pallida L. - **W**; 24
Elephantopus caroliniana Willd. - **I**; 24
E. tomentosus L. - **S**; 4, 7
Erechtites hieracifolia (L.) DC. - **I**; 20
Erigeron canadensis L. - **I**; 4, 7, 22
E. philadelphicus L. - **I**; 24
E. strigosus Muhl. - **I**; 2, 3, 4, 8, 10, 11, 13, 15, 16, 18, 19, 21, 22, 23, 24
Eupatorium album L. - **S**, 4, 19, 20
E. altissimum L. - **S**; 1, 4, 20, 21, 24
E. coelestinum L. - **I**; 7, 20, 24
E. fistulosum Barratt - **I**; 21, 22
E. hyssopifolium L. - **S**; 1, 20, 21, 22, 24
E. incarnatum Walt. - **S**; 9, 13
E. perfoliatum L. - **I**; 4, 13, 22, 24
E. rotundifolium L. - **S**; 1, 2, 3, 4, 19, 21, 24
E. rugosum Houtt. - **I**; 13, 19, 20
E. serotinum Michx. - **S**; 20, 22, 24
E. sessilifolium L. - **N**; 24
Euthamia graminifolia (L.) Nutt. - **N**; 1, 4, 20, 21, 22, 24
E. gymnospermoides Greene - **I**; 1
Gnaphalium obtusifolium L. - **I**; 1, 2, 4, 20, 24

Gnaphalium purpureum L. - **I**; 21, 22, 23
Gutierrezia dracunculoides (DC.) Blake - **X**, 4, 24
Helenium amarum (Raf.) Rock - **I**; 4, 13
H. autumnale L. - **I**; 24
H. flexuosum Raf. - **I**; 4
Helianthus angustifolius L. - **S**; 2, 4, 20, 21, 22, 24
H. atrorubens L. - **S**; 4, 20
H. divaricatus L. - **N**; 1, 14, 23, 24
H. hirsutus Raf. - **L**; 1, 2, 3, 7, 12, 14, 20, 22, 24
H. maximilianii Schrad. - **X**; 24
H. microcephalus T. & G. - **S**; 1, 5, 8, 15, 17, 24
H. mollis Lam. - **I**; 3, 4, 21, 22, 24
H. occidentalis Riddell - **I**; 13
H. silphioides Nutt. - **W**; 2, 19
H. tuberosus L. - **I**; 24
Heliopsis helianthoides (L.) Sw. - **I**; 24
Hieracium gronovii L. - **I**; 4, 19, 20, 21, 24
Krigia biflora (Walt.) Blake - **S**; 24
K. dandelion (L.) Nutt. - **S**; 13, 22
K. virginica (L.) Willd. - **I**; 4
Kuhnia eupatorioides L. - **S**; 10, 11, 12, 13, 15, 16
Lactuca canadensis L. - **I**; 13, 16, 21, 22
L. serriola L. - **X**; 22
Liatris aspera Michx. - **I**; 5, 13, 16
L. cylindracea Michx. - **N**; 14
L. scabra (Greene) K. Schum. - **I**; 4, 19
L. scariosa (L.) Willd. - **I**; 7
L. spicata (L.) Willd. - **I**; 1, 2, 4, 19, 24
L. squarrosa (L.) Michx. - **S**; 5, 23
Parthenium integrifolium L. var. *henryanum* Mears - **I**; 15
P. integrifolium L. var. *hispidum* Mears - **W**; 3
P. integrifolium L. var. *integrifolium* - **I**; 4, 14, 15, 16, 22
Pluchea camphorata (L.) DC. - **S**; 22
Prenanthes barbata (T. & G.) Milstead - **S**; 19, 24
P. serpentaria Pursh - **I**; 1, 4
Pyrrhopappus carolinianus (Walt.) DC. - **S**; 1, 15, 18, 21, 22
Ratibida pinnata (Vent.) Barnh. - **N**; 5, 14, 15, 22
Rudbeckia fulgida Ait. - **L**; 8, 10, 15, 16, 17
R. hirta L. - **L**; 1, 2, 3, 4, 14, 16, 19, 22
R. laciniata L. - **I**; 24
R. subtomentosa Pursh - **W**; 24
Senecio anonymus A. Wood - **S**; 11, 12, 15, 16, 21, 23
S. aureus L. - **S**; 24
S. plattensis Nutt. - **W**; 24
Silphium asteriscus L. - **S**; 4, 14
S. integrifolium Michx. - **W**; 4, 19, 24
S. laciniatum L. - **W**; 24
S. perfoliatum L. - **W**; 24
S. terebinthinaceum Jacq. - **W**; 14, 15
S. trifoliatum L. var. *latifolium* A. Gray - **L**; 5, 10, 11, 12
S. trifoliatum L. var. *trifoliatum* - **L**; 11, 24
Solidago canadensis L. var. *scabra* T. & G. - **I**; 1, 2, 4, 13, 22, 24
S. erecta Pursh - **S**; 4, 19, 20
S. gigantea Ait. - **I**; 14
S. juncea Ait. - **N**; 4, 15, 19, 20, 21, 24

Solidago nemoralis Ait. - **I**; 4, 8, 10, 11, 12, 13, 15, 16, 19, 20, 21, 24
S. odora Ait. - **I**; 1, 4
S. puberula Nutt. - **I**; 4
S. rigida L. - **I**; 4
S. rugosa Mill. subsp. *aspera* (Ait.) Cronq. - **I**; 4, 14, 15, 19, 21, 24
S. speciosa Nutt. - **I**; 4, 24
S. ulmifolia Muhl. - **N**; 21
Verbesina helianthoides Michx. - **S**; 4, 14, 15, 22, 24
V. virginica L.- **S**; 13
Vernonia gigantea (Walt.) Trel. - **I**; 4, 13, 20, 21, 22, 24
V. gigantea X *V. missurica* - **?**; 1, 24
V. missurica Raf. - **W**; 22, 24

Betulaceae
Corylus americana Walt. - **N**; 22
Ostrya virginiana (Mill.) K. Koch. - **N**; 5, 10, 11, 12, 13, 15, 16, 17

Bignoniaceae
Anisostichus capreolata (L.) Bureau - **S**; 5, 10, 15, 16
Campsis radicans (L.) Seem. - **S**; 11, 13, 16, 21, 22

Boraginaceae
Heliotropium tenellum Torr. - **S**; 5, 10, 11, 12, 14, 15, 16
Lithospermum arvense L. - **X**; 22
L. canescens (Michx.) Lehm. - **I**; 7, 8, 10, 11, 12, 13, 14, 15, 16, 17
L. tuberosum Rugel - **S**; 5
Onosmodium occidentale MacKenz. - **W**; 7, 15

Brassicaceae
Arabis glabra (L.) Bernh. - **N**; 8
A. laevigata (Muhl.) Poir. - **N**; 8, 15, 23
Draba cuneifolia Nutt. - **S**; 9, 15, 17
D. verna L. - **N**; 13
Leavenworthia exigua Rollins - **L**; 8, 15
Lepidium virginicum L. - **X**; 13, 22, 24

Cactaceae
Opuntia humifusa Raf. - **I**; 7, 12, 15, 16

Campanulaceae
Specularia perfoliata (L.) DC. - **I**; 22

Caprifoliaceae
Lonicera japonica Thunb. - **X**; 4, 8, 9, 11, 13, 15, 19, 21, 23
L. sempervirens L. - **I**; 9, 15, 19, 21, 23
Sambucus canadensis L. - **N**; 22
Symphoricarpos orbiculatus Moench - **I**; 3, 4, 8, 10, 11, 13, 14, 15, 23
Viburnum rufidulum Raf. - **S**; 10, 11, 12, 13, 14, 15, 16, 23

Caryophyllaceae
Arenaria patula Michx. - **S**; 8, 9, 15
Cerastium glomeratum Thuillier - **X**; 13
Dianthus armeria L. - **X**; 13, 22
Saponaria officinalis L. - **X**; 22
Silene antirrhina L. - **I**; 13

Celastraceae
Celastrus scandens L. - **I**; 7

Cistaceae
Lechea tenuifolia Michx. - **I**; 4
L. villosa Ell. - **I**; 3, 4, 24

Clusiaceae
Hypericum densiflorum Pursh - **S**; 8, 10, 13, 14
H. denticulatum Walt. var. *recognitum* Fern. & Schub. - **L**; 4
H. dolabriforme Vent. - **L**; 10, 15
H. drummondii (Grev. & Hook.) T. & G. - **S**; 4, 20
H. frondosum Michx. - **S**; 23
H. gentianoides (L.) BSP. - **I**; 4, 19, 21, 24
H. gymnanthum Engelm. & Gray - **S**; 1, 3
H. hypericoides (L.) Crantz - **S**; 4, 24
H. mutilum L. - **I**; 22, 24
H. prolificum L. - **I**; 16
H. punctatum Lam. - **I**; 4, 14, 16, 19, 20, 22, 23, 24
H. sphaerocarpum Michx. - **S**; 5, 8, 9, 10, 11, 12, 13, 14, 15, 16
H. stans Michx. - **S**; 13
H. stragalum Adams & Robson. - **S**; 3, 4, 14, 16, 20, 21, 24

Convolvulaceae
Calystegia sepium (L.) R. Browne - **I**; 19, 22
Ipomea pandurata (L.) G. F. W. Mey. - **I**; 3, 4, 13, 15

Cornaceae
Cornus florida L. - **I**; 3, 4, 8, 10, 13, 15, 21

Crassulaceae
Sedum pulchellum Michx. - **S**; 13, 15

Cyperaceae
Carex albolutescens Schwein. - **I**; 22
C. annectens Bickn. - **N**; 15, 22, 24
C. artitecta MacKenz. - **I**; 13
C. blanda Dewey - **I**; 24
C. complanata Torr. & Hook. - **S**; 3, 24
C. digitalis Willd. - **I**; 13
C. emmonsii Dew. - **I**; 13
C. festucacea Schkuhr - **I**; 24
C. flaccosperma Dewey - **I**; 24
C. frankii Kunth - **I**; 22, 24
C. granularis Muhl. - **I**; 4, 6, 11, 15
C. hirsutella MacKenz. - **I**; 2, 3, 4, 6, 8, 10, 13, 15, 16, 18, 19, 21, 22, 24
C. lupulina Muhl. - **I**; 24
C. meadii Dew. - **I**; 13, 14, 15, 17
C. muhlenbergii Schkuhr var. *enervis* Boott. - **I**; 4
C. normalis Mack. - **N**; 24
C. oxylepis Torr. & Hook. - **S**; 13
C. squarrosa L. - **N**; 21, 22, 24
C. tribuloides Wahlenb. - **I**; 22
C. vulpinoidea Michx. - **I**; 6, 21, 22, 24

Cyperus ovularis (Michx.) Torr. - **S**; 22, 24
C. pseudovegetus Steud. - **I**; 24
C. strigosus L. - **I**; 22, 24
Eleocharis compressa Sulliv. - **I**; 11
E. obtusa (Willd.) Schultes - **I**; 22
E. tenuis (Willd.) Schultes - **N**; 11, 22, 24
Fimbristylis autumnalis (L.) R. & S. - **I**; 22, 24
F. puberula (Michx.) Vahl. - **S**; 14, 15
Rhynchospora capitellata (Michx.) Vahl - **I**; 21, 22
R. corniculata (Lam.) Gray - **S**; 22, 24
R. globularis (Chapm.) Small - **S**; 4
Scirpus atrovirens Willd. - **N**; 21, 22
S. pendulus Muhl. - **I**; 11, 15, 21, 24
S. polyphyllus Vahl. - **N**; 24
Scleria oligantha Michx. - **S**; 5, 6, 11, 13, 15, 16, 24
S. pauciflora Muhl. - **S**; 4, 10, 19, 20, 21, 24
S. triglomerata Michx. - **I**; 13

Dioscoreaceae
Dioscorea quaternata (Walt.) J. F. Gmel. - **S**; 15

Ebenaceae
Diospyros virginiana L. - **I**; 1, 3, 4, 10, 11, 12, 13, 14, 15, 16, 18, 19, 20, 21, 22, 23

Ericaceae
Oxydendrum arboreum (L.) DC. - **S**; 1, 19, 20
Vaccinium arboreum Marsh. - **S**; 4, 10, 11, 14, 15, 16, 20, 23
V. atrococcum (Gray) Heller - **I**; 4
V. stamineum L. - **I**; 4, 10

Euphorbiaceae
Acalypha graciliens Gray - **I**; 13, 15
Croton monanthogynus Michx. - **S**; 3, 8, 10, 11, 12, 13, 14, 15, 16, 23
Crotonopsis elliptica Willd. - **S**; 16
Euphorbia corollata L - **I**; 1, 2, 3, 4, 7, 8, 10, 11, 12, 14, 15, 16, 19, 20, 21, 22, 23, 24
E. dentata Michx. - **I**; 13, 15, 17, 19, 22
E. maculata L. - **I**; 4, 8, 10, 11, 12, 13, 14, 15, 17, 22
Phyllanthus caroliniensis Walt. - **S**; 24

Fabaceae
Amphicarpa bracteata (L.) Fern. - **I**; 22, 24
Apios americana Medic. - **I**; 1, 6, 22, 24
Astragalus canadensis L. - **N**; 8, 24
Baptisia alba (L.) Vent. var. *macrophylla* (Lairsey) Isely - **W**; 21, 22, 24
Chamaecrista fasciculata (Michx.) Greene - **I**; 4, 8, 15, 20, 21, 22, 24
Cercis canadensis L. - **I**; 2, 8, 10, 11, 12, 13, 14, 15, 16, 17, 23
Clitoria mariana L. - **S**; 4, 19
Desmodium canescens (L.) DC. - **I**; 22
D. ciliare (Muhl.) DC. - **I**; 4, 8, 9, 10, 12, 14, 16, 19, 20
D. dillenii Darl. - **I**; 16
D. marilandicum (L.) DC. - **I**; 19, 21, 22
D. paniculatum (L.) DC. - **I**; 22
D. rotundifolium DC. - **I**; 13
D. sessilifolium (Torr.) T. & G. - **I**; 21, 22
Galactia volubilis (L.) Britt. - **S**; 4, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 19

Gleditsia triacanthos L - **I**; 13
Lespedeza capitata Michx. - **I**; 1, 24
L. cuneata (Dumont) G. Don - **X**; 13, 14, 15
L. hirta (L.) Hornem. - **I**; 4, 9, 13, 20
L. intermedia (S. Wats.) Britt. - **I**; 3, 4, 9, 13, 15
L. procumbens Michx. - **I**; 3, 4, 8, 9, 10, 11, 13, 15, 16, 18, 19, 20, 21
L. repens (L.) Bart. - **I**; 4, 13, 15, 16, 19, 21, 23
L. stipulacea Maxim. - **X**; 1, 3, 4, 13, 15
L. striata (Thunb.) H. & A. - **X**; 1, 20
L. virginica (L.) Britt. - **I**; 1, 4, 10, 11, 14, 15, 16, 19, 20, 21, 22, 23, 24
Melilotus alba Desr. - **X**; 10, 11, 15, 16, 17, 22
M. officinalis (L.) Lam. - **X**; 22
Orbexilum pedunculatum (Mill.) Rydb. var. *pedunculatum* - **S**; 1, 3, 6, 14, 15, 22, 24
Robinia pseudo-acacia L. - **I**; 8, 18, 23
Schrankia microphylla (Drylander) Macbr. - **S**; 2, 3, 4, 14, 19
Senna marilandica (L.) Link - **I**; 13, 14, 15, 16
S. nictitans (L.) Moench - **I**; 1, 2, 4, 6, 13, 14, 19, 20, 21
Strophostyles umbellata (Muhl.) Britt. - **S**; 4, 19, 20, 21
Stylosanthes biflora (L.) BSP. - **S**; 2, 3, 4, 10, 11, 13, 15, 16, 17, 19, 20, 21, 22, 24
Tephrosia virginiana (L.) Pers. - **I**; 1, 2, 3, 4, 6, 9, 10, 11, 14, 15, 16, 17, 20
Trifolium campestre Schreb. - **X**; 17

Fagaceae
Fagus grandifolia Ehrh. - **I**; 11
Quercus alba L. - **I**; 1, 3, 11, 14
Q. coccinea Muenchh. - **I**; 4
Q. falcata Michx. - **S**; 1, 4, 13, 16, 17, 20, 21
Q. laurifolia Michx. - **S**; 8
Q. imbricaria Michx. - **N**; 4
Q. marilandica Muenchh. - **S**; 1, 3, 4, 7, 10, 11, 13, 15, 16, 17, 18
Q. muhlenbergii Engelm. - **I**; 8, 10, 11, 12, 13, 15, 16, 17
Q. nigra L. - **S**; 1, 8
Q. palustris Muench. - **I**; 21, 24
Q. phellos L. - **S**; 4, 21, 24
Q. rubra L. - **I**; 13, 23
Q. shumardii Buckl. - **S**; 9, 10, 11, 12, 13, 15
Q. stellata Wang. - **I**; 1, 3, 4, 7, 10, 11, 13, 14, 15, 16, 18, 19, 20, 21, 23
Q. velutina Lam. - **I**; 1, 3, 8, 15

Gentianaceae
Frasera caroliniensis Walt. - **I**; 5, 10, 11, 15, 16
Gentiana saponaria L. - **I**; 24
Sabatia angularis (L.) Pursh - **I**; 3, 4, 5, 12, 19, 20, 21, 22
S. brachiata Ell. - **S**; 14, 15

Geraniaceae
Geranium carolinianum L - **I**; 13, 22

Hamamelidaceae
Liquidambar styraciflua L. - **I**; 1, 10, 19, 21, 22, 24

Iridaceae
Belamcanda chinensis (L.) DC. - **S**; 24
Iris virginica L. - **S**; 22
Sisyrinchium albidum Raf. - **I**; 4, 6, 7, 8, 10, 11, 12, 14, 15, 16, 19, 20, 23

Juglandaceae
Carya carolinae-septentrionalis (Ashe) Engelm & Graeb. - **S**; 13, 15, 18
C. glabra (Mill.) Sweet - **I**; 20, 23
C. ovata (Mill.) K. Koch - **I**; 13
C. pallida (Ashe) Engelm. & Graeb. - **S**; 23
C. tomentosa Nutt. - **I**; 4, 23, 24
Juglans nigra L. - **I**; 13, 15, 16, 23

Juncaceae
Juncus acuminatus Michx. - **I**; 19, 22, 24
J. biflorus Ell. - **I**; 1, 3, 20, 21, 22, 24
J. brachycarpus Engelm. - **I**; 1, 19, 21, 22, 24
J. coriaceus Mack. - **S**; 22
J. dudleyi Wieg. - **N**; 15, 19, 21
J. scirpoides Lam. - **I**; 3, 24
J. secundus Beauv. - **N**; 24
J. tenuis Willd. - **I**; 1, 3, 20, 22, 24
Luzula campestris (L.) DC. - **X**; 13
L. echinata (Small) F. J. Herm. - **S**; 4, 17, 20

Lamiaceae
Blephilia ciliata (L.) Benth. - **I**; 8, 10, 14, 15, 16
Hedeoma hispidum Pursh - **I**; 24
Isanthus brachiatus (L.) BSP. - **I**; 8, 11, 12, 13, 14, 15, 16, 17
Lamium amplexicaule L. - **X**; 22
L. purpureum L. - **X**; 22
Lycopus americanus Muhl. - **I**; 24
Monarda fistulosa L. - **I**; 2, 3, 8, 9, 10, 11, 12, 14, 15, 16, 18, 23, 24
Physostegia virginiana (L.) Benth. - **N**; 8, 10, 11, 12, 14, 15, 16, 17, 24
Prunella vulgaris L. var. *lanceolata* (Bart.) Fern. - **N**; 3, 4, 8, 10, 11, 14, 15, 16, 19, 24
Pycnanthemum loomisii Nutt. - **S**; 3
P. pilosum Nutt. - **W**; 21, 24
P. tenuifolium Schrad. - **S**; 1, 2, 3, 4, 10, 12, 14, 16, 19, 20, 21, 22, 23, 24
P. virginianum (L.) Dur. & Jack. - **N**; 24
Salvia azurea Lam. var. *grandiflora* Benth. - **S**; 10, 11
S. lyrata L. - **I**; 3, 4, 10, 11, 12, 13, 15, 16, 17, 18, 23
S. urticifolia L. - **S**; 10, 11, 12
Scutellaria australis Epl. - **I**; 15, 16
S. elliptica Muhl. - **I**; 19, 20
S. incana Biehler - **I**; 14, 24
S. leonardii Fern.- **I**; 10, 13, 15
S. ovata Hill - **S**; 22
Teucrium canadense L. - **I**; 22, 24
Trichostema dichotomum L. - **S**; 20, 24

Lauraceae
Sassafras albidum (Nutt.) Nees - **I**; 2, 4, 8, 15, 22

Liliaceae
Allium canadense L. - **I**; 11, 15, 23
A. cernuum Roth - **I**; 23
A. vineale L. - **X**; 4, 15, 19, 21, 22
Lilium michiganense Farw. - **N**; 24
Nothoscordum bivalve (L.) Britt. - **S**; 1, 8, 9, 10, 11, 12, 13, 14, 15, 16, 18, 23
Polygonatum canaliculatum (Muhl.) Pursh - **N**; 15, 23

Smilax bona-nox L. - **S**; 4, 23
S. glauca Walt. - **S**; 21, 22
S. rotundifolia L. - **I**; 8, 9, 11, 14
Yucca filamentosa L. - **X**; 11, 15, 17

Linaceae
Linum medium (Planch.) Britt. - **I**; 3, 4, 19, 21, 23, 24
L. sulcatum Riddell - **S**; 5, 9, 10, 11, 12, 13, 14, 15, 16, 17
L. virginianum L. - **I**; 15

Lobeliaceae
Lobelia cardinalis L. - **I**; 22
L. puberula Michx. - **S**; 19, 20, 21, 22, 24
L. spicata Lam. - **S**; 7, 8, 9, 10, 11, 12, 14, 15, 16, 17, 19, 24

Lythraceae
Lythrum alatum Pursh - **I**; 15, 24

Magnoliaceae
Liriodendron tulipifera L. - **I**; 7, 17, 19

Malvaceae
Hibiscus moscheutos L. - **S**; 22
Sida elliottii T. & G. - **S**; 8, 9, 17
S. spinosa L. - **X**; 19

Melastomataceae
Rhexia mariana L. - **S**; 1, 21, 22, 24
R. virginica L. - **N**; 1

Menispermaceae
Cocculus carolinus (L.) DC. - **S**; 13

Moraceae
Morus rubra L. - **I**; 9, 13, 15

Nyssaceae
Nyssa sylvatica Marsh. - **I**; 1, 3, 13, 15, 19, 20, 21

Oleaceae
Fraxinus americana L. - **I**; 5, 8, 9, 10, 11, 13, 15, 16, 19, 20
Ligustrum vulgare L. - **X**; 12, 13

Onagraceae
Gaura biennis L. - **N**; 10, 24
G. filipes Spach - **S**; 5, 10, 11, 12, 14, 15, 16, 17
Ludwigia alternifolia L. - **I**; 22, 24
Oenothera biennis L. - **I**; 4, 19, 22, 24
O. fruticosa L. subsp. *glauca* (Michx.) Straley - **I**; 4, 21, 24
O. laciniata Hill - **I**; 22
O. speciosa Nutt. - **W**; 24
O. tetragona Roth - **N**; 10, 11

Orchidaceae
Platanthera lacera (Michx.) G. Don - **I**; 21
P. peramoena (Gray) Gray - **I**; 21, 22
Spiranthes cernua (L.) Richard - **I**; 4, 20, 21, 24
S. gracilis (Bigel.) Beck - **I**; 24
S. vernalis Engelm. & Gray - **S**; 19, 22, 24

Oxalidaceae
Oxalis stricta L. - **I**; 4, 14, 22
O. violacea L. - **I**; 4, 13, 14, 17, 24

Passifloraceae
Passiflora incarnata L. - **S**; 22
P. lutea L. - **I**; 11

Phrymaceae
Phryma leptostachya L. - **I**; 24

Phytolaccaceae
Phytolacca americana L. - **I**; 22

Plantaginaceae
Plantago aristata Michx. - **W**; 1, 4, 9, 13
P. lanceolata L. - **X**; 3, 15
P. virginica L. - **I**; 3, 4, 11, 13, 15, 22

Plantanaceae
Platanus occidentalis L. - **I**; 6, 9

Poaceae
Agrostis alba L. - **X**; 21, 22
A. hiemalis (Walt.) BSP. - **I**; 2, 4, 10
A. perennans (Walt.) Tuckerm. - **I**; 4, 20, 24
Andropogon gerardii Vitman - **I**; 1, 2, 4, 5, 8, 10, 11, 12, 14, 15, 16, 21, 22, 24
A. gyrans Ashe - **S**; 1, 3, 4, 8, 19, 20, 21, 22, 24
A. ternarius Michx. - **S**; 2, 4, 20, 21
A. virginicus L. - **I**; 2, 4, 8, 16, 18, 21, 22, 23, 24
Aristida dichotoma Michx. - **I**; 1, 4
A. lanosa Muhl. - **S**; 4
A. longespica Poir. - **I**, 11, 19, 20, 21, 24
A. oligantha Michx. - **I**; 1, 4, 14, 20
A. purpurascens Poir. - **I**; 4, 14, 16, 19, 20, 21, 24
A. virgata Trin. - **S**; 24
Bromus commutatus Schrad./*B. racemosus* L. - **X**; 13, 15, 16, 22
B. japonicus Thurb. - **X**; 2, 3, 4, 13, 15
B. tectorum L. - **X**; 15
Chasmanthium latifolium (Michx.) H. O. Yates - **I**; 5
C. laxum (L.) H. O. Yates - **S**; 1, 7
C. sessilifolium (Poir.) H. O. Yates - **S**; 13, 15, 17
Cinna arundinacea L. - **I**; 22
Dactylis glomerata L. - **X**; 13
Danthonia spicata (L.) Beauv. - **I**; 1, 3, 4, 6, 8, 10, 11, 13, 15, 16, 18, 19, 23, 24
Elymus virginicus L. var. *glabriflorus* (Vasey) Bush - **I**; 1, 2, 13, 21, 22, 24
Eragrostis capillaris (L.) Nees - **I**; 21, 22
E. frankii C. A. Mey. - **I**; 15

Eragrostis hirsuta (Michx.) Nees - **S**; 19
E. spectabilis (Pursh) Steud. - **I**; 1, 4, 9, 13, 15, 19, 20, 21, 22, 24
Erianthus alopecuroides (L.) Ell. - **S**; 24
Festuca arundinacea Schreb. - **X**; 13, 16
Glyceria striata (Lam.) Hitchc. - **I**; 15, 22
Gymnopogon ambiguus (Michx.) BSP. - **S**; 4, 15, 20
Hordeum pusillum Nutt. - **S**; 15
Leersia oryzoides (L.) Swartz - **I**; 24
L. virginicus Willd. - **I**; 24
Melica mutica Walt. - **I**; 19
Muhlenbergia frondosa (Poir.) Fern. - **I**; 22
M. glabriflora Scribn. - **S**; 24
M. mexicana (L.) Trin. - **N**; 24
M. schreberi Gmel. - **I**; 24
M. tenuiflora (Willd.) BSP. - **N**; 13
Panicum agrostoides Spreng. - **S**; 22
P. anceps Michx. - **S**; 4, 8, 13, 14, 15, 19, 20, 21, 22, 24
P. angustifolium Ell. - **S**; 4
P. boscii Poir. - **I**; 11, 13, 14, 15, 16, 23
P. capillare L. - **I**; 20, 22, 24
P. commutatum Schultes - **I**; 5, 6, 13, 15, 16, 21
P. depauperatum Muhl. - **I**; 3, 4, 11, 13, 15, 16, 19, 23
P. dichotomum L. - **I**; 6, 18
P. flexile (Gattinger) Scribn. - **I**; 9, 10, 13, 14, 15
P. lanuginosum Ell. - **I**; 4, 6, 8, 9, 13, 14, 15, 19, 21, 22
P. laxiflorum Lam. - **S**; 4, 5, 13, 15, 16, 17, 18, 19, 20, 23
P. longiligulatum Nash - **S**; 21
P. malacophyllum Nash - **S**; 1, 15
P. microcarpon Muhl. - **I**; 1, 10, 13, 19, 20, 21, 22, 23, 24
P. oligosanthes Schultes - **S**; 4
P. philadelphicum Bernh. - **I**; 24
P. polyanthes Schultes - **I**; 19, 21, 24
P. scoparium Lam. - **I**; 1, 21, 22
P. sphaerocarpon Ell. - **I**; 2, 3, 4, 12, 13, 16, 18
P. verrucosum Muhl. - **I**; 22
P. villosissimum Nash - **I**; 13, 22
P virgatum L. - **I**; 4, 8, 24
Paspalum floridanum Michx. - **S**; 1, 15, 16
P. laeve Michx. - **S**; 4
P. setaceum Michx. var. *muhlenbergii* (Nash) D. Banks - **I**; 4, 13
Poa annua L. - **X**; 15
P. compressa L - **X**; 19
P. pratensis L. - **X**; 13, 22
Schizachyrium scoparium (Michx.) Nash - **I**; all sites
Setaria faberi Herrm. - **X**; 22, 24
S. geniculata (Lam.) Beauv. - **S**; 1, 4, 13, 15, 19, 22
S. viridis (L.) Beauv. - **X**; 22
Sorghastrum nutans (L.) Nash - **I**; 1, 4, 10, 14, 17, 21, 22, 24
Sorgum halepense (L.) Pers. - **X**; 22
Spartina pectinata Link - **W**; 1, 22
Sphenopholis intermedia Rydb. - **I**; 6, 13
S. nitida (Biehler) Scribn. - **I**; 13, 17
S. obtusata (Michx.) Scribn. - **I**; 22
Sporobolus asper (Michx.) Kunth - **I**; 15
S. clandestinus (Biehler) Hitchc. - **I**; 7, 10, 13

Sporobolus neglectus Nash - **I**; 9, 10, 12, 15, 16
S. vaginiflorus (Torr.) Wood - **I**; 7, 8, 11, 13
Tridens flavus (L.) Hitchc. - **I**; 4, 8, 10, 11, 12, 17, 19, 22
T. strictus (Nutt.) Nash - **S**; 24
Tripsacum dactyloides L. - **I**; 24
Vulpia octoflora Walt. - **S**; 1, 4, 21, 22

Polemoniaceae
Phlox amoena Sims - **S**; 5, 14, 15
P. paniculata L - **N**; 24
P. pilosa L. - **I**; 3, 24

Polygalaceae
Polygala ambigua Wood - **I**; 1, 3, 4, 10, 14, 19, 20, 21, 23, 24
P. curtissii Gray - **S**; 4
P. incarnata L. - **I**; 4, 19, 20
P. sanguinea L. - **I**; 19, 21, 22, 24
P. senega L. - **N**; 24
P. verticillata L. - **I**; 11

Polygonaceae
Polygonum coccineum Muhl. - **I**; 24
P. punctatum Ell. - **I**; 22

Primulaceae
Dodecatheon meadia L. - **S**; 23
Lysimachia ciliata L. - **I**; 24

Ranunculaceae
Anemone virginica L. - **I**; 8, 10, 12, 13, 14, 15, 17, 23
Clematis versicolor Small - **L**; 23
C. virginiana L. - **I**; 13
Ranunculus micranthus Nutt. - **S**; 24
R. pusillus Poir. - **S**; 22
Thalictrum revolutum DC. - **N**; 4, 22
T. thalictroides (L.) Eames & Boiv. - **I**; 19

Rhamnaceae
Berchemia scandens (Hill) K. Koch - **I**; 6, 7, 9, 10, 11, 12, 14, 15, 17
Ceanothus americanus L. - **I**; 3, 4, 9, 11, 15, 16, 17, 19, 24
Rhamnus caroliniana Walt. - **S**; 4, 5, 8, 9, 10, 11, 12, 13, 15, 16, 24

Rosaceae
Agrimonia parviflora Ait. - **I**; 13
A. pubescens Wallr. - **I**; 13
Amelanchier arborea (Michx. f.) Fern. - **I**; 10, 12, 13, 23
Crataegus crus-galli L. - **I**; 5, 15
C. viridis L. - **S**; 19
Fragaria virginiana Duch. - **N**; 24
Geum canadensis Jacq. - **N**; 9, 13
G. virginianum L. - **N**; 13
Gillenia stipulacea (Muhl.) Baill. - **I**; 3, 4, 23
Potentilla norvegica L. - **I**; 24
P. simplex Michx. - **I**; 1, 3, 4, 9, 10, 12, 13, 15, 16, 19, 20, 21, 22, 23
Prunus americana Marsh. - **I**; 23, 24

Prunus angustifolia Marsh. - **S**; 8, 15, 20
P. serotina Ehrh. - **I**; 3, 4, 10, 15, 19, 21, 24
Pyrus coronaria L. - **N**; 24
Rosa carolina L. - **I**; 4, 6, 8, 9, 10, 11, 14, 15, 16, 17, 19, 20, 21, 22, 23, 24
R. multiflora Thunb. - **X**; 19
R. setigera Michx. - **I**; 21
Rubus argutus L. - **I**; 19, 20
R. flagellaris Willd. - **I**; 19, 20, 21, 22
Spiraea tomentosa L. - **L**; 21, 24

Rubiaceae
Cephalanthus occidentalis L. - **I**; 22, 24
Diodia teres Walt. - **S**; 1, 4, 17, 19, 20, 21, 22
Galium circaezans Michx. - **I**; 6, 11, 13, 17
G. obtusum Biegel - **I**; 19
G. pilosum Ait. - **I**; 3, 4, 5, 9, 10, 13, 18, 19, 20, 21, 22
G. tinctorium L. - **I**; 1, 22
G. triflorum Michx. - **I**; 24
Houstonia caerulea L. - **I**; 1, 20
H. purpurea L. - **S**; 4, 6, 14, 19, 23
H. purpurea L. var. *calycosa* Gray - **I**; 8, 9, 10, 11, 13, 14, 15, 16
H. pusilla Schoepf - **S**; 13, 20

Salicaceae
Populus deltoides Marsh. - **I**; 1, 4, 22
Salix humilis Marsh. - **I**; 1, 9, 20, 22, 24
S. nigra Marsh. - **I**; 22
S. tristis Ait. - **I**; 1, 4, 6

Santalaceae
Comandra umbellata (L.) Nutt. - **I**; 8, 10, 11, 15, 24

Sapotaceae
Bumelia lycioides (L.) Gaertn. f. - **S**; 8, 13, 23

Saxifragaceae
Heuchera americana L. - **I**; 23
Parnassia grandiflora DC. - **L**; 6

Scrophulariaceae
Buchnera americana L. - **I**; 3, 4, 20
Gerardia gattingeri Small - **I**; 4
G. purpurea L. - **I**; 1, 10, 20
G. tenuifolia Vahl. - **I**; 1, 4, 14, 16, 19, 20, 21, 22, 23, 24
G. tenuifolia Vahl. var. *macrophylla* Benth. - **I**; 4
Mecardonia acuminata (Walt.) Small - **S**; 8, 12, 16
Mimulus alatus Aiton - **I**; 22
Penstemon brevisepalus Pennell - **L**; 10, 11, 13, 15, 16
P. hirsutus (L.) Willd. - **N**; 24
Verbascum thapsus L. - **X**; 11, 13, 17, 22, 23
Veronica arvensis L. - **X**; 13, 15
V. serpyllifolia L. - **X**; 15
Veronicastrum virginicum (L.) Farw. - **I**; 24

Solanaceae
Physalis heterophylla Nees - **I**; 13, 15, 22, 24
P. virginiana Mill. - **I**; 24
Solanum carolinense L. - **I**; 22

Styracaceae
Styrax grandifolia Ait. - **S**; 3, 4, 15

Ulmaceae
Celtis laevigata Willd. - **S**; 10, 11, 12, 13, 15
C. occidentalis L. - **I**; 11, 13, 23
C. tenuifolia Nutt. - **S**; 5, 7, 8, 10, 12, 13, 15, 16, 17
Ulmus alata Michx. - **S**; 8, 9, 10, 11, 13, 14, 15, 16, 21, 23
U. americana L. - **I**; 24
U. rubra Muhl. - **I**; 9, 11, 23

Urticaceae
Tragia cordata Michx. - **S**; 9, 14

Valerianaceae
Valerianella radiata (L.) Dufr. - **I**; 15

Verbenaceae
Callicarpa americana L. - **S**; 8, 16
Verbena hastata L. - **I**; 22
V. simplex Lehm. - **I**; 8, 10, 11, 15, 16, 17, 23
V. urticifolia L. - **I**; 22, 24

Violaceae
Viola cucullata Ait. - **N**; 13, 15, 17
V. pedata L. var. *lineariloba* DC. - **I**; 7, 10, 15, 16, 17
V. sagittata Ait. - **I**; 4
V. sororia Willd. - **N**; 24
V. triloba Schwein. - **I**; 9, 10, 13, 17

Vitaceae
Parthenocissus quinquefolia (L.) Planch. - **I**; 13, 23
Vitis aestivalis Michx. - **I**; 21, 24
V. cinerea Engelm. - **S**; 9
V. rotundifolia Michx. - **S**; 13

Xyridaceae
Xyris tennesseensis Kral - **L**; 6

A REVISED CHECKLIST OF MACROLICHENS IN THE LAND BETWEEN THE LAKES NATIONAL RECREATION AREA OF KENTUCKY AND TENNESSEE

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ABSTRACT. In 1970, H.C. Phillips of Austin Peay State University reported 20 genera and 82 species of fruticose and foliose lichens from the Land Between The Lakes National Recreation Area of Kentucky and Tennessee. In view of the many changes in generic and species concepts in the taxonomy of lichens since 1970, and the discovery of several additional macrolichen species in the LBL during limited field work in 1988, we initiated a new study in order to prepare a revised list of macrolichen species known to occur in LBL. To date our checklist includes 36 genera and 115 species. The revised checklist included in this report is based on an examination of specimens we collected during field work in 1988 and 1992, and on reexamination of Phillips' collections maintained in the Austin Peay State University Herbarium. Over 40 species are reported as new to LBL, mostly species of *Cladonia*, *Collema*, *Leptogium*, *Parmotrema* and *Phaeophyscia*. Not surprisingly, additions to the genera list are due largely to the division of heterogeneous genera such as *Parmelia* sensu lato and *Physcia* sensu lato by taxonomists into smaller, more homogeneous genera. Work continues on some of the specimens.

INTRODUCTION

During the mid to late 1960s, Haskell Phillips of Austin Peay State University studied the fruticose and foliose lichens of the Land Between the Lakes National Recreation Area (LBL) of Kentucky and Tennessee. In his well documented, annotated checklist published in 1970, Phillips reported 82 species and 20 genera of fruticose and foliose lichens from LBL. Phillip's illustrated booklet on "Lichens and Ferns of Land Between The Lakes" was subsequently published in 1974. One of us, J.P. Dey, briefly visited LBL in 1988 to sample lichens growing on calcareous substrates and noted the presence of several species not found by Phillips. In view of the discovery of additional species in the LBL, and the many changes in generic and species concepts in the taxonomy of lichens which have occurred since Phillips' studies, we initiated a new study of the macrolichens of the LBL. Our purposes were to provide an updated species list of LBL macrolichens that would be useful to managers as part of the inventory of the LBL biota, to provide data which could be used by lichen biogeographers to update the distributional ranges of lichens, and to provide a macrolichen species list which would be useful to anyone contemplating doing future air quality monitoring work in LBL, utilizing lichens as biomonitors.

THE STUDY AREA

The Land Between the Lakes National Recreation Area is an elongate, north-south peninsula between two reservoirs--Kentucky Lake (the impounded lower Tennessee River) and

Lake Barkley (the impounded lower Cumberland River). The LBL is located in parts of Lyon and Trigg counties in southwestern Kentucky and part of Stewart County in northwestern Tennessee. The backbone of the peninsula is a relatively even, north-south ridge whose highest elevation is approximately 200 m above sea level in the southernmost LBL and which gradually decreases to below 150 m in the north. The elevation of the reservoirs is generally 109 m. Erosion along closely-spaced streams on the flanks of the central ridge has created a dissected topography. The valleys are short with steep gradients in the headwaters and often include broad bottomlands downstream (Harris 1988). Bedrock consists mainly of cherty limestones. Natural exposures or limestone are uncommon, occurring mainly along the lake shores and along some stream channels. Layers of cherty gravels of Cretaceous and Tertiary-Quaternary ages topped by Pleistocene silty loess cover the underlying rock formations. Soils derived from parent materials are low in nutrients. Bottomland soils are composed of fluvial sediments derived from erosion of the upland (Harris 1988).

Average rainfall is approximately 1173 mm per year and is equally divided between summer and winter. Average winter temperature is 3° C; average summer temperature is 24° C. Prevailing wind is out of the southwest (Fralish & Crooks 1988).

Before purchase by the Tennessee Valley Authority (TVA) in 1964, portions of the land were non-forested due to periodic fires and/or clearing for farming or grazing. Many of the extensive forest areas were selectively cut for building lumber or for fuel wood used in the former iron and moonshine industries (Fralish & Crooks 1989). While some farming of bottom land, grazing activities, and timber harvests are being allowed under current TVA resource management, most of the abandoned homestead sites and farm/grazing acreage is succeeding back to forests.

Recent data on the forest communities of LBL can be found in the studies and summaries of Fralish and Crooks (1988, 1989), Carpenter and Chester (1988), and Chester and Ellis (1989). Upland dry ridge forests are open and dominated mostly by xerophytic oaks (*Quercus coccinea*, *Q. marilandica*, *Q. prinus*, *Q. stellata*, and *Q. velutina*). Hickories such as *Carya glabra*, *C. pallida*, and *C. tomentosa* are usually present, along with *Amelanchier arborea*, *Nyssa sylvatica*, and *Oxydendrum arboreum*. Ericaceous shrubs dominate the understory (Chester & Ellis 1989). In the southernmost areas yellow pine-mixed hardwoods stands dominated by *Pinus echinata*, the xerophytic oaks (mentioned previously), *Oxydendrum arboreum*, and *Nyssa sylvatica* are interspersed on dry, cherty backbones of the Tennessee Ridge and the Devil's Backbone area (Fralish & Crooks 1989).

Except for the most mesic north facing slopes, oaks dominate all slope community types. Drier slopes are dominated by various combinations of *Quercus falcata*, *Q. rubra*, *Q. stellata*, and/or *Q. velutina*, usually with two or more hickories and other hardwoods species. Drier site understories usually include *Cercis canadensis*, *Cornus florida*, and *Ostrya virginiana* (Chester & Ellis 1989). *Quercus alba* dominates moderately mesic slopes with the other oaks collectively being less important. While *Quercus alba* dominated communities are stable at many sites, Fralish & Crooks (1988) noted that periodic disturbances have enabled *Quercus alba* communities to occupy nearly all upland slopes where soil conditions are suitable for their existence. They predict that the highly productive, low, north and northeast facing slope stands will succeed to mesophytic hardwoods dominated by *Acer saccharum* and *Fagus grandifolia*. Mesophytic forests are already found on many of the most mesic, usually north facing slopes and non-flood ravines. Besides *Acer saccharum* and *Fagus grandifolia*, other dominants often include species such as *Carya cordiformis*, *C. ovata*, *Fraxinus americana*, *Juglans nigra*, *Liriodendron tulipifera*, *Nyssa sylvatica*, *Prunus serotina*, *Quercus alba* and other oaks (Carpenter & Chester 1988, Chester & Ellis 1989).

Xeric bluffs above bottomlands and the two major reservoirs/rivers support *Juniperus virginiana*-mixed hardwoods communities with hickories, ashes, oaks, and elms most often seen. The xeric bluffs west of the central, north-south ridge generally include a higher proportion of oaks and hickories than those east of the central ridge. A *Pinus virginiana*-mixed hardwoods community occurs on some west facing xeric bluffs (Chester & Ellis 1989). Only remnants of bottomland and streambank forests remain and usually include the following taxa: *Acer negundo*, *A. rubrum*, *A. saccharinum*, *Betula nigra*, *Carpinus caroliniana*, *Carya cordiformis*, *C. ovata*, *C. laciniosa*, *Celtis laevigata*, *C. occidentalis*, *Fraxinus americana*, *F. pennsylvanica.*, *Gleditsia triacanthos*, *Juglans nigra*, *Liquidamber styraciflua*, *Platanus occidentalis*, *Populus deltoides*, more mesic *Quercus* spp., *Salix nigra*, *Ulmus americana* and *U. rubra* (Carpenter & Chester 1988, Chester & Ellis 1989). There are some *Pinus strobus* and *P. taeda* plantations in LBL also.

METHODS

A series of short visits of 1/2 to 3 hours each were made to over 57 LBL localities in June, 1988 (Dey) and in June and July, 1992 (Dey & Eyer). Sites were selected to explore representative habitats of the region, including limestone outcrops, cemeteries, roadbanks, and a diversity of forest communities. Some of the sites visited by Phillips in the 1960s were revisited in an attempt to relocate some species he had found. At most sites a sample of macrolichens was taken for laboratory examination and identification, but no attempt was made to collect all available species at each locality. Voucher specimens are deposited at Illinois Wesleyan University.

All macrolichen specimens deposited by Phillips in the Austin Peay State University Herbarium were examined to verify identifications. Specimens requiring closer examination, chemical spot testing and/or chromatographic testing were borrowed for further study at Illinois Wesleyan University.

Identifications were carried out at Illinois Wesleyan University. Specimens were examined with a dissecting microscope for gross morphological characters (and for thallus chemical spot testing observations). When necessary, a compound microscope was used to examine free-hand thin sections of vegetative structures, such as lobes for cortical anatomy, or sexual reproductive structures, such as apothecia for ascospore septation patterns. Determination of chemical characters of the thalli aided the identification of species in many groups. Both the upper cortex and the medullary zone beneath the algal layer of individual thalli were tested with chemical reagents [such as a 10% potassium hydroxide solution (K reagent), a sodium hypochloride solution (C reagent) and a para-phenylenediamine in alcohol solution (PD reagent)] to look for color changes which are indicative of the presence of secondary metabolic products (Hale 1972). Standardized thin-layer chromatographic techniques (Culberson & Kristinsson 1970) were used to verify the identity of specific substances.

RESULTS AND DISCUSSION

Based on our examination of Phillips' specimens and our collections, we have identified to date 115 macrolichen species in 36 genera in LBL (Appendix 1). In addition to the species listed, several specimens remain to be identified. Forty-one species represent taxa new to LBL (labelled N in Appendix 1). Seven additional species new to LBL represent taxa which were recognized by Phillips under different names (labelled PN in Appendix 1). However, with taxonomic refinements the names of the seven taxa used by Phillips are now recognized as valid species occurring elsewhere in the United States, and the LBL specimens seen by Phillips must be assigned to different, often more recently described, species. Specimens recognized as *Physcia orbicularis* by Phillips are similarly now identified to several other species as a result of taxonomic refinements. Seven other species recognized by Phillips could not be verified from LBL collections.

Of the many species added to the known macrolichen flora of LBL during this study, most are species of *Cladonia*, *Collema*, *Leptogium*, *Parmotrema*, and *Phaeophyscia* (see Appendix 1 & 2). The additions to the list of genera are largely due to the division of heterogeneous genera such as *Parmelia* sensu lato and *Physcia* sensu lato by taxonomists into smaller, more homogeneous genera since 1970 (Appendix 2).

As Phillips (1970) noted, the most abundant growth and coverage of lichens occurs at sites and on suitable substrates where there is sufficient but not excessive light and where adequate precipitation/moisture regimes exist. In dense, closed-canopied forests, corticolous lichens, occurring on the bark of trees, are rare and less abundant on the completely shaded lower branches and trunks of trees (readily accessible to collectors). However, recently fallen canopy branches of trees found in such forests sometimes indicate a good macrolichen flora growing on the less shaded upper branches. In contrast, the best areas for corticolous lichens will be within the more open-canopied forests such as those dominated by xeric oaks on ridges and upper slopes, or on forest trees along the ecotone to open spaces such as fields, roads, cemeteries, picnic areas, etc., or on isolated trees in open areas. Lichens are often abundant from the tops of the trees all the way down the tree to the ground.

Lichens are much more common and abundant on hardwood trees than on conifers. Macrolichens occurring on hardwoods include *Anaptychia palmulata*, *Anzia colpodes*, *Candelaria concolor*, *C. fibrosa*, *Canoparmelia crozalsiana*, *C. texana*, *Catapyrenium tuckermanii*, *Cladonia* spp., *Coccocarpia palmicola*, *Collema conglomeratum*, *C. subflaccidum*. *Flavoparmelia caperata*, *Heterodermia albicans*, *H. hypoleuca*, *H. obscurata*, *H. speciosa*, *Hyperphysica syncolla*, *Hypotrachyna livida*, *Leptogium austroamericanum*, *L. burnetiae*, *L. cyanescens*, *L. millegranum*, *Myelochroa aurulenta*, *M. galbina*, *Pannaria lurida*, *P. tavaresii*, *Parmelia squarrosa*, *Parmelinopsis mniarum*, many *Parmotrema* spp., *Phaeophyscia adiastola*, *P. imbricata*, *P. pusilloides*, *P. rubropulchra*, *Physcia aipolia*, *P. americana*, *P. millegrana*, *P. stellaris*, *Physciella chloantha*, *Pseudocyphellaria aurata*, *Punctelia missouriensis*, *P. rudecta*, *P. subrudecta*, *Pyxine albovirens*, *P. sorediata*, *Ramalina americana*, *Rimelia cetrata*, *R. reticulata*, *R. subisidiosa*, *Usnea mutabilis*, *U. rubicunda*, *U. strigosa*, *Vulpicida viridis*, and *Xanthoria candelaria*. Macrolichens occurring on pines are infrequent and include occasional *Canoparmelia caroliniana*, *Cladonia* spp., *Flavoparmelia caperata*, *Hypotrachyna livida*, various *Parmotrema* spp., and *Punctelia rudecta*. Macrolichens are more common on cedars than on pines and include *Candelaria concolor*, *Canoparmelia* sp., *Myelochroa aurulenta*, *Parmotrema hypotropum*, *Phaeophyscia adiastola*, *P. pusilloides*, *P. rubropulchra*, *Physcia americana*, *P. millegrana*, *Physciella chloantha*, *Physconia detersa*, *Pyxine caesiopruinosa*, and *Xanthoria candelaria*.

In LBL, the best sites for soil macrolichens are: disturbed areas along roadsides, such as roadbanks not covered by dense grasses, the open edges of forests adjacent to roads, and open forests on ridges. *Baeomyces fungoides*, *Cladina subtenuis*, *Cladonia apodocarpa*, *C. caespiticia*, *C. chlorophaea*, *C. cristatella*, *C. dimorphoclada*, *C. grayii*, *C. peziziformis*, *C. piedmontensis*, *C. pleurota*, *C. polycarpoides*, *C. strepsilis*, *Peltigera canina*, *P. elizabethae*, *P. polydactyla*, and *P. praetextata* are examples. Macrolichens growing on decaying wood include *Cladonia bacillaris*, *C. cristatella*, *C. macilenta*, and *C. squamosa*. These species also occur on soil.

Exposed rock surfaces, mainly limestone, are less common and where they do occur the semishaded rocks are better for lichen growth than either densely shaded or totally exposed rocks. *Collema fuscovirens*, *C. pustulatum*, *Dematocarpon miniatum*, *Leptogium dactylinum*, *L. lichenoides*, *Phaeophyscia ciliata*, *P. imbricata*, and *P. insignis*, among others, occur on limestone rock. Saxicolous macrolichens occuring on non-calcarous rocks include *Flavoparmelia* cf. *baltimorensis*, *F. caperata*, *Phaeophyscia* spp., *Physcia subtilis*, *Physconia detersa*, *Punctelia rudecta*, *Xanthoparmelia cumberlandia*, and *X. hypomeleana*.

Cemeteries are scattered throughout LBL and grave headstones provide locally abundant lichen substrates. The headstones include limestone and various non-calcareous types of stone. In semishaded locations and/or on the semishaded surfaces of otherwise totally exposed headstones, saxicolous macrolichens often flourish. Included are *Candelaria concolor*, *Physcia* spp., *Phaeophyscia* spp. (such as *P. adiastola*, *P. ciliata*, *P. hirtella*, *P. kairamoi*, and *P. rubropulchra*), *Physciella chloantha*, *Physconia detersa*, and *Xanthoria candelaria*.

If attempts are ever made to initiate an air quality monitoring system in LBL, macrolichens could be useful as biomonitors. It has been well documented--as a result of studies showing correlations between lichen distributions and different level of air pollutants, as a result of studies involving the transplantation of healthy lichens into polluted and non-polluted sites, and as a result of laboratory and field fumigation studies on lichens--that lichens are differentially sensitive to air pollutants (see Nash & Wirth, 1988 and reviews by Nash, 1976, and Richardson, 1988). Among the measured effects of pollutants on lichens are visible changes in individual thalli (decreased size, decreased fertility, decay, death), increased accumulation of heavy metals and elements in thalli, physiological changes in thalli (decreased photosynthesis, decreased respiration, etc.), ultrastructural changes in thalli, and changes in lichen community structure (decreased numbers of species, decreased abundances of species, etc.). In fact, lichens are being used as biomonitors of air quality in several European countries as well as in the United States. It is interesting to note that mapping studies utilizing lichens as air quality biomonitors in London (Hawksworth & McManus 1989, Rose & Hawksworth 1981) and Ohio (Showman 1981) have documented recolonizations of previously highly polluted areas by pollution sensitive lichens as local air quality conditions have improved. In recent years in the United States the Air Quality Division of the National Park Service has funded baseline studies utilizing lichens as biomonitors of air quality in Air Quality Class I National Parks and Recreation Areas. Similarly, various federal agencies [U.S. Environmental Protection Agency (EPA), U.S. Forest Service, Tennessee Valley Authority, etc.] are currently funding "lichens as biomonitors" work as a part of the demonstration projects in the southeastern United States, the southern Appalachians, Colorado, and California as part of the Forest Health Monitoring Program of the Environmental Monitoring and Assessment Program of the EPA.

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Appendix 1. A revised checklist of macrolichens of the LBL. Species recognized are listed in **boldtype**. Additional names used by Phillips (1970) are listed in *italics*. The first column indicates the status of the species in the revised LBL macrolichen checklist: P=species recognized by Phillips, N=species new to the LBL, PN=species new to LBL (taxa recognized by Phillips but species in Phillips (1970) occur elsewhere in United States and are no longer recognized in the LBL). The nomenclature follows Egan (1988, 1989, 1990 & 1991) except where noted.

P **Anaptychia palmulata** (Michaux) Vainio
P **Anzia colpodes** (Ach.) Stizenb.
P **Baeomyces fungoides** (Swartz) Ach.--Syn: *Baeomyces roseus* Pers.; See nomenclatural note in Egan (1988); Known in LBL from Phillips single collection of immature material. Phillips original collecting site was revisited, but the species was not found there in 1992.
Baeomyces roseus Pers.=*Baeomyces fungoides* (Swartz) Ach.
N **Bulbothrix goebelii** (Zenker) Hale--Known in the LBL only from one of Phillips' collections.
P **Candelaria concolor** (Dickson) B. Stein
P **Candelaria fibrosa** (Fr.) Müll. Arg.
P **Canoparmelia caroliniana** (Nyl.) Elix & Hale--Syn.: *Parmelia caroliniana* Nyl.
P **Canoparmelia crozalsiana** (B. de Lesd. *ex* Harm.) Elix & Hale--Syn.: *Parmelia crozalsiana* B. de Lesd. *ex* Harm
P **Canoparmelia texana** (Tuck.) Elix & Hale--Syn.: *Parmelia texana* Tuck.
P **Catapyrenium tuckermanii** (Rav. *ex* Mont.) Thomson--Syn.: *Dermatocarpon tuckermanii* (Rav.*ex* Mont.) Zahlbr.
Cetraria juniperina (L.) Ach.=*Vulpicida viridis* (Schwein. *in* Halsey) E.-E. Mattsson & Lai
Cetraria viridis Schwein. *in* Halsey (Phillips, 1974)=*Vulpicida viridis* (Schwein. *in* Halsey) E.-E. Mattsson & Lai
P **Cladina subtenuis** (des Abb.) Hale & Culb.--Syn.: *Cladonia subtenuis* (des Abb.) Evans; Some forms might be confusing because they have low concentrations of usnic acid and do not appear very yellowish; Some specimens appear to have windswept branching patterns similar to *C. arbuscula* (Wallr.) Hale & Culb. but they differ from that species by having red pycnidial jelly and by lacking axillary pores.
P **Cladonia apodocarpa** Robb.
P **Cladonia bacillaris** Nyl.
P **Cladonia caespiticia** (Pers.) Flörke
Cladonia capitata (Michaux) Spreng.=*Cladonia peziziformis* (With.) Laundon
Cladonia caroliniana (Schwein.) Tuck. in the LBL=*Cladonia dimorphoclada* Robb.
P **Cladonia cervicornis** (Ach.) Flotow **subsp.*verticillata*** (Hoffm.) Ahti--Syn.: *Cladonia verticillata* (Hoffm.) Schaer.
P **Cladonia chlorophaea** (Flörke *ex* Sommerf.) Spreng.
P **Cladonia coniocraea** (Flörke) Spreng.
P **Cladonia cristatella** Tuck.
N **Cladonia cryptochlorophaea** Asah.
N **Cladonia cylindrica** (Evans) Evans
PN **Cladonia dimorphoclada** Robb.--As *Cladonia caroliniana* (Schwein.) Tuck. in the LBL.
Cladonia floerkeana (Fr.) Somm.=misidentification
N **Cladonia furcata** (Huds.) Schrader

Appendix 1 (continued)

N	***Cladonia grayi*** G.K. Merr. *ex* Sandst.
P	***Cladonia macilenta*** Hoffm.
	Cladonia pyxidata (L.) Hoffm.=misidentification
P	***Cladonia peziziformis*** (With.) Laundon--Syn.: *Cladonia capitata* (Michaux) Spreng.
N	***Cladonia piedmontensis*** G.K. Merr.
N	***Cladonia pleurota*** (Flörke) Schaerer
N	***Cladonia polycarpoides*** Nyl. *in* Zwackh
N	***Cladonia ramulosa*** (With.) Laundon--Until recently known as *Cladonia pityrea* (Flörke) Schaerer.
	Cladonia rangiferina (Scop.) Wigg.=misidentifications
N	***Cladonia sobolescens*** (Nyl.) Vainio--Until recently known as *Cladonia clavulifera* Vainio *in* Robb.
P	***Cladonia squamosa*** (Scop.) Hoffm.
P	***Cladonia strepsilis*** (Ach.) Vainio
	Cladonia subtenuis (des Abb.) Evans=*Cladina subtenuis* (des Abb.) Hale & Culb.
	Cladonia verticillata (Hoffm.) Schaer.=*Cladonia cervicornis* (Ach.) Flotow subsp.*verticillata* (Hoffm.) Ahti
	Coccocarpia cronia (Tuck.) Vainio=*Coccocarpia palmicola* (Sprengel) Arvidsson & D. Galloway
P	***Coccocarpia palmicola*** (Sprengel) Arvidsson & D. Galloway--Syn.: *Coccocarpia cronia* (Tuck.) Vain.
N	***Collema coccophorum*** Tuck.
P	***Collema conglomeratum*** Hoffm.
N	***Collema furfuraceum*** (Arnold) Du Rietz
N	***Collema fuscovirens*** (With.) Laundon--Until recently known as *Collema tuniforme* (Ach.) Ach.
N	***Collema pustulatum*** Ach.
N	***Collema subflaccidum*** Degel.
N	***Collema tenax*** *(Swartz) Ach.*
P	***Dermatocarpon miniatum*** (L.) Mann.
	Dermatocarpon tuckermanii (Rav. *ex* Mont.) Zahlbr.=*Catapyrenium tuckermanii* (Rav. *ex* Mont.) Thomson
N	***Flavoparmelia*** **cf. *baltimorensis*** (Gyelnik & Fóriss) Hale
P	***Flavoparmelia caperata*** (L.) Hale--Syn.: *Parmelia caperata* (L.) Ach.
P	***Heterodermia albicans*** (Pers.) Swinscow & Krog--Syn.: *Heterodermia domingensis* (Ach.) Trevisan
	Heterodermia domingensis (Ach.) Trevisan=*Heterodermia albicans* (Pers.) Swinscow & Krog
P	***Heterodermia hypoleuca*** (Muhl.) Trevisan
P	***Heterodermia obscurata*** (Nyl.) Trevisan
P	***Heterodermia speciosa*** (Wulfen) Trevisan--Syn.: *Heterodermia tremulans* (Müll. Arg.) W. Culb.
	Heterodermia tremulans (Müll. Arg.) W. Culb.=*Heterodermia speciosa* (Wulfen) Trevisan
N	***Hyperphyscia syncolla*** (Tuck. *ex* Nyl.) Kalb.
P	***Hypotrachyna livida*** (Taylor) Hale--Syn.: *Parmelia livida* Taylor
N	***Leptogium austroamericanum*** (Malme) Dodge
PN	***Leptogium burnetiae*** Dodge--As *Leptogium saturinum* (Dickson) Nyl. in the LBL
P	***Leptogium chloromelum*** (Swartz *ex* Ach.) Nyl.
P	***Leptogium cyanescens*** (Rabenh.) Körber

Appendix 1 (continued)

N	***Leptogium dactylinum*** Tuck.
N	***Leptogium juniperinum*** Tuck.
P	***Leptogium lichenoides*** (L.) Zahlbr.
N	***Leptogium millegranum*** Sierk
	Leptogium saturinum (Dickson) Nyl. in the LBL=*Leptogium burnetiae* Dodge
P	***Myelochroa aurulenta*** (Tuck.) Elix & Hale--Syn.: *Parmelia aurulenta* Tuck.
P	***Myelochroa galbina*** (Ach.) Elix & Hale--Syn.: *Parmelia galbina* Ach.
P	***Pannaria lurida*** (Mont.) Nyl.
N	***Pannaria tavaresii*** P. Jørg.
	Parmelia aurulenta Tuck.=*Myelochroa aurulenta* (Tuck.) Elix & Hale
	Parmelia bolliana Müll. Arg.=misidentifications
	Parmelia borreri (Sm.) Turn.=*Punctelia borreri* (Sm.) Krog
	Parmelia caperata (L.) Ach.=*Flavoparmelia caperata* (L.) Hale
	Parmelia caroliniana Nyl.=*Canoparmelia caroliniana* (Nyl.) Elix & Hale
	Parmelia cetrata Ach.=*Rimelia cetrata* (Ach.) Hale & Fletcher
	Parmelia crozalsiana B. de Lesd. *ex* Harm.=*Canoparmelia crozalsiana* (B. de Lesd. *ex* Harm.) Elix & Hale
	Parmelia cryptochorophaea Hale=misidentifications
	Parmelia cumberlandia (Gyelnik) Hale=*Xanthoparmelia cumberlandia* (Gyelnik) Hale
	Parmelia dilatata Vainio in the LBL=*Parmotrema gardnerii* (Dodge) Sérusiaux
	Parmelia dissecta Nyl.=*Parmelinopsis miniarum* (Vainio) Elix & Hale
	Parmelia galbina Ach.=*Myelochroa galbina* (Ach.) Elix & Hale
	Parmelia hypotropa Nyl.=*Parmotrema hypotropum* (Nyl.) Hale
	Parmelia livida Hoffm.=*Hypotrachyna livida* (Taylor) Hale
	Parmelia margaritata Hue=*Parmotrema margaritatum* (Hue) Hale
	Parmelia mellissii Dodge=misidentifications
	Parmelia michauxiana Zahlbr.=*Parmotrema michauxianum* (Zahlbr.) Hale
	Parmelia obsessa Ach.=misidentification
	Parmelia perforata (Jacq.) Ach.=*Parmotrema perforatum* (Jacq.) Massal.
	Parmelia rampoddensis Nyl.=*Parmotrema rampoddense* (Nyl.) Hale
	Parmelia reticulata Taylor *in* Mack.=*Rimelia reticulata* (Taylor *in* Mack.) Hale & Fletcher
	Parmelia rudecta Ach.=*Punctelia rudecta* (Ach.) Krog
	Parmelia saxatilis (L.) Ach. in the LBL=*Parmelia squarrosa* Hale
PN	***Parmelia squarrosa*** Hale--As *Parmelia saxatilis* (L.) Ach. in the LBL
	Parmelia subcrinta Nyl. in the LBL=*Parmotrema ultralucens* (Krog) Hale
	Parmelia subisidiosa (Müll. Arg.) Dodge=*Rimelia subisidiosa* (Müll. Arg.) Hale & Fletcher
	Parmelia subtinctoria Zahlbr.=*Parmotrema subtinctorium* (Zahlbr.) Hale
	Parmelia texana Tuck.=*Canoparmelia texana* (Tuck.) Elix & Hale
	Parmelia tinctorum Delise *ex* Nyl.=*Parmotrema tinctorum* (Delise *ex* Nyl.) Hale
N	***Parmelinopsis horrescens*** (Taylor) Elix & Hale
P	***Parmelinopsis miniarum*** (Vainio) Elix & Hale--Syn.: *Parmelia dissecta* Nyl.
N	***Parmotrema austrosinense*** (Zahlbr.) Hale
N	***Parmotrema eurysacum*** (Hue) Hale
N	***Parmotrema haitiense*** (Hale) Hale
P	***Parmotrema hypotropum*** (Nyl.) Hale--Syn.: *Parmelia hypotropa* Nyl.
PN	***Parmotrema gardnerii*** (Dodge) Sérusiaux--As *Parmelia dilatata* Vainio in the LBL; See Sérusiaux (1984) and Harris (1990)
P	***Parmotrema margaritatum*** (Hue) Hale--Syn.: *Parmelia margaritata* Hue

P	***Parmotrema michauxianum*** (Zahlbr.) Hale--Syn.: *Parmelia michauxiana* Zahblr.
P	***Parmotrema perforatum*** (Jacq.) Massal.--Syn.: *Parmelia perforata* (Jacq.) Ach.
P	***Parmotrema rampoddense*** (Nyl.) Hale--Syn.: *Parmelia rampoddensis* Nyl.
P	***Parmotrema subtinctorium*** (Zahlbr.) Hale--Syn.: *Parmelia subtinctoria* Zahlbr.
P	***Parmotrema tinctorum*** (Delise *ex* Nyl.) Hale--Syn.: *Parmelia tinctorum* Delise ex Nyl.
PN	***Parmotrema ultralucens*** (Krog) Hale--As *Parmelia subcrinta* Nyl. in the LBL
P	***Peltigera canina*** (L.) Willd.
N	***Peltigera elizabethae*** Gyelnik
P	***Peltigera polydactyla*** (Necker) Hoffm.
N	***Peltigera praetextata*** (Flörke *ex* Sommerf.) Zopf
N	***Phaeophyscia adiastola*** (Essl.) Essl.
P	***Phaeophyscia ciliata*** (Hoffm.) Moberg--Syn.: *Physcia ciliata* (Hoffm.) Du Rietz
N	***Phaeophyscia* cf. *erythrocardia*** (Tuck.) Essl.
N	***Phaeophyscia hirtella*** Essl.
P	***Phaeophyscia imbricata*** (Vainio) Essl.--Syn.: *Physcia lacinulata* Müll. Arg.
N	***Phaeophyscia insignis*** (Mereschk.) Moberg
N	***Phaeophyscia kairamoi*** (Vainio) Moberg
N	***Phaeophyscia pusilloides*** (Zahlbr.) Essl.
P	***Phaeophyscia rubropulchra*** (Degel.) Essl.--Syn.: *Physcia orbicularis f. rubropulchra* Degel.
N	***Physcia aipolia*** (Ehrh. *ex* Humb.) Fürnr.
P	***Physcia americana*** G.K. Merr. *in* Evans & Meyrow.--Syn.: *Physcia tribacoides* Nyl.
	Physcia ciliata (Hoffm.) Du Rietz=*Phaeophyscia ciliata* (Hoffm.) Moberg
	Physcia grisea (Lam.) Zahlbr..in the LBL=*Physconia detersa* (Nyl.) Poelt
	Physcia lacinulata Müll. Arg.=*Phaeophyscia imbricata* (Vainio) Essl.
P	***Physcia millegrana*** Degel.
	Physcia orbicularis (Neck.) Poetsch in the LBL=various *Phaeophyscia* spp.
	Physcia orbicularis f. rubropulchra Degel.=*Phaeophyscia rubropulchra* (Degel.) Essl.
P	***Physcia stellaris*** (L.) Nyl.
P	***Physcia subtilis*** Degel.
N	***Physciella chloantha*** (Ach.) Essl.
PN	***Physconia detersa*** (Nyl.) Poelt--As *Physcia grisea* (Lam.) Zahlbr. in the LBL
N	***Physconia kurokawae*** Kashiw.
P	***Pseudocyphellaria aurata*** (Ach.) Vainio
P	***Punctelia borreri*** (Sm.) Krog--Syn.: *Parmelia borreri* (Sm.) Turn.
N	***Punctelia missouriensis*** Wilhem & Ladd--See Wilhem and Ladd (1992).
P	***Punctelia rudecta*** (Ach.) Krog--Syn.: *Parmelia rudecta* Ach.
N	***Punctelia subrudecta*** (Nyl.) Krog
P	***Pyxine albovirens*** (G. Meyer) Aproot--Syn.: *Pyxine caesiopruinosa* (Nyl.) Imsh.
	Pyxine caesiopruinosa (Nyl.) Imsh.=*Pyxine albovirens* (G. Meyer) Aproot
P	***Pyxine sorediata*** (Ach.) Mont.
PN	***Ramalina americana*** Hale--As *Ramalina fastigiata* (Pers.) Ach. in the LBL
	Ramalina fastigiata (Pers.) Ach. in the LBL=*Ramalina americana* Hale
P	***Rimelia cetrata*** (Ach.) Hale & Fletcher--Syn.: *Parmelia cetrata* Ach.
P	***Rimelia reticulata*** (Taylor *in* Mack.) Hale & Fletcher--Syn.: *Parmelia reticulata* Tayl. *in* Mack.

Appendix 1 (continued)

P	***Rimelia subisidiosa*** (Müll. Arg.) Hale & Fletcher--Syn.: *Parmelia subisidiosa* (Müll. Arg.) Dodge
P	***Usnea mutabilis*** Stirton
P	***Usnea rubicunda*** Stirton
P	***Usnea strigosa*** (Ach.) A. Eaton
P	***Vulpicida viridis*** (Schwein. *in* Halsey) E.-E. Mattsson & Lai--Syn.: *Cetraria viridis* Schwein. *in* Halsey; *Cetraria juniperina* (L.) Ach.; See Mattsson and Lai (1993)
P	***Xanthoparmelia cumberlandia*** (Gyelnik) Hale--Syn.: *Parmelia cumberlandia* (Gyelnik) Hale
N	***Xanthoparmelia hypomeleana*** (Hale) Hale
P	***Xanthoria candelaria*** (L.) Th. Fr.

Appendix 2. Comparison of genera and species between Phillips' study (1970) and our study. Recognized genera and species numbers are indicated in **boldtype**. In first column (Genera in Phillips) we also indicate under *Parmelia* and *Physcia* the segregate genera created or widely accepted since 1970 with LBL species representation. In the second column (Species in Phillips) the minus (-) numbers indicate the number of species we can not verify in the LBL.

Genera in Phillips	Species	Genera our study	Species
Anaptychia	**1**	***Anaptychia***	**1**
Anzia	**1**	***Anzia***	**1**
Baeomyces	**1**	***Baeomyces***	**1**
Candelaria	**2**	***Candelaria***	**2**
Cetraria *s.l.*	**1**	(*Cetraria* s.s.)	(0)
		Vulpicida	**1**
Cladonia *s.l.*	**16** (-3)	***Cladina***	**1**
		Cladonia *s.s.*	**21**
Coccocarpia	**1**	***Coccocarpia***	**1**
Collema	**1**	***Collema***	**7**
Dermatocarpon *s.l.*	**2**	***Catapyrenium***	**1**
		Dermatocarpon	**1**
Heterodermia	**4**	***Heterodermia***	**4**
Leptogium	**4**	***Leptogium***	**8**
Pannaria	**1**	***Pannaria***	**2**
Parmelia	**28** (-4)	(*Parmelia* s.l.)	(33)
(*Bulbothrix*)	(0)	***Bulbothrix***	**1**
(*Canoparmelia*)	(4-1)	***Canoparmelia***	**3**
(*Flavoparmelia*)	(1)	***Flavoparmelia***	**2**
(*Hypotrachyna*)	(1)	***Hypotrachyna***	**1**
(*Myelochroa*)	(3-1)	***Myelochroa***	**2**
(*Parmelia* s.s.)	(1)	***Parmelia***	**1**
(*Parmelinopsis*)	(1)	***Parmelinopsis***	**2**
(*Parmotrema*)	(10-1)	***Parmotrema***	**12**
(*Punctelia*)	(3-1)	***Punctelia***	**4**
(*Rimelia*)	(3)	***Rimelia***	**3**
(*Xanthoparmelia*)	(1)	***Xanthoparmelia***	**2**
Peltigera	**2**	***Peltigera***	**4**
Physcia	**9** (-1)	(*Physcia* s.l).	(18)
(*Hyperphyscia*)	(0)	***Hyperphyscia***	**1**
(*Phaeophyscia*)	(3-1)	***Phaeophyscia***	**9**
(*Physcia*)	(5)	***Physcia***	**5**
(*Physciella*)	(0)	***Physciella***	**1**
(*Physconia*)	(1)	***Physconia***	**2**
Pseudocyphellaria	**1**	***Pseudocyphellaria***	**1**
Pyxine	**2**	***Pyxine***	**2**
Ramalina	**1**	***Ramalina***	**1**
Usnea	**3**	***Usnea***	**3**
Xanthoria	**1**	***Xanthoria***	**1**
TOTAL 20 Genera	82 (-8)	TOTAL 36 Genera	**115**

DETECTION OF THE LYME DISEASE BACTERIUM IN TICKS FROM WESTERN KENTUCKY UTILIZING PCR.

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ABSTRACT. Ticks of various species from western Kentucky were examined for the presence of the causative agent of Lyme disease, *Borrelia burgdorferi*, employing the polymerase chain reaction technique (PCR). Four tick species were examined: *Amblyomma americanum*, *Dermacentor albipictus*, *D. variabilis*, and *Haemaphysalis leporispalustris*. All ticks were removed from mammals suspected as potential reservoir hosts and analyzed for the presence of *B. burgdorferi*. Mammalian hosts included whitetail deer, *Odocoileus virginianus*, racoon, *Procyon lotor*, and eastern cottontail rabbit, *Sylvilagus floridanus*. Thirty-four of 100 samples consisting of pooled ticks were positive by PCR. The majority of the positive samples were from the genera *Amblyomma* and *Dermacentor*. One sample of *H. leporispalustris* was positive. The minimum prevalence of *B. burgdorferi* in tick hosts was 8.0 percent, based upon pooled samples. All tick species examined were positive by PCR testing. Subsequent confirmation of individual ticks from positive pools revealed that the actual prevalence was 15 percent, based upon a total of 418 ticks analyzed. These results indicate that multiple tick genera, primarily *Amblyomma* and *Dermacentor*, harbor *B. burgdorferi* in western Kentucky and may be potential vectors of Lyme disease.

EUGLENA VERMIFORMIS IN AN ACID MINE DRAINAGE STREAM OF THE WESTERN KENTUCKY COALFIELD

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ABSTRACT. The Western Kentucky coalfield has many active and inactive strip mines. The Coiltown mine in Hopkins county, which has not been active for over 50 years, still has high concentrations of heavy metals, low pH, and *Euglena vermiformis*. *Euglena vermiformis* has only been previously recorded in salt marsh areas (Carter 1937). This ongoing study is concerned with finding out how *E. vermiformis* can survive in such harsh conditions. Three study sites were chosen: site A has a moderate pH (5.0), site B has a low pH (3.0), and site C has the lowest pH (2.8). Heavy metal concentrations (Cd, Pb, Fe, Cu, Ni, and Al) follow the same continuum as the acidity, site A being lowest and site C being highest. Two studies were made to assess the effects of increased and decreased organic matter (with and without a light source), and changes in pH.

FOREST REGROWTH IN 10-12 YEAR OLD CLEARCUTS AT LAND BETWEEN THE LAKES, KENTUCKY AND TENNESSEE

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ABSTRACT. At Land Between The Lakes, six 10-12 year-old clearcuts of stands originally dominated by *Quercus* and *Carya* species were sampled for seedling, sapling, shrub, and vine composition and density. From two to eight 0.003 and 0.006 ha nested circular quadrats were sampled in each area. Density of shrubs, vines, and other mid-canopy arborescent species ranged from about 18,000/ha to over 45,000/ha. Seedlings and saplings of overstory canopy species ranged from 4,563/ha to 17,458/ha. On two xeric sites (steep rocky slopes and fragipan soil) and four xeric-mesic sites (moderately deep soil of south slopes), the relative density (importance) of *Quercus* and *Carya* seedlings and saplings ranged from 71 to 94% of all stems of overstory canopy species. These values indicate that *Quercus* and *Carya* will dominate the next mature forest community. On two mesic sites (north and east slopes at moderate to low elevation), the importance of *Quercus* and *Carya* was substantially lower (13 and 48%); here, mesophytes, primarily *Acer saccharum*, *Ulmus rubra*, and *Fraxinus americana*, with importance values of 52 and 76%, will dominate the developing community.

INTRODUCTION

A major objective of the resource management program (RMP) at LBL is "to restore and/or improve the natural resources to provide a wide variety of opportunities for outdoor recreation, environmental education, and interpretation for a rapidly urbanizing society" (Tennessee Valley Authority 1985). Under the forest land management section of the RMP, diversity of wildlife habitats and aesthetic quality are to be maintained by managing forest species composition, age class distribution, harvest size, and distribution of harvest areas. Inventory data on these variables are used by Tennessee Valley Authority resource managers to prescribe silvicultural techniques, including timber harvesting, reforestation, timber stand improvement, development of waterholes, planting to control soil erosion, and maintaining fire control access trails. Annually, these techniques are applied to approximately 1,400 ha.

Timber management (harvesting) has become, as elsewhere, the most controversial portion of the land management program. During the 1970s and 1980s, a "patch clearcut" of 2-3 ha was used to harvest timber, depending on the amount of forest land available under the management plan and the extent of its impact on aesthetic quality. If properly applied, clearcutting should have produced a sufficient number of seedlings and saplings (regeneration) for development of a new forest. A clearcut normally establishes an even-age class distribution which permits a larger number of seedlings to simultaneously receive the high light conditions required for survival. At LBL, approximately 200 ha were clearcut annually.

At present, clearcutting at LBL generally has been replaced by shelterwood cutting, a two-cut system. The first cut removes a portion of the overstory trees which increases light at ground level for seedling development. After seedlings and saplings are established, the second cut, which occurs 7 to 14 years after the first, removes the remaining overstory and permits development of an even-aged stand.

While previous research at LBL examined composition and successional patterns of mature hardwood and pine stands in relation to soil and topography (Fralish and Crooks 1988, 1989; Schibig and Chester 1988; Franklin 1990; Kettler 1990; Fralish et al. 1993a, 1993b), no intensive study of forest regrowth in clearcuts areas has been conducted. Data are not yet available from a long-term hardwood silviculture study set up at LBL by North Carolina State University. In related research, Smalley (1980) classified and assessed the productivity of LBL sites is his study of the Western Highland Rim and Pennyroyal sections of the Interior Low Plateau.

At LBL, data being collected in young forests resulting from clearcuts of the early 1980s will determine if dense stands of seedlings and saplings of desirable species presently exist. These stands are of sufficient age to provide information on stand composition, development, and conditions resulting from even-aged management. Specific objectives of the present research in 10-12 year-old clearcuts at LBL are to determine (1) the composition and density of shrubs, half-shrubs, and vines as well as seedlings and saplings of tree species, (2) if clearcut areas are well-stocked with desirable oak and hickory species, and (3) if stand composition and density is related to site conditions.

STUDY AREA

Land Between The Lakes is a 68,800 ha National Recreation Area between Kentucky and Barkley Lakes (the Tennessee and Cumberland Rivers, respectively). The area is approximately 65 km long and 10 km wide. It lies in the northwestern corner of the Highland Rim Section (Pennyroyal Formation) of the Interior Low Plateau Physiographic Division, where it interfaces with the Mississippi Embayment Section of the Coastal Plain Division (Harris 1988). The Highland Rim is composed of cherty limestone bedrock of Mississippian age (Harris 1988). The limestone forms the base of the Tennessee Ridge that runs nearly the entire length of LBL. Elevation ranges from approximately 110 m at lake level to 180 m on the Tennessee Ridge.

A Cretaceous Coastal Plain deposit (Tuscaloosa Formation) overlies the bedrock. A large proportion of the fine material has been carried away by mass wasting and erosion, making the pebbles (mostly white tripolitic chert) prominent so that the deposit is often referred to as "gravel" or white gravel (Harris 1988).

Remnants of Tertiary-Quaternary (Lafayette) gravel are found on the crests of some of the higher ridges. This deposit is yellowish-brown to reddish brown and contains rounded quartz pebbles. The gravel has a matrix of reddish sandy clay or sand. While the deposit is generally unconsolidated, a zone of massive dark brown iron oxide and pebbles (conglomerate) often is exposed; this type of material was mined for iron in the mid-1800s. The white and brown gravels of the Coastal Plain are over 30 m deep on the western one-half (Kentucky Lake side) of LBL. Overlying the Cretaceous and Lafayette gravels is a relatively thin loess deposit (Quaternary age) that is seldom more than 1.6 m deep on the ridgetops (Harris 1988).

Soils have developed in weathered limestone bedrock, both Tuscaloosa and Lafayette gravels, loess, and alluvial deposits. Common soil types are described by U. S. D. A. (1953, 1981), Fralish and Crooks (1988, 1989), Franklin (1990) and Kettler (1990).

The 1986 Continuous Forest Inventory indicated that LBL was 87.7% forested (Groton 1988). At present, the forest is approximately 10% old-growth, 56% sawtimber, 15% pole timber, 15% young-growth (seedlings and saplings), and 4% planted pine. Approximately 1,650 ha are under cultivation and 3,240 ha are kept open for wildlife by bush-hogging, discing, or food plantings.

The major natural upland communities are primarily dominated by *Pinus echinata, Quercus prinus, Q. stellata, Q. velutina, Q. alba, Fagus grandifolia,* and *Acer saccharum.* Compositionally-stable (climax) and successional forest community patterns and site relationships have been delineated and analyzed by Fralish and Crooks (1988, 1989), Franklin (1990), Kettler (1990), and Fralish et al. (1993a, 1993b). For management purposes, Land Between The Lakes is divided into 65 work areas set up on an eight year cutting cycle. Each work area is subdivided into approximately 20 to 30 units of which only one or two may be harvested at the appropriate point in the cycle.

In presettlement times (prior to 1850), the forest of the "land between the rivers" was moderately disturbed and relatively open due to fires set by Indians (S. B. Franklin, personal communication). Beginning about 1843, extensive tracts of forest were cleared to supply charcoal needed to operate eight iron furnaces located on the property. Timber cutters were kept busy supplying wood for the process, as approximately 60 cords of wood were needed to operate an iron furnace for 24 hours (Harris 1982). The last furnace to operate was Center Furnace which closed in 1912. In the early 1890s, much of the area again was logged for railroad ties and to operate whiskey stills. Stream terraces and other relatively level areas were maintained in open condition for farmland and adjacent wooded slopes were heavily grazed.

METHODS

Field Procedures

Six 10-12 year old clearcuts were selected for study. Work area maps and corresponding aerial photographs were used to locate old logging roads, trails, and to determine accessibility into the clearcuts. Each clearcut was examined to determine the range of topographic conditions and direction of the transect lines. Depending on topographic conditions, the transect line was oriented with the contour or was run on a specific compass bearing.

Because of topographic variability, two clearcuts were divided into two sites and each site sampled separately. In clearcuts with little topographic variability, eight points were located 20 m apart. Where two site conditions existed in a single clearcut, at least two points were located on each condition (Fig. 1).

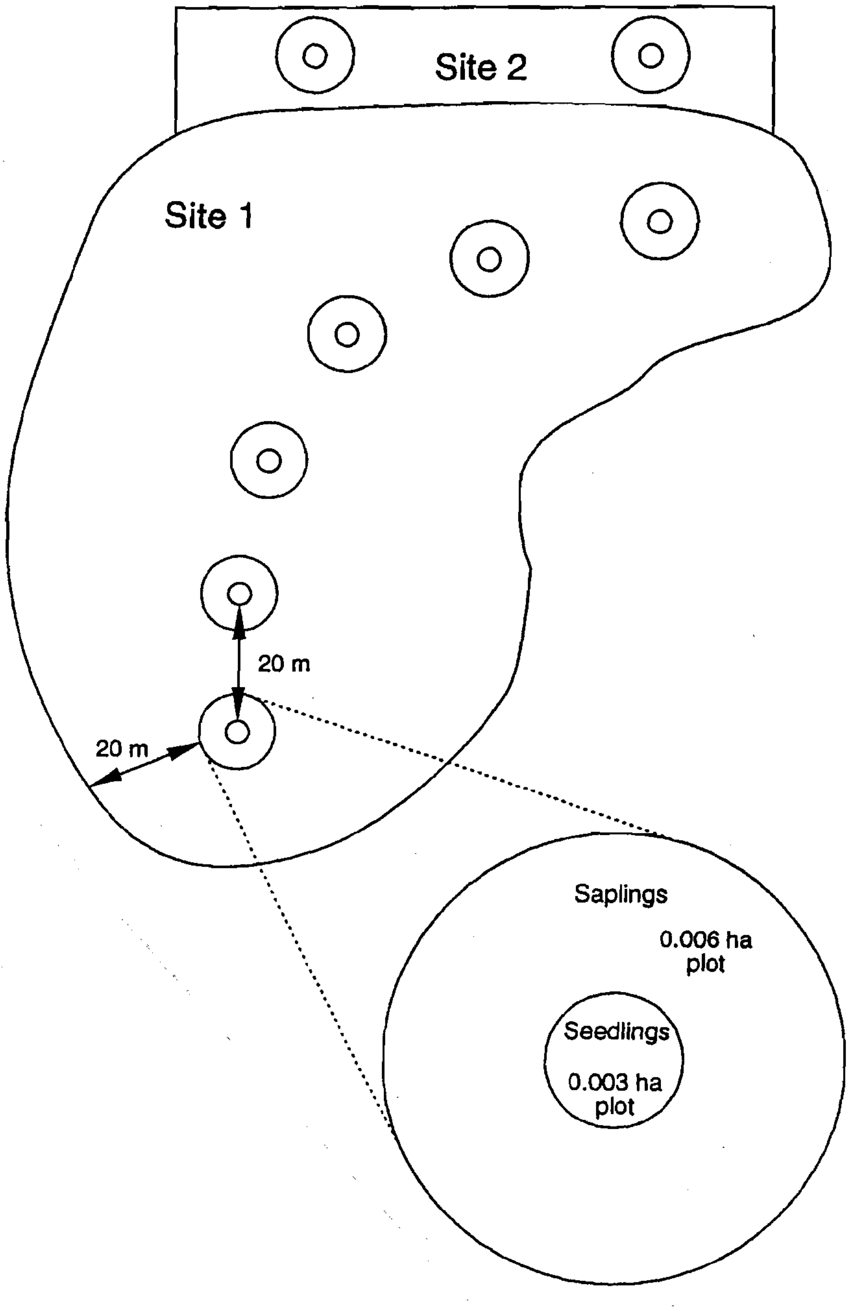

Figure 1. Sampling design used in clearcut stands.

Each point was the center of two circular nested quadrats. Seedlings (stems DBH <1.0) and saplings (stem DBH 1.0-9.0 cm) were counted on the 0.003 ha (30 m^2) and the 0.006 ha (60 m^2) plots, respectively, and recorded by species. Aspect, slope steepness, and general soil conditions were recorded. Elevation was obtained from topographic maps. Data were collected from a total of 50 plots.

Office Procedures

Seedling and sapling data for overstory canopy species (potential trees), for midcanopy species (shrubs and vines), and for four arborescent species (*Diospyros virginiana*, *Nyssa sylvatica*, *Prunus serotina*, and *Sassafras albidum*) were analyzed separately. The midcanopy and arborescent species were considered separately from the overstory canopy species since they seldom reach the mature forest canopy and often occur in such large numbers that the importance of overstory canopy species is often obscured.

For each stand, seedling counts from all plots on a site were used to calculate seedling density, total density, and species relative density or importance value [IV = (density for a given species/ density for all species) x 100] for overstory canopy species. Sapling density of overstory (or canopy) species and seedling and sapling density for midcanopy and arborescent species were calculated in a similar manner.

RESULTS

Site Environment

Using soil surface condition, aspect, elevation, and slope steepness, the eight clearcut sites were arranged in a general sequence from the most xerophytic to the most mesophytic site conditions. Variations in stand composition, density, and species importance were examined across this gradient.

The two most xeric sites were Woodlands Ridgetop (WLR) and Energy Lake South Slope (ELS) clearcuts. The Woodlands Ridgetop site was on relatively level soil containing a fragipan (Lax soil type) while the Energy Lake site was on cherty soil along a steep (> 30%) south slope; elevation of these sites was between 149 and 137 m, respectively. Four xeric-mesic sites had elevations between 140 and 170 m with sites at the lower end of this range located on a ridgetop (Old Ferry Road Ridgetop, FRR) or warm southwest to southeast slope (Crab Creek, CCS); sites at higher elevations (>150 m) were on cooler east slopes (The Trace, TTE, and Woodlands East Slope, WLE). The Trace site on the Tennessee Ridge had the highest elevation at 170 m. The most mesic sites were Old Ferry Road East Slope (FRE) and Energy Lake North Slope (ELN); both sites were located at a relatively low elevation of 140 and 130 m, respectively.

Stand Structure

Total number of stems (seedlings + saplings) for all species (midcanopy, arborescent, and overstory) in the eight stands ranged from 34,729 to 60,567 with six sites ranging between 34,729 and 41,277. Average density across all sites was 41,054 stems/ha. Midcanopy species generally had the greatest density (Fig. 2a) with an average of 41,054 stems/ha. Arborescent and overstory canopy species had a substantially lower density and relative similar averages of 10,589 and 10,712 stems/ha (Fig. 2a).

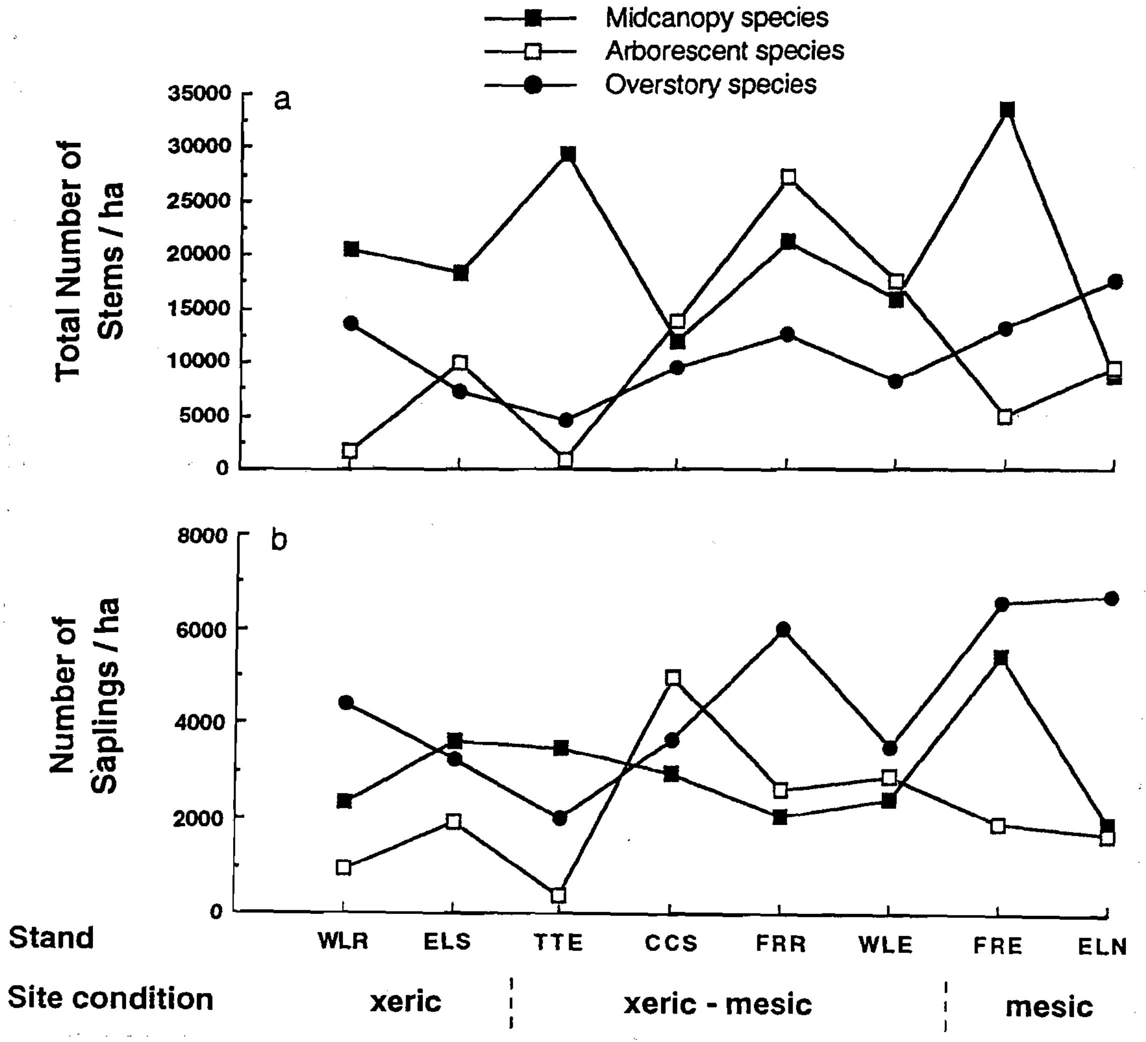

Figure 2. Density patterns for midcanopy, arborescent, and overstory tree species across a soil moisture gradient. Tables 1, 2, and 3 list the overstory, arborescent, and midcanopy species, respectively. Refer to text for full names of stands.

However, the overstory canopy species had the greatest proportion of stems (42%) in the sapling size class while the arborescent and midcanopy species had 20% and 15% in the sapling class, respectively. Thus, in six of the eight stands, overstory dominants had the greatest number of stems in the sapling size class (Fig 2b). In three stands (WLR, FRR, and ELN), the number of stems for overstory species exceeded the number of sapling stems for midcanopy and arborescent species combined. For overstory, arborescent, and midcanopy species, sapling density across all sites averaged 4,508, 2,157, and 3,019/ha, respectively. Average total density for stands on xeric, xeric-mesic, and mesic sites increased from 25,250 to 42,877 to 43,459 stems/ha.

Overstory Species

Species which had a moderate (IV = 25-50) or high (IV > 50) importance in either the seedling or sapling size class of one or more stands included *Quercus stellata*, *Q. marilandica*, *Q. velutina*, *Q. alba*, the *Carya glabra-ovalis* complex, *Ulmus rubra*, and *Acer saccharum* (Appendix 1). Generally, these species had a high IV in the sapling as well as the seedling strata. Other species of minor or secondary importance (IV < 25) which occurred in at least four stands were *Quercus coccinea*, *Q. falcata*, *Ulmus alata*, *Fraxinus americana*, and *Carya ovata*. *Quercus alba*, *Q. velutina*, and *Acer saccharum* had nearly equal importance (IV = 17-20) in the ELN stand.

The seedling class and sapling size classes of only four stands were dominated by the same species. *Quercus stellata* in stand WLR, *Q. velutina* in stand CCS, *Q. alba* in stand WLE, and *Ulmus rubra* in stand FRE had the highest IV in both seedling and sapling size classes. In four stands, the leading dominants (species with the highest IV) changed in the seedling and sapling size classes from *Q. velutina* to *Q. falcata* (ELR), *Q. marilandica* to *Q. stellata* (TTE), *Carya glabra-ovalis* to *Ulmus alata* (FRR), and from *Q. alba* to *Acer saccharum* (ELN) , respectively.

However, in the sapling size class, there was considerably more equitability between species compared to the seedling class (Appendix 1). For example, in stand WLR, *Quercus stellata* dominated the seedling class with an IV of 58, but in the sapling size class, *Q. stellata*, *Q. velutina*, *Q. coccinea*, and *Ulmus alata* had IVs ranging between 17 and 23. In stand ELS, *Q. velutina* was the single leading dominant in the seedling size class with an IV of 44, while in the sapling class, *Q. stellata* and *Q. falcata* had an IV of 27 to 29. Increases in equilability among species in the sapling class also occurred in stands FRR, WLE, and FRE. Three stands had high equilability among seedlings and saplings (TTE, CCS and ELN) although the dominant species changed between the seedling and sapling classes.

Total density of seedlings ranged from 1,876 to 10,792 stems/ha with an average of 6,120 stems/ha for the eight stands; saplings ranged from 1,856 to 6,667 stems/ha with an average of 4,487 stems/ha. There was a small decrease in the number of species from the seedling to the sapling size class.

Species Group Patterns Across the Gradient

For a given species group (*Quercus*, *Carya*, or mesophytes), IVs in the seedling and sapling classes had relatively similar patterns along the gradient (Fig. 3a, b). Both the xeric and xeric-mesic sections of the moisture gradient were dominated by a variety of *Quercus* species. However, there was a general decrease in *Quercus* importance across the gradient from xeric to mesic. Importance values in the xeric section varied between 80 and 90, while in the xeric-mesic section, IVs ranged from approximately 35 to nearly 80. Average *Quercus* IV at the mesic end of the gradient was approximately 30. *Quercus* species occurred in moderate to high densities and importance (2,918-11,416 stems/ha; IV = 16-88) in seven of the eight clearcuts. These parameters were extremely low on the FRE site (1,132 stem/ha; IV = 2).

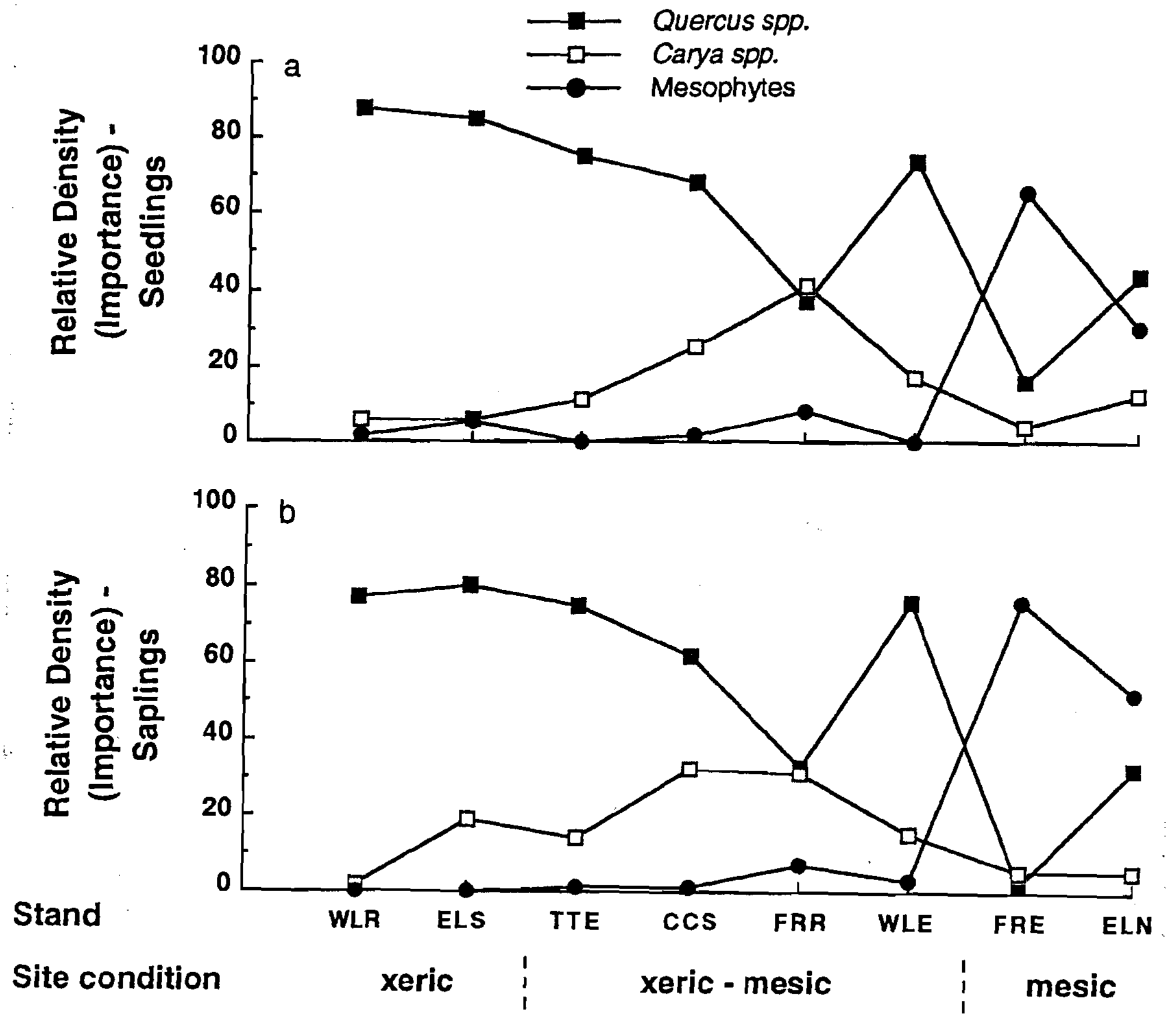

Figure 3. Relative density (importance values) for *Quercus*, *Carya*, and mesophytic species across a soil moisture gradient. Mesophytes include *Acer saccharum*, *Fraxinus americana*, and *Ulmus rubra*. Refer to text for full name of stands.

The pattern for *Carya* species was substantially different from that of *Quercus*. *Carya* had the lowest average importance in the xeric and mesic sections of the gradient and a moderately high importance (max IV = 43) in the xeric-mesic section. *Carya* density and importance was relatively low (501-4500 stems/ha; IV = 4-24).

Mesophytic species were absent or had low importance (21-900 stems/ha; IV < 5) in the xeric and xeric-mesic sections and relatively high importance (IV = 50-80) in the mesic section. On mesic sites, the density of *Acer saccharum* and other mesophytic species was 6,688-9,332 stems/ha.

Individual Species Patterns Across the Gradient

The importance of major tree species (*Q. stellata*, *Q. velutina*, *Q. alba*, and *Acer saccharum*) across the gradient is shown in Fig. 4a. *Quercus stellata* importance was highest

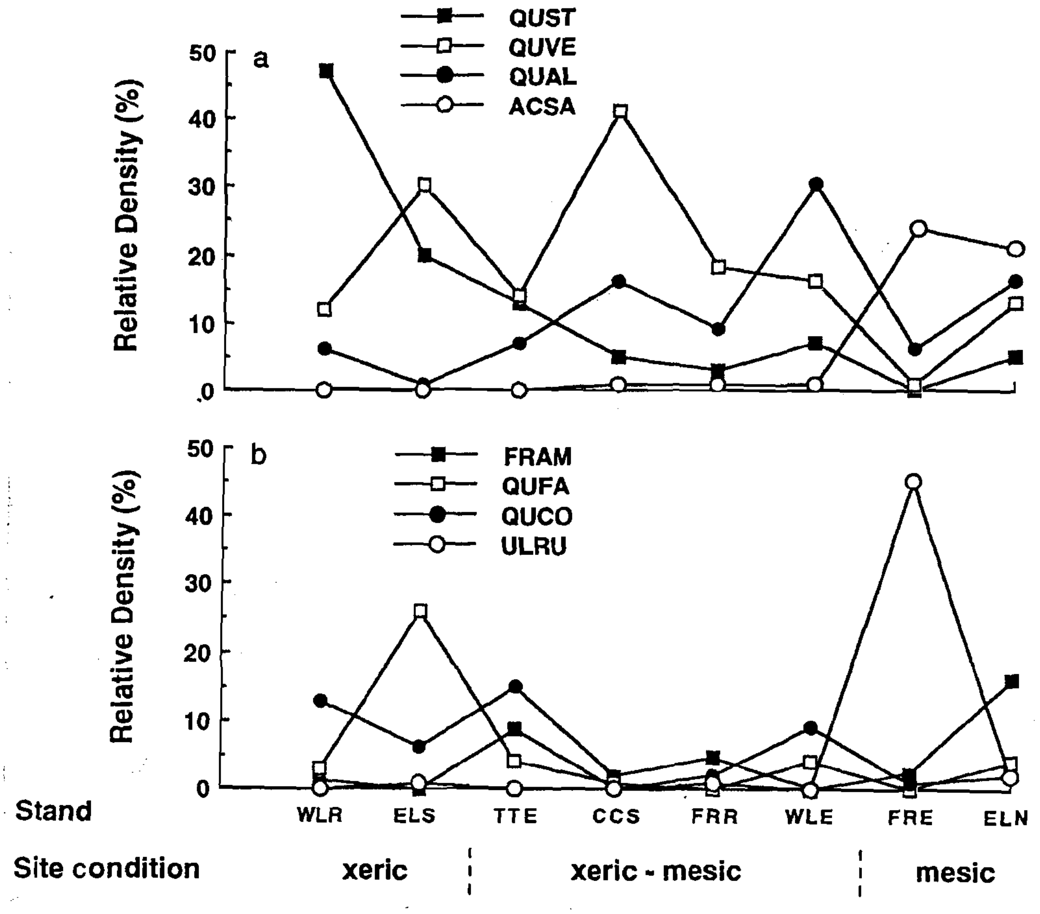

Figure 4. Relative density (importance values) for individual species across a soil moisture gradient. Acronyms are: QUST = *Quercus stellata*; QUVE = *Quercus velutina*; QUAL = *Quercus alba*; ACSA = *Acer saccharum*; FRAM = *Fraxinus americana*; QUFA = *Quercus falcata*; QUCO = *Quercus coccinea*; ULRU = *Ulmus rubra*.

on the most xeric site (WLR) and consistently decreased toward the mesic end of the gradient. *Quercus velutina* was the major dominant on the next four consecutive sites, which included one xeric and three xeric-mesic sites; it had secondary importance on the most xeric site and on the three sites at the mesic end of the gradient. The importance of *Q. alba* was at a maximum on the WLE site, a more mesic site than those on which *Q. velutina* was found. *Quercus falcata* and *Q. coccinea* had moderate to low importance on several sites toward the xeric end of the gradient (Fig. 4b).

Acer saccharum had maximum importance on the two most mesic sites. On one site (ELN), it shared dominance with *F. americana*, which had low importance (IV < 5) in five of the six stands where it was present (Fig. 4b). *Ulmus rubra* appeared only as a trace (IV < 5) on two xeric and xeric-mesic sites but dominated one site (IV = 44, FRE).

Arborescent Species

Total density for *Diospyros virginiana*, *Nyssa sylvatica*, *Prunus serotina*, and *Sassafras albidum* ranged from 833 to 27,100/ha (Fig. 2a; Appendix 2). Their collective importance in the stands ranged from 2.4% to 44.4%; their importance in three stands (WLR, TTE, and FRE) was < 10%, and in two stands (FRR and WLE) was > 40%. In the seedling size class, *D. virginiana* is the only species that consistently had moderate (IV = 25-50) to low importance (IV < 25). In the sapling size class, each species in this group had major importance (IV > 50) in at least one stand. *Prunus serotina* had high importance values in three stands.

Along the moisture gradient, *Diospyros virginiana* seedlings and saplings had highest importance at the xeric end of the gradient (WLR, ELE and TRE sites) and had low importance or were absent at the mesic end. *Nyssa sylvatica* had highest importance at the mesic portion of the gradient (WLE, FRE and ELN sites) while *Sassafras albidum* was most important in the xeric-mesic portion. *Prunus serotina* was important at the xeric and mesic ends but not in the xeric-mesic portion.

Midcanopy Species

The most important species in the midcanopy seedlings size class was *Rubus*, primarily *R. allegheniensis*, but *R. occidentalis* also was a component (Appendix 3). Other woody and semi-woody species that appeared as moderately important (IV = 25-50) in at least one stand included *Cornus florida*, *Corylus americana*, *Smilax* spp, and *Symphoricarpos orbiculatus*. Seedling density ranged from 8,833 to 27,000 stems/ha.

The sapling size class of the midcanopy species was dominated by *Cornus florida* and *Rhus copallina*; these species were found on all sites and frequently with a moderate to high (IV = 50+) importance. *Corylus americana* was the only other species to have an IV > 25.

In the seedling size class, the lowest number of species occurred on the xeric sites (WLR and ELS). The WLR site also had the lowest number of species (2) in the sapling size class. For a given stand, the number of species substantially declined (16 to 71%) from the seedling to the sapling size class.

DISCUSSION

The study areas, created for the wildlife habitat improvement program (WHIPs), are among the oldest forest clearcuts at LBL. They are sufficiently old so that the present composition and density indicate if stands of desirable species are developing.

At present, midcanopy and arborescent species have a combined density between approximately 18,000 and 48,000 stems/ha and an IV between 50 to 85, compared to a density between approximately 4,500 and 17,500 stems/ha and an IV between 13 and 49 for overstory tree species. However, these data are deceiving in that when only saplings are considered, only 15 and 20% of midcanopy and arborescent stems, respectively, are saplings while 42% of stems of overstory species are saplings. The limited growth potential of the midcanopy species is shown by the substantial drop in number of species between the seedling and sapling strata. Furthermore, the number of saplings of overstory species exceeds the combined number of midcanopy and arborescent stems on three of eight sites and exceeds either the midcanopy or arborescent species on the other five sites. These data indicate that the sapling strata of overstory species is presently emerging from the mass of vegetation that has characterized these clearcuts for the past 10 to 12 years.

Considering only stems of overstory species, *Quercus* and *Carya* seedlings and saplings have a moderate to high density (5,938 to 11,416 stems/ha) and high importance (IV = 48-94) on six of the eight clearcuts, indicating that substantial regeneration of desirable species has developed. Since *Quercus* and *Carya* have fewer serious natural enemies in the region that could cause high mortality, the present young stands are likely to produce moderately dense mature stands of these species. However, on two sites, mesophytes such as *Acer saccharum* and *Ulmus rubra* or *Fraxinus americana* were the dominant species, although *Quercus* and *Carya* also were present. However, because *Quercus* and *Carya* are less shade tolerant than mesophytes, their importance can be expected to decrease as the stands mature.

Based on the composition of stands adjacent to the clearcuts and on the community-site relationships developed by Fralish and Crooks (1988, 1989), Franklin (1990), Kettler (1991), Fralish et al. (1993a, 1993b), there appears to be little difference in the composition of pre-harvest forest and the present stand of seedlings and saplings on xeric and xeric-mesic sites. *Quercus stellata*, *Q. marilandica*, and *Q. falcata* were most important on xeric sites, while *Q. velutina* and *Q. alba*, along with *C. glabra-ovalis* were the most important species on xeric-mesic sites. The two communities of mesic sites (north and east slopes) presently dominated by *Acer saccharum*, *Ulmus rubra*, and *Fraxinus americana* represent a major change in forest composition from pre-harvest to the present condition. Prior to clearcutting, all stands were dominated by *Quercus*, but in the absence of preharvest operations to remove the understory of mesophytic tree species, clearcutting immediately converted the stand from

Quercus to mesophytes.

Although becoming subordinate to stems of overstory tree species, midcanopy and arborescent species density remains high and important for wildlife food and cover, for maintaining diversity, and for retaining soil nutrients and particulates (sand, silt and clay) on the site. *Diospyros virginiana*, *Prunus serotina*, *Amelanchier arborea*, *Corylus americana*, *Crataegus*, *Morus rubra*, *Rubus*, *Rhus*, and *Vitis* are important wildlife species that occur in high number in clearcut forest. It would appear that although the objective of clearcutting was to produce food and cover for wildlife in a surrounding matrix of relatively mature forest, the objective of revegetating the sites to *Quercus*, a major wildlife food species, also was achieved on xeric and xeric-mesic sites.

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Appendix 1. Relative density (%) and total density of overstory tree seedlings and saplings for eight clearcut areas at Land Between The Lakes in Kentucky and Tennessee. Seedlings have a DBH < 1.0 cm and saplings a DBH of 1.0 - 9.0 cm. Species density can be determined by multiplying relative density by total stems/ha and dividing by 100.

	CLEARCUT SITES							
SPECIES	WLR	ELS	TTE	CCS	FRR	WLE	FRE	ELN
				Seedling Relative Density (%)				
Quercus prinus	2					1		
Quercus marilandica			27					
Quercus stellata	58	16	16	8	3	8		5
Quercus coccinea	11	2	7			7		
Ulmus alata	4		7	3	14	10	11	8
Carya pallida				1		1		
Quercus velutina	7	44	19	41	22	17	2	18
Quercus alba	2	1	2	17	9	35	12	20
Quercus falcata	4	22	4	1		5		
Carya glabra-ovalis	4	2	9	24	32	14	3	6
Carya tomentosa		3			4			
Fraxinus americana	2			1	4			10
Carya ovata	2	1	2		5	2	1	4
Ulmus rubra		1			2		48	2
Acer saccharum				1	1		16	17
Liquidambar styraciflua		4						6
Other Species	4	4	7	3	4	.	7	4
TOTAL	100	100	100	100	100	100	100	100
Density (Stems/ha)	9,000	3,917	1,876	5,833	6,400	4,611	6,533	10,792
Number of Species	11	12	12	13	13	10	11	16
				Sapling Relative Density (%)				
Quercus prinus						15		
Quercus marilandica						1		
Quercus stellata	23	27	17	2	3	6		7
Quercus coccinea	17	10	30	2	5	11	1	4
Ulmus alata	21		1	4	28	5	14	6
Carya pallida				3				
Quercus velutina	20	14	14	42	13	14		5
Quercus alba	13	1	16	14	9	24	1	8
Quercus falcata	2	29	5	1	2	5		9
Carya glabra-ovalis	2	2	12	26	21	14	1	
Carya tomentosa		13	3	2	6		1	1
Fraxinus americana					6		4	23
Carya ovata		3			4		2	1
Ulmus rubra							41	1
Acer saccharum				1		1	31	27
Liquidambar styraciflua								5
Other Species	2	1	2	3	3	3	4	3
TOTAL	100	100	100	100	100	100	100	100
Density (Stems/ha)	4,417	3,229	1,856	3,667	6,000	3,500	6,567	6,667
Number of Species	8	10	12	12	13	13	13	16

Appendix 2. Relative density and total density of four arborescent species for eight clearcut sites at Land Between The Lakes in Kentucky and Tennessee. Seedlings have a DBH < 1.0 cm and saplings a DBH of 1.0 - 9.0 cm. Species density can be determined by multiplying relative density by total stems/ha and dividing by 100.

	CLEARCUT SITES							
SPECIES	WLR	ELS	TTE	CCS	FRR	WLE	FRE	ELN
				Seedling Relative Density (%)				
Diospyros virginiana	25	4	27	3	1	2	-	-
Nyssa sylvatica	-	19	9	34	3	46	67	32
Prunus serotina	75	4	9	7	4	4	28	23
Sassafras albidum	-	73	55	56	92	48	4	44
TOTAL	100	100	100	100	100	100	100	100
Density (Stems/ha)	677	7,833	458	8,708	24,467	14,500	3,067	7,750
				Sapling Relative Density (%)				
Diospyros virginiana	9	48	72	4	9	1	2	9
Nyssa sylvatica	-	24	28	12	12	64	37	15
Prunus serotina	91	9	-	-	49	21	56	70
Sassafras albidum	-	19	-	84	30	13	5	6
TOTAL	100	100	100	100	100	100	100	100
Density (Stems/ha)	917	1,896	375	4,958	2,633	2,889	1,900	1,688

Appendix 3. Species relative density and total density of midcanopy tree, shrub and vine seedlings and saplings for eight clearcut sites at Land Between The Lakes in Kentucky and Tennessee. Seedlings have a DBH < 1.0 cm and saplings a DBH of 1.0 - 9.0 cm. Species with a relative density < 0.5% are not listed. Species density can be determined by multiplying relative density by total stems/ha and dividing by 100.

	CLEARCUT SITES							
SPECIES	WLR	ELS	TTE	CCS	FRR	WLE	FRE	ELN
				Seedling Relative Density (%)				
Amelanchier arborea	-	-	-	1	-	-	-	-
Aralia spinosa	-	-	4	24	6	-	3	-
Cercis canadensis	-	-	-	-	5	-	3	1
Corylus americana	-	5	-	-	4	2	69	24
Cornus florida	55	2	-	6	5	9	-	14
Crataegus spp.	-	-	-	-	-	-	-	-
Lonicera japonica	-	-	-	-	-	-	3	-
Morus rubra	-	-	-	-	-	-	5	2
Ostrya virginiana	-	-	-	-	-	-	1	9
Rosa multiflora	24	-	-	1	-	12	-	-
Rubus spp.1/	16	71	84	44	3	25	6	6
Rhus copallina	1	15	6	1	1	12	2	5
Rhus glabra	-	-	-	-	2	-	-	-
Smilax spp.2/	3	-	2	8	4	29	1	-
Symphoricarpos orbiculatus	-	-	2	1	64	3	4	27
Vaccinium arboreum	-	7	-	1	2	-	-	-
Vaccinum stamineum	-	-	-	-	-	3	-	11
Vitis spp.	1	-	2	13	4	5	3	1
TOTAL	100	100	100	100	100	100	100	100
Density (Stems/ha)	18,167	14,542	25,875	8,833	19,000	13,333	27,000	6,625
Number of Species	7	7	11	11	15	11	12	11
				Sapling Relative Density (%)				
Albizzia julibrissin	-	-	-	-	-	-	-	1
Amelanchier arborea	-	-	-	5	-	-	-	1
Aralia spinosa	-	-	5	2	-	-	-	-
Cercis canadensis	-	-	-	-	15	-	13	-
Corylus americana	-	3	-	-	2	2	58	2
Cornus drummondi	-	1	-	-	-	-	-	-
Cornus florida	96	8	18	36	35	61	4	24
Crataegus spp.	-	-	1	-	6	-	-	-
Morus rubra	-	-	-	-	2	-	1	3
Ostrya virginiana	-	-	1	-	-	-	-	12
Rhus copallina	4	74	71	54	29	36	22	46
Rhus glabra	-	-	4	1	6	-	-	-
Vaccinium arboreum	-	14	-	1	5	-	-	11
Viburnum rufidulum				1				
Vitis spp.	-	-	-	-	-	1	2	-
TOTAL	100	100	100	100	100	100	100	100
Density (Stems/ha)	2,333	3,583	3,458	2,938	2,067	2,444	5,433	1,896
Number of Species	2	5	6	7	8	4	6	8

1/ Primarily *Rubus allegheniensis*. 2/ Primarily *Smilax glauca* and *S. bona-nox.*

FROM PLEISTOCENE TO PRESENT: A VEGETATIONAL HISTORY OF LAND BETWEEN THE LAKES, KENTUCKY AND TENNESSEE

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ABSTRACT. The vegetational history of Land Between The Lakes (LBL) was summarized beginning with the Pleistocene Series. During glacial extensions, LBL became a refuge for northern boreal species (e.g., *Picea, Abies, Larix,* and *Pinus*). Due to the Gulf Coast climatic influence, the zonation of boreal, northern deciduous, and southern deciduous/pine species seen in North America today was compacted, allowing these vegetation zones to coexist. Boreal and northern deciduous trees dominated LBL during peak glacial extensions, alternating with southern and prairie constituents during warmer and drier periods.

The Holocene, a warming and drying period, followed the Pleistocene. During the height of this period, the Hypsithermal, prairie expanded eastward, creating the Prairie Peninsula. Mesophytic species retreated to bottomlands and protected coves while prairie and savanna dominated uplands. As the climate became cooler and more moist, southern *Pinus* and *Quercus* migrated north, invading prairie and open forest. However, this succession was delayed by aboriginal disturbances. Fires were set annually and timber was used relentlessly.

When Europeans first explored the LBL area, they found bottomland hardwoods of enormous size and upland park-like forests containing an herbaceous understory. Europeans settled the area around 1800. Their influence on the vegetation included farming, grazing, whiskey distilling, timber cutting for iron manufacturing, railroad ties and other wood products, and damming the Cumberland and Tennessee Rivers. Agrodeforestation and the control of wildland fire led to the reversal of forest dominance across the landscape. Bottomland forests were converted to agricultural land and were later inundated by Kentucky Lake and Lake Barkley. Previously open uplands succeeded to closed forest.

Information about vegetation and disturbance history is helpful for land management, including restoration of "lost" communities (e.g., prairie, savanna, and canebrake). Restoring "lost" communities is necessary for maximizing biodiversity on the landscape.

THE YELLOW-PIGMENTED BACTERIA OF KENTUCKY LAKE

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ABSTRACT. Yellow-pigmented bacteria (YPB) are emerging as important pathogens of fish and shellfish. Diseased and moribund mussels have been shown to harbor higher numbers of these bacteria than their healthier counterparts. Studies on the ecology of fish and shellfish pathogens, such as the YPB, have been limited but the available data indicate that bacterial pathogens of aquatic animals represent members of the normal bacterial flora of water. The water column at two different sites on Kentucky Lake were analyzed for the presence of YPB. Since the YPB represent heterotrophic bacteria, specific study sites were selected based upon the extent of influx of organic material. The West Sandy Embayment was selected as the nutrient rich site because of the heavy organic inflow from the West Sandy Creek Dewatering area. The second site was located in Panther Bay, which represents an area of low organic inflow. The membrane filter technique was used to enumerate the YPB and to obtain a total heterotrophic plate count. Interestingly, neither the total plate counts nor the counts of YPB showed any significant variation between the two sites. The densities of YPB ranged from a low of 1.2 x 10^3 colony forming units (cfu)/ml to a high of 5.1 x 10^3 cfu/ml. Both counts were obtained from the West Sandy site. The YPB represented approximately 10% of the total heterotrophic plate counts at both sites. Seasonal variations were observed in the numbers of bacteria present but the ratio of the YPB to the total plate counts remained constant. Typical colonies of YPB were randomly selected. Both Gram-positive and Gram-negative bacteria were identified. None of the isolates characterized thus far belong to the Gram-negative gliding bacteria. Some of the genera that have been isolated include *Flavobacterium* spp. and *Pseudomonas* spp.

THE WETLAND VASCULAR FLORA OF CROSS CREEKS NATIONAL WILDLIFE REFUGE, STEWART COUNTY, TENNESSEE

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ABSTRACT. The refuge is a 3,566-ha, mostly wetland tract astride 10 river miles of the Cumberland River (Lake Barkley) between Dover and Cumberland City. The area has been owned and managed since 1962 by the U.S. Fish and Wildlife Service, primarily as a feeding and resting site for migrating waterfowl. Much of the refuge is river bottomland that was formerly agricultural. Present management practices include moist-soil crops for wildlife, some agricultural production (hay, soybeans, small grains), successional fields, and 16 managed pools where dams, levees, and floodgates allow for water level manipulation. The Cumberland River and its tributaries are permanently impounded with seasonal variations in pool levels. Various wetland habitat and community types occur, including marshes, swamps, dewatered zones, bottomland forests, and permanent deep water. This research involved a floristic survey of the area, excluding peripheral uplands. Specific objectives were to (1) qualitatively delineate community types, (2) determine their floristic composition, and (3) seek listed rare taxa. During 1990-1992, 77 collecting trips yielded 636 taxa (including seven rare elements) representing 367 genera and 116 families.

SEED GERMINATION ECOLOGY OF *SOLIDAGO ALTISSIMA* L. (ASTERACEAE)

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ABSTRACT. *Solidago altissima* L. is a hexaploid (2n=54) member of the *S. canadensis* L. complex and has been treated as an infraspecific taxon, *S. canadensis* L. var. *scabra* (Muhl.) Torr. & Gray (Croat, T. 1972. *Solidago canadensis* complex of the Great Plains. *Brittonia* 24:317-326; Gleason, H.A. and A. Cronquist. 1991. *Manual of vascular plants of northeastern United States and adjacent Canada*. The New York Botanical Garden, Bronx, NY). However, several workers have treated *S. altissima* as a distinct species (Melville, M.R. and J.K. Morton. 1982. A biosystematic study of the *Solidago canadensis* (Compositae) complex. I. The Ontario populations. *Can. J. Bot.* 60:976-997; Semple, J.C., G.S. Ringius, C. Leeder, and G. Morton. 1984. Chromosome numbers of goldenrods, *Euthamia* and *Solidago* (Compositae: Astereae). II. Additional counts with comments on cytogeography. *Brittonia* 36:280-292). Most ecological works do not make clear which variant(s) of *S. canadensis* were studied.

Solidago canadensis is a C_3 herbaceous polycarpic hemicryptophyte with vegetative reproduction by rhizomes (Werner, P.A., I.K. Bradbury, and R.S. Gross. 1980. The biology of Canadian weeds. 45. *Solidago canadensis* L. *Can. J. Plant Sci.* 60:1393-1409). The geographical range of the complex extends throughout most of North America, from Alaska to Labrador south to Mexico and Florida; *S. altissima* is confined to eastern North America (Croat. *op. cit.*; Melville and Morton. *op. cit.*; Semple *et al. op. cit.*). Members of this complex occur in fairly moist situations in abandoned farmland, infrequently grazed pastures, waste areas, and tall-grass prairies. *Solidago canadensis* is an important component of the vegetation on sites undergoing secondary succession (Werner *et al. op. cit.*).

Freshly-matured seeds of *S. altissima* are conditionally dormant at maturity; they require high temperatures (25/15, 30/15, 35/20°C) and light to germinate to 90% or more. Seeds cold stratified at 5°C for 12 weeks gained the ability to germinate at low temperatures (15/6, 20/10°C); stratified (nondormant) seeds germinated to high percentages at 15/6, 20/10, 25/15, 30/15, and 35/20°C. Seeds required light for germination at all thermoperiods, but the light requirement could be fulfilled either during the stratification or incubation period. Thus, in spring, high percentages of seeds can germinate over a wide range of thermoperiods (15/6 to 35/20°C). These results differ somewhat with those of R. Cornelius, who reported that although freshly-matured seeds of *S. canadensis* germinated in light to 95% or higher at constant temperatures of 25, 30, and 35°C, germination at 10, 15, and 20°C ranged from only 1 to 59%. However, Cornelius did not test the effect of cold stratification on seeds of *S. canadensis*, and further stated that "No dormancy [in freshly-matured seeds] could be observed." (Cornelius, R. 1990. The strategies of *Solidago canadensis* L. in relation to urban habitats. III. Conformity to habitat dynamics. *Acta Oecol.* 11:301-310). We suggest that the freshly-matured seeds in Cornelius' study were in conditional dormancy and that cold stratification would have promoted higher percentages of them to germinate at 10, 15, and 20°C.

Seeds of *S. altissima* sown in flats on 14 November 1991 in a nontemperature-controlled greenhouse in Lexington, Kentucky, began germinating between 17 and 24 February 1992, when average daily maximum and minimum temperatures were 13.8 and 5.0°C, respectively. However, most seeds germinated between 2 and 9 March, when average daily maximum and minimum temperatures were 17.4 and 5.4°C, respectively. Forty percent (360/900) of the seeds germinated in spring 1992, and 4 additional seeds germinated between 24 August and 14 September 1992. In marked contrast to these results, Werner *et al.* (*op. cit.*) reported that seedlings of *S. canadensis* emerged in June or early July in southern Ontario and southern Michigan.

Seeds of *S. canadensis* have been reported to be present in persistent seed banks in soil. In the majority of these studies, soil samples were collected between September and December (*e.g.*, Roberts, T.L. and J.L. Vankat. 1991. Floristics of a chronosequence corresponding to old field-deciduous forest succession in southwestern Ohio. II. Seed banks. *Bull. Torrey Bot. Club* 118:377-384). Soil collected in September and October (*i.e.*, before seed dispersal) could have contained seeds slightly less than one year old and/or seeds more than one year old. Whereas, soil collected in November and December (*i.e.*, after seed dispersal) could have contained seeds greater than one year old, about one year old, and/or a few days to a few weeks old. Thus, one cannot determine if the seeds were part of a transient or of a persistent seed bank.

Cornelius (*op. cit.*) reported that 131 seeds/m^2 and 110 seeds/m^2 germinated over "two germination seasons" in soil samples collected in August from an "industrial derelict site" and in a "derelict garden," respectively, in West Berlin. From these observations, he concluded that *S. canadensis* forms a persistent seed bank. However, one cannot determine from his pooled data if any seeds that germinated were greater than one year old, which is the criterion that K. Thompson and J.P. Grime use to distinquish between a transient and persistent seed bank (Thompson, K. and J.P. Grime. 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. *J. Ecol.* 67:893-921).

However, we suggest that in goldenrods the criterion for a persistent seed bank should not be survival of seeds in the soil for at least one calender year, but rather the ability of the seeds to remain viable until at least the second (spring) germination season - *i.e.*, for 16 months or longer. A conceptial model will be used to compare our definition of persistent seed bank with that of Thompson and Grime, and preliminary results of a study on the potential of *S. altissima* to form a persistent seed bank will be presented.