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XERIC LIMESTONE PRAIRIES OF EASTERN UNITED STATES

Patrick Joseph Lawless
University of Kentucky

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ABSTRACT OF DISSERTATION

Patrick Lawless

The Graduate School

University of Kentucky

2005

XERIC LIMESTONE PRAIRIES OF EASTERN UNITED STATES

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ABSTRACT OF DISSERTATION
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**A dissertation submitted in partial fulfillment of the
requirements for the degree of Doctor of Philosophy in the
College of Arts and Sciences
at the University of Kentucky**

**By
Patrick Joseph Lawless**

Lexington, Kentucky

**Co-Directors: Dr. Jerry M. Baskin, Professor of Biology
and   Dr. Carol C. Baskin, Professor of Biology and
                          of Plant and Soil Science**

Lexington, Kentucky

2005

ABSTRACT OF DISSERTATION

XERIC LIMESTONE PRAIRIES OF EASTERN UNITED STATES

Xeric limestone prairies (XLPs) are open, nonforested communities dominated by native, C_4 perennial grasses. In eastern United States, they occur on shallow, rocky calcareous soils in various physiographic provinces from Missouri and Pennsylvania south to Arkansas and Georgia. Floristic, vegetation, and physical environmental data were collected from 18 XLPs in Kentucky and used in conjunction with data collected in other studies to provide a synthesis for XLP vegetation in eastern United States and a comparison of this vegetation type with limestone cedar glades and deep-soil barrens. XLPs occur on 33 soil series in five orders (Alfisols, Mollisols, Ultisols, Inceptisols, and Vertisols) and on limestone, dolomite, and calcareous shale of Cambrian through Tertiary systems. In Kentucky, XLPs are restricted to the Interior Low Plateaus, where they are most frequent on the Upper Mississippian Salem Limestone in the Knobstone Escarpment and Knobs. Three hundred and thirty-five taxa were recorded in the 18 sites sampled in Kentucky, of which 20 (6.0%) are nonnative and 24 (7.2%) state-listed as rare. The majority of the flora is intraneous C_3 hemicryptophytes. Thirteen taxa are endemic to XLPs of eastern United States, but none to those in Kentucky. The native, C_4 perennial grass *Schizachyrium scoparium* was dominant in 10 of 12 community types in Kentucky identified at a scale of 100-m^2 and in 21 of 23 studies of XLPs in eastern United States. The C_4 annual grass *Sporobolus vaginiflorus* had high frequency values in the majority of sites in Kentucky, where it often was dominant in the most shallow-soil zones. Variability among XLPs in Kentucky and among the floras of XLPs in different

regions is largely attributable to differences in forb species composition. Soil depth is the primary abiotic source of variability in XLP community types in Kentucky and in many other regions of eastern United States. Dendrochronological and aerial photographic studies support the conclusion that the vast majority of XLPs are not primary communities. XLPs on the Cambrian Ketona Dolomite in the Ridge and Valley in Bibb County, Alabama, are perhaps the only sites which represent an edaphic climax

KEYWORDS: barrens, floristics, glades, vegetation, xeric limestone prairies

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1
GENERAL INTRODUCTION

INTRODUCTION

Variability in vegetation from global to local spatial scales has prompted scientists to classify it into discrete types or categories for the purposes of both description and communication. Classification is a systematic means of categorizing things based upon predefined sets of characteristics or variables. To devise classification systems for vegetation, ecologists have used physiognomy, taxonomic composition, geographic/physiographic distribution, and/or phenological characteristics (e.g. Transeau, 1948; Walter, 1979; Barbour and Billings, 2000). The desired outcome of vegetation classification is to be able to recognize all the different types in an area and to understand how they relate to each other. Consequently, a considerable amount of information (e.g. composition and structure) about the plant cover in a particular area can be communicated with a limited number of descriptive terms, i.e. one or more vegetation type(s).

The forest classification system of Braun (1950) for eastern North America is particularly exemplary of the utility of vegetation classification systems. Dominance of broad-leaf deciduous tree species (sometimes co-dominant with the needle-leaf evergreen *Tsuga canadensis*) in forests in southeastern Canada and eastern United States led Braun to classify this region of North America as the Eastern Deciduous Forest Formation (hereafter EDF). Based on her extensive sampling and observations of vegetation, Braun recognized trends in the composition and dominance structure of forests in the EDF and divided it into nine forest regions, principally in accordance with the dominant taxa in climatic climax vegetation in each region.

Braun also discussed many of the nonforested openings that occur within the EDF (e.g. limestone cedar glades and deep-soil barrens in the western mesophytic forest region). Subclimax and edaphic climax herbaceous communities are broadly distributed in the EDF and generally can be divided into two categories, those with deep soils and those associated with rock outcrops of various substrates. In order to provide greater

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perspective on the focal vegetation (xeric limestone prairies) of my dissertation research, I will briefly review the geographic distribution and structural, floristic, and physical environmental characteristics of **prominent nonforested, herbaceous communities** within the EDF region.

Forest Openings: Deep Soil

Deep-soil barrens, Black Belt prairies, and grassy balds are extremely susceptible to invasion by woody species and currently occupy only a small proportion of their former area. Prior to European settlement, **deep-soil barrens** (sensu Baskin et al., 1994; Chester et al., 1997; Baskin et al., 1999) covered broad expanses of the Pennyroyal (PP) and Elizabethtown (EP) plains in Kentucky and of the PP in northwestern Tennessee. This mostly karstic area underlain by Upper Mississipian limestones was commonly referred to as the "Big Barrens Region" and was included in various maps of the Prairie Peninsula by E.N. Transeau (Transeau, 1935; Baskin et al., 1995). Extensive areas of deep-soil barrens in the Jackson Purchase region in Kentucky (Loughridge, 1888) also were considered by Transeau to be part of the Prairie Peninsula. Deep-soil barrens originated from burning practices of Native Americans and rapidly came under cultivation or succeeded to secondary forest upon European settlement (Baskin and Baskin, 1981; Baskin et al., 1994; Chester et al., 1997; Baskin et al., 1999). Chester et al. (1997) and Chester (1999) conducted floristic surveys and vegetation sampling, respectively, in some of the few remaining barrens in this region, all of which are located in or near Fort Campbell Military Reservation (southwestern PP, Kentucky and Tennessee). These barrens represent a stage of old field succession, and they are maintained by burning. Chester et al. (1997) recorded 342 taxa in 22 sites, including 13 taxa state-listed as rare in Kentucky and/or Tennessee. The C_4 perennial prairie grass *Schizachyrium scoparium* was dominant (average percent importance value = 32.69) in all ten barrens sampled by Chester (1999). **[Note: Taxonomy follows USDA, NRCS (2004) throughout this dissertation.]**

Black Belt prairies once ranged from northeastern Mississippi to central Mississippi and central Alabama (DeSelm and Murdock, 1993), and their distribution was strongly correlated with that of the Cretaceous Selma Chalk (Jones and Patton,

1966). Low density of woody taxa in these prairies is attributed to alkaline clay soils (Jones and Patton, 1966). The majority of grasslands in the Black Belt, like those in the Big Barrens region in Kentucky, came under cultivation soon after European settlement (Jones and Patton, 1966). In the only vegetation sampling I am aware of in the Alabama portion of the Black Belt, *Hypoxis hirsuta*, *Schoenolirion croceum*, *Sporobolus vaginiflorus*, *Echinacea purpurea*, and *Schizachyrium scoparium* had the highest relative density values (Schuster and McDaniel, 1973). The only vegetation sampling data for the Mississippi portion of the Black Belt is for Harrell Prairie, where *Sporobolus asper*, *Dalea purpurea*, *Ratibida pinnata*, *Schizachyrium scoparium*, and *Symphyotrichum dumosum* had the highest frequency values (DeSelm and Murdock, 1993).

   Grassy balds occur at high elevations (~ 1400 to 1800 m) in the southern Appalachian Mountains (principally eastern Tennessee and western North Carolina) (Mark, 1958). Although the origin(s) of this vegetation type has been widely debated, there is general agreement that grassy balds were used as summer pastures for livestock of early European settlers (Wiser and White, 1999). Currently, management (grazing, cutting, herbicide use) is necessary to prevent or retard encroachment of woody species in these areas and thus maintain their open nature. Grassy balds support many rare and endangered species (Wiser and White, 1999). None of these is endemic to grassy balds, but many are endemic/near endemic to regionally co-occuring high elevation rock outcrop communities (see below). The geographically widespread, native, C_3 perennial grass *Danthonia compressa* is the dominant taxon in the vast majority of grassy balds that have been sampled (DeSelm and Murdock, 1993).

Forest Openings: Rock Outcrops

   Many open, nonforested vegetation types in the EDF are associated with rock outcrops. These long-persisting herbaceous vegetation types have received much attention from North American ecologists due to the sizeable number of rare and endangered heliophytic taxa they support, many of which are endemic (Baskin and Baskin, 1988). Because vegetation of these areas often differs considerably between geologic substrates, ecologists have distinguished rock outcrop plant communities primarily on the basis of substrate composition (Anderson et al., 1999), i.e. serpentine

barrens, shale barrens, granite rock outcrops, high elevation rock outcrops, sandstone rock outcrops, alvars, and limestone cedar glades.

Serpentine barrens range from Newfoundland, Canada, to Georgia (Brooks, 1987), but they are most numerous in northeastern Maryland and southeastern Pennsylvania (Tyndall and Hull, 1999). The term serpentine specifically refers to minerals composed of antigorite and chrysotile, but it is generally used to describe weathered ultramafic rock, which contains high concentrations of magnesium and iron (Brooks, 1987). Taxa with the highest mean importance values of all herbaceous layer species in four sites in Maryland were *Schizachyrium scoparium* (52.0%), *Scleria pauciflora* (13.8), *Cerastium arvense* var. *villosum* (13.8), *Aristida purpurascens* (11.9), and *Arabis lyrata* (10.0). *Schizachyrium scoparium* and *Scleria pauciflora* also were abundant in Pennsylvania serpentine barrens, in addition to *Panicum philadelphicum*, *P. sphaerocarpon*, *Aristida dichotoma*, and *A. longespica* (Tyndall and Hull, 1999).

With the exception of *S. scoparium*, dominant herbaceous taxa (*Senecio plattensis*, *Andropogon gerardii*, *Hexastylis arifolia* var. *ruthii*, and *Thalictrum macrostylum*) in an olivine-serpentine outcrop in western North Carolina differed considerably from serpentine sites in Maryland and Pennsylvania (Mansberg and Wentworth, 1984). Radford (1948) described eight community types associated with olivine and serpentine in North Carolina and Georgia. Of these, the pine-*Andropogon*, oak-grass, grass-weed, and grass-weed-oak communities were dominated by herbaceous taxa. Vegetation data largely are lacking for serpentine rock outcrops in Delaware, New York, Vermont, and eastern Canada (Quebec and Newfoundland).

Shale barrens are concentrated in the Ridge and Valley physiographic province (sensu Fenneman 1938, 1946 [1949]) in West Virginia, Virginia, and Pennsylvania (Braunschweig et al., 1999). This vegetation type is characterized by an open canopy of xerophytic shrub and tree species and supports numerous xerophytic, herbaceous taxa, 18 of which are endemic/near endemic. Interestingly, although all of these endemic/near endemic taxa are herbaceous, ground layer vegetation data are lacking for shale barrens. *Pinus virginiana* and *Juniperus virginiana* each had the highest importance value of all woody species in one of two sites in southwestern Virginia (Braunschweig et al., 1999).

Herbaceous vegetation types on **granite rock outcrops** occur in the Piedmont physiograpic province from east-central Alabama to southeastern Virginia (Shure, 1999), in the southern Appalachian Mountains (see high elevation rock outcrops below), in the Minnesota River Valley (Nietering, 1984), and in the Canadian Shield in southern Ontario, Canada (Catling and Brownell, 1999a). In the Piedmont of southeastern United States, these rock outcrops contain habitats at opposite ends of the moisture gradient. Shallow depressions on the surface of outcrops form pools (especially in winter and spring) that support uniquely adapted hydrophytic taxa, particularly the granite rock outcrop endemics *Isoetes melanospora*, *Isoetes tegetiformans*, and *Amphianthus pusillus*.

Vegetation mats and soil islands develop on flat exposed rock and in exfoliation depressions, respectively. These habitats are extremely xeric and are characterized by distinct successional stages in which community composition is highly correlated with soil depth, which generally increases over time (Oosting and Anderson, 1939; Burbanck and Platt, 1971; Shure and Ragsdale, 1977). Lichens and xerophytic mosses are typical pioneers on flat exposed rock. The winter annual succulent *Diamorpha* (*Sedum*) *smallii* often forms monospecific colonies in the first primary successional stage in exfoliation depressions. As organic (plant and lichen) and mineral materials accumulate in these pioneer communities, soil formation results in increased soil depth and areal coverage of mats and islands in their respective habitats. Areas on the periphery of these communities generally have the shallowest soils and continue to support pioneer stage vegetation. Conversely, maximum soil depth typically occurs in the interior of these vegetated areas, and this is the characteristic recruitment region for less xerophytic taxa. Burbanck and Platt (1964) used soil depth and characteristic flora to distinguish four successional communities (*Diamorpha*, lichen-annual herb, annual-perennial herb, herb-shrub) in exfoliation depressions. Species richness and proportion of perennial species increased along this successional sequence.

Significant habitat variability also is present in southern Ontario granite barrens and in granite rock outcrops in the Minnesota River Valley. Southern Ontario granite barrens contain exposed rock, lichen mats, grasslands, forests, and wetlands associated with rivers and streams (Catling and Brownell, 1999a). Nietering (1984) distinguished six microhabitats in granite rock outcrops in the Minnesota River Valley, including bare

rock, shallow depressions with dry soil, shallow depressions with soil saturated in spring, narrow rock cracks, rock pools, and deeper soils on rock surfaces.

Sixteen taxa are endemic to granite outcrops in southeastern United States (Shure, 1999). However, no plant taxa are known to be endemic to granite outcrops in other regions of eastern United States. Many of the so-called granite rock outcrop endemics [e.g. *Arenaria uniflora*, *Diamorpha* (*Sedum*) *smallii*, and *Talinum mengiesii*] also occur on other substrates, particularly Pennsylvanian and Tertiary sandstones (Baskin and Baskin, 1988).

High elevation rock outcrop vegetation types occur on granite, gneiss, schist, gabbro, and amphibolite in the southern Appalachian Mountains, primarily eastern Tennessee and western North Carolina from ~1,200 – 2,000 m (Wiser and White, 1999). Floristic composition and vegetation structure in these high elevation rock outcrop communities are correlated with elevation, geologic substrate, insolation, soil depth, and percent cover of bedrock. *Dichanthelium acuminatum*, *Carex umbellata*, *Kalmia latifolia*, and *Krigia montana* (an endemic) are common on rock outcrops from 1,200 to 1,600 m. *Aster acuminatus*, *Picea rubens*, *Abies fraseri*, *Solidago glomerata* (a southern Appalachian endemic), *Menziesia pilosa*, *Vaccinium erythrocarpum*, and *Carex brunescens* are characteristic of higher elevation outcrops (> 1600 m). Thirteen taxa are endemic to high elevation rock outcrops in the southern Appalachians. However, many of these so-called endemic taxa also occur in grassy balds (see above). **Heath balds** also are prominent landscape features on rock outcrops in the southern Appalachians. However, these communities are dominated by woody, evergreen species in the Ericaceae (primarily *Rhododendron* spp. and *Kalmia latifolia*) and are typified by low herbaceous species richness (Wiser and White, 1999).

Nonforested, **sandstone rock outcrop communities** primarily occur in the Ozark Plateaus (Arkansas and Missouri), Interior Low Plateaus (Illinois), Cumberland Plateau (Alabama, Georgia, Tennessee, Kentucky), and Coastal Plain (Louisiana, Georgia, Florida) (Baskin and Baskin, 1988; DeSelm and Murdock, 1993). *Coreopsis grandiflora*, *Crotonopsis elliptica*, and *Schizachyrium scoparium* had the highest average frequency values in 25 Calico Sandstone glades in the Arkansas Ozarks sampled by Jeffries (1985). Jeffries (1987) also sampled five sandstone glades in Devil's Den State Park (Arkansas

Ozarks), in which *Schizachyrium scoparium*, *Coreopsis palmata*, *Aristida dichotoma*, and *Helianthus hirsutus* had the highest average frequency values. According to Nelson and Ladd (1983), *Schizachyrium scoparium*, *Crotonopsis elliptica*, *Juniperus virginiana*, *Quercus stellata*, and *Vaccinium arboreum* are dominant taxa in sandstone glades in Missouri.

Woody taxa (particularly *Juniperus virginiana*), *Euphorbia corollata*, and *Manfreda virginica* had the highest average cover values in eight sandstone glades in the Shawnee Hills in southern Illinois sampled by Heikens and Robertson (1995). The lichen *Xanthoparmelia conspersa* and mosses *Polytrichum virginianum* and *Grimmia olneyi* were most abundant in Caseyville Sandstone rock ledges (i.e. glades) in the Shawnee Hills in southern Illinois sampled by (Winterringer and Vestal, 1956), particularly on exposed rock and in shallow soils. In less xeric zones of these outcrops, *Sedum pulchellum*, *Manfreda virginica*, *Asclepias verticillata*, and *Diodia teres* had high abundance values. *Juniperus virginiana*, *Quercus marilandica*, *Rhus radicans*, *Ulmus alata*, and *Vaccinium arboreum* were the dominant woody taxa in areas of deeper soils. *Quercus stellata*, *Ulmus alata*, *Schizachyrium scoparium*, and *Danthonia spicata* had the highest importance values in two sandstone barrens in the Shawnee Hills in southern Illinois sampled by Taft and Solecki (2002).

Perkins (1981) identified lithophyte (bare rock), cryptogram-herb, shrub-herb, and tree zones along a soil depth gradient in sandstone outcrops in the Cumberland Plateau in Tennessee and Alabama. Lithophyte zone communities included only nonvascular plants (lichens, mosses, algae). Cryptogam-herb communities were characterized by high cover of cryptogams and low cover of xerophytic herbaceous taxa [e.g. *Symphyotrichum surculosus*, *Liatris microcephala*, *Talinum teretifolium*, *Bigelowia nuttallii* (a near endemic to sandstone outcrops), and *Panicum dichotomum*]; shrub-herb communities by woody, evergreen ericaceous taxa (*Vaccinium* spp., *Kalmia latifolia*, *Gaylussacia baccata*), *Smilax rotundifolia*, *Tephrosia virginiana*, *Danthonia sericea*, *Helianthus longifolius*, *Symphyotrichum surculosus*, and *Schizachyrium scoparium*; and tree zone communities by *Pinus virginiana*.

Although they did not collect vegetation data, MacRoberts and MacRoberts (1992, 1993) reported *Schizachyrium scoparium* and *Bigelowia nuttallii* were the most

frequent taxa in three sandstone glades in the Gulf Coastal Plain in Louisiana (Kisatchie National Forest). All three of these glades occur within locally dominant long-leaf pine savannas and show evidence of erosion (gullied slopes). Harper (1906) reported *Packera* [*Senecio*] *tomentosa*, *Bigelowia nuttallii*, *Penstemon dissectus* (an endemic), *Lindernia monticola*, *Crotonopsis*, *Talinum*, and *Selaginella acanthonota* were "usual plants … on broad exposed horizontal ledges" in the Altamaha Grit region in the Coastal Plain in Georgia.

Limestone cedar glades and alvars are restricted to calcareous rock outcrops. **Limestone cedar glades** (sensu Baskin and Baskin, 1999; Baskin & Baskin, 2003, 2004) are an edaphic climax vegetation type limited to north-central southeastern United States. This vegetation type supports 21 endemic/near endemic taxa and is characterized by dominance of C_4 annual grasses and/or C_3 perennial or annual forbs. Soil depth is the primary factor determining community composition and structure in cedar glades (Somers et al., 1986; Rollins, 1997; Baskin and Baskin, 1999). In general, cover of C_3 winter annual forbs, many of which are endemic (i.e. *Leavenworthia* spp.), is negatively correlated with soil depth, and cover of C_3 perennial forbs is positively correlated with soil depth. C_4 annual grasses (particularly *Sporobolus vaginiflorus*, *Panicum flexile*, *P. capillare*) are abundant over the entire range of soil depth, except on pavements, where lichens and the N_2-fixing cyanobacterium *Nostoc commune* are common.

Alvars primarily occur on the shores of rivers and lakes and in limestone plateaus in the Great Lakes region (Catling & Brownell, 1999b). Shallow soils, scouring action of adjacent water bodies (shoreline alvars only), and/or fire are responsible for absence or low cover of woody vegetation in open alvar community types, principally alvar pavements and alvar grasslands. Alvar pavement communities are restricted to shallow (< 2 cm), rocky soils and support annual and perennial herbs. Alvar grassland communities occur in areas with deeper soils (> 2 cm) and little exposed rock, are characterized by dominance of perennial graminoids (*Carex scirpoidea*, *Danthonia spicata*, *Poa compressa*, *Schizachyrium scoparium*, *Sporobolus heterolepis*, *Bouteloua curtipendula*), and are the primary habitat for the only alvar endemic, *Hymenoxys herbacea*.

JUSTIFICATION AND PURPOSE OF DISSERTATION RESEARCH

Many sites with shallow, rocky calcareous soils (sometimes with ledges and often rock outcrops) in the EDF support herbaceous communities that resemble xeric grasslands in the Central Plains and Prairies Formation (sensu Barbour and Billings, 2000), particularly those in rocky uplands in western and west-central Kansas (Albertson, 1937; Hulett and Tomanek, 1969; Heitschmidt et al., 1970; Hladek et al., 1972). In eastern United States, these sites are distributed from Missouri and Pennsylvania south to Arkansas and Georgia, where they have been referred to as "glades" (e.g. Erickson et al., 1942), "barrens" (e.g. Heikens and Robertson, 1995), "prairies" (Braun, 1928), "prairie barrens" (Webb et al., 1997), and "xeric limestone prairies" (e.g. Baskin et al., 1994). Unlike limestone cedar glades, these grasslands apparently do not support rich endemic floras (Baskin et al., 1994) and are susceptible to invasion by woody species (Beilmann and Brenner, 1959; Kimmel and Probasco, 1980; Annala and Kaputska, 1983; Ver Hoef et al., 1993; Batek et al., 1999; Laughlin, 2004). C_4 perennial prairie grasses (principally *Schizachyrium scoparium*, *Boutleoua curtipendula*, *Andropogon gerardii*, *Sorghastrum nutans*) typically are dominant taxa in these sites (e.g. Braun, 1928; Kucera and Martin, 1957; Baskin and Baskin 1978 a,b; Keeland, 1978; Hicks, 1981; DeSelm, 1988, 1991, 1993; Logan, 1992; Bartgis, 1993; Ver Hoef et al., 1993; Heikens and Robertson, 1995; George, 1996; DeSelm and Webb, 1997; Ludwig, 1999; McClain and Ebinger, 2002; Laughlin and Uhl, 2003). However, C_4 annual grasses (particularly *Sporobolus vaginiflorus* and *S. neglectus*) are locally dominant in the shallow soil regions of some sites (Skinner, 1979; Ver Hoef et al., 1993; Baskin & Baskin, 2000).

A survey of available information on C_4 perennial grasslands associated with calcareous rock outcrops in eastern United States leads to the question: do all of these grasslands represent the same vegetation type, or are they different types of somewhat similar vegetation? In other words, are people studying different kinds of calcareous rock outcrop communities, or do these grasslands all share structural and compositional characteristics? Should the same term be used to designate this vegetation throughout its broad geographic range?

Baskin et al. (1994) referred to these grassland communities in the Big Barrens and adjacent regions in Kentucky as "xeric limestone prairies (XLPs)." Subsequently, this term has been conserved in describing similar sites in the Kentucky Karst Plain (=Pennyroyal Plain + Elizabethtown Plain, sensu Quarterman and Powell, 1978) (Baskin and Baskin, 1997), Ozarks and Midwest (Baskin and Baskin, 2000), and Ridge and Valley in Pennsylvania (Laughlin and Uhl, 2003; Laughlin, 2004). However, detailed comparisons have not been made to determine if the term xeric limestone prairie could be used justifiably as a descriptive term for these calcareous perennial grasslands throughout their geographic range in eastern United States. Further, although floristic and/or vegetation data are available for what has been called XLPs in other regions of eastern United States (Baskin and Baskin, 2000; Laughlin and Uhl, 2003), limited data are available for sites in Kentucky. Baskin and Baskin (1978) surveyed the flora of five xeric grasslands (portions of which fit the description of XLPs) in the Big Barrens Region of Kentucky. In his floristic survey of Hardin County, Cranfill (1991) included data collected from XLPs. White et al. (1994) conducted an endangered species survey in Fort Knox Military Reservation (Hardin County), which supports several XLPs. Data obtained by Baskin and Baskin (1978), Cranfill (1991), and White et al. (1994) suggest that XLPs in Kentucky are a significant repository for regionally rare heliophytic taxa; however, these studies focused on small geographic areas and/or a limited number of sites and did not include vegetation sampling.

Thus, given the 1) inconsistency in terminology used to describe these shallow-soil, calcareous grasslands throughout eastern United States, 2) limited comparisons between sites in different states and phyiographic regions, and 3) lack of adequate floristic and vegetation sampling in XLPs in Kentucky, I undertook an investigation of XLPs of eastern United States. After a survey of the literature, I developed five hypotheses, and these have provided the framework for my studies.

1. These sites are characterized by a single *vegetation type* defined by dominance of C_4 perennial grasses; a rich forb flora containing numerous regionally rare heliophytic taxa; shallow, rocky soils derived from calcareous substrates; and susceptibility to woody plant invasion.

2. *Community composition* and *structure* vary considerably throughout the geographic extent of this single vegetation type due to differences in geography, physiography, geology, and local soil conditions.

3. Taxa are endemic/near endemic to this vegetation type. However, lack of an integrated classification system for these calcareous rock outcrop communities has prevented thorough assessment of the fidelity of taxa to XLPs.

4. Soil depth is a primary determinant of fine-scale community composition and structure in all sites fitting the description of this vegetation type, as was true in the studies conducted by Skinner (1979) and Ver Hoef et al. (1993) in the Ozarks.

5. XLPs throughout eastern United States are of anthropogenic origin, which is in accordance with the conclusions of Baskin et al. (1994) and Baskin et al. (1997) concerning sites in the Interior Low Plateaus in Kentucky.

In addition to the paucity of information about the flora and vegetation of XLPs in Kentucky, another advantage of centering my studies in this state is that conservation organizations currently own and/or manage eleven high quality XLPs in the Commonwealth. These sites are broadly distributed among four physiographic regions in the Interior Low Plateaus province (sensu Quarterman and Powell, 1978), and thus they present an excellent opportunity to determine the effect(s), if any, of landform, geology, and soils on distribution, composition, and structure of XLPs. However, vegetation data are lacking for these preserves and other XLPs on private land; floristic data have not been collected systematically (i.e. in multiple surveys conducted throughout the growing season); and geology (formations/members) and soils (orders, subgroups, series) associated with these sites have not been documented. Collection of these data will fill a significant void in our knowledge of XLPs, and in conjunction with data collected in other studies, they will enable a thorough characterization of this vegetation type throughout its broad geographic distribution in eastern United States.

DISSERTATION CONSPECTUS

The purpose of this study was to collect floristic, vegetation, and physical environmental data from xeric limestone prairies (XLPs) in Kentucky in order 1) to compare XLPs in Kentucky with those in other regions in eastern United States, 2) to gain further insight into factors affecting composition, structure, and distribution of XLPs, and 3) to characterize the XLP vegetation type(s) throughout eastern United States. Occurrence of these sites in four physiographic regions in Kentucky afforded a unique opportunity to examine the fidelity of XLPs and of XLP community types to landforms/topographic positions, geologic formations/members, and soil types (orders, subgroups, series). Regional co-occurrence of XLPs, limestone cedar glades, and deep-soil barrens in the Interior Low Plateaus physiographic province in Kentucky (Baskin et al., 1994) also provided impetus for further comparison of these regionally rare herbaceous vegetation types based upon floristic and vegetation data obtained from XLPs in the current study.

In **chapter 2**, life form (sensu Raunkiaer, 1934), photosynthetic pathway, geographic affinity, and conservation status were determined for each taxon present in the 18 XLPs sampled in Kentucky. These data were used in floristic comparisons of XLPs in Kentucky with limestone cedar glades of southeastern United States (Baskin and Baskin, 1999; Baskin and Baskin, 2003) and deep-soil barrens of the southwestern Pennyroyal Plain (Chester et al., 1997). Furthermore, physiography, geologic formation(s)/member(s), and soil series associated with each XLP were documented. Three hundred and thirty-five taxa were recorded in the 18 XLPs, of which 20 are nonnative and 24 state-listed. The floras of XLPs in Kentucky and deep-soil barrens in the southwestern Pennyroyal Plain had higher percentages of woody taxa and lower percentages of therophytes (annuals) than did the flora of limestone cedar glades of southeastern United States. Furthermore, only the limestone cedar glade flora contains endemic/near endemic taxa. Typically, the XLPs surveyed occurred on moderate to steep slopes with south to west aspects and were associated with soils mapped as rock outcrop complexes. Nine of 18 XLPs surveyed were in the Knobstone Escarpment and Knobs subsection of the Interior Low Plateaus, and all of these sites occurred on Upper Mississippian Salem Limestone.   Coefficients of community (CC) calculated from floristic checklists prepared for each site suggested all but two of the 18 sites (Crooked

Creek Barrens Sites 1 and 2) belong to a single association [sensu the association criterion (CC's $\geq$ 0.50) of Barbour and Billings (2000), which is based entirely on floristic data].

In **chapter 3**, XLP community types were identified at multiple scales (0.01, 0.1, 1.0, 10, and 100 m^2) via flexible beta linkage cluster analysis of presence and cover class data. Nonmetric multidimensional scaling was used to determine primary sources of variability among 100-m^2 community types. *Schizachyrium scoparium* was the dominant taxon in 10 of 12 100-m^2 community types and had the highest percent occurrence of all taxa in the majority of fine-scale community types (0.01-10 m^2). Therefore, XLPs in Kentucky, like those in other regions of eastern United States, are characterized by dominance of C$_4$ perennial grasses. *Sporobolus vaginiflorus*, a C$_4$ annual grass, had the highest frequency of all taxa in many fine-scale community types and often co-occurred with *Schizachyrium scoparium*. Soil depth and herbaceous species composition were significant sources of variability among 100-m^2 community types.

Fidelity of multiple-scale XLP community types to sites and Level IV ecoregions of Kentucky (sensu Woods et al., 2002) was analyzed via site and ecoregional dispersion indices in **chapter 4**. Dispersion of community types among sites and among ecoregions was negatively correlated with grain (i.e. quadrat size). Strong fidelity of coarse-grain community types (10 and 100-m^2) to sites and ecoregions in this study suggests that a considerable number of less abundant taxa, or of unique sets of less abundant taxa, are restricted to particular sites and ecoregions. Restriction of these taxa or sets of taxa to particular sites and, more importantly to ecoregions, suggests regional processes such as colonization and extinction significantly affect community composition and thus classification and dispersion of community types.

Geographic, physiographic, geologic, soils, vegetation, and floristic data from sites throughout the range of this vegetation type were synthesized in a broad characterization of XLPs in eastern United States in **chapter 5**. In addition, the aforementioned data were used in conjunction with aerial photographic (Missouri, Indiana, Ohio, and Pennsylvania) and dendrochronological (Missouri and Indiana) data to make inferences about the origin and maintenance of XLPs throughout their broad geographic range in eastern United States. Synthesis of floristic, vegetation, and physical

13

environmental data for XLPs of eastern United States resulted in recognition of a single XLP vegetation type, to which 13 taxa apparently are endemic/near endemic. This vegetation type occurs in six physiographic provinces (Ozark Plateaus, Central Lowland, Interior Low Plateaus, Appalachian Plateaus, Ridge and Valley, and Coastal Plain) (sensu Fenneman 1938, 1946 [1949]) and is associated with 33 soil series (in five orders, including Alfisols, Ultisols, Mollisols, Inceptisols, and Vertisols) derived from limestones, dolomites, and calcareous shales of Cambrian through Tertiary systems. With the exception perhaps of sites on Ketona Dolomite in Bibb County, Alabama, this vegetation type is characterized by dominance of C_4 perennial grasses and is not an edaphic climax.

The **final chapter (6)** summarizes results of my dissertation research and presents conclusions relevant to classification and distribution of xeric limestone prairies throughout eastern United States. Furthermore, comparisons are made between 1) XLPs and other nonforested herbaceous vegetation types on calcareous substrates in the EDF region (specifically limestone cedar glades and deep-soil barrens), and 2) XLPs and xeric grasslands in the Central Plains and Prairies Formation.

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CHAPTER 2

THE FLORISTIC ECOLOGY
OF XERIC LIMESTONE PRAIRIES IN KENTUCKY,
AND A COMPARISON TO
LIMESTONE CEDAR GLADES AND DEEP-SOIL BARRENS

SYNOPSIS

The flora of 18 xeric limestone prairies (XLPs) in the Interior Low Plateaus physiographic province in Kentucky was surveyed and a checklist of vascular plants prepared for each site. Nine of the 18 sites are in the Knobstone Escarpment and Knobs, four in the Mammoth Cave Plateau, two in the Pennyroyal Plain, and three in the Outer Blue Grass. Life form, photosynthetic pathway, geographic affinity, conservation status and presence were determined for each taxon.   Community coefficients were calculated from site floristic lists, and the physiography, geology, and soils associated with each site were documented. The flora of XLPs was compared to that of limestone cedar glades of the southeastern United States and of deep-soil barrens of the southwestern Pennyroyal Plain in Kentucky and Tennessee. Three hundred and thirty-five taxa were identified in this vegetation type, of which 20 are nonnative and 24 state-listed as rare. Families with the highest number of taxa were Asteraceae (70), Poaceae (32), and Fabaceae (29); genera with the highest number of taxa were *Symphyotrichum* (15), *Panicum* sensu lato (=*Panicum* + *Dichanthelium*) (10), *Carex* (7), *Solidago* (7), and *Hypericum* (6). Intraneous C_3 hemicryptophytes make up the majority of the flora.   Community coefficients indicate high similarity among all sites except those in the eastern Outer Blue Grass, which belong to a second association or community type.   Endemic species, a higher percentage of therophytes (i.e. annuals, especially winter annuals), and a higher number of taxa with western and northwestern geographic affinities distinguish the limestone cedar glade flora from those of XLPs and deep-soil barrens.

INTRODUCTION

Xeric limestone prairies (XLPs) are characterized by high cover of C_4 perennial grasses (*Schizachyrium scoparium*, *Andropogon gerardii*, *Sorghastrum nutans*, and *Bouteloua curtipendula*), moderate to steep slopes with south to west aspects, and shallow rocky soils derived from calcareous substrates (Baskin and Baskin, 2000). In Kentucky, these herbaceous plant communities occur in the western mesophytic forest region (sensu Braun, 1950) and are rare at the landscape scale. The flora of XLPs in Kentucky has not been adequately characterized, and the soils, geology, and physiography associated with this vegetation type have not been documented systematically. Thus, the primary objectives of the present study were to: 1) provide a checklist of vascular plants in XLPs in Kentucky based upon my recent field work; 2) determine the geographic relationships, life forms, and photosynthetic pathways of the constituent taxa; and 3) document the soils, geology, and physiography associated with XLPs in Kentucky. A fourth objective was to further compare XLPs to limestone cedar glades and deep-soil barrens, both of which also are developed on calcareous substrates and occur in the western mesophytic forest region.

In their comparison of XLPs, limestone cedar glades and deep-soil barrens in the Kentucky Karst Plain and adjacent areas, Baskin et al. (1994) focused primarily on vegetation, edaphic characteristics, and origins. Like XLPs, deep-soil barrens are characterized by high cover of C_4 perennial grasses (*Schizachyrium scoparium*, *Andropogon gerardii*, and *Sorghastrum nutans*). However, deep-soil barrens originated from periodic burning by Native Americans prior to European settlement, whereas XLPs resulted from clearing of land for agricultural purposes, overgrazing, and subsequent soil erosion (Baskin et al., 1994). Conversely, limestone cedar glades are an edaphic climax community and typically have high cover of the C_4 summer annual grass *Sporobolus vaginiflorus* (Baskin and Baskin, 1999).

Baskin and Baskin (2003) published the flora of limestone cedar glades of the southeastern United States, and Chester et al. (1997) published the flora of deep-soil barrens in the southwestern Pennyroyal Plain of Kentucky and Tennessee. By providing a flora of XLPs in Kentucky, the current study affords the opportunity for floristic comparisons among these three herb-dominated vegetation types. Comparative data on

species richness, geographic affinities, photosynthetic pathways, life form, and taxonomic distribution of the three respective floras are essential for accurate characterization of these vegetation types and will provide further insight into their ecological differences.

SITE CHARACTERISTICS

A site was defined as a single forest opening (Figure 2.1), many of which contained small patches of woody vegetation. In two sample areas (Crooked Creek Barrens and Fort Knox Military Reservation), two forest openings occurred on the same land parcel. However, in both of these properties the two openings are separated by at least 100 m, and thus each opening was considered a site. An attempt was made to determine the exact area of each site using GIS software. However, the large perimeter to area ratios and patches of woody vegetation in many sites prevented accurate measurement. In general, sample sites ranged from less than 0.5 to approximately 2.25 hectares. Site characteristics are summarized in Table 2.1.

Physiography

In Kentucky, XLPs occur in the Blue Grass, Shawnee, and Highland Rim sections of the Interior Low Plateaus physiographic province (sensu Quarterman and Powell, 1978) (Figure 2.2). The Knobstone Escarpment and Knobs subsection of the Blue Grass supports the largest number of XLPs in the state, containing nine of the 18 sites surveyed in this study. The relatively high number of XLPs in this area is most likely due to the rugged terrain in the region, since moderate to steep slopes with fine-textured soils are particularly susceptible to soil erosion. XLPs also occur in the western (Pine Creek Barrens) and eastern (Crooked Creek Barrens 1 and 2) Outer Blue Grass.   In the Shawnee Hills section, all four sample sites (Grayson County Barren, Knight's Barren, Lapland Barrens, and Lapland Road Barrens) are located in the Mammoth Cave Plateau. Logan County Glade and Logan County Barrens also are shown in the Mammoth Cave Plateau on the map of Quarterman and Powell map (Figure 1, page 30). However, I consider them to be in the Pennyroyal Plain subsection of the Highland Rim, which is in agreement with Fenneman (1938, Figure 123, page 436) and an unpublished map of the Pennyroyal Plain by Baskin and Baskin.

Geology

The XLPs in Kentucky occur on Upper Silurian and Upper Mississippian calcareous substrates including limestone, dolomite and shale (Figure 2.3). The sample sites in the Knobstone Escarpment and Knobs, Mammoth Cave Plateau, and Pennyroyal Plain all occur on Upper Mississippian limestones, many of which also contain shale and/or dolomite. All nine XLPs surveyed in the Knobstone Escarpment and Knobs are developed on Salem Limestone of the Meramecian Series (Keperfele, 1966, 1967; Peterson, 1966). Keperfele (1967) defines two main units within the Salem Limestone and describes the second unit in association with characteristic surface and vegetation features of XLPs as follows: "an argillaceous limestone and shale" with a "surface marked by rounded gullied slopes barren except for scattered junipers."

All sample sites in the Mammoth Cave Plateau and Pennyroyal Plain occur on Upper Mississippian limestones of the Chesterian Series, many of which contain a significant shale component. Three of the four XLPs in the Mammoth Cave Plateau (Lapland Road Barrens, Lapland Barrens, and Knight's Barren) are on Reelsville Limestone, and two of the three sites (Lapland Road Barrens and Lapland Barrens) extend onto Beech Creek Limestone (Moore, 1965; Amos, 1972). The fourth site in the Mammoth Cave Plateau (Grayson County Barren) is restricted to Glen Dean Limestone (Gildersleeve, 1978). The two sites in the Pennyroyal Plain are developed on Paint Creek Limestone (Logan County Barrens) and Girkin Limestone (Logan County Glade) (Rainey, 1965; Miller, 1968).

The single sample site in the western Outer Blue Grass (Pine Creek Barrens) is on Louisville Limestone (Upper Silurian), which is composed of dolomite and dolomitic limestone (Keperfele, 1968). The two XLPs in the eastern Outer Blue Grass (Crooked Creek Barrens 1 and 2) are formed on the Upper Part of the Crab Orchard formation, a variegated clay-shale, and the Lower Part of the Crab Orchard and Brassfield formations (undivided, Upper Silurian), which is composed of dolomite, dolomitic limestone, and interbedded clay-shale (Peck and Pierce, 1966).

Soils

Soils of XLPs in Kentucky have mixed mineralogy, are fine-textured (Table 2.2), moderately to severely eroded, and shallow to moderately deep (0 to ca. 1 m, Baskin et al., 1994). Forty-two percent of 376 soil depth measurements in the 18 sites were $\leq$ 10 cm, 76% $\leq$ 30 cm, 91% $\leq$ 60 cm, and only 6% > 1 m. Ten of the 13 soil series upon which XLPs occur are Alfisols, and the remaining three series are Mollisols (Corydon), Ultisols (Gilpin), and Inceptisols (Garmon). Nine of the 18 sample sites are developed on the Caneyville series, a Typic Hapludalf (Figure 2.4). In addition, many of the soil mapping units in XLPs are rock outcrop complexes (e.g. Caneyville-Rock Outcrop Complex, Rock Outcrop-Corydon Complex, and Rock Outcrop-Fredonia-Colbert Complex). All soil mapping units associated with sample sites in the Knobstone Escarpment and Knobs are members of the Garmon-Caneyville-Lenberg Soil Association, which in this region also includes the Corydon, Cumberland, Hagerstown, and Vertrees series (Arms et al., 1979). Three of the four sites in the Mammoth Cave Plateau (Grayson County Barren, Lapland Road Barrens, and Knight's Barrens) occur on the Caneyville series (Whitaker et al., 1972; Arms et al., 1979; Haagen, 2001), and the fourth (Lapland Barrens) is the only site on the Rosine-Gilpin-Lenberg complex (Haagen, 2001). Both sites in the Pennyroyal Plain (Logan County Barrens and Logan County Glade) are restricted to the Rock Outcrop-Fredonia-Colbert complex (Dye et al., 1975). The sample sites in the Outer Blue Grass occur on the Caneyville series (Pine Creek Barrens) (Whitaker and Waters, 1986) and Beasley and Shrouts series (Crooked Creek Barrens 1 and 2) (USDA, NRCS, Soil survey of Lewis County, Kentucky, unpublished).

METHODS

In 2002 and 2003, each of 18 sites was visited a minimum of once per season in spring, summer, and autumn. All vascular plant species were recorded and a species list prepared for each site. Gleason and Cronquist (1991) was used for field identification, and taxa not identified in the field were collected and determined in the University of Kentucky Herbarium (KY) with the aid of a stereomicroscope. Each taxon was assigned a presence value based on the percentage of sites in which it was recorded and placed in one of the following five presence classes (Cain and Castro, 1959): 1 (1-20%), 2 (21-

40%), 3 (41-60%), 4 (61-80%), and 5 (81-100%) . *Sporobolus vaginiflorus* was treated as a single taxon, since the two varieties found in this study are primarily distinguished by microscopic characters in both vegetative and reproductive states (FNEC 2003). Community coefficients (CC) were calculated for all possible pair-wise site comparisons using PC-ORD (McCune and Mefford, 1999). Community coefficients [CC= 2W/(A+B)] are based on the number of taxa shared between sample sites (W) and the total number of taxa in site A and in site B. The life form (sensu Raunkiaer, 1934) of each taxon was obtained from Gibson (1961), Hansen (1952), Ennis (1928), and Baskin and Baskin (1978) and the photosynthetic pathway from Baskin and Baskin (2003) and Waller and Lewis (1978). Life form and photosynthetic pathway also were determined for each of the 342 taxa reported by Chester et al. (1997) in the deep-soil barrens of the southwestern Pennyroyal Plain of Kentucky and Tennessee for comparisons with the floras of XLPs in Kentucky and limestone cedar glades of the southeastern United States (Baskin and Baskin, 1999). I reviewed the list of state endangered, threatened and special concern species published by the Kentucky State Nature Preserves Commission (2002) and noted all state-listed taxa occurring in XLPs in Kentucky.

The geographic relationships of all taxa were determined by examining distribution maps obtained from Plants (USDA, NRCS, 2004). Taxa in which Kentucky is in the central region of their current distribution were defined as intraneous, and those in which Kentucky is at the edge of their current distribution were defined as extraneous. When considering the geographic relationships of taxa in which Kentucky is near the edge of their range, the conservation status or rank and/or county distribution in the adjacent state was (were) considered, if available. If Kentucky is near the edge of the taxon's current distribution and the taxon is listed (endangered, threatened, or special concern) in the adjacent state or only distributed in counties adjacent to the Kentucky border, the taxon was considered extraneous. The extraneous species were divided further into extraneous northern, southern, eastern and western groups in accordance with the position of Kentucky in relation to the center of distribution of the taxon of interest.

RESULTS

A total of 335 vascular plant taxa representing 333 species, 215 genera and 72 families were recorded in the 18 XLPs surveyed (Appendix). The genera *Crataegus* and

Rubus were each treated as a single taxon, because no flowering individuals were observed in either genus, both of which are characterized by intergradation of vegetative characters between/among species and high taxonomic diversity. Three hundred and fifteen (94.0%) of the 335 taxa are native to Kentucky, and the remaining 20 (6.0%) nonnative (Figure 2.5). Asteraceae, Poaceae and Fabaceae had the highest richness values of all families, containing 70 (20.9%), 32 (9.6%) and 29 (8.7%) taxa, respectively. Genera with the largest number of taxa were *Symphyotrichum* (15), *Panicum* sensu lato (=*Panicum* + *Dichanthelium*) (10), *Carex* (7), *Solidago* (6), and *Hypericum* (6). The XLPs in Kentucky support 24 state-listed taxa (9 endangered, 8 threatened and 7 special concern), including three species (*Delphinium carolinianum* ssp. *calciphilum*, *Leavenworthia exigua* var. *laciniata*, and *Talinum calcaricum*) listed by Baskin and Baskin (1999) as cedar glade endemics. However, none of these state-listed taxa is federally listed, and none of the taxa recorded in this study is endemic to XLPs in Kentucky. Furthermore, the three cedar glade endemics occur in areas of XLPs that fit the description of limestone cedar glades when categorized at small spatial scales (Figure 2.1).

The flora of XLPs in Kentucky is composed primarily of native C_3 hemicryptophytes with broad geographical distributions encompassing Kentucky. Ninety-two and eight-tenths percent of the taxa are C_3 plants, and with the exception of *Manfreda virginica*, *Opuntia humifusa* (CAM plants), and *Cuscuta cuspidata* (nonphotosynthetic), the remaining taxa are C_4 plants. The hemicryptophyte life form group contains more taxa (52.9% of native species) than all other life form groups combined (Figure 2.5). Seventy-three and five-tenths percent of the native taxa in the xeric limestone prairie flora in Kentucky (230 taxa) is intraneous (Figure 2.6), and taxa with southern geographic affinities (44 taxa, 14.1%) make up the largest extraneous component of the flora.

Although species richness values varied considerably across the 18 XLP sites surveyed, species composition among the sites was quite similar. Average site richness was 113 taxa (CV=13%) and ranged from 88 (Thompson Creek Glade) to 151 (Pine Creek Barrens) (Table 2.1). Calculation of community coefficients (CCs) for all possible pair-wise site comparisons determined that the majority of XLPs surveyed form a single

association or community type. Only 11 of the 153 CCs calculated were less than 0.50, the generally accepted association criterion (Barbour et al., 1999). Nine of the 11 CCs less than 0.50 included either site 1 or site 2 in Crooked Creek Barrens, and the CC resulting from comparison of Crooked Creek Barrens site 1 and site 2 is high (0.71). These data suggest the two sites in Crooked Creek Barrens may belong to a second association. Particularly noteworthy was the absence of *Echinacea simulata* and *Hypericum dolabriforme* in both Crooked Creek Barrens sites, since these taxa had high frequency values in the majority of the remaining sites (Chapter 3). CCs ranged from 0.39 to 0.80, and the average CC (x=0.58) minus one standard deviation (s = 0.07) exceeds the generally accepted 0.50 association criterion.

As expected, the presence diagram for the XLP flora in Kentucky (Figure 2.7) shows that the majority of species are in presence classes 1 and 2. However, the percentage of taxa in presence class four (15.3%) is similar to that in presence class two (18.0%), and thus class four approaches a second maximum (Oosting, 1956). Only 13 taxa were present in all 18 sites, and all of them are native. Five of these 13 taxa are broadly distributed phanerophytes (*Cercis canadensis*, *Diospyros virginiana*, *Fraxinus americana*, *Juniperus virginiana*, and *Rhamnus caroliniana*), two are dominant perennial (*Schizachyrium scoparium*) and annual (*Sporobolus vaginiflorus*) grass species in this community type (Baskin and Baskin, 2000; Chapter 3), and the remaining six species (*Euphorbia corollata*, *Helianthus hirsutus*, *Lobelia spicata*, *Physostegia virginiana*, *Ruellia humilis*, and *Solidago nemoralis*) are relatively abundant forbs in XLPs in Kentucky (Chapter 3).

DISCUSSION

The taxonomic distribution of the flora of XLPs in Kentucky is very similar to that in the floras of cedar glades of the southeastern United States (Baskin and Baskin, 1999) and of the deep-soil barrens of the Southwestern Pennyroyal Plain in Kentucky and Tennessee (Chester et al., 1997). However, the percentage of nonnative taxa in the XLP flora of Kentucky (6.0%) is considerably less than the percentage of nonnative taxa in the flora of the state of Kentucky (21.8%, Jones, 2005), of cedar glades of the Central Basin of Tennessee (18.7%, Baskin and Baskin, 2003), and of southeastern United States (17.9%, Baskin and Baskin, 1999) and of deep-soil barrens of the southwestern

Pennyroyal Plain in Kentucky and Tennessee (9.1%, Chester et al., 1997) (Figure 2.6). Furthermore, the vast majority of nonnative species in the XLP flora in Kentucky have low presence values. Nine of the 20 taxa were present in only one site, and 18 occurred in four sites or less. The low percentage of nonnative taxa in the flora of XLPs in Kentucky may be due to erosion of the organic horizon in these sites, which results in reduced nutrient availability in the soil surface layer (Rhoades et al., 2004). This reduction in surface layer nutrient availability may significantly decrease survivorship of nonnative seedlings, as these taxa typically are adapted to nutrient-rich sites (Grime, 1974).

Asteraceae and Poaceae have the highest richness values of all families in the floras of XLPs in Kentucky, cedar glades of the southeastern United States, and deep-soil barrens of the southwestern Pennyroyal Plain, collectively accounting for 30.4%, 20.9%, and 33.3%, respectively, of taxa in these floras. Fabaceae ranks third in species richness in the floras of XLPs in Kentucky and deep-soil barrens, whereas species richness in the Cyperaceae exceeds that in Fabaceae in the flora of cedar glades of the southeastern United States. The flora of cedar glades also is distinguished by 19 endemic and two near-endemic taxa. The genus *Panicum* sensu lato contains the largest number of taxa in the floras of cedar glades (16) and deep-soil barrens (10). The flora of XLPs in Kentucky also is rich in *Panicum* species sensu lato (10 taxa); however, *Symphyotrichum* had the highest richness of all genera (15 taxa).

The geographic affinities, photosynthetic pathway, and life form distributions among the floras of XLPs in Kentucky, limestone cedar glades, and deep-soil barrens are similar. However, the flora of limestone cedar glades differs from that of the other two community types in three important aspects. The floras of XLPs and deep-soil barrens contain a strong extraneous southern component (14.1 % and 24.0% of floras, respectively). In contrast, taxa with western or northwestern geographical affinities make up the largest percentage of extraneous taxa (12.6% of flora) in the limestone cedar glade flora (Baskin and Baskin, 1999). The phanerophyte life form group contains a considerably smaller percentage of native taxa in the flora of limestone cedar glades (11.5) in comparison with the floras of XLPs in Kentucky (19.4) and deep-soil barrens (18.6) (Figure 2.5). The flora of limestone cedar glades also is distinguished by a relatively high percentage of native therophytes (23.0), many of which are winter

annuals. The cedar glade flora contains eight winter annuals in the genus *Leavenworthia* alone, which partially accounts for the richness of the Brassicaceae (17 taxa) in this community type and for the near endemic status of the genus *Leavenworthia* in the southeastern United States (Estill and Cruzan, 1999; Baskin and Baskin, 2003). Conversely, the XLP flora in Kentucky contains only three native winter annuals, *Leavenworthia uniflora*, *Leavenworthia exigua* var. *laciniata*, and *Minuartia patula*, all of which occur in cedar glade-like areas of the perennial grassland matrix (Figure 2.1), and this life cycle type is absent in the deep-soil barrens flora.

The winter annual life cycle is an adaptive phenological strategy in limestone cedar glades. It assures completion of the life cycle prior to summer-dry conditions, which winter annuals pass in the drought-tolerant seed stage (Baskin and Baskin, 1985). The paucity of winter annuals in the floras of XLPs in Kentucky and deep-soil barrens of the southwestern Pennyroyal Plain suggest the edaphic conditions in these habitats are considerably less severe, and/or these communities have not existed for a sufficient period to allow for evolution of the annual life cycle in a comparable proportion of resident taxa.

Although the XLPs surveyed support no endemic or federally listed taxa, this community type is the primary habitat in Kentucky for almost all of the 24 state-listed rare species recorded in the present study. Therefore, preservation of these species in Kentucky is dependent upon conservation of the XLP vegetation type. Presently, nine of the 18 sites surveyed are owned by conservation organizations (Kentucky State Nature Preserves Commission and The Nature Conservancy) or by the federal government (Fort Knox Military Reservation). Three of the remaining nine sites (Hardin County Cedar Glade, Knight's Barrens, and Lapland Barrens) are under management agreement with The Nature Conservancy, and the Logan County NRCS office is currently in the process of purchasing Logan County Barrens, one of the two sites surveyed in the Pennyroyal Plain. The most significant threat to XLP conservation is all terrain vehicle (ATV) usage, which damages or destroys vegetation, thus promoting further erosion of denuded soils.

Baskin et al. (1994) proposed the following sequence of events for the origin of XLPs in Kentucky: clearing of marginal agricultural lands by European settlers →

cultivation and/or grazing → significant erosion of the topsoil → abandonment → colonization of these degraded areas by the XLP flora → succession to hardwood forest in the absence of disturbance or maintenance of XLP with periodic management (i.e. disclimax). Forest succession is retarded by the highly eroded soils of these abandoned hillsides and by large heat loads (sensu McCune and Grace, 2002) associated with the moderate to steep slopes with south to west aspects. However, succession to hardwood forest eventually occurs in the absence of management, which typically consists of mechanical removal of large trees, particularly *Juniperus virginiana*, and periodic prescribed fire (2-5 year burning interval, David Skinner, KSNPC Eastern Preserve Manager, personal communication).

The species composition of this vegetation type is relatively consistent despite 1) their relatively recent origin, 2) the rarity of XLPs at the landscape scale, and 3) the small area occupied by these communities in the matrix of deciduous forests and agricultural lands. The richness of Asteraceae and Poaceae in the XLP flora of Kentucky is primarily responsible for the relatively high CCs (x = 0.58) observed in this study, since both of these families are characterized by large regional species pools and high proportions of wind-dispersed taxa. Furthermore, I have observed many taxa in the XLP flora (e.g. *Schizachyrium scoparium*, *Panicum flexile*, *Liatris squarrulosa*, *Ratibida pinnata*, *Croton monanthogynus*, *Hypericum dolabriforme*, etc.) in open forests with shallow rocky soils, on rock ledges, and on rocky stream banks. These habitats, in addition to deep-soil barrens and limestone cedar glades, are the likely sources of the XLP flora in Kentucky, since they existed prior to European settlement.

CONCLUSIONS

XLPs are broadly distributed throughout the Interior Low Plateaus physiographic province in Kentucky and are most frequent in the Knobstone Escarpment and Knobs, where they primarily occur on eroded Alfisols derived from the Upper Mississippian Salem Limestone. The flora is rich in species of Asteraceae and Poaceae and contains 24 state-listed rare taxa, many of which are restricted to XLPs in this part of their geographic range. Community coefficients suggest that all sample sites except those in the eastern Outer Blue Grass (Crooked Creek Barrens 1 and 2) belong to a single association. XLPs

32

are relatively well protected in Kentucky; the majority of sites are owned and/or managed by conservation organizations and the federal government.

The majority of taxa in the floras of XLPs in Kentucky, limestone cedar glades of the southeastern United States, and deep-soil barrens of the southwestern Pennyroyal Plain in Kentucky and Tennessee are intraneous C_3 hemicryptophytes. The very low percentage (6.0) of nonnative species in the XLP flora of Kentucky is noteworthy. Among XLPs, limestone cedar glades, and deep-soil barrens, the flora of limestone cedar glades is particularly unique due to 1) 21 endemic/near endemic taxa, 2) relatively high percentage of therophytes, and 3) an extraneous component with strong western and northwestern affinities (Baskin and Baskin 1999). In contrast, the floras of XLPs in Kentucky and deep-soil barrens of the southwestern Pennyroyal Plain 1) contain no endemic taxa, 2) have higher percentages of phanerophyte taxa, and 3) have an extraneous component with strong southern geographic affinities.

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Table 2.1.   Site characteristics of 18 xeric limestone prairies surveyed in the Interior Low Plateaus physiographic province in Kentucky.

	Site	County	Physiographic Subsection of Interior Low Plateaus	Ownership	Soil Order(s)	Geologic Formation(s) (System)	Site Richness
1	Fort Knox Military Reservation 1	Hardin	Knobstone Esc. & Knobs	Dept. of Defense	Alfisols, Mollisols	Salem Limestone (UM)	99
2	Fort Knox Military Reservation 2	Hardin	Knobstone Esc. & Knobs	Dept. of Defense	Alfisols	Salem Limestone (UM)	126
3	Cedar Creek Farms	Hardin	Knobstone Esc. & Knobs	Private	Alfisols	Salem Limestone (UM)	123
4	Scudder Glade	Hardin	Knobstone Esc. & Knobs	KSNPC	Alfisols	Salem Limestone (UM)	125
5	Hardin Co. Cedar Glade	Hardin	Knobstone Esc. & Knobs	Private*	Alfisols	Salem Limestone (UM)	99
6	Muldraugh's Barren	Hardin	Knobstone Esc. & Knobs	Private	Alfisols	Salem Limestone (UM)	93
7	Mixed Grass Barrens	Larue	Knobstone Esc. & Knobs	Private	Alfisols	Salem Limestone (UM)	104
8	Spalding Glade	Larue	Knobstone Esc. & Knobs	KSNPC,Private**	Alfisols, Inceptisols	Salem Limestone (UM)	129
9	Thompson Creek Glade	Larue	Knobstone Esc. & Knobs	KSNPC	Alfisols	Salem Limestone (UM)	88
10	Pine Creek Barrens	Bullitt	Outer Blue Grass	TNC	Alfisols	Louisville Limestone (US)	151
11	Crooked Creek Barrens 1	Lewis	Outer Blue Grass	KSNPC	Alfisols	Upper Part of Crab Orchard (US), Lower Part of Crab Orchard (US), Brassfield (US)	121
12	Crooked Creek Barrens 2	Lewis	Outer Blue Grass	KSNPC	Alfisols	Upper Part of Crab Orchard (US), Lower Part of Crab Orchard (US), Brassfield (US)	114

Table 2.1 (continued)

13	Grayson Co. Barren	Grayson	Mammoth Cave Plateau	Private	Alfisols	Glen Dean Limestone (UM)	117
14	Knight's Barren	Hardin	Mammoth Cave Plateau	Private*	Alfisols	Reelsville Limestone (UM)	95
15	Lapland Barrens	Meade	Mammoth Cave Plateau	Private*	Alfisols, Ultisols	Reelsville Limestone (UM), Beech Creek Limestone (UM)	108
16	Lapland Road Barrens	Meade	Mammoth Cave Plateau	Private	Alfisols	Reelsville Limestone (UM), Beech Creek Limestone (UM)	104
17	Logan Co. Glade	Logan	Pennyroyal Plain	KSNPC	Alfisols	Girkin Limestone (UM)	131
18	Logan Co. Barrens	Logan	Pennyroyal Plain	Private	Alfisols	Paint Creek Limestone (UM)	98

Ownership: KSNPC = Kentucky State Nature Preserves Commission **TNC** = The Nature Conservancy - Kentucky Chapter

*Under management agreement with The Nature Conservancy   ******Portion of site owned by KSNPC, remainder under private ownership

Geologic System: UM = Upper Mississippian, US = Upper Silurian

Table 2.2. Series, family, and great group of soils in the 18 xeric limestone prairies sampled in Kentucky. For site identification, see Table 2.1.

Soil Series	Family	Great Group	Site(s)
Beasley	Fine, mixed, active, mesic	Typic Hapludalfs	11, 12
Caneyville	Fine, mixed, active, mesic	Typic Hapludalfs	2, 3, 7, 8, 9, 10, 13, 14, 16
Colbert	Fine, smectitic, thermic	Vertic Hapludalfs	17, 18
Corydon	Clayey, mixed, superactive, mesic	Lithic Argiudolls	1, 5
Cumberland	Fine, mixed, semi-active, thermic	Rhodic Paleudalfs	6
Fredonia	Fine, mixed, active, mesic	Typic Hapludalfs	17, 18
Garmon	Fine-loamy, mixed, semi-active, mesic	Dystric Eutrudepts	8
Gilpin	Fine-loamy, mixed, active, mesic	Typic Hapludults	15
Hagerstown	Fine, mixed, semi-active, mesic	Typic Hapludalfs	3
Lenberg	Fine, mixed, semi-active, mesic	Ultic Hapludalfs	15
Rosine	Fine-silty, mixed, semi-active, mesic	Ultic Hapludalfs	15
Shrouts	Fine, mixed, mesic	Typic Hapludalfs	11, 12
Vertrees	Fine, mixed, semi-active mesic	Typic Paleudalfs	2, 4, 6

Figure 2.1. Three xeric limestone prairies in the Interior Low Plateaus physiographic province in Kentucky. Top, Scudder Glade State Nature Preserve, Hardin County (photo by Carol Baskin, August 1980); middle, Pine Creek Barrens (The Nature Conservancy), Bullitt County, XLP = xeric limestone prairie and LCG-LA = limestone cedar glade-like area (photo by Patrick Lawless, October 2003); bottom, Crooked Creek Barrens State Nature Preserve, Lewis County (photo by Patrick Lawless, May 2002).
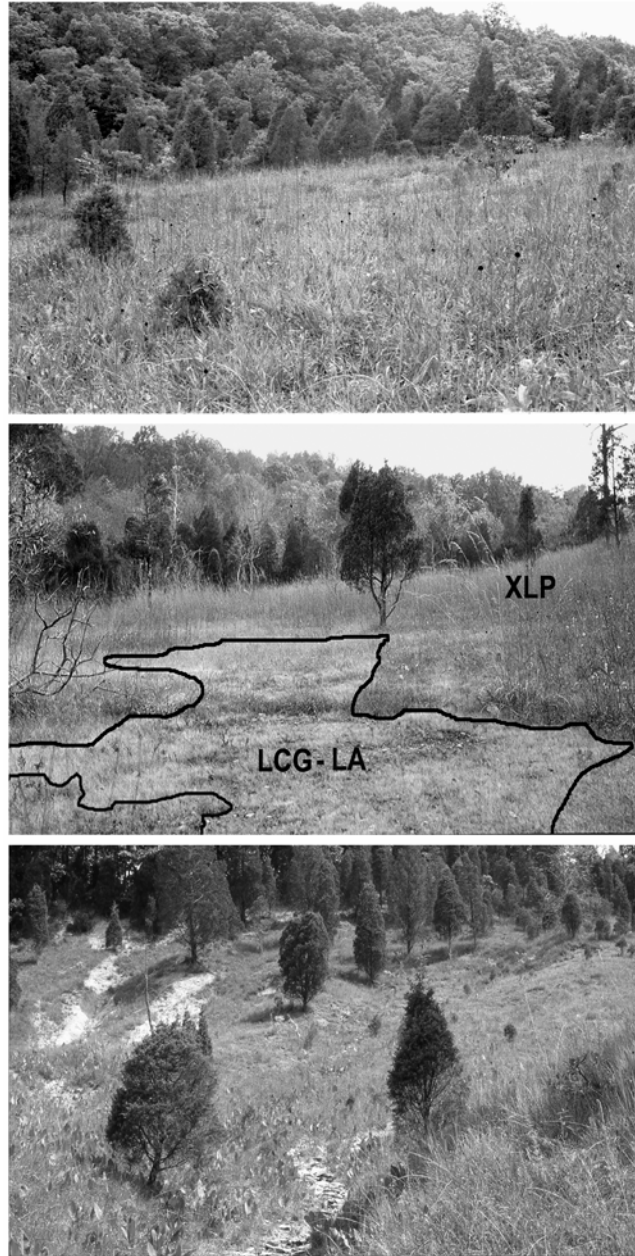
Figure 2.2. Locations of sample sites in the Interior Low Plateaus physiographic province (map from Quarterman and Powell, 1978). Subsections of Highland Rim Section: H1 =Eastern Highland Rim, H2=Southern Highland Rim, H3=Western Highland Rim, H4=Southwestern Highland Rim, H5=Little Mountain, H6=Moulton Valley, H7=Pennyroyal Plain, H8=Elizabethtown [Plain], H9=Mitchell Plain, H10=Greensburg Upland, H11=Cumberland Enclave, H12=Norman Upland. Subsections of Central Basin Section: C1=Cumberland River Basin, C2=Harpeth River Basin, C3=Duck River Basin, C4=Elk River Basin. Subsections of Blue Grass Section: B1=Knobstone Escarpment and Knobs, B2=Northeastern Blue Grass, B3=Outer Blue Grass, B4=Eden Shale Belt, B5=Inner Blue Grass. Subsections of Shawnee Hills Section: S1=Mammoth Cave Plateau, S2=Marion [Area], S3=Illinois Ozarks, S4=Ohio River Hills & Lowlands, S5=Brush Creek Hills.
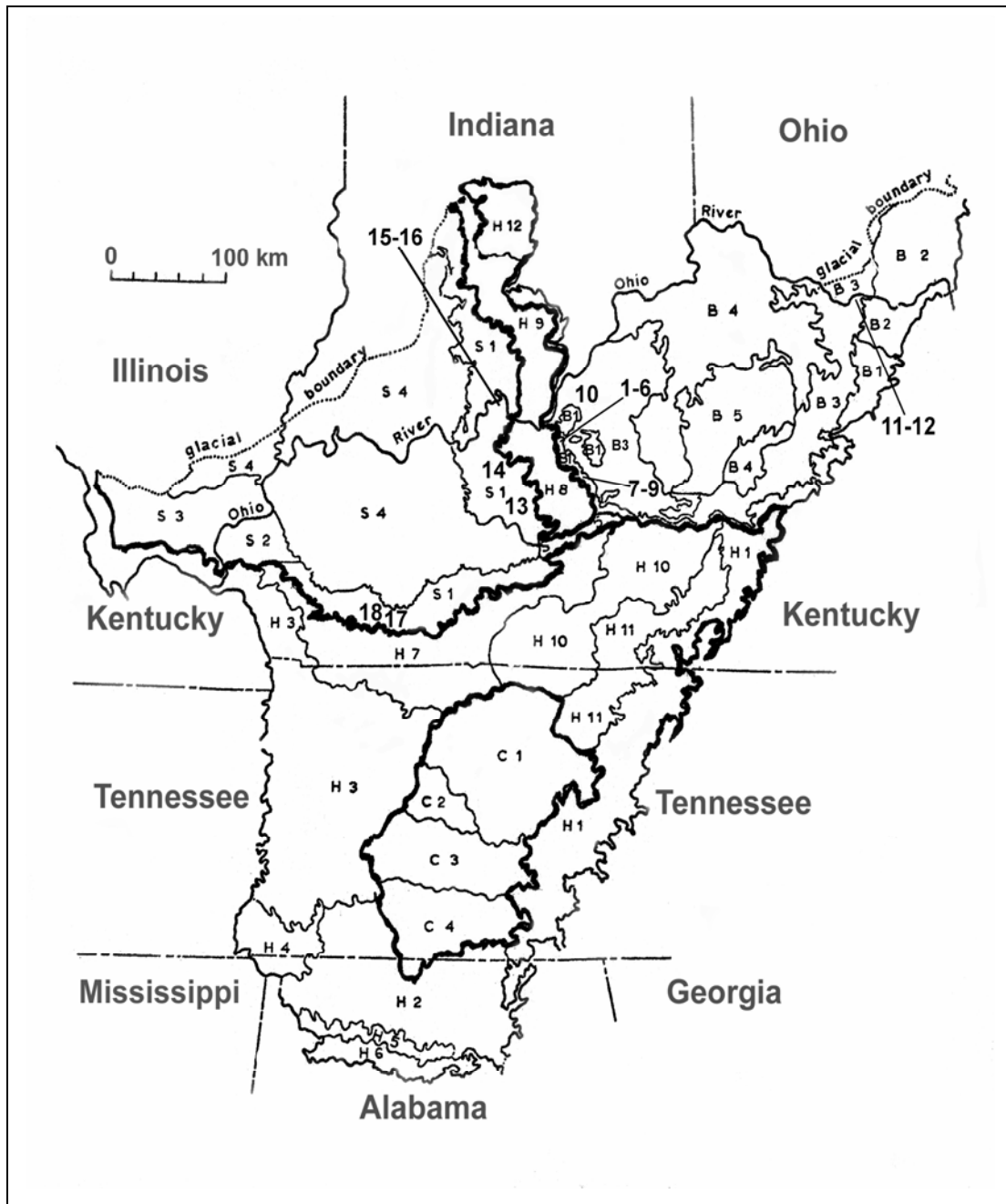
Figure 2.3. Bedrock geology of xeric limestone prairies in the Outer Blue Grass (western and eastern), Pennyroyal Plain, Mammoth Cave Plateau, and Knobstone Escarpment and Knobs subsections of the Interior Low Plateaus physiographic province in Kentucky (from McDowell 1981). Numbers refer to site numbers in Table 1. The break between Upper Mississippian and Upper Silurian is for the Upper Devonian upon which xeric limestone prairies do not occur in Kentucky.

Figure 2.4. A block diagram of the topography and soil series in the Knobs and Knobstone Escarpment section of the Interior Low Plateaus physiographic province in Hardin and Larue counties Kentucky. Soil series: Cn=Caneyville, Cr=Crider, Gm=Garmon, Hn=Hagerstown, Lf=Lenberg-Frondorf, No=Nolin-Newark-Melvin, V=Vertrees.
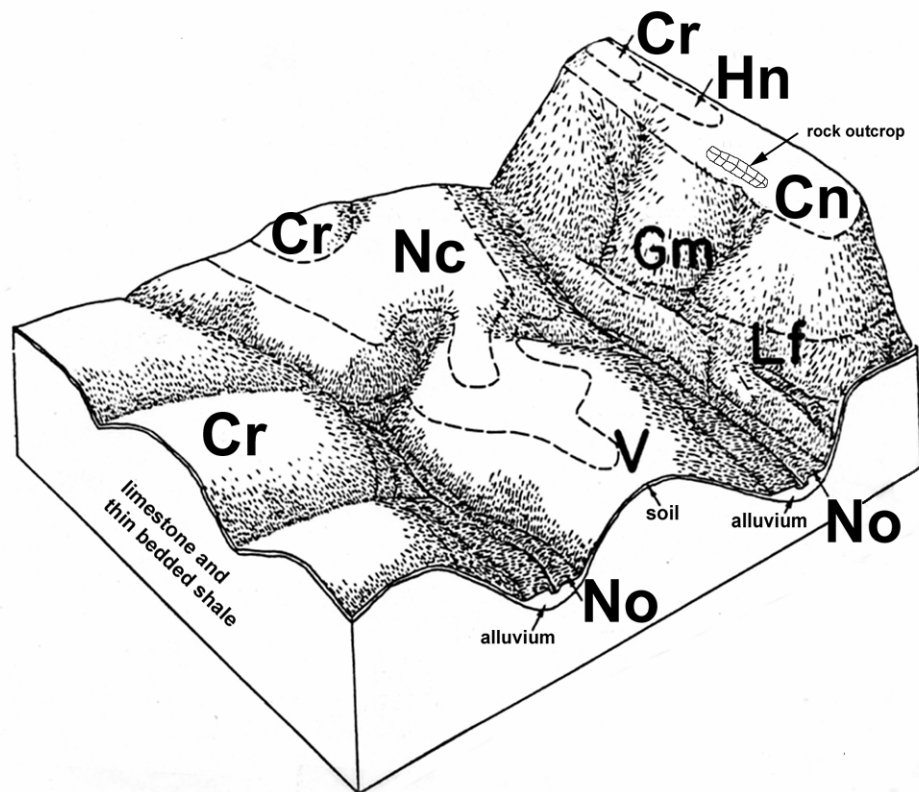
Figure 2.5. Life form distribution of native species in the floras of xeric limestone prairies in Kentucky (XLP), deep-soil barrens of the southwestern Pennyroyal Plain (DSB), and limestone cedar glades of the southeastern U.S. (LCG-SE).
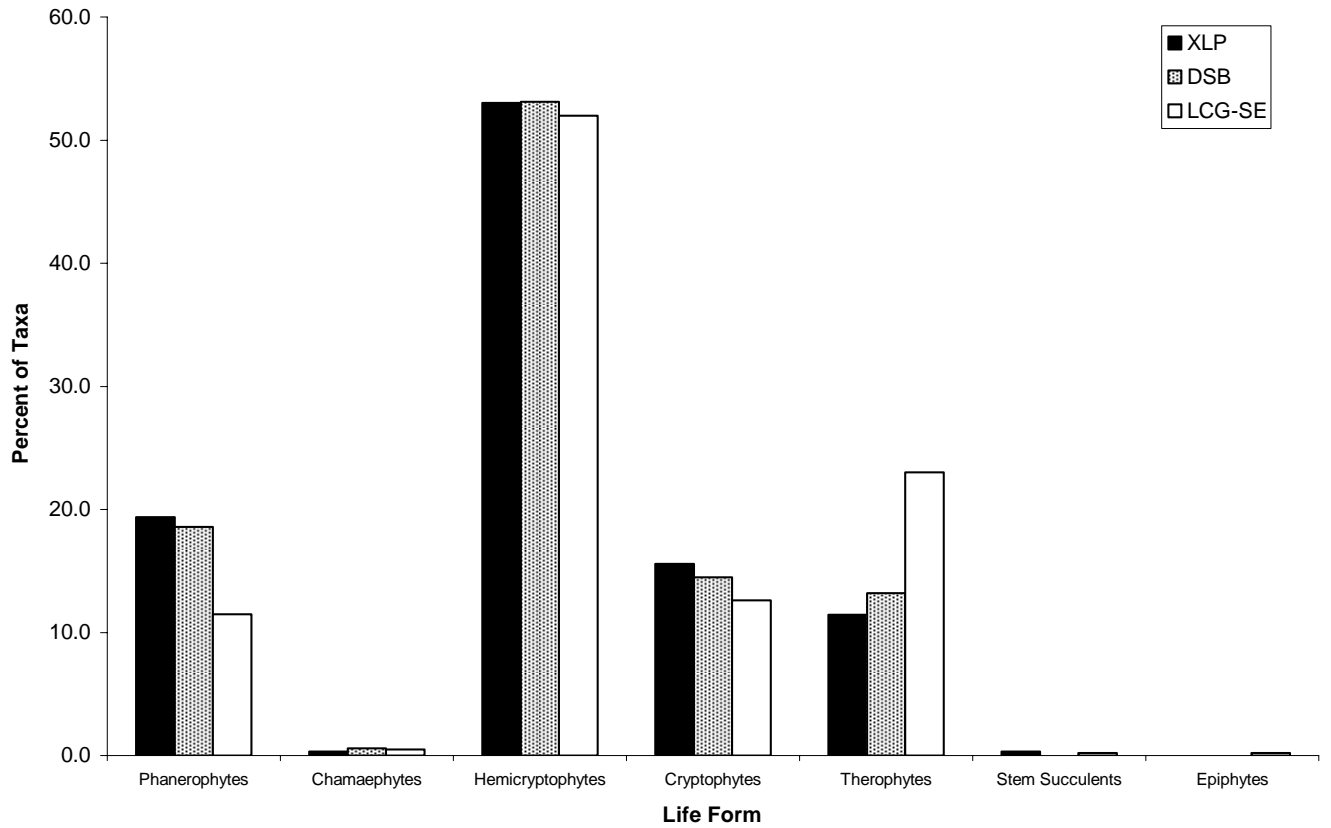
Figure 2.6. Geographic affinities of the floras of xeric limestone prairies in Kentucky (XLP) , deep-soil barrens of the southwestern Pennyroyal Plain (DSB), and cedar glades in the Central Basin of Tennessee (LCG-CB).
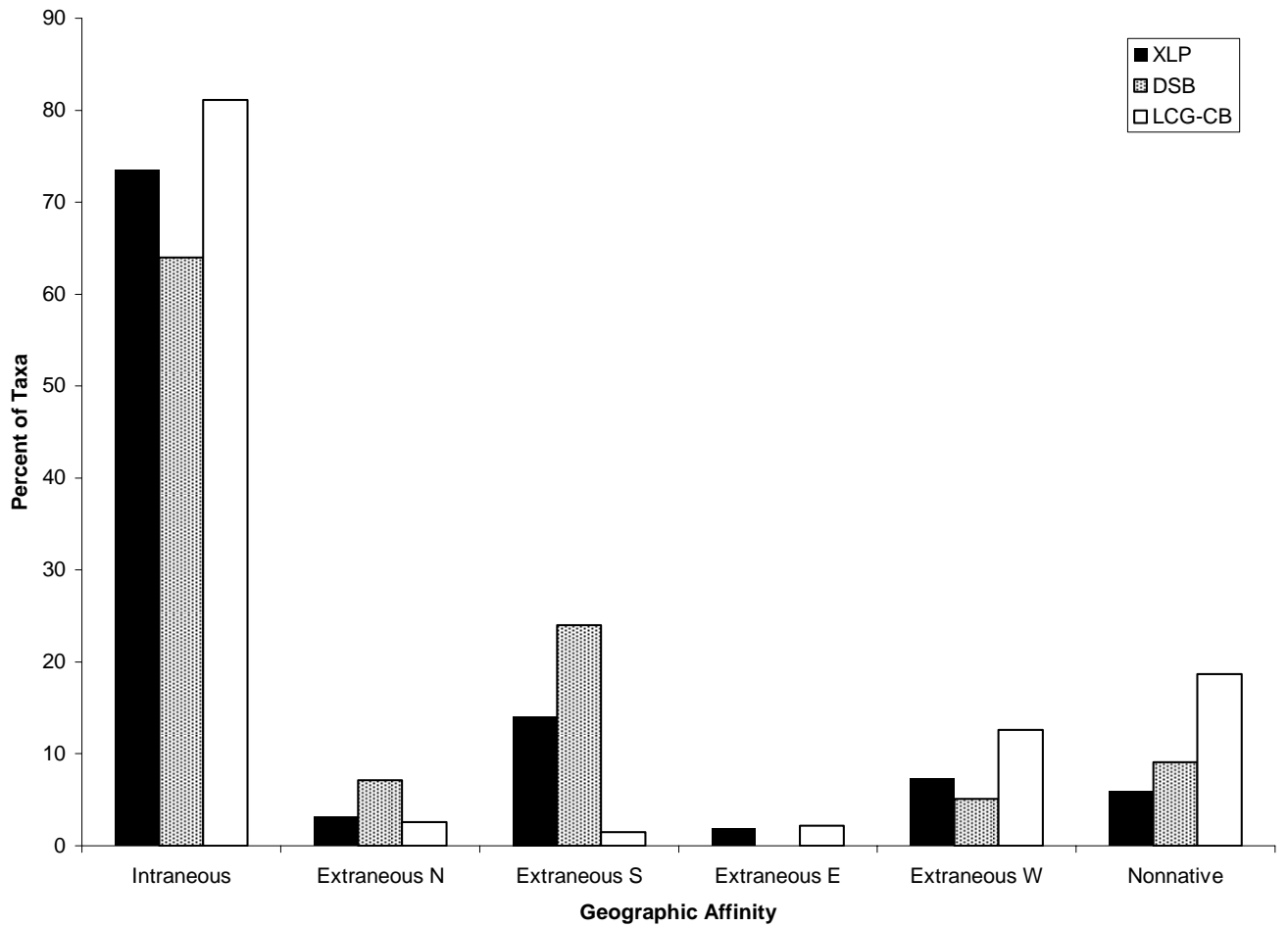
Figure 2.7. Percent of taxa in each of five presence classes in 18 xeric limestone prairies surveyed in the Interior Low Plateaus physiographic province in Kentucky. Presence classes are as follows: 1=1-20%, 2=21-40%, 3=41-60%, 4=61-80%, and 5=81-100%. Number of taxa in presence class above each bar.
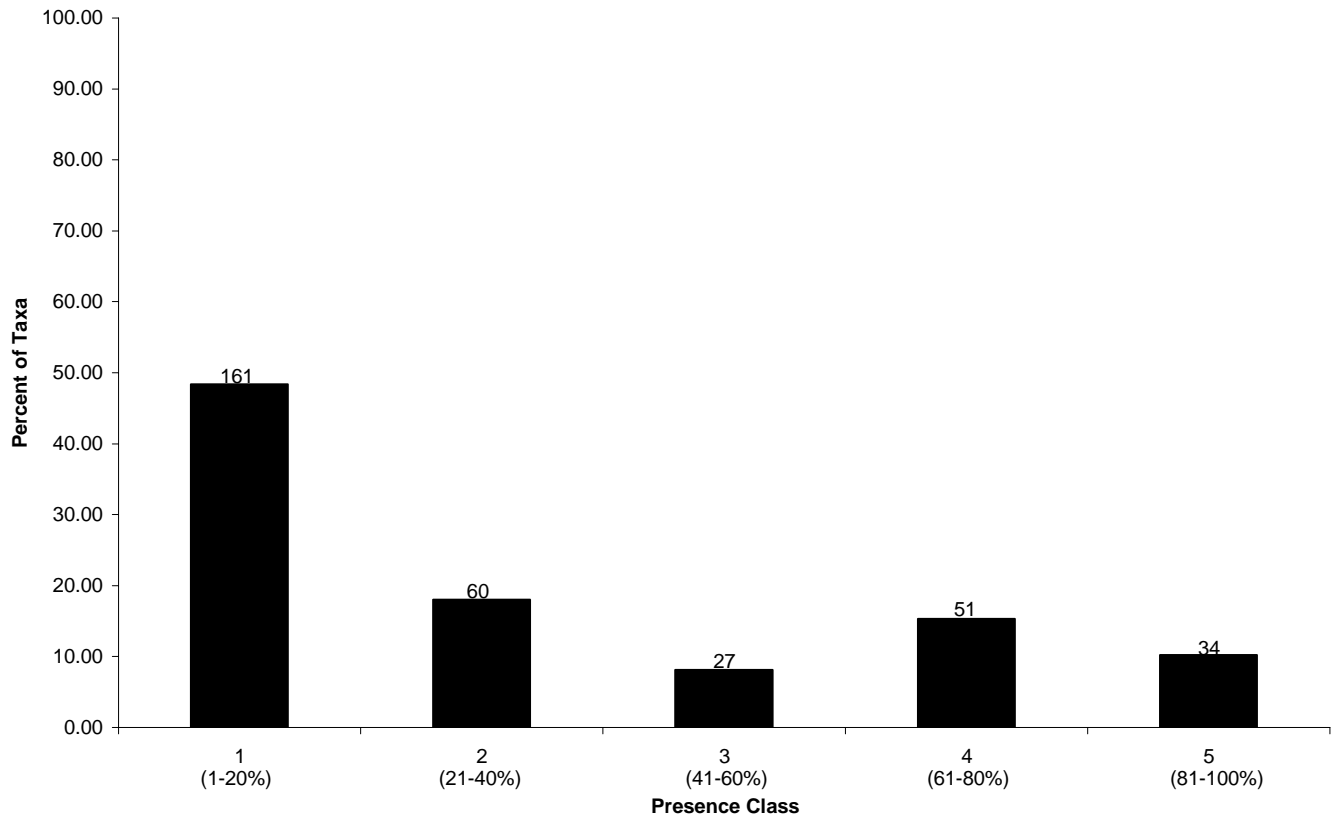
CHAPTER 3

SCALE-DEPENDENT CLASSIFICATION OF XERIC LIMESTONE PRAIRIES: ANNUAL OR PERENNIAL GRASSLANDS?
SYNOPSIS

The vegetation of 18 xeric limestone prairies (XLPs) in the Interior Plateau ecoregion in Kentucky was sampled using a multi-scale sampling design. Presence was determined at five spatial scales (0.01, 0.1, 1.0, 10 and 100 m^2). Cover and abiotic environmental data were collected at the largest scale (100 m^2). Agglomerative cluster analysis and nonmetric multidimensional scaling were used to identify multi-scale community types and sources of variability among 100-m^2 community types, respectively. Distribution of multi-scale XLP community types among Level IV ecoregions was determined. Percent occurrence (0.01-100-m^2 scales) and average cover (100-m^2 scale) of C_4 annual and perennial grass species were used to assess the relative importance of these taxa in multi-scale community types. *Schizachyrium scoparium* was the dominant taxon in 10 of 12 100-m^2 community types and had the highest percent occurrence of all taxa in the majority of fine-scale community types (0.01-10 m^2). Soil depth and herbaceous species composition were significant sources of variability among community types. Distribution of community types was inversely proportional to quadrat size and corresponding scale of community characterization. Cover of C_4 perennial grasses exceeded that of the C_4 annual grass *Sporobolus vaginiflorus* in all 12 100-m^2 community types. However, *Sporobolus vaginiflorus* often was dominant locally at the extreme lower limits of soil depth and is capable of competing with perennial grasses over a range of environmental conditions. Therefore, XLPs are best described as C_4 perennial grasslands with a significant C_4 annual grass component.

INTRODUCTION

Xeric limestone prairies (XLPs) occur on shallow rocky soils derived from calcareous substrates (limestone, dolomite, and shale) and are distributed from Missouri (Nelson and Ladd, 1983; Baskin and Baskin, 2000) and Pennsylvania (Laughlin and Uhl, 2003) south to Arkansas (Keeland, 1978; Baskin and Baskin, 2000) and Georgia (DeSelm, 1993). Baskin et al. (1994) and Baskin and Baskin (2000) describe these herbaceous communities as C_4 perennial grasslands dominated by *Schizachyrium scoparium* and/or *Bouteloua curtipendula*. However, community composition and structure in XLPs often are quite heterogeneous within sites and can shift abruptly over small spatial scales (Ver Hoef et al., 1993). Most notably, transitions in dominance from C_4 perennial prairie grasses to C_4 annual grasses (*Sporobolus* spp.) often occur in response to decreased soil depths (Ver Hoef et al., 1993; Baskin and Baskin, 2000). Forb composition in XLPs also varies considerably both within and among sites (Lawless et al., 2004 [Chapter 2]). This study uses a multiple-grain sampling design to determine variability in community composition and structure over a range of spatial scales in XLPs in Kentucky. Furthermore, we assess abiotic and biotic sources of community variability, focusing on the relative importance of C_4 perennial grasses and the C_4 annual grass *Sporobolus vaginiflorus* in multiple-scale community types.

In Kentucky, XLPs occur in the Crawford-Mammoth Cave Uplands, Knobs-Norman Upland and Outer Bluegrass Level IV ecoregions of the Interior Plateau (Level III ecoregion; sensu Woods et al., 2002) (Figure 3.1). Two XLPs (Site #'s 17 and 18) are located at the southern boundary of the Crawford-Mammoth Cave Uplands. However, we place these sites in the Western Pennyroyal Karst Plain ecoregion, which is in agreement with Fenneman (1938, Figure 123, page 436) and an unpublished map of the Pennyroyal Plain by Baskin and Baskin (Lawless et al., 2004 [Chapter 2]). Sites occur on moderate to steep slopes with south to west aspects and primarily are developed on Alfisols derived from Mississipian (Western Pennyroyal Karst Plain, Crawford-Mammoth Cave Uplands, and Knobs-Norman Upland) and Silurian (Outer Bluegrass) limestones, dolomites and shales (Lawless et al., 2004 [Chapter 2]). In Kentucky, this vegetation type is of anthropogenic origin, is maintained by prescribed fire and cutting, and is an aberration to

49

regionally dominant deciduous forests (Baskin and Baskin, 1994; Lawless et al., 2004 [Chapter 2]). Furthermore, XLPs support a significant number of state-listed rare species, many of which are restricted to this vegetation type in this portion of their geographic range (Lawless et al., 2004 [Chapter 2]).

In Kentucky and many other areas within the geographic range of this vegetation type, XLPs are referred to as "cedar glades" or "glades" (Baskin et al., 1994; Baskin and Baskin, 2000; Baskin and Baskin, 2004; Rhoades et al., 2004). Cedar glades (sensu Baskin and Baskin, 1994; Baskin and Baskin, 2003) are an edaphic climax community characterized by dominance of C_4 annual grass species, particularly *Sporobolus* species, in contrast to the C_4 perennial grass species (*Schizachyrium scoparium*, *Bouteloua curtipendula*, *Sorghastrum nutans*, and *Andropogon gerardii*) characteristic of XLPs. However, *Sporobolus vaginiflorus*, a C_4 annual grass, is locally dominant in XLPs in Kentucky (Rhoades et al., 2004). Therefore, classification of these grasslands may be influenced significantly by the scale (i.e. grain) at which community sampling and characterization are conducted. In this study, I identify XLP community types over a range of scales and assess the relative importance of C_4 perennial grass species versus *Sporobolus vaginiflorus* within these community types. Furthermore, I determine the distribution of these community types among sites and Level IV ecoregions of Kentucky (sensu Woods et al., 2002). This is the first quantitative study of XLPs in Kentucky conducted in multiple sites and ecoregions and thus provides data necessary for effective conservation of this vegetation type.

METHODS

Vegetation Sampling

In July through October of 2002 and 2003, the vegetation of 18 XLPs in the Interior Plateau ecoregion in Kentucky was sampled using a nested quadrat sampling design adapted from Peet et al. (1998). Sampling plots consisted of two to six 100-m^2 modules arranged adjacent to one another. Only one plot was sampled in each site with the exception of Pine Creek Barrens (Site #10), in which two plots of 6 modules each were sampled. The number of modules sampled per site ranged from two to 12 (200 to 1200 m^2) and was determined primarily by area of site, which ranged from less than 0.5 to approximately 2.25 hectares (Lawless et al., 2004 [Chapter 2]). In each sample module

ground layer vegetation (≤ 1.5 m) was sampled in one or two series of nested quadrats increasing logistically in area from 0.01 to 10 m^2. Taxa present in each nested quadrat were recorded, and all species rooted in the module were assigned to one of ten cover classes (1, trace; 2, 0-1%; 3, >1-2%; 4, >2-5%; 5, >5-10%; 6, >10-25%; 7, >25-50%; 8, >50-75%; 9, >75-95%; and 10, >95-100%). In each module, all trees and shrubs ≥ 1.5 m in height were identified and diameter at breast height (dbh) measured for placement into size categories (0-2.5, >2.5-5, >5-10, >10-15, >15-20, >20-25, >25-30, >30-35, ≥ 40 cm). Density (individuals/m^2) and basal area (m^2/hectare, based on size class midpoints) of trees and shrubs ≥ 1.5 m in height were determined both by species and in aggregate (i.e. summed for all species) for each module.

Sampling of Abiotic Environment

Soil depth was recorded to the nearest centimeter in the four corners of all modules (2-m diagonal from the corner), and soil samples were collected from the top 25 cm of soil in the same locations. A composite soil sample was prepared for each module after field samples were air-dried and sieved. Composite soil samples then were submitted to the University of Kentucky Soil Testing Laboratory for the following analyses: pH (Thomas, 1996), buffered pH (SPAC, 2000), texture (Burt et al., 1993), water holding capacity (Barnhisel, unpublished), percent organic matter and total N via dry combustion (LECO CNS-2000; St. Joseph, MI, USA), cation exchange capacity (total and individually for K, Ca, Mg, and Na), and base saturation (Hendershot, et al. 1993) and concentrations of the following elements: P, K, Ca, Mg, Zn, Cu, Mn, Na, Fe, and Al (Mehlich, 1984).

Three measurements of slope (%) and aspect of slope (in degrees east of true north) were collected for each module using a compass and clinometer, respectively, and an average calculated for both parameters. The average aspect of slope (Φ) for each module then was used to calculate a corresponding heat load index (HLI) using the following equation: HLI = (1- cos ($\Phi - 45$))/2. The heat load index ranges from zero to one with zero corresponding to the coolest slope (northeast - 45°) and one corresponding to the warmest slope (southwest - 225°) (McCune and Grace, 2002).

Identification of Community Types at Multiple Scales

The flexible beta linkage agglomerative clustering method in PC-ORD (MJM Software Design, 1999) was used to identify community types (i.e. groups) at multiple spatial scales (0.01, 0.1, 1.0, 10, and 100-m^2). A beta value of -0.25 and Sorensen's distance measure were used in all analyses. Analyses were performed on presence-absence data at each of the five scales sampled and on cover class data at the 100-m^2 scale. Indicator species analysis was used to determine the optimal number of groups at each scale via selection of the group number with the lowest average p-value (Dufrêne and Legendre, 1997). Percent occurrence data within groups were used to characterize and compare community types identified at the 0.01, 0.1, 1.0, and 10-m^2 spatial scales. The percent occurrence criterion for defining characteristic taxa in each community type was scale-dependent as follows: 0.01 m^2 ≥ 30%, 0.1 m^2 ≥ 40%, 1.0 m^2 ≥ 50%, and 10 m^2 ≥ 60%. At the 100-m^2 scale, taxa with average cover values ≥ 3% were used to characterize community types. These characteristic taxa were further divided into dominant (avg. cover ≥10%) and subdominant (3%≤ avg. cover<10%) categories in each community type. Average cover values were obtained from column summaries generated by PC-ORD (MJM Software Design, 1999) after all taxa were assigned percent cover values corresponding to cover class midpoints. The number of characteristic graminoids, forbs, shrubs, herbs, trees, lianas, and succulents was calculated at each scale to determine variability in the relative importance of these physiognomic classes.

Ordination

Nonmetric multidimensional scaling (NMS) (Kruskal, 1964; Mather, 1976) was used to determine variability in community structure at the 100-m^2 scale and to investigate potential sources of variability. A random starting configuration and Sorensen's distance measure were used in the analysis of ground-layer cover class data, which included 40 runs with real data and 50 runs with randomized data (PC-ORD; MJM Software Design, 1999). Monte Carlo tests were performed to determine the statistical significance of each ordination axis, and only axes generating a p-value < 0.05 were considered for inclusion in the final analysis. The results of Monte Carlo tests, stress reduction with increasing dimensionality (scree plot), and instability analyses were all considered in selecting the number of dimensions in the final analysis. Data collected

from the abiotic environment (slope, aspect of slope, soil depth, and soil chemistry) and total density and basal area of all woody taxa ($\geq$ 1.5 m in height) were entered into a second matrix for calculation of coefficients of determination (r^2) with ordination axes. In addition, the cover class data set from the primary matrix was used as a second matrix to assess correlations between species abundances and ordination axes. Only abiotic variables and taxa with an r^2 value $\geq$ 0.35 were included in joint plots.

RESULTS

Cluster Analysis

0.01-m^2 Community Types

One hundred and fifty-nine of 174 0.01-m^2 quadrats sampled contained one or more individuals and were included in cluster analysis. Four community types (i.e. groups) were identified at the 0.01-m^2 scale (Figure 3.2), and percent occurrence data resulted in only four characteristic taxa (% occurrence $\geq$ 30), all of which are graminoids (Table 3.1). Three taxa, *Schizachyrium scoparium* (Groups 1 and 2), *Sporobolus vaginiflorus* (Groups 2 and 3) and *Carex crawei* (Groups 1 and 3), were characteristic in two community types, and *Sorghastrum nutans* was a characteristic taxon in a single community type (Group 1). The *Schizachyrium scoparium-Sporobolus vaginiflorus* community type (Group 2) contained more quadrats (48) and occurred in more sites (15) than any other community type. The *Sporobolus vaginiflorus-Carex crawei* community type (Group 3) contained 46 quadrats and occurred in 14 of 18 sites. Group 4 contained the smallest number of quadrats (22), supported no characteristic taxa, and was present in only eight sites.

0.1-m^2 Community Types

One hundred and seventy-three of 174 0.1-m^2 quadrats contained one or more individuals and were included in cluster analysis. Ten community types were identified at the 0.1-m^2 scale (Figure 3.3), and percent occurrence data resulted in a total of 19 characteristic taxa (% occurrence $\geq$ 40) among these community types (Table 3.2). Thirteen (68.4%) of these taxa are forbs, and six are graminoids (31.6%). *Schizachyrium scoparium* was a characteristic taxon in six of these community types, more than any

other taxon, and was followed by *Sporobolus vaginiflorus* (4) and *Carex crawei* (3). Eight taxa had a percent occurrence ≥ all other taxa in one or more community types, including *Schizachyrium scoparium* (4 community types), *Sporobolus vaginiflorus* (2), *Andropogon gerardii* (1), *Sorghastrum nutans* (1), *Carex meadii* (1), *Carex crawei* (1), *Ruellia humilis* (1), and *Rosa carolina* (1).

The *Schizachyrium scoparium-Solidago nemoralis-Croton capitatus* community type (Group 8) was most narrowly distributed occurring in only nine quadrats from two sites [Muldraugh's Barren (Site #6) and Fort Knox #1 (Site #1)] in the Knobs-Norman Upland ecoregion. The *Schizachyrium scoparium-Sporobolus vaginiflorus-Echinacea simulata-Hedyotis nigricans* community type (Group 3) and *Sporobolus vaginiflorus-Heliotropium tenellum-Hypericum dolabriforme* community type (Group 7) occurred in the largest number of sites (9). The *Carex crawei-Schizachyrium scoparium-Sporobolus vaginiflorus-Ruellia humilis* community type (Group 6) occurred in the largest number of quadrats (40) and was distributed in eight sites in three ecoregions.

1.0-m^2 Community Types

All 174 of the 1.0-m^2 quadrats sampled contained one or more individuals and were included in cluster analysis. Ten community types were identified at the 1.0-m^2 scale (Figure 3.4), and percent occurrence data resulted in a total of 39 characteristic taxa (% occurrence ≥ 50) among these community types (Table 3.3). Twenty-seven (69.2%) of these taxa are forbs, eight (20.5%) graminoids, three (7.7%) trees (*Cercis canadensis*, *Fraxinus americana* and *Celtis tenuifolia*), and one (2.6%) a liana (*Smilax bona-nox*). *Schizachyrium scoparium* was a characteristic taxon in 9 of 10 community types and was followed by *Sporobolus vaginiflorus* (6 community types), *Echinacea simulata* (5), *Euphorbia corollata* (5), *Physostegia virginiana* (5), *Sorghastrum nutans* (4), and *Ruellia humilis* (4). *Schizachyrium scoparium* had a percent occurrence ≥ all taxa in five community types. Other taxa with a percent occurrence ≥ all taxa in two or more community types included *Echinacea simulata* (Groups 2, 3, 6, and 9) and *Sporobolus vaginiflorus* (Groups 1 and 4).

Only the *Schizachyrium scoparium-Dichanthelium sphaerocarpon-Gaura filipes-Smilax bona-nox* community type (Group 5) was restricted to a single site [Logan County Glade (Site #17)]. The *Schizachyrium scoparium-Echinacea simulata-Sporobolus vaginiflorus* community type (Group 2) occurred in the most sites (8) and contained the largest number of quadrats (51). With the exception of one quadrat from Pine Creek Barrens (Site #10), Group 2 was composed entirely of quadrats from the Knobs-Norman Upland ecoregion. Only the *Carex meadii-Schizachyrium scoparium* community type (Group 10) was restricted to a single ecoregion (Crawford-Mammoth Cave Uplands).

<u>10-m^2 Community Types</u>

Twelve community types were identified at the 10-m^2 scale (Figure 3.5), and percent occurrence data resulted in a total of 73 characteristic taxa (% occurrence $\geq$ 60) among these community types (Table 3.4). Forty-nine (68.1%) of these are forbs, 12 (16.7%) graminoids, seven (9.7%) trees, two (2.8%) shrubs (*Rosa carolina* and *Rhus aromatica*), one (1.4%) a liana (*Smilax bona-nox*), and one (1.4%) a succulent (*Manfreda virginica*). *Schizachyrium scoparium* was a characteristic taxon in all 12 community types. Only eight additional taxa were characteristic in seven or more community types, including *Sporobolus vaginiflorus* (8), *Sorghastrum nutans* (8), *Echinacea simulata* (8), *Physostegia virginiana* (8), *Euphorbia corollata* (8), *Ruellia humilis* (7), *Solidago nemoralis* (7), and *Juniperus virginiana* (7). *Schizachyrium scoparium* had a percent occurrence $\geq$ all other taxa in 8 community types and was followed by *Sporobolus vaginiflorus* (4) and *Echinacea simulata* (4).

Seven of the 12 community types (Groups 1, 2, 6, 9, 10, 11, and 12) occurred in a single site, two (Groups 7 and 8) in two sites, one (Group 4) in three sites, and two (Groups 3 and 5) in five sites. Nine of the 12 community types were restricted to a single ecoregion. The *Schizachyrium scoparium-Sorghastrum nutans-Echinacea simulata-Sporobolus vaginiflorus* community type (Group 5) occurred in five sites in the Knobs-Norman Upland ecoregion and was represented in more quadrats (36) than any other community type.

<u>100-m^2 Community Types</u>

Cluster analyses of both presence-absence data and ground-layer cover class data at the 100-m^2 scale identified twelve community types (Figure 3.6), and with the exception of two quadrats from Mixed Grass Barrens (Site #7), these data sets yielded clusters (i.e. community types) that were identical with regards to their constituent quadrats. Community types identified from both data sets occurred in one to three sites (x=1.64) and one or two ecoregions (x=1.1 ± 0.3), with only the standard deviation in number of sites differing slightly (s=0.9 presence-absence data vs. 0.8 cover class data) between the two analyses. In both analyses, all community types that occurred in the Western Pennyroyal Karst Plain and Outer Bluegrass ecoregions were restricted to a single site. In contrast, community types present in the Knobs-Norman Upland often occurred in two or more sites in both community classifications. Because quantitative data provide an estimate of the abundance of taxa in particular community types, summary and comparison of community types were based on the cluster analysis performed on ground-layer cover class data (Figure 3.5).

Forty-one taxa had an average cover value ≥ 3% (i.e. were dominant or subdominant) in one or more community types (Table 3.5). Twenty-two (53.7%) of these are herbs, 13 (31.7%) graminoids, four (9.8%) trees (*Juniperus virgiana*, *Cercis canadensis*, *Fraxinus americana*, and *Celtis tenuifolia*), one (2.4%) a shrub (*Rhus aromatica*), and one (2.4%) a liana (*Smilax bona-nox*). Fifteen taxa were dominant (avg. cover ≥ 10%) in one or more community type(s), and of these eight (53.3%) are graminoids, five (33.0%) herbs, one (6.7%) a tree (*Juniperus virginiana*), and one (6.7%) a liana (*Smilax bona-nox*). Six of these 15 taxa were dominant in three or more community types, including *Schizachyrium scoparium* (10 community types), *Sporobolus vaginiflorus* (5), *Sorghastrum nutans* (5), *Echinacea simulata* (5), *Andropogon gerardii*, (4) and *Carex crawei* (3). *Schizachyrium scoparium* had the highest average cover in 10 of 12 community types, and *Andropogon gerardii* and *Silphium terebinthinaceum* each had the highest cover in one community type. *Schizachyrium scoparium* and *Sporobolus vaginiflorus* were co-dominant in five of 12 community types, and *Schizachyrium scoparium* and *Sorghastrum nutans* were co-dominant in four of 12 community types. Only seven taxa were subdominant in three or more community types. *Andropogon*

gerardii was subdominant in seven community types, and six taxa, including *Echinacea simulata, Carex meadii, Hedyotis nigricans, Sorghastrum nutans, Juniperus virginiana,* and *Cercis canadensis*, each were subdominant in three community types.

Ordination

Monte Carlo test results were statistically significant ($p \leq 0.02$) for each of the six ordination axes analyzed. The final NMS ordination consisted of 400 iterations of a three-dimensional solution and resulted in final stress =15.33 and instability =0.00829. Percent of variance (=cumulative r^2 x 100) collectively explained by the three axes was 82.9%, and the increment r^2 values of the three axes were as follows: 1=0.234, 2=0.226 and 3=0.369. Orthogonality between axis pairs ranged from 97.2 to 99.1%.

Only quadrats from the two sites in the eastern Outer Bluegrass [Crooked Creek Barrens Sites 1 and 2 (Site #'s 11 and 12)] had relatively large negative eigenvectors (~ -1) on axis three, and as a result the distances between these quadrats and all others were high (Figure 5.7b). There was a strong negative correlation between soil depth and axis three, and cover of eleven taxa also was correlated (r^2 value ≥ 0.35) with axis three. Cover of *Silphium terebinthinaceum, Symphyotrichum laeve, Hypericum prolificum, Pycnanthemum tenuifolium, Liatris cylindracea, Cornus drummondii, Castilleja coccinea, Oligoneuron rigidum* var. *glabratum* and *Desmodium glabellum* was correlated negatively with axis three, and cover of *Sporobolus vaginiflorus* and *Echinacea simulata* was correlated positively with this axis. Axis three eigenvectors of quadrats from Logan County Glade and Logan County Barrens (Site #18) were large (≥ 0.59) (Figure 5.7c). Only quadrats from Pine Creek Barrens had relatively large positive eigenvectors (≥ 0.6) on axis two (Figure 5.7a). Cover of *Carex crawei, Aristida purpurascens, Euphorbia corollata, Symphotrichum urophyllum* and *Liatris squarrosa* was correlated positively with axis two.

DISCUSSION

Results of this study confirm that XLPs in Kentucky are C_4 perennial grasslands as described by Baskin et al. (1994) and Baskin and Baskin (2000). *Schizachyrium scoparium* was the dominant graminoid (i.e. had the highest avg. cover) in 10 of 12 100-

m^2 community types, and collective average cover of C$_4$ perennial grasses (primarily *Schizachyrium scoparium*, *Sorghastrum nutans*, and *Andropogon gerardii*) exceeded cover of *Sporobolus vaginiflorus* in all 12 100-m^2 community types. However, *Sporobolus vaginiflorus* was a dominant taxon (avg. cover ≥ 10%) in five of 12 100-m^2 community types and was a characteristic taxon in the majority of community types identified at scales ≤100-m^2. In one of four 0.01-m^2 community types and two of 10 0.1-m^2 community types, *Sporobolus vaginiflorus* was the only characteristic grass taxon, thus indicating local dominance of this taxon in a considerable number of sites. Therefore, when considered at fine spatial scales, portions of XLPs sampled in this study fit the physiognomic description of cedar glades provided by Baskin and Baskin (2003). This finding is consistent with those of Hall (1955), Kucera and Martin (1957), Skinner (1979), Hicks (1981), Nelson (1985), Logan (1992), and Ver Hoef et al. (1993) in the XLPs of midwestern United States, which were summarized by Baskin and Baskin (2000). Surprisingly, *Sporobolus vaginiflorus* and *Schizachyrium scoparium* were both characteristic in the 0.01-m^2 and 0.1-m^2 community types containing the largest number of quadrats. Therefore, *Sporobolus vaginiflorus* is not necessarily confined to portions of sites in which perennial grasses are absent, typically where soil depths are extremely shallow (≤ 0.1 m), and apparently is capable of competing with these grasses over a range of local environmental conditions. As a result, XLPs in Kentucky would best be described as C$_4$ perennial grasslands with a significant C$_4$ annual grass component (i.e. *Sporobolus vaginiflorus*), the latter often locally dominant at the extreme lower limits of soil depth.

Cover of *Sporobolus vaginiflorus* also was a significant source of variability at the largest scale (100 m^2). However, 13 of the 17 taxa with r^2 values ≥ 0.35 were herbs. This phenomenon largely is due to the small number of characteristic graminoid taxa and their high percent occurrence values in this vegetation type. Conversely, the number of characteristic herbs is much greater, and many of these are distributed patchily among sites. *Melilotus alba* was the only nonnative taxon characteristic of one or more community types (Table 5.3, Group 7; Table 5.4, Group 1) and was not abundant (i.e. dominant or subdominant) in any of the 100-m^2 community types. Cover (ground layer vegetation), density, and basal area of trees and shrubs generally were not a significant

source of variability in this vegetation type. *Cornus drummondii* was the only tree or shrub with an r^2 value ≥ 0.35, which is due to its restriction to the two sites (Crooked Creek Barrens Sites 1 and 2) in the eastern Outer Bluegrass ecoregion. *Juniperus virginiana* and *Cercis canadensis* generally were the dominant woody taxa, often having both relatively high ground-layer cover and basal area.

Geographic distribution of community types generally decreased with increasing grain (i.e. quadrat size). At the 100-m^2 scale, strong fidelity of community types to ecoregions was apparent (Table 5.5). One-half of the sites (nine of 18) sampled in this study are in the Knobs-Norman Upland ecoregion, and quadrats from these sites occupied the central region of ordination space. Consequently, primary sources of variation among community types in this ecoregion were generally indiscernible in the ordination. Quadrats from the Western Pennyroyal Karst Plain, Crawford-Mammoth Cave Uplands and Outer Bluegrass ecoregions generally were well separated from the central cluster of quadrats on one or more ordination axes. Absence of *Echinacea simulata* and *Hypericum dolabriforme*, abundance of *Silphium terebinthinaceum*, and high average soil depths in the quadrats sampled in the eastern Outer Bluegrass (Crooked Creek Barrens Sites 1 and 2) and northern Crawford-Mammoth Cave Uplands [Lapland Barrens (Site #15) and Lapland Road Barrens (Site #16)] ecoregions largely account for the distance between quadrats from these sites and all remaining quadrats on axis three. The abundance of *Carex crawei*, *Aristida purpurascens*, *Euphorbia corollata*, *Symphyotrichum urophyllum*, and *Liatris squarrosa* in quadrats sampled in the western Outer Bluegrass (Pine Creek Barrens) ecoregion resulted in large distances between quadrats from this site and all remaining quadrats on axis two. Quadrats from the two sites (Logan County Glade and Logan County Barrens) in the Western Pennyroyal Karst Plain ecoregion and one site (Grayson County Barren, Site #13) from the Crawford-Mammoth Cave Uplands ecoregion had large eigenvectors on axis two and low to moderate eigenvectors on axis three, which largely resulted from high average cover of *Echinacea simulata* and *Hypericum dolabriforme* in these quadrats. In addition, Grayson County Barren was the only site in which the average cover of *Andropogon gerardii* exceeded that of *Schizachyrium scoparium*.

However, strong correspondence of cluster analyses performed on presence-absence and ground layer cover class data sets at the 100-m^2 scale suggests a large proportion of variability in these community types is explained by differences in species composition as opposed to differences in species abundances. The patchy distribution of herbaceous taxa among sites is largely responsible for differences in species composition among sites, since the dominant graminoids are present in the vast majority of sites. This patchy distribution pattern is likely attributable to the rarity of this vegetation type at the landscape scale and small area of XLPs in comparison with the regionally dominant deciduous forests and agricultural lands (Lawless et al., 2004 [Chapter 2]). Therefore, colonization and extinction, and factors that affect such processes (e.g. site area, distance from nearest site, regional species pools, etc.) strongly influence species composition in XLPs and are primary sources of variability in this vegetation type throughout its range in the eastern deciduous forest biome.

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Note: In tables 3.1 through 3.5, the following acronyms are used for Level IV ecoregions of the Interior Plateau (Level III ecoregion, sensu Woods et al. 2002): WPKP=Western Pennyroyal Karst Plain; CMCU=Crawford-Mammoth Cave Uplands; KKU=Knobs-Norman Upland; OBG=Outer Bluegrass.

Table 3.1. Community types identified at the 0.01-m^2 scale by cluster and indicator species analyses of presence data. Characteristic taxa (percent occurrence $\geq$ 30) in each community type are listed in order of decreasing percent occurrence.

Group 1 45 quadrats from 14 sites	Group 2 48 quadrats from 15 sites
KKU - 16 quadrats	KKU - 30 quadrats
OBG - 14	OBG - 9
CMCU - 11	CMCU - 5
WPKP - 4	WPKP - 4
Schizachyrium scoparium (33%)	*Schizachyrium scoparium* (100%)
Sorghastrum nutans (40%)	*Sporobolus vaginiflorus* (31%)
Carex crawei (38%)	

Group 3 46 quadrats from 14 sites	Group 4 20 quadrats from 8 sites
KKU - 24 quadrats	KKU - 10 quadrats
CMCU - 12	OBG - 5
OBG - 6	WPKP - 3
WPKP - 4	CMCU - 2
Sporobolus vaginiflorus (96%)	
Carex crawei (30%)	

Table 3.2. Community types identified at the 0.1-m^2 scale by cluster and indicator species analyses of presence data. Characteristic taxa (percent occurrence ≥ 40) in each community type are listed in order of decreasing percent occurrence.

Group 1	Group 2
14 quadrats from 8 sites	**9 quadrats from 8 sites**
OBG - 7 quadrats	KKU - 3 quadrats
KKU - 4	CMCU - 3
CMCU - 2	WPKP - 1
WPKP - 1	OBG - 2
Schizachyrium scoparium (100%)	*Ruellia humilis* (89%)
	Schizachyrium scoparium (67%)
	Physostegia virginiana (56%)

Group 3	Group 4
35 quadrats from 9 sites	**5 quadrats from 2 sites**
KKU - 25 quadrats	OBG - 4 quadrats
WPKP - 5	CMCU - 1
CMCU - 3	
OBG - 2	
Schizachyrium scoparium (89%)	*Sorghastrum nutans* (100%)
Sporobolus vaginiflorus (89%)	*Silphium terebinthinaceum* (80%)
Echinacea simulata (80%)	*Carex meadii* (80%)
Hedyotis nigricans (40%)	*Lithospermum canescens* (40%)

Group 5	Group 6
8 quadrats from 5 sites	**40 quadrats from 8 sites**
OBG - 4 quadrats	KKU - 22 quadrats
KKU - 2	OBG - 12
WPKP - 1	CMCU - 6
CMCU - 1	
Andropogon gerardii (50%)	*Carex crawei* (100%)
Rosa carolina (50%)	*Schizachyrium scoparium* (93%)
	Sporobolus vaginiflorus (90%)
	Ruellia humilis (50%)

Table 3.2 (continued)

Group 7	Group 8
20 quadrats from 9 sites	**9 quadrats from 2 sites**
KKU - 9 quadrats	KKU - 9 quadrats
CMCU - 6	
WPKP - 4	
OBG - 1	
Sporobolus vaginiflorus (100%)	*Schizachyrium scoparium* (89%)
Heliotropium tenellum (50%)	*Solidago nemoralis* (78%)
Hypericum dolabriforme (50%)	*Croton capitatus* (67%)

Group 9	Group 10
23 quadrats from 8 sites	**10 quadrats from 5 sites**
KKU - 12 quadrats	CMCU - 5 quadrats
CMCU - 5	WPKP - 4
OBG - 5	KKU - 1
WPKP - 1	
Schizachyrium scoparium (100%)	*Carex meadii* (80%)
Sorghastrum nutans (70%)	*Lobelia spicata* (50%)
Echinacea simulata (57%)	*Sporobolus vaginiflorus* (50%)
Symphyotrichum laeve (52%)	*Carex crawei* (40%)
Carex crawei (52%)	*Symphyotrichum laeve* (40%)

Table 3.3. Community types identified at the 1.0-m^2 scale by cluster and indicator species analyses of presence data. Characteristic taxa (percent occurrence ≥ 50) in each community type are listed in order of decreasing percent occurrence.

Group 1	Group 2
19 quadrats from 2 sites	**51 quadrats from 8 sites**
OBG - 17 quadrats	KKU - 50 quadrats
CMCU - 2	OBG - 1
Carex crawei (95%)	*Schizachyrium scoparium* (98%)
Sporobolus vaginiflorus (95%)	*Echinacea simulata* (98%)
Schizachyrium scoparium (89%)	*Sporobolus vaginiflorus* (88%)
Euphorbia corollata (79%)	*Solidago nemoralis* (67%)
Dichanthelium acuminatum (74%)	*Silphium trifoliatum* (67%)
Ruellia humilis (68%)	*Sorghastrum nutans* (61%)
Sorghastrum nutans (68%)	*Euphorbia corollata* (55%)
Liatris squarrosa (63%)	*Physostegia virginiana* (55%)
Echinacea simulata (63%)	*Galactia volubilis* (51%)

Group 3	Group 4
7 quadrats from 5 sites	**21 quadrats from 4 sites**
KKU - 4 quadrats	KKU - 20 quadrats
OBG - 2	CMCU - 1
CMCU - 1	
Schizachyrium scoparium (57%)	*Schizachyrium scoparium* (100%)
Echinacea simulata (57%)	*Sporobolus vaginiflorus* (100%)
Euphorbia corollata (57%)	*Heliotropium tenellum* (81%)
	Carex crawei (71%)
	Viola pedata (71%)
	Allium cernuum (62%)
	Croton capitatus (57%)
	Echinacea simulata (52%)
	Physostegia virginiana (52%)
	Solidago nemoralis (52%)

Table 3.3 (continued)

Group 5	Group 6
6 quadrats from 1 site	**20 quadrats from 3 sites**
WPKP - 6 quadrats	WPKP - 10 quadrats
	CMCU - 9
	KKU - 1
Schizachyrium scoparium (100%)	*Echinacea simulata* (100%)
Dichanthelium sphaerocarpon (85%)	*Sporobolus vaginiflorus* (88%)
Gaura filipes (83%)	*Schizachyrium scoparium* (70%)
Smilax bona-nox (83%)	*Sorghastrum nutans* (67%)
Croton capitatus (77%)	*Physostegia virginiana* (65%)
Carex meadii (67%)	*Hypericum dolabriforme* (65%)
Dichanthelium acuminatum (67%)	*Ruellia humilis* (65%)
Lobelia spicata (67%)	*Silphium pinnatifidum* (55%)
Hypericum dolabriforme (67%)	
Viola pedata (67%)	
Cercis canadensis (67%)	
Allium cernuum (67%)	
Galactia volubilis (50%)	
Celtis tenuifolia (50%)	
Polygala verticillata (50%)	
Fraxinus americana (50%)	

Group 7	Group 8
9 quadrats from 2 sites	**9 quadrats from 2 sites**
OBG - 8 quadrats	OBG - 9 quadrats
CMCU - 1	
Silphium terebinthinaceum (89%)	*Schizachyrium scoparium* (100%)
Coreopsis tripteris (78%)	*Liatris cylindracea* (78%)
Pycnanthemum tenuifolium (78%)	*Hedyotis nigricans* (67%)
Carex meadii (67%)	*Silphium terebinthinaceum* (67%)
Lithospermum canescens (56%)	*Symphyotrichum laeve* (56%)
Euphorbia corollata (56%)	
Melilotus alba (56%)	

Table 3.3 (continued)

Group 9	Group 10
16 quadrats from 5 sites	**16 quadrats from 3 sites**
KKU - 13 quadrats	CMCU - 16 quadrats
CMCU - 2	
WPKP - 1	
Echinacea simulata (100%)	*Carex meadii* (100%)
Ruellia humilis (75%)	*Schizachyrium scoparium* (88%)
Croton capitatus (75%)	*Ruellia humilis* (75%)
Schizachyrium scoparium (63%)	*Sorghastrum nutans* (69%)
Liatris squarrosa (56%)	*Sporobolus vaginiflorus* (69%)
Sporobolus vaginiflorus (56%)	*Physostegia virginiana* (69%)
Physostegia virginiana (50%)	*Euphorbia corollata* (63%)
Hypericum dolabriforme (50%)	*Symphyotrichum laeve* (63%)
Isanthus brachiatus (50%)	*Solidago nemoralis* (63%)
Houstonia canadensis (50%)	*Dichanthelium acuminatum* (56%)
	Carex crawei (56%)
	Lithospermum canescens (56%)

Table 3.4. Community types identified at the 10-m^2 scale by cluster and indicator species analyses of presence data. Characteristic taxa (percent occurrence $\geq$ 60) in each community type are listed in order of decreasing percent occurrence.

Group 1	Group 2
8 quadrats from 1 site	**8 quadrats from 1 site**
OBG - 8 quadrats	OBG - 8 quadrats
Schizachyrium scoparium (100%)	*Pycnanthemum tenuifolium* (100%)
Liatris cylindracea (100%)	*Silphium terebinthinaceum* (100%)
Hedyotis nigricans (88%)	*Sorghastrum nutans* (88%)
Symphyotrichum laeve (88%)	*Oligoneuron rigidum* (88%)
Melilotus alba (88%)	*Melilotus alba* (88%)
Silphium terebinthinaceum (88%)	*Lithospermum canescens* (88%)
Lobelia spicata (75%)	*Coreopsis tripteris* (88%)
Physostegia virginiana (75%)	*Euphorbia corollata* (75%)
Allium cernuum (63%)	*Castilleja coccinea* (75%)
Juniperus virginiana (63%)	*Cornus drummondii* (75%)
Oligoneuron rigidum (63%)	*Physostegia virginiana* (63%)
Solidago nemoralis (63%)	*Schizachyrium scoparium* (63%)
Houstonia canadensis (63%)	*Symphyotrichum laeve* (63%)
	Carex meadii (63%)

Table 3.4 (continued)

Group 3	Group 4
24 quadrats from 5 sites	**19 quadrats from 3 sites**
KKU - 19 quadrats	KKU - 18 quadrats
CMCU - 5	CMCU - 1
Schizachyrium scoparium (100%)	*Croton capitatus* (100%)
Sporobolus vaginiflorus (100%)	*Schizachyrium scoparium* (95%)
Solidago nemoralis (92%)	*Echinacea simulata* (95%)
Echinacea simulata (92%)	*Solidago nemoralis* (89%)
Ruellia humilis (92%)	*Isanthus brachiatus* (89%)
Physostegia virginiana (88%)	*Houstonia canadensis* (79%)
Sorghastrum nutans (83%)	*Euphorbia corollata* (79%)
Euphorbia corollata (83%)	*Lobelia spicata* (74%)
Silphium trifoliatum (83%)	*Sporobolus vaginiflorus* (74%)
Carex crawei (79%)	*Ruellia humilis* (74%)
Linum sulcatum (79%)	*Hypericum dolabriforme* (74%)
Cercis canadensis (75%)	*Linum sulcatum* (68%)
Liatris aspera (75%)	*Blephilia ciliata* (63%)
Heliotropium tenellum (75%)	*Juniperus virginiana* (63%)
Houstonia canadensis (71%)	*Cercis canadensis* (63%)
Gaura filipes (71%)	
Sabatia angularis (71%)	
Viola pedata (67%)	
Allium cernuum (63%)	
Juniperus virginiana (63%)	
Lobelia spicata (63%)	

Table 3.4 (continued)

Group 5	Group 6
36 quadrats from 5 sites	**9 quadrats from 1 site**
KKU - 36 quadrats	CMCU- 9 quadrats
Schizachyrium scoparium (100%)	*Sporobolus vaginiflorus* (100%)
Sorghastrum nutans (100%)	*Echinacea simulata* (100%)
Echinacea simulata (97%)	*Carex meadii* (100%)
Sporobolus vaginiflorus (94%)	*Ruellia humilis* (100%)
Solidago nemoralis (89%)	*Physostegia virginiana* (100%)
Silphium trifoliatum (83%)	*Houstonia canadensis* (100%)
Lithospermum canescens (81%)	*Schizachyrium scoparium* (89%)
Liatris aspera (81%)	*Sorghastrum nutans* (89%)
Galactia volubilis (81%)	*Solidago nemoralis* (89%)
Euphorbia corollata (79%)	*Juniperus virginiana* (78%)
Physostegia virginiana (75%)	*Hypericum dolabriforme* (78%)
Juniperus virginiana (72%)	*Silphium pinnatifidum* (78%)
Hedyotis nigricans (72%)	*Heliotropium tenellum* (67%)
Symphyotrichum laeve (69%)	*Ambrosia atermisiifolia* (67%)
Gaura filipes (67%)	*Potentilla simplex* (56%)
Blephilia ciliata (67%)	
Andropogon gerardii (67%)	

Table 3.4 (continued)

Group 7	Group 8
3 quadrats from 2 sites	**18 quadrats from 2 sites**
KKU - 2 quadrats	CMCU - 18 quadrats
CMCU - 1	
Schizachyrium scoparium (100%)	*Schizachyrium scoparium* (100%)
Echinacea simulata (100%)	*Sorghastrum nutans* (100%)
Fraxinus americana (100%)	*Silphium terebinthinaceum* (100%)
Helianthus hirsutus (100%)	*Euphorbia corollata* (94%)
Rosa carolina (100%)	*Physostegia virginiana* (94%)
Houstonia canadensis (67%)	*Ruellia humilis* (94%)
Juniperus virginiana (67%)	*Hedyotis nigricans* (89%)
Apocynum cannabinum (67%)	*Symphyotrichum laeve* (89%)
Potentilla simplex (67%)	*Liatris squarrulosa* (89%)
Cercis canadensis (67%)	*Sporobolus vaginiflorus* (83%)
Coreopsis tripteris (67%)	*Carex crawei* (83%)
Liatris aspera (67%)	*Carex meadii* (83%)
Quercus muhlenbergii (67%)	*Linum sulcatum* (78%)
Sorghastrum nutans (67%)	*Andropogon gerardii* (78%)
Andropogon gerardii (67%)	*Lobelia spicata* (72%)
Brickellia eupatoriodies (67%)	*Solidago nemoralis* (72%)
Diospyros virginiana (67%)	*Galactia volubilis* (61%)
Danthonia spicata (67%)	*Asclepias viridiflora* (61%)
Galactia volubilis (67%)	*Lithospermum canescens* (61%)
Croton monanthogynous (67%)	
Eupatorium altissimum (67%)	
Monarda fistulosa (67%)	
Panicum flexile (67%)	
Galium circaezans (67%)	

Table 3.4 (continued)

Group 9	Group 10
11 quadrats from 1 site	**6 quadrats from 1 site**
WPKP - 11 quadrats	WPKP - 6 quadrats
Sporobolus vaginiflorus (100%)	*Schizachyrium scoparium* (100%)
Echinacea simulata (100%)	*Bouteloua curtipendula* (100%)
Lobelia spicata (100%)	*Dichanthelium acuminatum* (100%)
Silphium pinnatifidum (100%)	*Croton capitatus* (100%)
Hedyotis nigricans (91%)	*Lobelia spicata* (100%)
Schizachyrium scoparium (91%)	*Lespedeza virginica* (100%)
Ruellia humilis (91%)	*Cercis canadensis* (100%)
Hypericum dolabriforme (91%)	*Celtis tenuifolia* (100%)
Physostegia virginiana (82%)	*Smilax bona-nox* (100%)
Celtis tenuifolia (73%)	*Dichanthelium sphaerocarpon* (83%)
Juniperus virginiana (73%)	*Polygala verticillata* (83%)
Sisyrinchium albidum (73%)	*Hypericum dolabriforme* (83%)
	Gaura filipes (83%)
	Rhus aromatica (83%)
	Viola pedata (67%)
	Sporobolus vaginiflorus (67%)
	Allium cernuum (67%)
	Euphorbia corollata (67%)
	Ruellia humilis (67%)
	Linum sulcatum (67%)
	Galactia volubilis (67%)
	Carex meadii (67%)
	Manfreda virginica (67%)
	Eupatorium altissimum (67%)

Table 3.4 (continued)

Group 11	Group 12
21 quadrats from 1 site	**11 quadrats from 1 site**
OBG - 21 quadrats	KKU - 11 quadrats
Schizachyrium scoparium (100%)	*Schizachyrium scoparium* (100%)
Echinacea simulata (100%)	*Sporobolus vaginiflorus* (100%)
Euphorbia corollata (100%)	*Echinacea simulata* (100%)
Sporobolus vaginiflorus (90%)	*Lobelia spicata* (100%)
Carex crawei (90%)	*Physostegia virginiana* (100%)
Aristida purpurascens (86%)	*Silphium trifoliatum* (100%)
Liatris squarrosa (86%)	*Melilotus alba* (91%)
Ruellia humilis (76%)	*Sisyrinchium albidum* (91%)
Sorghastrum nutans (76%)	*Euphorbia corollata* (91%)
Dichanthelium acuminatum (71%)	*Solidago nemoralis* (91%)
Gaura filipes (67%)	*Liatris aspera* (91%)
Silphium trifoliatum (67%)	*Liatris squarrosa* (91%)
Symphyotrichum urophyllum (62%)	*Galactia volubilis* (91%)
	Polygala verticillata (82%)
	Sabatia angularis (82%)
	Hypericum dolabriforme (73%)
	Hedyotis nigricans (73%)
	Sorghastrum nutans (73%)
	Croton monanthogynous (73%)
	Asclepias viridiflora (64%)
	Houstonia canadensis (64%)
	Lithospermum canescens (64%)
	Parthenium integrifolium (64%)
	Agalinis tenuifolia (64%)

Table 3.5. Community types identified at the 100-m^2 scale by cluster and indicator species analyses of ground-layer cover class data. Dominant (avg. cover ≥ 10%) and subdominant (3%≤ avg. cover<10%) taxa in each community type are listed in order of decreasing average percent cover.

Group 1	Group 2
3 quadrats from 1 site	**9 quadrats from 2 sites**
WPKP - 3 quadrats	KKU - 9 quadrats
Schizachyrium scoparium (27.5%)	*Schizachyrium scoparium* (35.3%)
Dichanthelium sphaerocarpon (14.8%)	*Sorghastrum nutans* (14.4%)
Andropogon gerardii (13.8%)	*Echinacea simulata* (11.7%)
Smilax bona-nox (10.8%)	*Liatris aspera* (10.2%)
Celtis tenuifolia (9.5%)	*Sporobolus vaginiflorus* (9.1%)
Rhus aromatica (8.2%)	*Parthenium integrifolium* (8.4%)
Bouteloua curtipendula (8.2%)	*Cercis canadensis* (5.3%)
Cercis canadensis (7.5%)	*Carex crawei* (4.7%)
Hypericum dolabriforme (5.2%)	*Allium cernuum* (3.9%)
Eupatorium altissimum (5.0%)	*Sporobolus compositus* (3.4%)
Dichanthelium acuminatum (3.2%)	*Andropogon gerardii* (3.1%)
Clematis pitcheri (3.2%)	
Carex meadii (3.0%)	

Table 3.5 (continued)

Group 3	Group 4
12 quadrats from 1 site	**10 quadrats from 3 sites**
OBG - 12 quadrats	KKU - 8 quadrats
	CMCU - 2
Schizachyrium scoparium (31.7%)	*Schizachyrium scoparium* (30.0%)
Sporobolus vaginiflorus (27.6%)	*Sporobolus vaginiflorus* (24.1%)
Fimbristylis puberula (20.7%)	*Echinacea simulata* (12.5%)
Echinacea simulata (16.7%)	*Juniperus virginiana* (10.0%)
Sorghastrum nutans (12.4%)	*Andropogon gerardii* (9.4%)
Carex crawei (11.2%)	*Sorghastrum nutans* (8.9%)
Hedyotis nigricans (10.2%)	*Cercis canadensis* (3.5%)
Liatris squarrosa (7.9%)	*Manfreda virginica* (3.2%)
Euphorbia corollata (5.0%)	*Solidago nemoralis* (3.0%)
Carex meadii (4.4%)	
Comandra umbellata (4.4%)	
Heliotropium tenellum (4.3%)	
Andropogon gerardii (3.9%)	
Silphium trifoliatum (3.6%)	
Ruellia humilis (3.4%)	

Group 5	Group 6
6 quadrats from 1 site	**4 quadrats from 1 site**
CMCU - 6 quadrats	OBG - 4 quadrats
Andropogon gerardii (43.3%)	*Schizachyrium scoparium* (73.1%)
Echinacea simulata (15.8%)	*Liatris cylindracea* (12.1%)
Carex meadii (13.0%)	*Silphium terebinthinaceum* (6.5%)
Sporobolus vaginiflorus (10.2%)	*Hedyotis nigricans* (4.0%)
Schizachyrium scoparium (6.8%)	*Symphyotrichum laeve* (3.5%)
Silphium pinnatifidum (4.3%)	*Juniperus virginiana* (3.3%)
Hypericum dolabriforme (3.9%)	
Juniperus virginiana (3.8%)	

Table 3.5 (continued)

Group 7	Group 8
4 quadrats from 1 site	**14 quadrats from 3 sites**
OBG - 4 quadrats	KKU - 14 quadrats
Silphium terebinthinaceum (45.0%)	*Schizachyrium scoparium* (24.6%)
Sorghastrum nutans (32.0%)	*Sporobolus vaginiflorus* (14.2%)
Andropogon gerardii (31.3%)	*Sorghastrum nutans* (10.2%)
Schizachyrium scoparium (4.5%)	*Carex crawei* (5.8%)
Pycnanthemum tenuifolium (3.8%)	*Allium cernuum* (5.3%)
Cornus drummondii (3.5%)	*Echinacea simulata* (4.5%)
Liatris spicata (3.0%)	*Aristida purpurascens* (4.4%)
Coreopsis tripteris (3.0%)	*Andropogon gerardii* (3.2%)
	Liatris aspera (3.1%)

Group 9	Group 10
6 quadrats from 1 site	**11 quadrats from 2 sites**
KKU - 6 quadrats	KKU - 11 quadrats
Schizachyrium scoparium (20.8%)	*Schizachyrium scoparium* (28.4%)
Sorghastrum nutans (16.5%)	*Andropogon gerardii* (25.7%)
Carex crawei (13.2%)	*Hedyotis nigricans* (10.4%)
Hedyotis nigricans (9.2%)	*Sorghastrum nutans* (9.3%)
Echinacea simulata (9.2%)	*Echinacea simulata* (9.1%)
Andropogon gerardii (9.2%)	*Carex umbellata* (6.4%)
Sporobolus compositus (6.8%)	
Sporobolus vaginiflorus (6.5%)	
Liatris aspera (5.5%)	

Table 3.5 (continued)

Group 11	Group 12
9 quadrats from 2 sites	**6 quadrats from 1 site**
CMCU - 9 quadrats	WPKP - 6 quadrats
Schizachyrium scoparium (16.4%)	*Schizachyrium scoparium* (14.2%)
Carex crawei (13.8%)	*Echinacea simulata* (14.2%)
Sporobolus vaginiflorus (12.4%)	*Sporobolus vaginiflorus* (9.5%)
Sorghastrum nutans (8.6%)	*Silphium pinnatifidum* (6.8%)
Andropogon gerardii (8.4%)	*Juniperus virginiana* (4.0%)
Carex meadii (7.9%)	*Andropogon gerardii* (3.2%)
Silphium terebinthinaceum (7.1%)	
Hedyotis nigricans (6.6%)	

Figure 3.1. Map of continental United States showing the location of Kentucky (shaded) and ecoregional map of Kentucky (from Woods et al., 2002) with sample site locations (1-18). Level III Ecoregions (bold font) and constituent Level IV ecoregions (regular font): 68 Southwestern Appalachians, 68a Cumberland Plateau, 68c Plateau Escarpment; 69 Central Appalachians, 69d Dissected Appalachian Plateau, 69e Cumberland Mountain Thrust Block; 70 Western Alleghany Plateau, 70b Monongahela Transition Zone, 70d Knobs-Lower Scioto Dissected Plateau, 70f Ohio/Kentucky Carboniferous Plateau, 70g Northern Forested Plateau Escarpment, 70h Carter Hills; 71 Interior Plateau, 71a Crawford-Mammoth Cave Uplands, 71b Mitchell Plain, 71c Knobs-Norman Upland, 71d Outer Bluegrass, 71e Western Pennyroyal Karst Plain, 71f Western Highland Rim, 71g Eastern Highland Rim, 71h Outer Nashville Basin, 71k Hills of the Bluegrass, 71l Inner Bluegrass; 72 Interior River Valleys and Hills, 72a Wabash-Ohio Bottomlands, 72c Green River-Southern Wabash Lowlands, 72h Caseyville Hills; 73 Mississippi Alluvial Plain, 73a Holocene Meander Belts; 74 Mississippi Valley Loess Plains, 74a Bluff Hills, 74b Loess Plains.

Figure 3.2. Cluster dendrogram of 0.01-m^2 community types obtained from cluster and indicator species analyses of presence data. Group numbers correspond with Table 3.1.
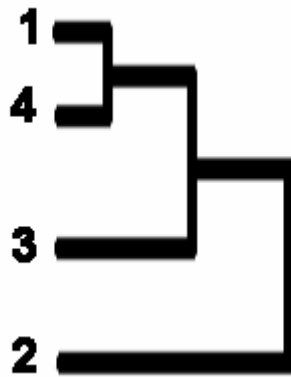
Figure 3.3. Cluster dendrogram of 0.1-m^2 community types obtained from cluster and indicator species analyses of presence data. Group numbers correspond with Table 3.2.
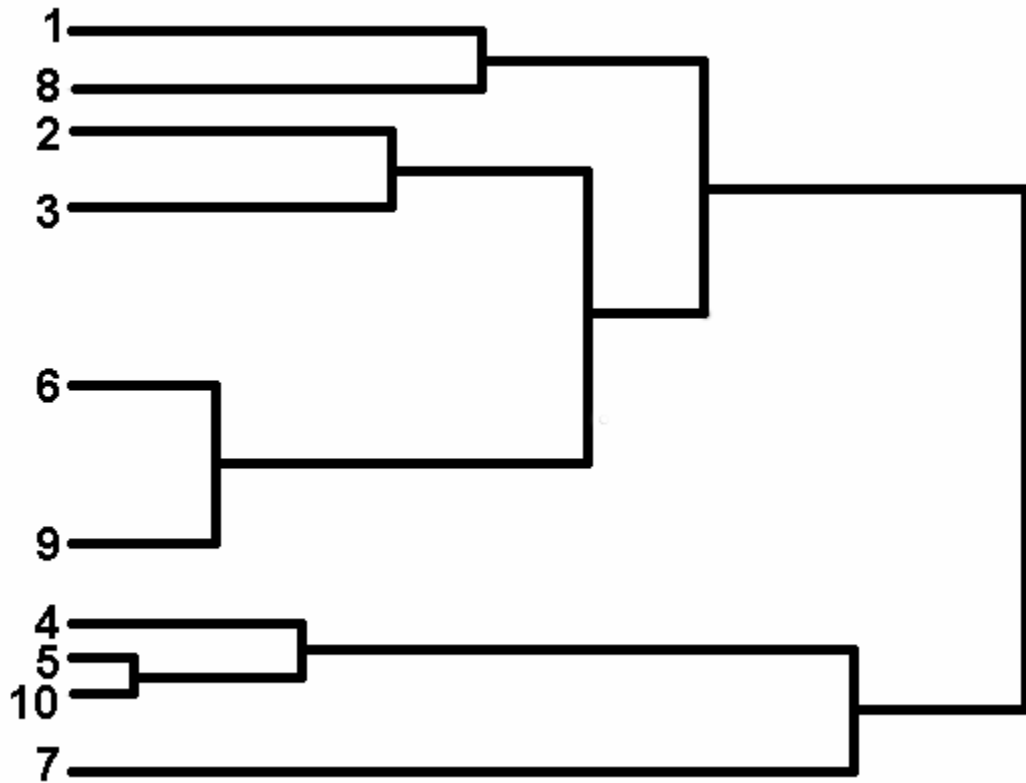
Figure 3.4. Cluster dendrogram of 1.0-m^2 community types obtained from cluster and indicator species analyses of presence data. Group numbers correspond with Table 3.3.
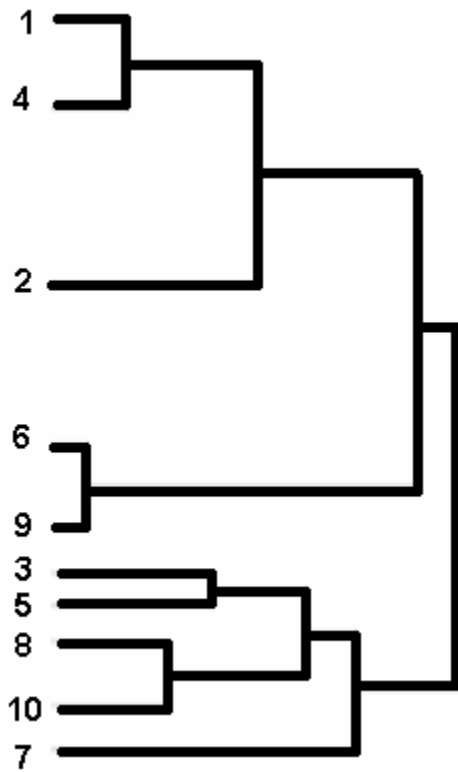
Figure 3.5. Cluster dendrogram of 10-m^2 community types obtained from cluster and indicator species analyses of presence data. Group numbers correspond with Table 3.4.
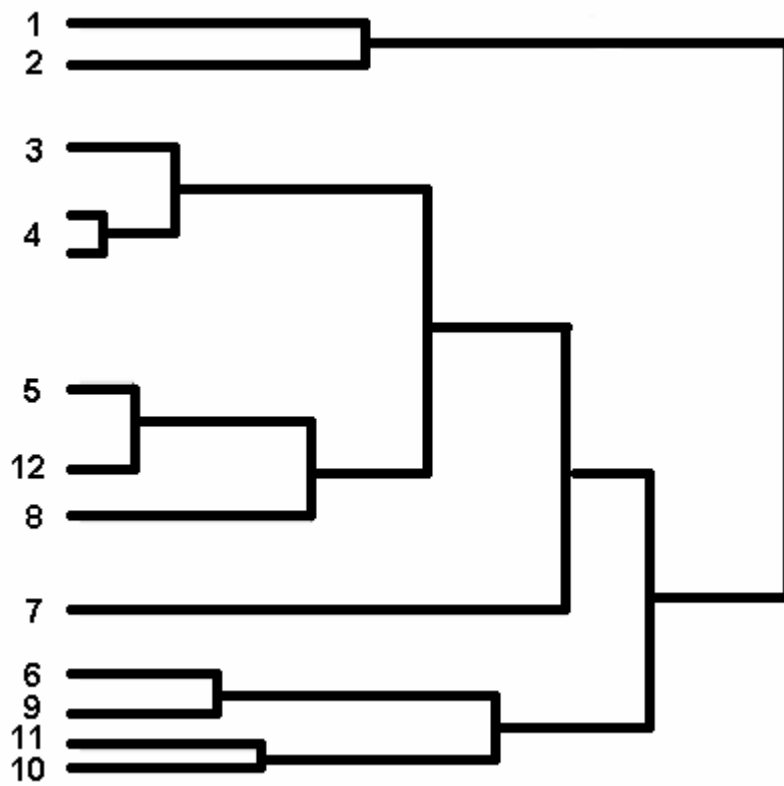
Figure 3.6. Cluster dendrogram of 100-m^2 community types obtained from cluster and indicator species analyses of ground-layer cover class data. Group numbers correspond with Table 3.5.
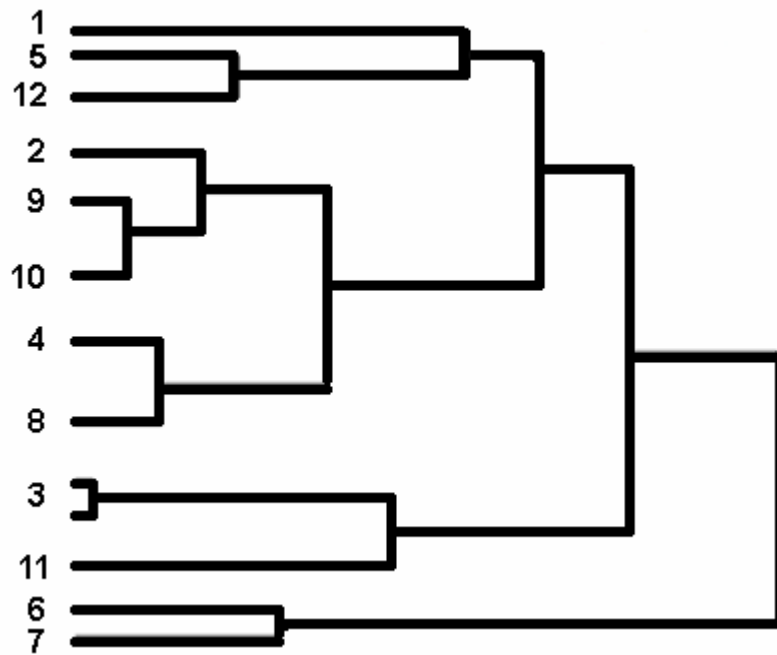
Figure 3.7. Joint plots including abiotic environmental variables and taxa with r^2 values ≥ 0.35; a) axis 1 vs. 2, b) axis 1 vs. 3 and c) axis 2 vs. 3. Each 100-m^2 quadrat is represented by a triangle labeled with site number (from Figure 1) followed by quadrat number within site. Taxon codes are formed by the first three letters of the genus and species epithet, respectively. "Depth" symbolizes soil depth.

3.7 a.
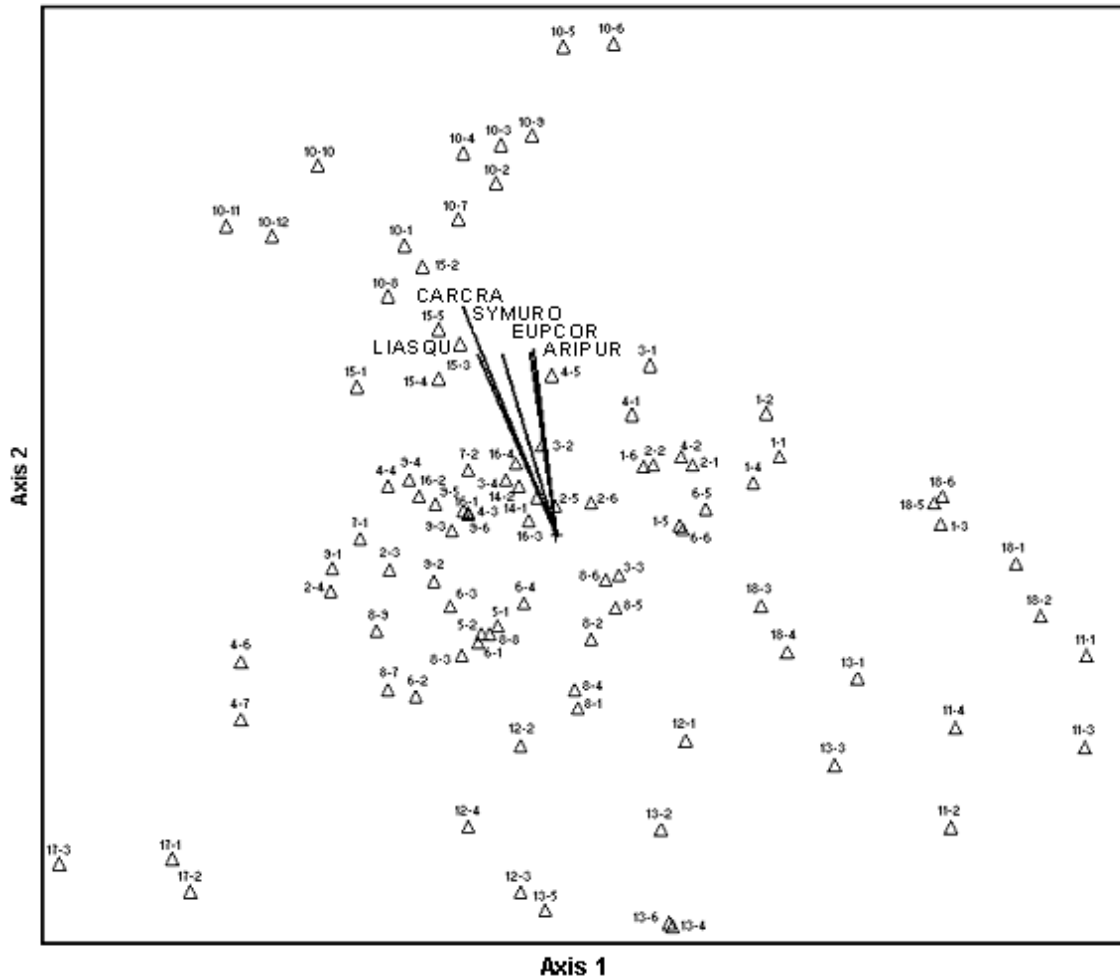
3.7 b.
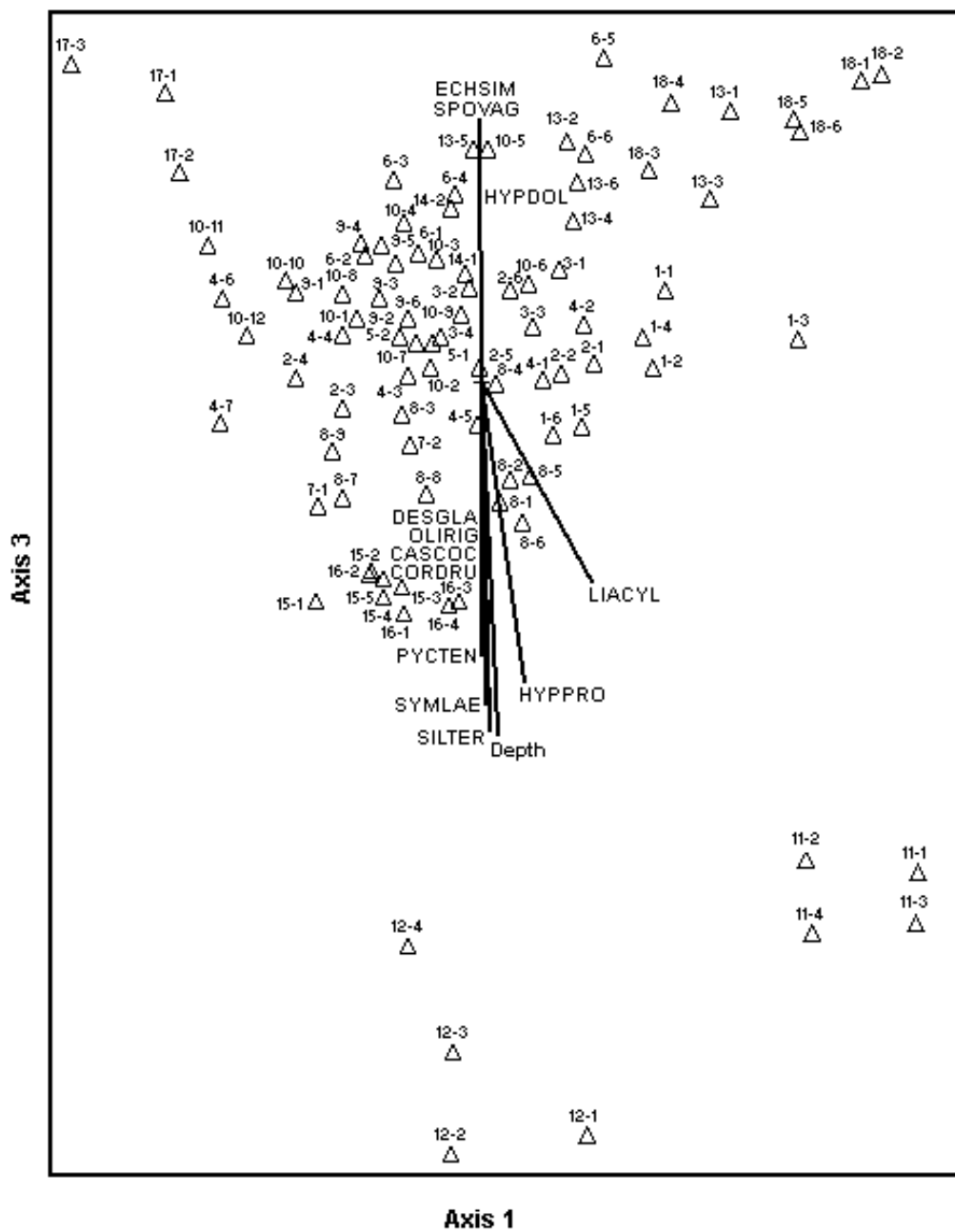
3.7 c.
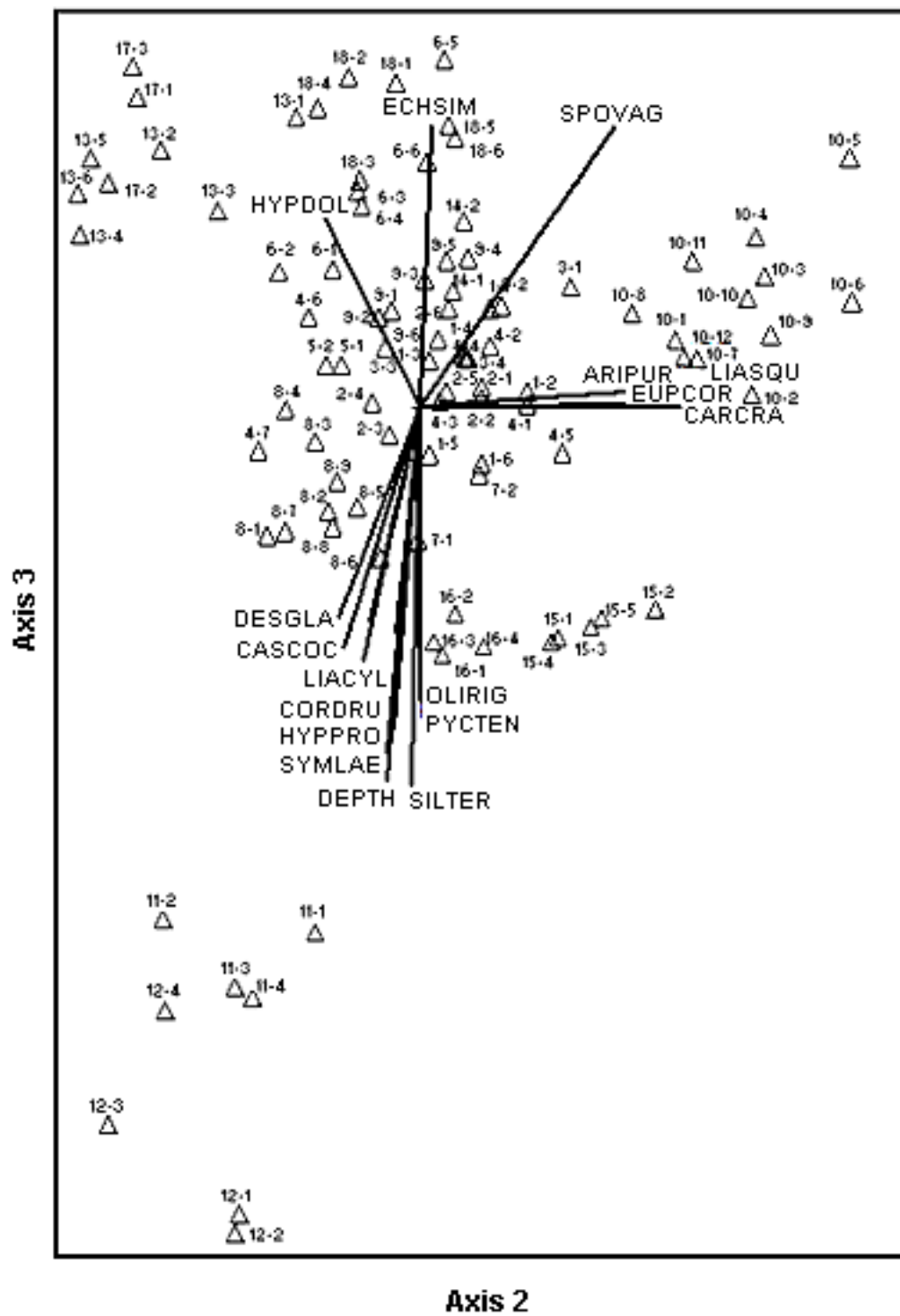
CHAPTER 4

EFFECTS OF GRAIN ON CLASSIFICATION AND DISPERSION
OF CALCAREOUS GRASSLAND COMMUNITIES:
IMPLICATIONS FOR CONSERVATION

SYNOPSIS

The vegetation of eighteen xeric limestone prairies (XLPs) in the Interior Plateau ecoregion in Kentucky (U.S.A.) was sampled with a multiple-grain sampling design to determine the effects of grain on community classification and dispersion. Flexible beta linkage cluster analysis was used to identify community types at scales commensurate with grain (0.01, 0.1, 1.0, 10, and 100 m^2). Total number of community types identified among sites and patch diversity within sites were calculated for each grain. Fidelity of community types to sites and to ecoregions was determined via dispersion indices. Ecoregional dispersion indices were used to assess the physiography-based ecoregional classification of Kentucky by Woods et al. (2002). There was a general positive correlation between grain and number of community types identified. Patch diversity reached a maximum at the 0.1 m^2 grain and decreased at grains ≥ 1.0 m^2. Dispersion of community types among sites and among ecoregions was negatively correlated with grain. Dispersion of community types among sites consistently exceeded dispersion of community types among ecoregions. The low dispersion of coarse-grain (≥ 10-m^2) community types among ecoregions suggests physiography-based ecoregional classification systems are capable of explaining vegetation dynamics in patchy vegetation types such as XLPs. However, further assessment of physiography-based ecoregional classification systems will require similar multiple-grain analyses in regionally dominant vegetation types.

INTRODUCTION

Conservation biologists increasingly have been focusing on protection of biodiversity at hierarchical ranks above the species level (Franklin, 1993; Poiani et al., 2000). This transition in conservation strategy resulted from recognition of both the broad range of spatial and temporal scales over which ecological processes operate (Brand and Parker, 1995) and the necessity to protect these processes for effective biodiversity conservation (Peterson and Parker, 1998). Due to the extent of anthropogenic disturbance in the majority of contemporary landscapes, it is impossible to protect the range of community types and intrinsic ecological processes that occur in any particular landscape. Therefore, ecologists are routinely charged with the task of identifying and preserving the best examples of the remaining community types within a landscape. Consequently, conservation of biodiversity is strongly dependent upon accurate inventory and classification of ecological communities.

The sampling design used to collect biotic and abiotic data strongly affects community classification (Barbour et al., 1999) and ultimately protection of biodiversity. The three fundamental components of sampling design are grain, sample number, and sampling extent. Grain is the smallest sampling unit from which data are collected; sample number the total number of samples collected in a study; and sampling extent the maximum distance between sample units, thus defining the study area. Of these three components of sampling design, Palmer and White (1994) determined that grain most strongly influences the species-area relationship due to the positive correlation between grain and sample disaggregation. Grain also has been shown to shift patch occupancy frequency distributions from left to right, which corresponds to a decrease in the number of low-frequency species (i.e. satellite species; sensu Hanski, 1982) and an increase in the number of middle- to high-frequency species (see review in McGeoch and Gaston, 2002). Consequently, grain is expected to indirectly affect community classification due to the dependence of commonly employed distance measures (e.g. Sorensen's distance) upon both average species richness and the frequency distribution of species among samples. This study utilizes a multiple-grain sampling design to determine the effect(s) of grain on

classification and dispersion of xeric limestone prairie community types in the Interior Plateau Level IV ecoregion in Kentucky (sensu Woods et al., 2002).

Xeric limestone prairies (XLPs) (sensu Baskin et al., 1994; Baskin and Baskin, 2000) occur on shallow rocky soils in the deciduous forest biome in the eastern United States from Missouri (Nelson and Ladd, 1983; Baskin and Baskin, 2000) and Pennsylvania (Laughlin and Uhl, 2003) south to Arkansas (Keeland, 1978; Baskin and Baskin, 2000) and Georgia (DeSelm, 1993). They are dominated by C_4 perennial prairie grasses (*Schizachyrium scoparium*, *Boutelous curtipendula*, *Sorghastrum nutans* and *Andropogon gerardii*) and support a significant number of rare heliophytic taxa (DeSelm, 1993; Allison and Stevens, 2001; Baskin and Baskin, 2000; Laughlin and Uhl, 2003; Lawless et al., 2004 [Chapter 2]). Soil depth is heterogeneous within sites (Lawless et al., 2004 [Chapters 2]; Chapter 3) and often results in relatively abrupt transitions in community structure at local spatial scales, thus producing a mosaic of patch types (Chapter 3). There is also significant variation in the composition of nondominant taxa among sites, which most likely is attributable to the rarity of this vegetation type at the landscape scale and the small area of sites in relation to regionally dominant deciduous forests (Lawless et al., 2004 [Chapter 2]). Thus, I expected a negative correlation between grain and both dispersion of community types among sites and ecoregions and patch diversity within sites.

In Kentucky, XLPs occur on Mississipian and Silurian calcareous substrates (limestone, dolomite and clay-shale) (Lawless et al., 2004 [Chapter 2]) in the Crawford-Mammoth Cave Uplands, Knobs-Norman Upland and Outer Bluegrass Level III ecoregions in the Interior Plateau (sensu Woods et al., 2002). Two XLPs (Figure 4.1, site #'s 17 and 18) are at the southern boundary of the Crawford-Mammoth Cave Uplands ecoregion of Woods et al. (2002). However, I consider them to be in the Western Pennyroyal Karst Plain ecoregion, which is in agreement with Fenneman (1938, Figure 123, page 436) and an unpublished map of the Pennyroyal Plain by Baskin and Baskin (Lawless et al., 2004 [Chapter 2]).

The ecoregional classification systems of Omernik (1987) for the continental United States and of Woods et al. (2002) for Kentucky largely are based on physiographic units commensurate with provinces and sections (sensu Fenneman, 1938),

respectively. These physiographic units are defined by similar topography and geology (Fenneman, 1938), are typified by ecological patterns and characteristic biotas, and thus often are used in the delimitation of ecoregions. A considerable number of studies have determined the fidelity of riparian community types to ecoregions and corresponding physiographic regions (Harding, 1997; Feminella, 2000; Gerritsen et al., 2000; van Sickle and Hughes, 2000; Dovciak and Perry, 2002). These studies are pivotal in assessing the validity of ecoregional classification as an effective partitioning of habitat for the establishment of conservation priorities and standard management practices. Wright et al. (1998) determined the areal proportion of vegetation types (fine- to coarse-scale classification) in Idaho, Oregon, and Washington occurring in ecoregional provinces of Bailey (1976) and Level III ecoregions of Omernik (1987) and found poor correspondence between current vegetation type distributions and ecoregional classification. However, extensive empirical testing of the fidelity of fine-scale terrestrial plant community types to ecoregions has not been conducted. By quantifying the dispersion of fine-scale XLP community types among Level IV ecoregions of Kentucky, this project also will provide data necessary for a more thorough critique of ecoregional classification and its physiographic basis.

METHODS

Vegetation Sampling

In July through October of 2002 and 2003, the vegetation of 18 XLPs in the Interior Plateau ecoregion in Kentucky (Figure 5.1) was sampled using a nested quadrat sampling design adapted from Peet et al. (1998). Sampling plots consisted of two to six 100-m^2 modules arranged adjacent to one another. A single plot was sampled in each site, with the exception of Pine Creek Barrens, in which two plots of six modules each were sampled. Number of modules sampled per site ranged from two to 12 (200 to 1200 m^2) and was determined primarily by area of site, which ranged from less than 0.5 to approximately 2.25 hectares (Lawless et al., 2004 [Chapter 2]). In each sample module, ground layer vegetation (≤ 1.5 m) was sampled in one or two series of nested quadrats increasing logistically in area from 0.01 to 10 m^2. Taxa present in each nested quadrat and module were recorded. Average species richness per sample was calculated at each grain across all sample sites.

Identification of Community Types at Multiple Scales

The flexible beta linkage (beta = -0.25) agglomerative clustering method in PC-ORD (MJM Software Design, 1999) was used to identify community types (i.e. groups) at multiple spatial scales (0.01, 0.1, 1.0, 10, and 100-m^2), which correspond to the grains used in vegetation sampling. A beta value of -0.25 and Sorensen's distance measure were used in analyses of presence-absence data at each of the five grains. Indicator species analysis was used to determine the optimal number of groups at each grain via selection of the group number with the lowest average p-value for the set of species present in one or more quadrats (Dufrêne and Legendre, 1997).

Community Type Dispersion Indices and Patch Richness, Diversity and Evenness Indices

The Shannon-Wiener diversity index $[H' = -\Sigma (p_i) (\ln p_i)]$(Shannon and Weaver, 1949) was used for the determination of community type dispersion among sites and ecoregions and of patch diversity within a site (Romme and Knight, 1982; Glenn and Collins, 1990). In the ecoregional dispersion index, p_i is calculated for each community type as the number of quadrats in the community type that is in a particular ecoregion divided by the total number of quadrats assigned to that community type. Similarly, in the site dispersion index, p_i, is calculated for each community type as the number of quadrats in the community type that is in a particular site divided by the total number of quadrats assigned to that community type. Thus, the ecoregional and site dispersion indices are measures of the number of ecoregions and sites, respectively, within which a community type occurs and the relative frequency of the community type within ecoregions and sites, respectively.

In the patch diversity index (H'), the proportional dominance index (p_i) for each community type within a site is calculated as the number of quadrats assigned to that community type (via cluster analysis) divided by the total number of quadrats sampled in the site. Consequently, H' is a measure of the number (richness) and evenness of relative frequencies of community types within a site. Patch diversity indices were not calculated at the 100-m^2 grain due to the reduction in sample number resulting from the nested

sampling design, which would tend to underestimate patch diversity. The average number of community types per site (community type richness = C) and average evenness (J') of community types within sites were also calculated at the 0.01 to 10-m^2 grains. J' was obtained by dividing H' by C.

RESULTS

Grain and number of community types identified via cluster analysis generally were positively correlated in this study (Figure 4.2). However, number of community types identified at grains of 0.1 and 1.0 m^2 and at 10 and 100 m^2 did not differ. Dispersion of community types among ecoregions and sites was negatively correlated with grain (Figure 4.2). Dispersion of community types among sites was higher than among ecoregions over the entire range of grains. Rate of decrease of both dispersion indices decreased considerably from the 10 to 100-m^2 grains. The ecoregional dispersion index decreased from 0.11 at the 10-m^2 grain, where nine of the 12 community types were restricted to a single ecoregion, to 0.04 at the 100-m^2 grain, where 11 of the 12 community types occurred in a single ecoregion. At both grains, the remaining community types were present in only two ecoregions. The site dispersion index decreased from 0.42 at the 10-m^2 grain, where seven of the 12 community types were restricted to one site, to 0.30 at the 100-m^2 grain, where only six of the 12 community types were present in a single site. Maximum number of sites in which a community type occurred at the 10-m^2 grain was five (two community types) and at the 100-m^2 grain three (three community types).

Patch diversity was not directly correlated with grain and was relatively low at each of the four grains (0.01, 0.1, 1.0, and 10 m^2) (Figure 4.3). Diversity increased from 0.85 at the 0.01-m^2 grain to 1.00 at the 0.1-m^2 grain and then decreased considerably to 0.32 at the 10-m^2 grain. There was no difference in average evenness of community types identified at the 0.01-m^2 and 0.1-m^2 grains, and average community type evenness decreased at grains > than 0.1 m^2. Average site community type richness increased from 2.83 at the 0.01-m^2 grain to 3.56 at the 0.1-m^2 grain and then decreased at grains > 0.1 m^2. Fourteen of the 18 sites contained three or four of the four 0.01-m^2 community types. However, only two of the eighteen sites supported five or more of the 10 0.1-m^2

community types. Seven of the 18 sites contained only one of the 1-m^2 community types, and thirteen sites supported only one of the 10-m^2 community types.

DISCUSSION

Community Classification and Dispersion

  The negative correlation between grain and dispersion of community types among sites and ecoregions is most likely attributable to the superior accuracy of coarse-grain samples in estimating local and regional species pools and thus the site and ecoregion, respectively, from which individual samples were collected. At fine grains (0.01 to 0.1 m^2), only the dominant C$_4$ perennial prairie grasses (*Schizachyrium scoparium*, *Sorghastrum nutans*, and *Andropogon gerardii*), the C$_3$ sedge *Carex crawei*, and the C$_4$ annual grass *Sporobolus vaginiflorus* had high percent occurrence values (Chapter 3). However, the low average species richness of samples at these grains (Figure 4.2), clonal growth form of the C$_4$ perennial grasses and *Carex crawei* and differences in habitat preferences among these taxa typically prevented the co-ocurrence of more than two of these taxa at grains ≤ 0.1-m^2 (Chapter 3). Consequently, these taxa are the chief indicator species of fine-grain community types (Figure 4.4), and the community types, like their indicator species, are broadly distributed geographically. These data are consistent with the ubiquitous positive correlations between local abundance and frequency (Gotelli and Simberloff, 1987; Collins and Glenn, 1990; Guo et al., 2000; Partel et al., 2001) and between local abundance and geographic range size (Brown, 1984; Gotelli and Simberloff, 1987; Collins and Glenn, 1990; Hanski et al., 1993; Collins and Glenn, 1997; Gaston et al., 1997; Gonzalez et al., 1998; Lawton, 1999; Guo et al., 2000; Bossuyt et al., 2004), both of which have been documented in a variety of taxonomic groups and community types.

  At relatively coarse grains (10 to 100 m^2), percent occurrence values of the dominant taxa (*Schizachyrium scoparium*, *Sporobolus vaginiflorus*, *Sorghastrum nutans*, *Echinacea simulate*, and *Andropogon gerardii*) are high in almost all community types identified in this study (Chapter 3). Therefore, the dominant taxa are not significant indicator species of coarse grain community types (Figure 4.4). Glenn and Collins (1990, 1993) documented the same pattern, though at coarser grains (≥ 100 m^2), in tallgrass

prairies of the midwestern United States, which share the same dominant C_4 perennial prairie grasses as XLPs in Kentucky. Consequently, classification of coarse-grain tallgrass prairie and XLP community types is dependent upon less abundant taxa. The strong fidelity of coarse-grain community types (10 and 100-m^2) to sites and ecoregions in this study suggests that a considerable number of less abundant taxa or unique sets of less abundant taxa are restricted to particular sites and ecoregions, which also is in agreement with the correlation between local abundance and frequency. Restriction of these taxa or sets of taxa to particular sites and, more importantly ecoregions, suggests regional processes such as colonization and extinction significantly affect community composition and thus classification and dispersion of community types. The isolation of XLP sites among regionally dominant deciduous forests most likely results in decreased rates of colonization, increased rates of extinction, and thus significant differences in community composition even between proximate sites, which results in low dispersion of community types among sites and ecoregions at large grains.

Patch Diversity

The high patch diversity observed at small grains (0.01 and 0.1-m^2) is attributable to both richness and evenness of patch types (i.e. community types) within sites. Maximization of patch diversity at the 0.1-m^2 grain resulted from an increase in patch richness with grain, since patch evenness within sites did not differ between 0.01 and 0.1-m^2 grains. The sharp decrease in patch diversity observed at the 1.0-m^2 grain resulted from large decreases in both patch richness and patch evenness within sites. This reduction in patch diversity most likely resulted from both decreased dispersion of community types at coarse grains and positive correlation between grain and proportion of environmental heterogeneity present within sample units. When the proportion of environmental heterogeneity within sample units approaches the total heterogeneity within a site, fine-scale environmental conditions within samples become indiscernible (Wiens, 1989; McGeoch and Gaston, 2002); therefore, patch types may represent aggregations of species assemblages adapted to dissimilar habitats.

Implications for Conservation

This study was not designed to identify the most appropriate grain for classification of grassland communities or other vegetation types. However, results obtained from it suggest grain significantly influences the number of community types identified in a study, the distribution of community types among sites and ecoregions, and patch diversity within and among sites, all of which may profoundly affect conservation strategy and protection of biodiversity. The appropriate grain in any particular study is perhaps best determined by total environmental heterogeneity within sites (McGeoch and Gaston, 2002) and the rate at which environmental conditions fluctuate in space, both of which are difficult to quantify at the outset of an experiment and presumably vary significantly among vegetation types.

Low dispersion of community types among ecoregions, particularly at grains $\geq$ $10m^2$, suggests physiography is a useful indicator of regional processes, and thus is a reasonable basis for the delimitation of ecoregions. However, XLPs are an aberration from the regionally dominant deciduous forests and are of limited areal extent at the landscape scale. In the majority of instances, the geographic distances between sites from the same ecoregion are relatively small in comparison with average distances between sites from different ecoregions. Therefore, the low dispersion of community types among ecoregions may simply result from distance decay of similarity (Nekola and White, 1999) in species composition among sites and not the restriction of environmental conditions and unique community dynamics to particular ecoregions. Conversely, spatial autocorrelation of environmental conditions is one of the primary impetuses for the grouping of land areas into physiographic regions and perhaps is the most parsimonious explanation for the restriction of patchy community types such as XLPs to small portions of a given ecoregion. Further assessment of physiography-based ecoregional classification would be strengthened significantly by similar analyses of regionally dominant vegetation types across Level IV ecoregions or other ecoregional units of an equivalent scale.

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Figure 4.1. Map of continental United States showing the location of Kentucky (shaded) and ecoregional map of Kentucky (from Woods et al., 2002) with sample site locations (1-18). Level III Ecoregions (bold font) and constituent Level IV ecoregions (regular font): 68 Southwestern Appalachians, 68a Cumberland Plateau, 68c Plateau Escarpment; 69 Central Appalachians, 69d Dissected Appalachian Plateau, 69e Cumberland Mountain Thrust Block; 70 Western Alleghany Plateau, 70b Monongahela Transition Zone, 70d Knobs-Lower Scioto Dissected Plateau, 70f Ohio/Kentucky Carboniferous Plateau, 70g Northern Forested Plateau Escarpment, 70h Carter Hills; 71 Interior Plateau, 71a Crawford-Mammoth Cave Uplands, 71b Mitchell Plain, 71c Knobs-Norman Upland, 71d Outer Bluegrass, 71e Western Pennyroyal Karst Plain, 71f Western Highland Rim, 71g Eastern Highland Rim, 71h Outer Nashville Basin, 71k Hills of the Bluegrass, 71l Inner Bluegrass; 72 Interior River Valleys and Hills, 72a Wabash-Ohio Bottomlands, 72c Green River-Southern Wabash Lowlands, 72h Caseyville Hills; 73 Mississippi Alluvial Plain, 73a Holocene Meander Belts; 74 Mississippi Valley Loess Plains, 74a Bluff Hills, 74b Loess Plains.

Figure 4.2. Number of community types, site and ecoregional dispersion indices, and species richness versus grain.
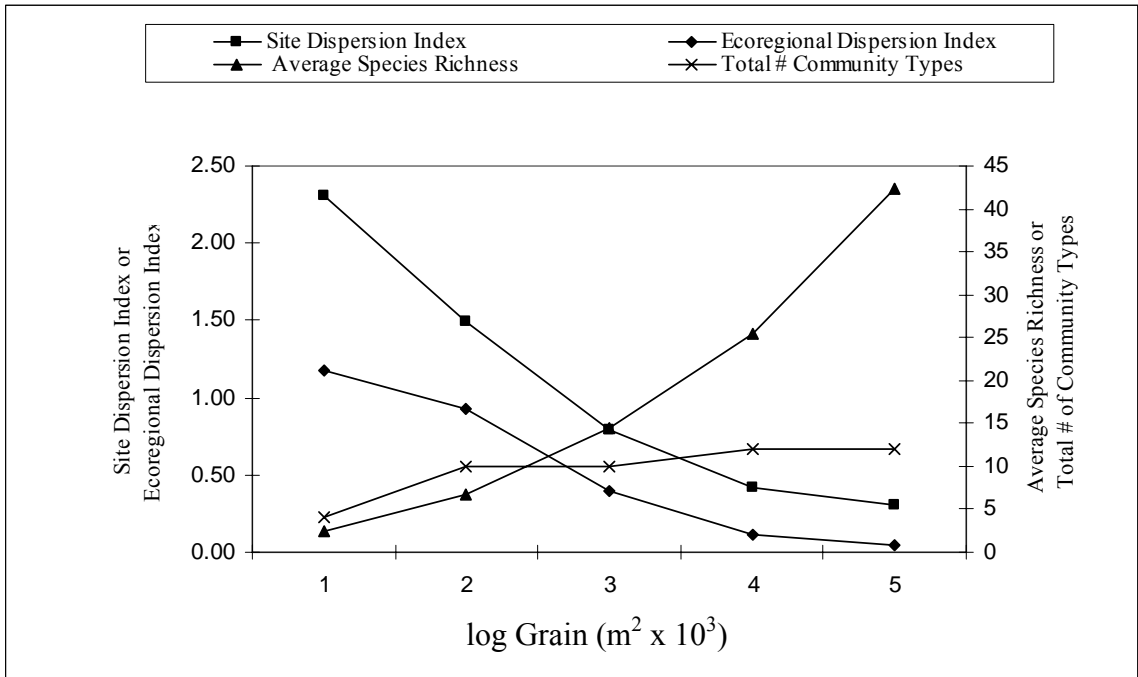
Figure 4.3. Average patch richness, diversity, and evenness per site versus grain.
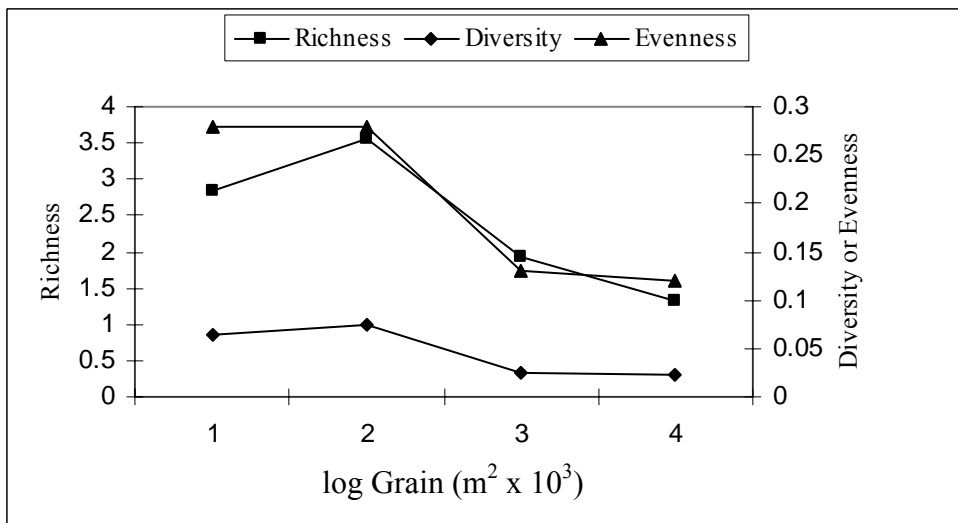
Figure 4.4. Indicator values of dominant taxa versus grain.
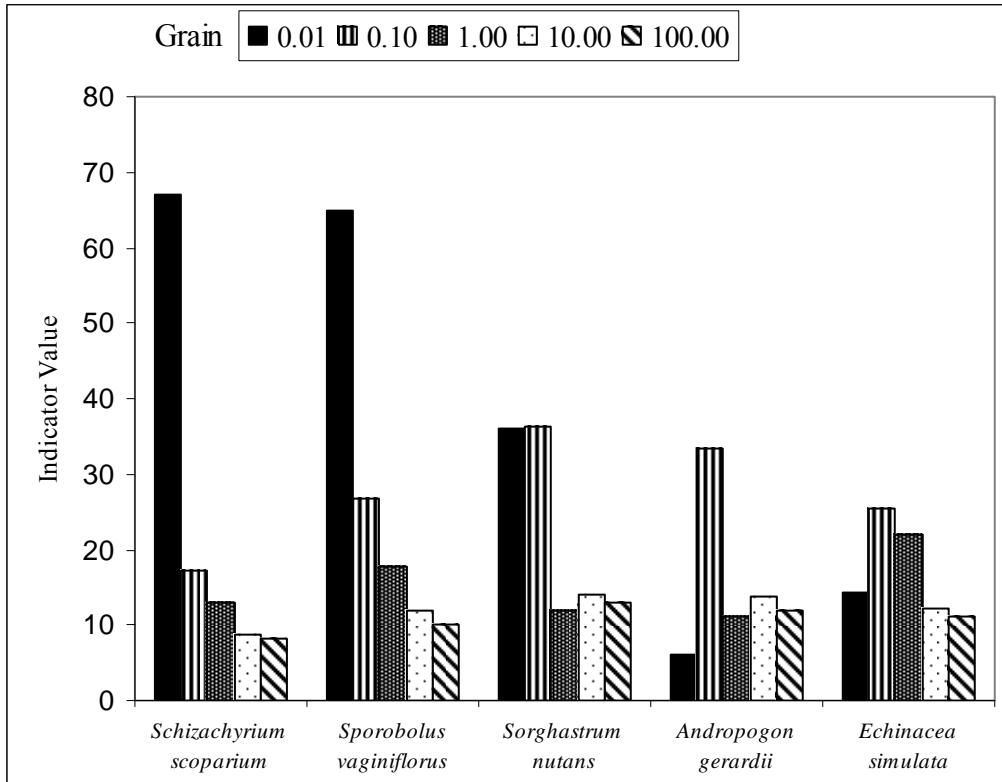
CHAPTER 5

XERIC LIMESTONE PRAIRIES OF EASTERN UNITED STATES:
REVIEW AND SYNTHESIS

SYNOPSIS

Xeric limestone prairies (XLPs) are open, nonforested areas in which herbaceous plant communities occur on shallow, rocky soils derived from calcareous substrates. These grasslands are characterized by dominance of C_4 perennial grasses and are distributed in the eastern United States from Missouri and Pennsylvania south to Arkansas and Georgia. XLPs occur in the Ozark Plateaus, Central Lowland, Interior Low Plateaus, Appalachian Plateaus, Ridge and Valley, and Coastal Plain physiographic provinces, and they are developed on Alfisols, Ultisols, Mollisols, Inceptisols, and Vertisols derived from limestones, dolomites, and calcareous shales of Cambrian through Tertiary (Eocene) systems. The C_4 perennial prairie grasses *Schizachyrium scoparium*, *Bouteloua curtipendula*, *Andropogon gerardii*, *Sorghastrum nutans*, and *Sporobolus clandestinus* typically are dominant taxa in XLPs. However, C_3 perennial forbs are dominant in some sites, and C_4 annual grasses (*Sporobolus* spp.) may be locally dominant in shallow soil zone microsites. Thirteen taxa apparently are endemic, or nearly so, to this vegetation type, including eight in the Ridge and Valley in Alabama (Cahaba River Valley), four in the Ozark Plateaus in Missouri and Arkansas, and one in the Ridge and Valley of West Virginia and Virginia. Various types of information are used to construct a conceptual model of the origin, maintenance, and successional dynamics of XLPs.

INTRODUCTION

Xeric limestone prairies (XLPs) (sensu Baskin et al., 1994; Baskin and Baskin, 2000) are open, nonforested areas in which herbaceous plant communities are developed on shallow, rocky soils derived from calcareous substrates including limestone, dolomite and shale (Lawless et al., 2004 [Chapter 2]) (Figure 5.1). This vegetation type is characterized by dominance of C_4 perennial grasses (Baskin and Baskin, 2000; Laughlin and Uhl, 2003; Baskin et al., 2004; Chapter 3) and relatively high taxonomic richness of heliophytic C_3 perennial forbs, many of which are rare at the state, regional, and/or global levels (White et al., 1994; Laughlin and Uhl, 2003; Lawless et al., 2004 [Chapter 2]). XLPs often contain islands of woody vegetation within the grassland matrix and typically are surrounded by dry, rocky upland forests. Expansion of islands of woody vegetation and encroachment of adjacent forests into XLPs has been documented in some regions and can result in drastic reductions in the size of openings (e.g. Annala and Kaputska, 1983; Kimmel and Probasco, 1980).

This vegetation type is broadly distributed throughout a large portion of the eastern deciduous forest formation (sensu Braun, 1950)(Figure 5.2), where it has been referred to as "glades" (Missouri, Arkansas, Illinois, Indiana, Kentucky, West Virginia, Tennessee, Georgia, and Alabama), "barrens" (Illinois, Indiana, Ohio, West Virginia, Virginia, Kentucky, Tennessee, Georgia, and Alabama), "prairies" (Alabama and Ohio), "prairie barrens" (Alabama), and "xeric limestone prairies" (Pennsylvania and Kentucky). Inconsistency in terminology used to describe XLPs throughout their broad geographic range has resulted in failure to recognize similarities among sites (Ludwig, 1999) and in confusion of these herbaceous communities with limestone cedar glades (Baskin et al. 1994; Baskin and Baskin 1999), an herbaceous edaphic climax community in north-central southeastern United States characteristically dominated by C_4 summer annual grasses (sensu Baskin and Baskin, 1999; Baskin and Baskin, 2003).

Although many individual studies have been done on the flora, vegetation, physical environment, and history of XLPs in various states and physiographic regions, heretofore no attempt has been made to synthesize information on this vegetation type throughout eastern United States. Thus, the purpose of this paper is to synthesize data on

the geographic/physiographic distribution, geology, soils, climate, vegetation, and endemic and other noteworthy plant taxa of XLPs in eastern United States and to provide a conceptual model of the origin, maintenance, and succesional trajectories of this vegetation type.

Physiography

Physiographic provinces follow Fenneman (1938, 1946 [1949]), lower tiers in the hierarchy of land form classification various sources (cited in Table 5.1), and physiographic regions (sections and subsections) of the Interior Low Plateaus Quarterman and Powell (1978).

XLPs occur in six physiographic provinces in eastern United States: Ozark Plateaus, Central Lowland, Interior Low Plateaus, Appalachian Plateaus, Ridge and Valley, and Coastal Plain (Figure 5.2; Table 5.1). In the Ozark Plateaus, this vegetation type is distributed broadly in the Springfield and Salem plateaus and extends south into the Boston Mountains of northern Arkansas (Keeland, 1978; Kurz, 1981; Ladd and Nelson, 1982; Nelson and Ladd, 1982a; Heikens 1991). Sites in the Central Lowland occur in the Osage Plains of west-central Missouri, Eastern Glaciated Plains and Lincoln Hills of east-central Missouri, and the Muscatatuck Flats and Canyons and Switzerland Hills of southeastern Indiana (Ladd and Nelson, 1982; Homoya, 1987; Maxwell, 1987). In the Interior Low Plateaus, XLPs range from the Mammoth Cave Plateau in southern Indiana to the Northeastern Blue Grass in southeastern Ohio and south to the Moulton Valley in northern Alabama (Braun, 1928; Bacone and Casebere, 1983; Webb et al., 1987). This vegetation type is distributed over its maximum latitudinal range in the Ridge and Valley, where it extends from north-central Pennsylvania to central Alabama (DeSelm, 1993; Allison and Stevens, 2001; Laughlin, 2002). The distribution of XLPs in the Coastal Plain and Appalachian Plateaus is extremely limited, where they apparently are restricted to the Southern Red Hills in southern Alabama and to the Marietta Plateau in eastern Ohio, respectively (Harper, 1920; Rick Gardner, personal communication).

Bedrock Geology

XLPs are developed on Cambrian through Tertiary (Eocene) calcareous substrates (Table 5.2). In the Ozark Plateaus, this vegetation type occurs on Cambrian, Ordovician, and Mississippian limestones and dolomites; in the Central Lowland (principally) on Mississippian and Ordovician limestones; in the Interior Low Plateaus on limestones and dolomites of Mississippian, Silurian and Ordovician systems; and in the Ridge and Valley on limestones and dolomites of Cambrian through Devonian systems. In the East Gulf Coastal Plain in Alabama, Harper (1920) described XLPs restricted to Tertiary (Eocene) Midway Limestone. Apparently, limestone of the Pennsylvanian Conemaugh formation is the only substrate upon which this vegetation type is developed in the (unglaciated) Allegheny Plateaus, in Belmont County, Ohio (Rick Gardner, personal communication).

Soils

Soils of XLPs typically are shallow (≤ 1.0 m) and rocky, and often they are mapped as rock outcrop complexes with one or more associated soil series (Baskin et al., 1994; Lawless et al., 2004 [Chapter 2]). Despite circumneutral pH values ($\sim 6.0 - 8.0$), soil fertility often is quite low, and many researchers have documented low soil phosphorus levels (Keeland, 1978; Heikens, 1991; Ludwig, 1999; Allison and Stevens, 2001; Rhoades, 2004; Trammell et al., 2004). Soil moisture varies considerably throughout the growing season, characteristically decreasing from saturated conditions in early spring to xeric conditions in summer and autumn (Aldrich et al., 1982). Literature review and personal communication revealed this vegetation type is associated with 5 soil orders and 33 series: 22 Alfisols; five Mollisols; three Ultisols; three Inceptisols; and one Vertisols (Table 5.3).

The vast majority of sites occur on moderate to steep slopes, where soil erosion generally exceeds soil genesis (Ware, 2002). Therefore, topographic position and soil texture may profoundly affect the distribution of XLPs. Many of the soil series upon

which sites occur are clay loams and silty clay loams that are relatively fine-textured and extremely susceptible to erosion on moderate to steep slopes. In Kentucky, many of the soil mapping units associated with XLPs are moderately to severely eroded (Lawless et al., 2004 [Chapter 2]). However, other studies include only the soil series, rather than mapping units per se, upon which sites occur and thus do not include detailed descriptions of these series under localized conditions. Heikens (1991) reported only soil associations for sites in southern Illinois, but each of the five series (Alford, Hormer, Muren, Stoy, and Weir) that make up these associations are Alfisols.

Climate

Climates in which XLPs occur in eastern United States are categorized as humid subtropical and humid temperate sensu Köppen's classification system (Ackerman, 1941). In areas of the southeastern United States (Arkansas, Alabama, Georgia, Tennessee, Kentucky, and Virginia) and in southern portions of certain midwestern states (Missouri, Illinois, Indiana, and Ohio), this vegetation type occurs in humid subtropical climates (Cfa) with rain in all seasons and hot summers (avg. temperature of warmest months $\geq 22.2°C$) (Trewartha, 1968 from Ackerman, 1941). XLPs in central to northern portions of midwestern United States (Missouri, Illinois, Indiana, and Ohio) and in the Ridge and Valley of West Virginia and Pennyslvania have a humid temperate climate (Dfa) with rain in all seasons and hot summers (Trewartha, 1968 from Ackerman, 1941). The primary difference between Cfa and Dfa climatic regions is the number of inclusive months with mean monthly temperatures $\geq 10°C$. Subtropical climates (Cfa) have eight to 12 inclusive months with mean monthly temperatures $\geq 10°C$ and temperate climates (Dfa) 4 to 7 months (Trewartha, 1968 from Ackerman, 1941).

Precipitation patterns and amounts differ considerably between XLP sites in the eastern United States and grasslands of the central plains and prairies formation (sensu Barbour and Billings, 2000). Seasonality of precipitation throughout the range of XLPs is considerably less (Figure 5.3) than that in the central plains and prairies formation (Markham, 1970), where amounts of precipitation are relatively high during the growing season and significantly less during the remainder of the year (Borchert, 1950). Mean

annual precipitation generally decreases from south to north in the range of XLPs, varying from about 100 cm in midwestern United States to 150 cm in southeastern United States (Figure 5.3). Conversely, mean annual precipitation in the central plains and prairies formation decreases from east to west and typically is $\leq$ 90 cm (NCDC, 2001).

Vegetation

The perennial C_4 grasses (*Schizachyrium scoparium*, *Bouteloua curtipendula*, *Andropogon gerardii*, *Sorghastrum nutans*, and *Sporobolus clandestinus*) typically are the dominant taxa in XLPs. However, in some sites perennial C_3 herbs (e.g. *Silphium terebinthinaceum* and *Monarda fistulosa* var. *brevis*) and/or taxa in the Cyperaceae, particularly *Carex* spp. and *Fimbristylis* spp., have cover values that equal or exceed those of dominant grasses. When examined at fine spatial scales (≤ 1.0 m^2), the C_4 summer annual grasses *Sporobolus vaginiflorus* and *Sporobolus neglectus* are locally dominant in shallow-soil zones of some sites (Skinner, 1979; Ver Hoef et al., 1993; Baskin and Baskin, 2000; Chapter 3).

In virtually all sites, species richness of dominant and subdominant perennial graminoids in any particular site is low, and that of perennial C_3 forbs is relatively high. However, the forb component of xeric limestone prairie floras varies considerably among sites and especially across ecoregions (Lawless et al., 2004 [Chapters 2]; Chapter 4). Therefore, vegetation of xeric limestone prairies, like that of the tall grass prairie (Glenn and Collins, 1990), is characterized by a stable matrix of dominant graminoids and a forb component that varies considerably both within and among sites (Chapter 3).

XLP Vegetation by Physiographic Province

In the following section, vegetation of XLP communities in the eastern United States will be reviewed and discussed by physiographic province. This review focuses on quantitative vegetation data, but it also includes qualitative descriptions for regions where quantitative data are unavailable. For quantitative studies conducted by DeSelm (1988, 1991, 1993) and DeSelm and Webb (1997), average cover values have been recalculated

to incorporate quadrats that did not include the taxon of interest (i.e. cover = 0%), because DeSelm only included quadrats in which the taxon of interest was present.

Ozark Plateaus

Hall (1955) compared ground-layer species composition and *Juniperus virginiana* seedling distribution and population structure in an old field and "glade" [= xeric limestone prairie] in the Missouri Botanical Garden Arboretum in the northeastern section of the Salem Plateau. In the glade, *Sporobolus neglectus* had the highest frequency (1.00) in 1-m^2 quadrats, followed by *Carex crawei* (0.90), *Schizachyrium scoparium* (0.80), *Houstonia longifolia* (0.75), *Euphorbia corollata* (0.60), and *Rudbeckia missouriensis* (0.55). Hall described glade community structure and vegetation dynamics as follows: "In a good year the clumps of Andropogon [=*Schizachyrium scoparium*] are larger, denser, and more frequent. The [*annual*] *Sporobolus* effectively fills in between the clumps. In a dry or unseasonable year the *Andropogon* may lose ground, the *Sporobolus* to a lesser extent, but the *Bouteloua* [*curtipendula*] may increase considerably." Of 6,694 *J. virginiana* seedlings recorded in the glade, 99.7% were in the smallest size class ($\leq$ 0.46 m in height), thus indicating extremely high seedling mortality in the glade. Hall concluded "In general, juniper population density is proportional to the degree of land abuse, so that glades may support junipers distributed as dense 'brakes,' open stands with evenly but widely spaced individuals, or scattered, clumped colonies."

Schizachyrium scoparium had both the highest average cover and frequency in sites sampled by Kucera and Martin (1957) in the White River region of the Salem Plateau in southwestern Missouri. Locally dominant graminoids included *Andropogon gerardii*, *Bouteloua curtipendula*, *Panicum virgatum*, *Sorghastrum nutans*, *Sporobolus heterolepis*, and *Tridens flavus*. *Hedyotis nigricans*, a C$_3$ herbaceous perennial, was the only forb with a relatively high frequency (57%). Kucera and Martin also reported increased frequencies of C$_3$ summer annuals (*Ambrosia artemisiifolia*, *Croton capitatus*,

and *Croton monanthogynus*) "during the drouth [=drought] years." They also noted increased densities of *Juniperus virginiana* in some sites, which in some instances resulted in "enclosure."

Skinner (1979) sampled vegetation associated with three threatened glade species (*Penstemon cobaea* var. *purpureus*, *Centaurium texense*, and *Stenosiphon linifolius*) using 0.01-m^2 and 0.1-m^2 quadrats centered around individuals of focal species. As noted by Baskin and Baskin (2000), "*Sporobolus neglectus* had the highest percent occurrence in quadrats of both sizes placed around *Penstemon* and *Centaurium*, and *Schizachyrium scoparium* had the highest percent occurrence in those of both sizes placed around *S. linifolius*, which grows in deeper soil (15.7 ± 6.1 cm) than *Penstemon* (10.9 ± 5.6 cm) or *Centaurium* (5.3 ± 2.8 cm)."

Schizachyrium scoparium had the highest average importance value (29.2%) in 20 sites sampled by Hicks (1981) in Hercules Glade Wilderness in the Salem Plateau. Importance values were obtained from frequency and cover data collected in 50 20 cm x 50 cm quadrats per site. Other taxa with average importance values $\geq 5\%$ included *Hedyotis nigricans* (10.5%), *Sporobolus neglectus* (9.5%), *Rudbeckia missouriensis* (7.3%), *Panicum virgatum* (6.4%), and *Croton* spp. (*C. capitatus* and *C. monanthogynous*) (5.1%). Woody species data were collected in one or two 15 m x 25 m macroplots per site. *Juniperus virginia* had the highest average importance value (41.2%) of all tree species, followed by *Cotinus obovatus* (19.2%) and *Diospyros virginiana* (12.5%). The average importance value of *Rhus aromatica* (58.8%) exceeded all other shrubs and all vines.

Ver Hoef et al. (1993) sampled 24 sites on Gasconade Dolomite and seven sites on Eminence Dolomite in the vicinities of the Current and Jack's Fork rivers in the Salem Plateau of southeastern Missouri. Average percent cover values reported in this study actually represent average geometric means (range = 0 to 31.6), since cover class midpoints were converted to geometric midpoints prior to calculations of means. On both substrates, *Schizachyrium scoparium* had the highest mean cover value (31.6 on each) in 7 m x 7 m quadrats. Average cover of *Rudbeckia missouriensis* (Gasconade,

31.6, Eminence, 14.1) and of the perennial C_4 grass *Sporobolus clandestinus* (Gasconade = 9.6, Eminence = 15.4) also was high on both substrates. *Fimbristylis caroliniana* had the second highest average cover value (23.0) on Eminence Dolomite glades, followed by *Hedyotis nigricans* (15.4) and *Liatris cylindracea* (15.4). TWINSPAN analysis of cover class data collected in 7 m x 7 m quadrats identified *Bouteloua curtipendula* and *Sorghastrum nutans* as significant indicator species of Gasconade Dolomite sites. *Aristida purpurascens* was the only significant indicator species of Eminence Dolomite sites. Average cover of *Sporobolus vaginiflorus* exceeded that of all perennial grasses in 70 cm x 70 cm quadrats sampled in the "shallow soil glade" (avg. soil depth = 7.5 cm) microhabitat in the Brandewiede Hollow East A site and in the "rocky glade" (avg. soil depth = 5.9 cm) and "shallow soil glade" (10.7 cm) microhabitats in the Cave Spring E site, both of which are on Gasconade Dolomite. *Juniperus virginiana* had the highest average basal area on both substrates. However, woody species richness and total basal area in Gasconade Dolomite sites was significantly higher than those in Eminence Dolomite sites.

The only vegetation data for the Springfield Plateau region in Missouri were collected by George (1996). Sampling was conducted in two sites in both spring (June) and autumn (October) using 1-m^2 quadrats. *Panicum virgatum* had the highest average cover in both seasons in the Cross Timbers site and in autumn in the Silver Mine Ridge Road site. *Schizachyrium scoparium* had the second highest cover in both seasons at the Cross Timbers site and the highest cover in spring in the Silver Mine Ridge Road site. Cover of C_4 perennial grasses increased from 10 to 70% between spring and autumn sampling. Other species with relatively high cover values in one of these sites included *Rudbeckia missouriensis*, *Echinacea paradoxa* var. *paradoxa*, *Bouteloua curtipendula*, *Liatris aspera*, *Liatris squarrosa*, *Fimbristylis puberula*, *Hedyotis nigricans*, *Andropogon gerardii*, and *Silphium terebinthinaceum*. *Juniperus virginia* was the dominant woody taxon in both sites.

Of the four "glade" community types (grassland-cedar, cedar, cedar-hardwood, and hardwood) described by Keeland (1978) in the Springfield Plateau, Salem Plateau, and Boston Mountains regions of northern Arkansas, only the grassland-cedar type fits

the description of XLPs. The other community types also presumably represent seral stages from a grassland-cedar community type to a hardwood forest (Baskin and Baskin 2000). In the grassland-cedar community type, *Schizachyrium scoparium* had the highest average cover value (22%), followed by *Desmodium rotundifolium*, *Sorghastrum nutans*, and *Desmodium paniculatum*. *Juniperus virginiana* and *Quercus stellata* were the dominant overstory species, and *Rhus glabra* had the highest importance value of all understory species.

In the Buffalo National River in north-central Arkansas, Logan (1992) estimated abundance of species in limestone and sandstone "glades" "using a subjective five point scale," ranging from "5 [=] abundant (widespread with high cover, a dominant or near-dominant species" to "1 [=] rare (only one or two individuals)." *Schizachyrium scoparium* was in the highest abundance class in 18 of 20 limestone "glades." *Andropogon gerardii*, *Sporobolus vaginiflorus*, and *Bouteloua curtipendula* were dominant or codominant in these sites. *Coreopsis tinctoria*, *Acalypha gracilens*, *Eupatorium altissimum*, and *Rudbeckia missouriensis* were the only forbs in abundance classes 4 and/or 5 in 3 or more sites. Abundant woody species included *Juniperus virginiana*, *Quercus marilandica*, and *Quercus stellata*.

Central Lowland

Only one of five limestone "barrens" sampled by Heikens (1991) in southern Illinois is in the Central Lowland (Fults Limestone Glade, Monroe County, Illinois). The only taxon with an average cover value $\geq 1.0\%$ in 15 50-m^2 circular plots was *Schizachyrium scoparium* (12.0 %). *Bouteloua curtipendula*, *Dalea purpurea*, *Lespedeza capitata*, *Rudbeckia missouriensis*, *Solidago nemoralis*, and the site dominant, *S. scoparium*, were present in 100% of these quadrats. Woody taxa present in five or more of the 15 quadrats were *Cornus drummondii* (7 quadrats) and *Ceanothus americanus* (6).

Community structure differed markedly between three "limestone glades" sampled by McClain and Ebinger (2002) in Calhoun County, Illinois. In Schleeper Glade, *Hedyotis nigricans* [percent importance value (%IV) = 35.9] and *Bouteloua curtipendula* (35.6) were codominant, and *Croton capitatus* (9.4) was the only other

taxon with a %IV ≥ 5. *Bouteloua curtipendula* had the highest %IV (= 20.2) in Kamp's Glade, followed by *Ruellia humilis* (11.2), *Croton capitatus* (10.6), *Schizachyrium scoparium* (8.0), and *Hedyotis nigricans* (5.5). Lead Hollow Glade was the only site in which *S. scoparium* was dominant (%IV = 30.5). *Hedyotis nigricans* (%IV = 16.0) and *B. curtipendula* (13.1) were subdominant, and *R. humilis* (7.5), *Eupatorium altissimum* (6.0), and *Croton capitatus* (5.7) were the only other taxa with %IVs ≥ 5.

Vegetation data are not available for sites in the Central Lowland in Indiana. Homoya (1987) qualitatively described the vegetation of a "limestone glade" in Versailles State Park (Ripley County) as follows: "… *Andropogon gerardii*, *Aster sagittifolius* [*Symphyotrichum urophyllum*], *Silphium trifoliatum*, *Physostegia virginiana*, *Lithospermum canescens*, *Kuhnia eupatoriodies*, *Helianthus hirsutus*, and *Euphorbia corollata* are the herbaceous species with the highest estimated importance values." Important woody species included *Quercus muhlenbergii*, *Viburnum rufidulum*, *Celastrus scandens*, *Cercis canadensis*, *Ceanothus americanus*, and *Juniperus virginiana*." In two "glades" in the Indiana Army Ammunition Plant (Clark County), Maxwell (1987) reported "Little bluestem [*Schizachyrium scoparium*] dominates both glades as a xeric, bunch-grass surrounded by patches of rocky pavement." The following herbaceous species were present in both the "little bluestem glades" and the limestone cedar glades surveyed by Baskin and Baskin (1978) in nearby Bullit County, Kentucky: *Ruellia humilis*, *Manfreda virginica*, *Isanthus brachiatus*, *Ophioglossum engelmannii*, *Sporobolus vaginiflorus*, *Heliotropium tenellum*, *Scutellaria parvula*, *Houstonia canadensis*, *Sisyrinchium albidum*, *Asclepias verticillata*, and *Croton monanthogynous*. *Juniperus virginiana* also was common in the "open glades" surveyed by Maxwell (1987).

The distribution map of "limestone glades" in Missouri compiled by Ladd and Nelson (1982), shows a concentration of sites in the vicinity of the Salt, Missouri, and Mississippi rivers in the glaciated portion of the state. However, to our knowledge, vegetation data are not available for this region. Density of glades (measured as areal coverage per 7.5 minute quadrangle) in this region is low (≤ 10 acres/7.5 minute quadrangle) in comparison with the Ozark Plateaus (Ladd and Nelson, 1982). This

inequity in glade development between regions (Ozark Plateaus and Central Lowland) may have prompted vegetation scientists to focus their research on the Ozarks, where glades are both more numerous and typically larger in comparison with those in the Central Lowland (Nelson and Ladd, 1982). However, collection of vegetation data in XLPs in the glaciated portion of the Central Lowland in Missouri would fill a gap in our knowledge of this vegetation type in eastern United States.

<u>Interior Low Plateaus</u>

Four of five "limestone glades" sampled by Heikens (1991) in southern Illinois are in the Interior Low Plateaus. According to Heikens, diagnostic features of these limestone glades include: cover of "prairie species" ≥ 10%, cover of woody species < 50%, soil depth < 10 cm, and exposed rock ≥ 5%. *Schizachyrium scoparium* was the dominant taxon in three sites, with average cover values ranging from 15.7% to 25.5%. *Silphium terebinthinaceum* (avg. cover = 9.1%) and *S. scoparium* (7.9%) were codominant in the fourth site (Whoopie Cat Bluff). *Symphyotrichum oblongifolium* (avg. cover = 6.9%) and *Echinacea pallida* (4.9%) were subdominant taxa in the Cave Creek site. *Quercus muhlenbergii* and *Juniperus virginiana* were the only additional taxa with average cover values ≥ 5% in one or more sites. TWINSPAN analysis of "natural forest openings" sampled by Heikens (1991) identified *Physostegia virginiana*, *Manfreda virginica*, and *Asclepias verticillata* as significant indicator species of the limestone glade community type.

Twenty-three of 32 "limestone glades" sampled by Kurz (1981) are in extreme southern Illinois in the Interior Low Plateaus. The remaining nine sites occur "along the Mississippi River valley" (Jersey, Monroe, St. Clair, and Union counties) and "on the uplands above the Illinois River" (Calhoun and Pike counties) in the Central Lowland. For select taxa, Kurz (1981) provided frequency data averaged across all sites. However, as mentioned above, the majority of sites (71.9%) are in the Interior Low Plateaus (Shawnee Hills), and thus the cursory data provided are discussed in the context of this physiographic province. In 30 of 32 sites, *Schizachyrium scoparium* had the highest frequency in 0.25-m^2 circular quadrats. *Bouteloua curtipendula* and *Sorghastrum nutans*

each had the highest frequency in one of the other sites. According to Kurz (1981), "Dominant species of forbs occurring in several glades were *Aster oblongifolius* [= *Symphyotrichum oblongifolium*], *Echinacea pallida*, *Croton monanthogynous*, *Hedyotis nigricans*, *Manfreda virginica*, *Euphorbia corollata*, *Physostegia virginiana*, and *Brickellia eupatoriodies*."

Braun (1928) sampled "prairies" and "cedar barrens" on Crab Orchard Shale (=Estill Shale), Cedarville Dolomite (= Peebles Dolomite), and Monroe Dolomite (=Lilley and Bisher formations) in the Mineral Springs Region of Adams County, Ohio. She described sites developed on Crab Orchard Shale as "barren cleared slopes, everywhere showing the effects of slumping." According to Braun (1928), *Juniperus virginiana*, *Panicum flexile*, *Allium cernuum*, *Cuphea viscosissima*, *Sabatia angularis*, *Ratibida pinnata*, *Monarda fistulosa*, and *Cassia marilandica* are characteristic and *Hedyotis nigricans* is "particularly characteristic" of sites developed on this susbstrate. She reported frequency data for sites developed on Cedarville [Turkey Creek (two sites) and Cedar Fork (three sites)] and Monroe [Turkey Creek (two sites)] dolomites (Table 4, pages 427-431). *Andropogon gerardii* had the highest frequency (100%) in both sites on Monroe Dolomite (=Lilley and Bisher formations), followed by *Silphium terebinthinaceum* (90% and 82%, respectively). *Schizachyrium scoparium* had the highest frequency in three (Turkey Creek, site 1; Cedar Fork, sites 1 and 3) of five sites on Cedarville Dolomite. In Turkey Creek site 2, *Fragaria virginiana* had the highest frequency (55%), followed by *Blephilia ciliata* (52%), *Helianthus occidentalis* (50%), *Lithospermum canescens* (47%), *Schizachyrium scoparium* (43%), *Andropogon gerardii* (40%), and *Delphinium exaltatum* (40%). In Cedar Fork site 1, *Manfreda virginica* and *Bouteloua curtipendula* had the highest frequency values (90% and 78%, respectively). Remaining taxa with frequency values ≥ 50% in one or more sites include *Agrimonia pubescens*, *Carex crawei*, *Chrysanthemum leucanthemum* (nonnative species), *Comandra umbellata*, *Pycnanthemum tenuifolium*, *Ruellia humilis*, *Euphorbia corollata*, *Helianthus hirsutus*, *Isanthus brachiatus*, *Scutellaria parvula*, *Packera* (*Senecio*) *plattensis*, *Solidago nemoralis*, and *Sorghastrum nutans*. With regard to woody species encroachment, Braun stated: "Among the tree invaders, *Juniperus virginiana* and *Thuja occidentalis* are most prominent; with these are *Ostrya*, *Cercis*, and *Quercus muhlenbergii*."

As is the case for the Central Lowland, vegetation data are lacking for XLPs in the Interior Low Plateaus in Indiana. Bacone et al. (1983) surveyed "glades" and "barrens" of Crawford and Perry counties and provided the following qualitative description: "On the barrens, prairie dock [*Silphium terebinthinaceum*] was very common, and Elliott's bluestem [*Andropogon elliottii*] was an important grass, in addition to big bluestem [*Andropogon gerardii*], little bluestem [*Schizachyrium scoparium*], and Indian grass [*Sorghastrum nutans*]." Aldrich et al. (1982) mentions very little about vegetation in "limestone glades" in Harrison County, except for the following general statement: "They are dominated by prairie grasses and forbs."

Lawless (Chapter 3) used a multiple-scale sampling design to identify XLP community types (0.01- to 100-m^2) in 18 sites in the Interior Low Plateaus in Kentucky. Cluster analysis of cover class data obtained from 100-m^2 quadrats identified 12 community types. *Schizachyrium scoparium* had the highest average cover value in 10 of these community types, and *Andropogon gerardii* and *Silphium terebinthinaceum* each had the highest average cover value in one of the two remaining 100-m^2 community types. Dominant taxa (avg. cover $\geq$ 10%) in three or more community types include *S. scoparium* (10 community types), *Sporobolus vaginiflorus* (5), *Sorghastrum nutans* (5), *Echinacea simulata* (5), *Andropogon gerardii* (4), and *Carex crawei* (3). *Andropogon gerardii* was subdominant (5% $\leq$ avg. cover < 10%) in seven community types, and six taxa, including *Echinacea simulata*, *Carex meadii*, *Hedyotis nigricans*, *Sorghastrum nutans*, *Juniperus virginiana*, and *Cercis canadensis*, each were subdominant in three community types. *Sporobolus vaginiflorus* was locally dominant in portions of many sites, as evidenced by its high percent occurrence values in numerous fine-scale community types (0.01 and 0.1-m^2). In addition, high percent co-occurrence values of *S. vaginiflorus* and *S. scoparium* in certain fine-scale community types suggests *S. vaginiflorus* is capable of coexisting with the dominant perennial grass over a range of environmental conditions. Characteristic trees and shrubs in this vegetation type in Kentucky include *Juniperus virginiana*, *Cercis canadensis*, *Diospyros virginiana*, *Fraxinus americana*, *Rhamnus caroliniana*, *Rhus aromatica*, *Cornus florida*, and *Rosa carolina* (Lawless et al., 2004 [Chapter 2]).

Schizachyrium scoparium also is the dominant taxon in XLPs in the Interior Low Plateaus in Tennessee. DeSelm (1991) studied "small remnants of barrens" in the Central Basin, which "occur on shallow soil … as an alternative to the cedar forest which borders glades." *Schizachyrium scoparium* had the highest average cover value in each of the three sites for which data were reported [Mt. Juliet Road "glade" (avg. cover = 40%); Mt. Juliet Road barren (40%); and Cedars of Lebanon glade border (76%)]. *Sporobolus asper* was codominant (avg. cover = 35%) in Mt. Juliet Road barren. Although *Bouteloua curtipendula* was subdominant in Cedars of Lebanon glade border (avg. cover = 15%), its distribution apparently was restricted within the site, as evidenced by low frequency value (15%). *Hedyotis nigricans* had the highest frequency (100%) and highest average cover (19%) in the Mt. Juliet Road "glade." No other taxon had an average cover value ≥ 5% in any site. *Schizachyrium scoparium*, *Sporobolus vaginiflorus*, and the N_2-fixing cyanobacterium *Nostoc commune* had the highest frequency values in another site in Cedars of Lebanon State Forest sampled by Baskin and Baskin (1977). *Schizachyrium scoparium* also was the dominant taxon in three "barrens" in the Western Highland Rim (Perry and Decatur counties) sampled by DeSelm (1988). Other taxa with percent importance values ≥ 5% in one or more sites include *Galactia volubilis*, *Opuntia humifusa*, *Euphorbia corollata*, *Sporobolus clandestinus*, *Solidago nemoralis*, *Croton monanthogynous*, *Fimbristylis puberula*, *Andropogon gerardii*, and *Sorghastrum nutans*.

DeSelm and Webb (1997) sampled the "lower flat" (0-5% slope), "footslope" (11-20%), and "steep sideslope" (32-70%) in two grasslands in the Southern Highland Rim in northwestern Alabama. In both sites (Littleville and Cedar Creek), footslopes and steep sideslopes had the lowest mean soil depths (6.5 cm to 13.5 cm) and highest average combined cover values of rock and gravel (24.4% to 86.0%), and thus portions of sites occupying these slope positions can be categorized as XLPs. In the footslope of Littleville Barren, average total plant cover was only 46.3%, and *Schizachyrium scoparium* (avg. cover = 5.0%) was the only taxon with an average cover value ≥ 2.0%. *Sporobolus clandestinus* (avg. cover = 30.2%) and *Schizachyrium scoparium* (avg. cover = 16.2%) were the dominant and subdominant taxa, respectively, in the steep sideslope. *Schizachyrium scoparium* was the dominant taxon in both the footslope (avg. cover = 18.7%) and steep sideslope (avg. cover = 21.3%) of Cedar Creek Barren. *Bouteloua*

curtipendula, Fimbristylis puberula, Sorghastrum nutans, and *Celtis tenuifolia* were the only other taxa with average cover values > 1.0% in either landform in this site.

Ridge and Valley

Boutleoua curtipendula, Danthonia spicata, and *Schizachyrium scoparium* "dominated in terms of abundance" in XLPs in Pennsylvania studied by Laughlin and Uhl (2003). However, quadrat sampling was not performed, and therefore, abundance values reported in this study are semiquantitative. According to Laughlin (2002), common forbs in these sites are *Anemone virginiana, Solidago nemoralis, Monarda fistulosa, Lithospermum canescens, Asclepias tuberosa, Asclepias verticillata, Asclepias viridiflora, Penstemon hirsutus*, and *Senecio obovatus*, and common trees are *Juniperus virginiana, Juglans nigra, Celtis occidentalis, Pinus strobus*, and *P. virginiana*. Percentage of nonnative species in the flora of XLPs in Pennsylvania is particularly high (25% and 28% in two sites) (Laughlin, 2004). Consequently, Laughlin and Uhl (2003) concluded "Exotic invasion is likely a significant reason for the loss of native species from limestone prairies."

Schizachyrium scoparium was the dominant taxon in 14 of 16 plots (11 sites total) sampled by Ludwig (1999) in southwestern Virginia. *Andropogon gerardii* was the dominant taxon in two plots. Other herbaceous taxa with cover values ≥ 5% in one or more sites include *Symphyotrichum sericeum* (nomenclature updated), *Carex eburnea, C. hirsutella, Liatris aspera, Minuartia patula, Oxypolis rigidior, Scleria verticillata, Sorghastrum nutans, Sporobolus clandestinus*, and *S. vaginiflorus*. In the "shrub layer" (height 1-6 m), *Cercis canadensis, Cornus florida, Frangula caroliniana, Juniperus virginiana*, and *Quercus muhlenbergii* were the only taxa with cover values ≥ 5%. In 12 of 16 plots, no taxa were present in the "tree layer" (6-10 m), and in the remaining four plots *J. virginiana* and/or *Q. muhlenbergii* were present.

Bartgis (1993) sampled "glades," "barrens," and "cedar woodlands" on Knobly and Cave mountains in West Virginia. Glades had shallower soils (mean depth 3.9 cm) and higher cover of cobble and bedrock (mean cover 74%) than did limestone barrens (mean soil depth 8.9 cm, mean cover cobble/bedrock 14%). However, perennial C_4

grasses and/or perennial C_3 herbs were the dominant taxa in both of these shallow-soil community types, and thus they can be classified as XLPs. In Knobly Mountain cedar glades, *Bouteloua curtipendula* (avg. cover 8%) and *Solidago arguta* var. *harrisii* (avg. cover 4%) were the dominant herbaceous taxa. *Phlox subulata* and *Paronychia virginica* were the only remaining herbaceous taxa with average cover values > 1%. According to Bartgis (1993), "*Bouteloua* is much less important at the Cave Mountain cedar glades, where the dominants are typically *Solidago arguta* var. *harrisii*, *Monarda fistulosa* var. *brevis*, and *Paronychia virginica; Carex eburnea* is locally dominant." Important woody taxa in these sites include *Juniperus virginiana*, *Cercis canadensis*, *Quercus muhlenbergii*, and *Thuja occidentalis* (Cave Mountain sites only). Total herbaceous cover was considerably higher in the Knobly Mountain limestone barrens, where *B. curtipendula* (avg. cover 35%), *Hystrix patula* (12%), and *Schizachyrium scoparium* (5%) were the dominant taxa.

Eighty-six sites, including "glades" and "barrens," in the Ridge and Valley of Alabama, Georgia, Tennessee, and Virginia were studied by DeSelm (1993). He distinguished barrens from glades based upon percentage of perennial grass cover, with the former having perennial grass cover > 50% and the latter < 50%. Data were reported for three barrens, all of which are consistent with our definition of XLPs. In Crowder Cemetery Barren (Roane County, Tennessee), *Andropogon gerardii* (avg. cover 17.5%) and *Schizachyrium scoparium* (16.1%) were codominant, and *Liatris cylindracea* and *Hypericum dolabriforme* were the only other taxa with average cover values > 1%. *Schizachyrium scoparium* (avg. cover 20.7%) and *Bouteloua curtipendula* (16.6%) were codominant in the Elementary School Barren (Catoosa County, Georgia). Subdominant taxa (5% < avg. cover ≤10%) include *Panicum virgatum*, *Andropogon gerardii*, and *Hypericum dolabriforme*. *Schizachyrium scoparium* (avg. cover 22.2%) and *Aristida purpurascens* (avg. cover 21.8%) were codominant in the third site (Centre, Alabama), and they were the only taxa with average cover values ≥ 1%.

Schizachyrium scoparium also is the dominant graminoid in the Ketona Dolomite Glades in the Ridge and Valley near its southwestern terminus, in Alabama. However, as noted by Allison and Stevens (2001), "… it usually does not achieve great density and is

an aspect dominant only in late fall and winter, when the strong forb component is muted." *Onosmodium decipiens* and *Erigeron strigosus* var. *dolomiticola*, both Ketona Dolomite Glade endemics, were abundant at the majority of sites. Allison and Stevens (2001) also report "*Amsonia ciliata* var. *tenuifolia* is often abundant and dense enough to be an aspect dominant in spring, and *Rudbeckia triloba* var. *pinnatiloba* is occasionally an aspect dominant in summer." Ketona Dolomite Glades also are noteworthy for supporting a number of woody taxa that typically do not occur in the remainder of the range of xeric limestone prairies, including *Pinus palustris*, *Sabal minor*, and *Croton alabamensis* var. *alabamensis*.

According to Allison and Stevens (2001), "Ketona Glades fail several to many criteria" for each of the three community types (limestone cedar glades, XLPs, and deep-soil barrens) described by Baskin et al. (1994) in the Big Barrens Region of Kentucky and Tennessee. The authors conclude "Ketona Glades come closest to the 'xeric limestone prairie' class" but point out the following characteristics of Ketona Glades that differ from those of xeric limestone prairies described by Baskin et al. (1994): 1) their occurrence on dolomite rather than limestone, 2) multiple endemic taxa, and 3) presence of two species of *Leavenworthia*. However, as discussed above, XLPs occur on dolomite in various regions throughout the geographic range of this community type in the eastern United States. Furthermore, XLP endemics (Table 5.4) occur in regions other than the Cahaba River Valley in Alabama, particularly in the Ozark Plateaus in Missouri and Arkansas. In addition, *Leavenworthia* spp., some of which are limestone cedar glade endemics (e.g. *Leavenworthia alabamica*, *Leavenworthia exigua* var. *exigua*, and *Leavenworthia exigua* var. *laciniata*), occur in other XLPs in the eastern United States (Baskin and Baskin, 1977; Maxwell, 1987; DeSelm, 1988, 1991, 1993; DeSelm and Chester, 1993; Ver Hoef et al., 1993; Webb et al., 1997; Gardner and Minnie, 2004; Lawless et al., 2004 [Chapter 2]).

<u>Appalachian Plateaus</u>

Vegetation data are not available for XLPs in the unglaciated Allegheny Plateau, which apparently are restricted to Beaumont County, Ohio (Rick Gardner, personal communication).

<u>Coastal Plain</u>

Harper (1920) is the only source of information on vegetation of "limestone prairies" in the Coastal Plain, in Alabama. He provided a cursory species list and estimated "the commonest species in the areas of natural prairie, in order of abundance," the first five of which are as follows: *Schizachyrium scoparium*, *Polygala grandiflora*, *Fimbristylis puberula*, *Hedyotis nigricans*, and *Prunella vulgaris*. He also states "*Juniperus virginiana* is practically the only tree" throughout the geographically restricted area in which "natural prairie vegetation" is developed on limestone, a very uncommon substrate in the Coastal Plain of Alabama.

Affinities of XLPs to other vegetation types in eastern United States

A number of other vegetation types in eastern North America are remarkably similar to XLPs due to their association with calcareous rock outcrops and dominance by C_4 perennial grasses. Dry lime prairies (sensu Anderson, 1954) and hill prairies (sensu Ugarte, 1987) in upper midwestern United States and "cedar glades" (sensu Curtis, 1959) in Wisconsin are developed on shallow, rocky soils derived from limestone and dolomite (calcareous gravels in some glaciated regions). Furthermore, these vegetation types typically occur on moderate to steep slopes with south to west aspects and are susceptible to invasion by woody species, particularly *Juniperus virginiana*.

Dry lime prairies are concentrated in the "rugged topography of the Driftless Area of southwestern Wisconsin" and extend into northwestern Illinois, northeastern Iowa and southeastern Minnesota (Anderson, 1954). In 41 stands sampled by Anderson, *Schizachyrium scoparium* had the highest average frequency (71.3%), followed by *Bouteloua curtipendula* (62.4) and *Andropogon gerardii* (50.2). Additional taxa with average frequency values ≥ 25% were *Symphyotrichum sericeum* (nomenclature

updated), *Euphorbia corollata, Amorpha canescens, Solidago nemoralis, Panicum perlongum*, and *Dalea purpurea. Rhus glabra* and *Juniperus virginiana* were dominant woody invaders in dry lime prairies, along with *Juniperus communis*.

Schizachyrium scoparium, Andropogon gerardii, Sporobolus heterolepis, and *Bouteloua curtipendula* had the highest total cover values in 32 hill prairies in northeast Iowa sampled by Ugarte (1987). *Solidago nemoralis, Aster azureus, Amorpha canescens*, and *Coreopsis palmata* were characteristic forbs. Interestingly, Ugarte described a *Bouteloua curtipendula-Sporobolus* aff. *vaginiflorus* community type which developed on gravelly, heavily grazed sites. Furthermore, total cover of *Juniperus virginiana* exceeded that of all other woody species, with the exception of *Rhus glabra*. Ugarte attributed "encroachment of hill prairies by woody species" to "suppression of fire and overgrazing." Portions of some hill prairies described by Evers (1955) (e.g. Sunset Trail, Bielema, and Clendenny) apparently are shallow and rocky and are dominated by C$_4$ perennial grasses, and thus they resemble XLPs.

According to Curtis (1959), "… a steep hillside of thin loess over limestone… or a gravelly glacial moraine" are typical habitats for "cedar glades," which he and Bray (1955) considered a type of savanna. *Schizachyrium scoparium* had the highest average frequency (38.0%) in this vegetation type, followed by *Euphorbia corollata* (27.1), *Andropogon gerardii* (26.6), *Arenaria stricta* (23.0), *Solidago nemoralis* (20.8), *Amorpha canescens* (20.8), and *Anemone cylindrica* (20.1). *Juniperus virginiana* is the only dominant woody taxon in this vegetation type (data of J.R. Bray from Curtis, 1959).

"Calcareous prairies" in the Kisatchie National Forest in Louisiana described by MacRoberts and MacRoberts (1995) are difficult to characterize due to the complex geology in this region and lack of information on vegetation and soil depth. "Calcareous concretions" were reported in the soil surface in both sites. However, rock outcrops in proximity to these sites are primarily sandstone and support glade communities. The calcareous prairies " … are on or near the summits of hills …, " where soil depth is considerably greater than in adjacent sandstone glade communities (Michael Macroberts, personal communication). Composites, grasses, and legumes are dominant taxa in these

prairies, and both sites currently are being invaded by woody species (*Crataegus* spp., *Rhus copallina*, *Viburnum dentatum*, *Cornus drummondii*, *Diospyros virginiana*, and *Prunus* spp.) from calcareous forests in the region. Both the calcareous prairies and sandstone glades are embedded within locally dominant long-leaf pine savanna vegetation, and the authors attribute woody encroachment in the calcareous prairies to decreased fire frequency in the latter. Due to uncertainty about whether these areas fit the definition of XLP, I have not included them on the map (Figure 5.2) showing the distribution of XLPs in eastern United States.

In eastern North America, alvars are restricted to the Great Lakes Region, where they are developed on Ordovician limestones and dolomites (Catling and Brownell, 1999). Catling and Brownell describe two principal alvar types: shoreline and plateau. They acknowledge disparate origins for these two community types in the following statement: "Lack of tree cover on shoreline alvars may be largely a result of flooding and erosion, whereas fire may be the most important factor in limiting woody cover on plateau alvars." Alvar grasslands most closely resemble XLPs and occur in both of these habitats. In contrast to alvar pavement community types, alvar grasslands typically occur in soils > 2 cm. Xeric grasslands are dominated by C_4 (e.g. *Schizachyrium scoparium*, *Sporobolus heterolepis*, and *Bouteloua curtipendula*) and/or C_3 (e.g. *Carex scirpoidea*, *Danthonia spicata*, and *Poa compressa*) perennial graminoids and are extremely variable with regard to forb composition (Catling and Brownell, 1999).

Endemic taxa and other noteworthy floristic elements

Thirteen taxa are endemic/near endemic to XLPs of eastern United States (Table 5.3). The Cahaba River Valley in the Ridge and Valley in Alabama and the Ozark Plateaus in Missouri and Arkansas are centers of endemism in this vegetation type. Allison and Stevens (2001) described eight new taxa endemic to XLPs on Ketona Dolomite rock outcrops in the Cahaba River Valley in Bibb County, Alabama, including *Castilleja kraliana*, *Coreopsis grandiflora* var. *inclinata*, *Dalea cahaba*, *Erigeron strigosus* var. *dolomiticola*, *Liatris oligocephala*, *Onosmodium decipiens*, *Silphium glutinosum*, and *Spigelia gentianoides*. *Delphinium treleasei*, *Echinacea paradoxa* var.

paradoxa, and *Scutellaria bushii* are restricted to XLPs in the Ozark Plateaus in Missouri and Arkansas. *Valerianella ozarkana* occurs in the Ozark Plateaus in Missouri, Arkansas, and Oklahoma and in the Ouachita Mountains in eastern Oklahoma (USDA, NRCS, 2004; Hoagland et al., 2004), and thus should be considered an Ozark-Ouachita endemic. According to Bartgis (1993), "*Monarda fistulosa* var. *brevis* appears to be endemic to cedar glades, limestone barrens, glade woodlands, and dry limestone cliffs of West Virginia and Virginia." This is the only XLP endemic outside the Ozarks Plateaus not restricted to XLPs on Ketona Dolomite.

The flora of XLPs also contains taxa considered to be endemic to other vegetation types, most notably shale barrens and limestone cedar glades. Bartgis (1993) noted the occurrence of eight mid-Appalachian shale barren endemics (sensu Keener, 1983) in XLPs in West Virginia, including *Calystegia spithamaea* ssp. *purshianus*, *Oenothera argillicola*, *Solidago arguta* var. *harrisii*, *Taenidia montana*, *Trifolium virginicum*, *Antennaria virginica*, *Helianthus laevigata* (not an endemic), and *Paronychia montana*. Twelve of the 19 taxa considered to be limestone cedar glade endemics by Baskin and Baskin (1999) also occur in XLPs of eastern United States (Table 5.5), including *Dalea gattingeri*, *Echinacea tennesseensis*, *Leavenworthia alabamica*, *Leavenworthia exigua* var. *exigua*, *Leavenworthia exigua* var. *laciniata*, *Leavenworthia exigua* var. *lutea*, *Leavenworthia stylosa*, *Lobelia appendiculata* var. *gattingeri*, *Onosmodium molle*, *Pediomelum subacaule*, *Talinum calcaricum*, and *Trifolium calcaricum*. Interestingly, Allison and Stevens (2001) suggested *Pediomelum subacaule*, a C_3 perennial cryptophyte lacking long-distance dispersal mechanisms, was introduced in XLPs on Ketona Dolmite. The limestone cedar glade near-endemics *Astragalus tennesseensis* and *Dalea foliosa* (sensu Baskin and Baskin, 1999) also are known from XLPs in the Cumberland River Basin in Tennessee (Rutherford and Davidson counties) (DeSelm, 1991).

As noted by DeSelm (1991, 1993, 1994), limestone cedar glade endemic/near endemic taxa often occur in XLPs that are adjacent or in close proximity to limestone cedar glades. Exceptions include *Pediomelum subacaule* and *Leavenworthia exigua* var. *lutea* in sites on Ketona Dolomite in Bibb County, Alabama, and *Talinum calcaricum* in an XLP in Logan County, Kentucky. In virtually all instances, occurrence of limestone

cedar glade endemic/near endemic taxa are restricted to microsites which fit the description of limestone cedar glades yet exist within the perennial grass matrix of XLPs.

Other floristic elements of XLPs also are restricted to vegetation types developed on calcareous rock outcrops. Catling et al. (1993) described a new sedge, *Carex juniperorum,* based on collections from alvars in the Napanee limestone plain in Ontario and from XLPs and similar habitats in southeastern Ohio (Adams County) and northeastern Kentucky (Lewis and Bath counties). Recently, Wieboldt (Belden et al., 2004) reported a new station for this species in Montgomery County, Virginia, where it occurs "in dry or seasonally wet spots in a small barren or in the thin chinquapin oak-redbud-red cedar woodland." *Echinacea simulata* apparently is restricted (or nearly so) to XLPs and similar habitats in Missouri, Illinois, Indiana, Kentucky and Tennessee. However, inconsistent taxonomic treatment of this taxon (Baskin et al., 1993; Kim et al., 2004), its remarkable similarity to *Echinacea pallida* (Nutt.) Nutt. (Binns et al., 2002), and sympatry of *Echinacea pallida* and *Echinacea simulata* throughout much of the latter's apparent geographic range (Missouri, Illinois, Indiana, and Tennessee) make it difficult to discern the true distribution of this species and assess its fidelity to XLPs. The winter annual *Lesquerella filiformis* is narrowly distributed in southwestern Missouri (Jasper, Dade, Lawrence, Greene, and Christian counties) (USFWS, 1988) and northwestern Arkansas (Izard and Washington counties) (ANHC, 2004), where it "… occurs in shallow soils on limestone glades, outcrops in pastures and rarely in rocky open woods (USFWS, 1988)." *Viola egglestonii* ranges from southern Indiana (Harrison County) south to northern Alabama (Franklin County) and northern Georgia (Catoosa and Walker counties) (Baskin et al., 1987) and was once considered to be a limestone cedar glade endemic (sensu Baskin and Baskin, 1978a, b, 1986, 1989; Baskin et al., 1987). However, this species also occurs in XLPs and other glade-like habitats (DeSelm, 1993; Baskin and Baskin, 2003; Lawless et al., 2004 [Chapter 2]), and thus it is no longer considered to be a limestone cedar glade endemic or even a near endemic (sensu Baskin and Baskin, 2003).

Floras of XLPs in the Ozark Plateaus in Missouri and Arkansas have western and southwestern affinities. Many taxa reach the eastern edge of their geographic range in

XLPs in this region (Nelson and Ladd, 1982b); examples are *Acacia angutissima* var. *hirta*, *Castilleja purpurea*, *Centaurium texense*, *Juniperus ashei*, *Marshallia caespitosa* var. *signata*, *Nemastylis nuttallii*, *Palafoxia callosa* var. *callosa*, *Parthenium hispidum*, *Penstemon arkansana*, and *Yucca glauca* var. *glauca*. *Evolvulus nuttallianus*, *Onosmodium molle* var. *subsetosum*, and *Solidago gattingeri* occur in XLPs in the Ozarks and are absent further east with the exception of limestone cedar glades in Middle Tennessee (Baskin and Baskin, 1986; Adams et al., 2003).

Origin and maintenance

There is no general consensus regarding the origin of XLPs. Current distribution of this vegetation type in the eastern United States likely reflects interaction of multiple factors over variable time intervals ranging from decades to millennia. DeSelm and Murdock (1993) astutely acknowledged, "The scattered occurrence of grassland and related communities [in southeastern United States] does not argue strongly for climate nor great soil group control over community distribution." XLPs in the Ozark and midwestern regions of United States also are scattered geographically and occur on numerous soil series and orders. Shallow soils (including 33 series in five orders), calcareous bedrocks resistant to weathering, moderate to steep slopes (typically with south to west aspects), anthropogenically increased fire frequencies (native Americans and/or European settlers), land clearing for cultivation or pasturage, grazing (by both native and nonnative mammals), and erosion are factors frequently mentioned, singly or in concert, as potential sources of origin and/or maintenance for this vegetation type (Figure 5.4).

Braun (1928), Steyermark (1940), and Logan (1992) suggest XLPs are a primary vegetation type. Logan (1992) states, "Glades are primary natural communities" which are "… maintained indefinitely at an early stage of succession by the substrate or by natural forces such as erosion or microclimate." Steyermark (1940) regarded "glades" as the first two seral stages [1) *Bouteloua curtipendula-Rudbeckia missouriensis* and 2) *Rhus aromatica-Diospyros virginiana-Juniperus virginiana*] of a six-stage primary succession culminating in an *Acer saccharum-Quercus alba* climatic climax (see review

in Baskin and Baskin, 2000 and Hicks, 1981). Braun (1928) offered a compelling argument against the notion of a recent, anthropogenic origin for "extensive prairie vegetation" developed on Cedarville [=Peebles] Dolomite in the Mineral Springs region of Ohio.

> Clearing, the entrance and occupancy by a prairie community and its gradual elimination by forest invasion - which on the edges is extremely slow - would have had to take place within a period of 125 years. It seems far more plausible that the forest is a stage in primary succession, representing the slow migration of the sub-climax prairie of ridges.

Braun (1928) goes on to state, "There is no vegetational evidence that this community ["prairie"] is not primary; and the oldest inhabitants say that there never have been anything but tall grasses and cedars in these places." Conversely, Braun (1928) refers to the "cedar barrens" developed on Crab Orchard [=Estill] Shale in this same region as "barren cleared slopes, everywhere showing the effects of slumping." Thus, she suggests an anthropogenic origin for these community types. Furthermore, Braun makes the following statement regarding the "*Andropogon gerardii-Silphium* [*terebinthinaceum*] prairies" developed on Monroe Dolomite [=Lilley and Bisher formations] in the region: "Their position in relation to cultivated fields and to cleared slopes suggests they may be secondary." Therefore, she (Braun 1928) considered XLPs developed on Peebles Dolomite to be primary and those developed on other substrates in Adams County to be secondary.

Other researchers also implicate agriculture as a potential source of origin and/or expansion for this vegetation type. Baskin et al. (1994) and Baskin and Baskin (1997) attributed formation of this vegetation type in the Kentucky Karst Plain [= Pennyroyal Plain + Elizabethtown (Plain) sensu Quarterman and Powell, 1978] to the following sequence of events: clearing of marginal agricultural lands by European settlers → cultivation and/or grazing → significant erosion of the

129

topsoil → abandonment → colonization of these degraded areas by XLP flora → succession to hardwood forest in the absence of disturbance or maintenance of XLP with periodic management (i.e. disclimax) (Lawless et al., 2004 [Chapter 2]). DeSelm (1993) suggested land use patterns of both native American and colonial European cultures affected the maintenance and possible expansion, respectively, of "barrens" (including XLPs) in the Ridge and Valley of Alabama, Georgia, Tennessee, and Virginia.

> 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.

For the Central Basin of Tennessee, DeSelm (1991) stated the "… crescentic ring of barren-like vegetation between the glade and cedar thicket or forest" was the result of "clearing of the cedar or burning and grazing of this vegetation" and subsequent extension of perennial grasses.   According to Bartgis (1993), "Most glades and barrens in West Virginia have been pastured, typically for sheep." However, he attributes the maintenance of XLPs to "periodic severe droughts," such as the one recorded in 1987 "which promote[s] prominence of *Juniperus virginiana* over deciduous species."

The vast majority of researchers attribute the origin and maintenance of XLPs to interaction of two or more of the following endogenous or exogenous factors: shallow soils, weathering-resistant bedrock, moderate to steep slopes (typically with south to west aspects), erosion, fire, and grazing. According to Heikens (1999), "The Ozark Plateaus supports a mosaic of prairies, forests, glades, barrens, and savannas depending on such factors as topography, bedrock, soils, fire, and native herbivores." Ver Hoef et al. (1993) stated, "Studies have indicated that bedrock type, topography, weathering, soil conditions, drought, and fire are some of the major factors influencing both the distribution of glade types and patterns within and around glades." Laughlin (2004) focused on maintenance rather than origin(s) of XLPs, yet he suggested anthropogenic

fire and/or overgrazing (of nonnative ungulates) in combination with extremely xeric edaphic conditions (particularly in sites on Opequon soil series) were likely responsible for establishment of XLPs in the Ridge and Valley of Pennsylvania. Despite Logan's (1992) previously mentioned assertion that XLPs are primary communities, he also stated, "Xeric prairie and glade floras have evolved with drought and fire and need one or both to survive and compete with or displace encroaching species." According to Hicks (1981), "Prior to settlement by people of European origin, fires, either naturally occurring or set by Indians, and grazing by large herbivores such as elk and bison, now absent in the area may have played an important role in maintaining the glade ecosystem." Kurz (1981) offers two possible explanations for the origin of sites in the glaciated portion of Illinois, both of which are plausible and not mutually exclusive.

> The slope of the glades usually faces south and it is suggested that the wind-blown silt [loess] was not deposited in these areas because of their position. Another suggestion is that the soils eroded over a period of time because of some disturbance leaving little loess covering the bedrock.

According to Aldrich et al. (1982), the persistence of limestone glades in Harrison County, Indiana, "… involves a complex interplay of factors including thin soils, a southerly aspect, seven to twenty degree slopes, xeric conditions and fire." Homoya (1994) attributes the xeric, open nature of barrens in Indiana to "… excessive drainage …; southern or western aspects …; excessive steepness of slope …; presence of a hardpan …; presence of bedrock at or near the surface …; and a fire regime that increases radiant heating and consumes moisture-retaining litter."

Mann et al. (1999) and Lowell and Astroth (1989) developed geographic information system (GIS) models to predict locations of XLPs in the Cedar Creek Preserve in Fort Knox Military Reservation (Kentucky) and in Hercules Glade Wilderness Area in the Mark Twain National Forest (Missouri), respectively. Soil series were not a significant indicator

of this habitat in Cedar Creek Preserve. However, when soil subgroup and depth ("depth of lithologic contact") were included, efficacy of the model increased considerably. Incorporation of additional soils (presence of flagstone on surface) and geologic (formation/member) data further increased predictive capability of the Mann et al. (1999) model. Presence of a mollic epipedon was determined to be the most diagnostic characteristic of "threatened calcareous habitat" in Cedar Creek Preserve. In contrast to the Mann et al. (1999) model, Lowell and Astroth (1989) found soil series (Gasconade) to be the best predictor of glade distribution in Hercules Glade Wilderness Area. Elevation and aspect of slope also were strong "controlling factors" of distribution and quality (high quality = limited redcedar invasion; low quality = extensive redcedar invasion) of XLPs in this region.

Several studies of aerial photographs obtained over relatively short chronological sequences (< 50 years) suggest XLPs are quite susceptible to woody plant invasion. Laughlin (2004) reported areal reductions of 78% and 92% in Great Plains and Westfall Ridge "prairies" in the Ridge and Valley of Pennsylvania from 1949 to 1994. In limestone glades in the Ozarks of south-central Missouri, Kimmel and Probasco (1980) reported a 34% decrease in glade area with 0% to 15% woody plant cover and a 31% increase in glade area with 50% to 100% woody plant cover from 1938 to 1975. The authors attributed this phenomenon to decreased burning and grazing over the previous 30 years. Ver Hoef et al. (1993) documented average reductions in "glade" area of 14.4% and 32.4% from 1955 to 1984 on sites developed on Eminence Dolomite and Gasconade Dolomite, respectively.   Rates of forest encroachment in XLPs in Hercules Glade Wilderness Area from 1938 to 1986 generally decreased when sites were burned (Lowell and Astroth, 1989). However, fire significantly increased the area of some low quality sites (i.e. sites with significant encroachment of woody species) but failed to retard encroachment and corresponding decline in other low quality sites.

Referring to limestone glades in Harrison County, Indiana, Aldrich et al. (1982) stated that "Aerial photographs document the continuing shrinkage of these glades, as they were nearly double their present size in the 1940's." Similarly, Bacone et al. (1983) reported "Aerial photographs [of glades and barrens in Crawford and Perry counties, Indiana] show a remarkable decrease in size over the last forty years due to encroachment by woody species." In two "prairies" developed on Cedarville Dolomite in Adams County, Ohio, Annala et al. (1983) documented a 31% reduction in prairie areas between 1938 and 1971. The authors concluded, "The edaphic conditions of the prairie remnants [Lynx Prairie and Bohl Property] in Adams County [Ohio; Edge of Appalachia Preserve] undoubtedly have helped to retain them. Nevertheless, the successional process clearly is converting these areas to forest." In other sites in the Edge of Appalachia Preserve (The Wilderness, Buzzardroost Rock, Hanging Prairie, and Cave Hollow), Annala and Kaputska (1983) reported "… some degree of forest encroachment in all sites" from 1938 to 1971. Particularly interesting were the authors' observations that, "Many of the present-day prairie remnants have been established (or reestablished) on cultivated or pasture land," and "other areas were prairie in 1938 and indicated no evidence of agricultural disturbance."

Despite the susceptibility of many XLPs to encroachment by woody species, some sites apparently are quite stable. Although large perimeter to area ratios and patches of woody vegetation prevented accurate measurement of the area of XLPs in Kentucky (Lawless et al., 2004 [Chapter 2]), comparison of aerial photographs taken of Muldraugh's Barren and Scudder Glade (Hardin County, Kentucky) in 1958 and 1988 does not show dramatic changes in these two sites. However, proximity of old homesteads (circa 1850-1900) to the latter and to Spalding Glade (Larue County, Kentucky) (Lane Linnenkohl, Kentucky State Nature Preserves Commission, personal communication) does not rule out anthropogenic disturbance (e.g. timber harvesting and grazing) as a possible cause of origin for these sites and others in Kentucky. It also is not known whether disturbance is the reason why succession is not evident in these sites between 1958 and 1988.

Because endogenous factors such as bedrock type, soil depth, and degree and aspect of slope are relatively static over geologic time periods, some researchers have focused on the frequency of exogenous disturbance events, particularly fire, as a potential source of variability in the area of XLPs in recent times. *Juniperus virginiana* individuals often are the source of dendrochronological data in XLPs due to their abundance and relatively long life spans. In a study of seven live and 14 dead redcedars (*J. virginiana*) in Burtram Hollow "glades" (Ava Ranger District; Missouri Ozarks), Guyette and McGinnes (1982) reported that "Prior to 1870, fires, as marked by tree scars, were present somewhere on the study area (2.59 km^2) every 3.2 years. After 1870, the frequency of scarring drops to one every 22 years." In conclusion, the authors made the following statement:

> Much of this change in fire frequency is due to fire suppression, possibly by early settlers, and after 1940 by the U.S. Forest Service. Other possible reasons for the change in fire frequency are the removal of a major ignition source (Osage Indians), the building of roads (firebreaks), severe overgrazing and erosion (reduced fuel loads).

Variable fire-return intervals were also detected in the dendrochronological records obtained by Batek et al. (1999) in the Current River watershed in the Missouri Ozarks. Batek et al. made the following statement regarding the influence of Native Americans on historical fire frequencies and corresponding vegetation patterns.

> Fires exerted strong constraints on vegetation composition and patterns. Historical patterns of Native American occupancy in the region are consistent with the reconstructed vegetation and fire histories suggest that anthropogenic fire regimes played an overriding role in the development of Ozark vegetation in the 1800's.

Although Beilmann and Brenner (1951) did not study dendrochronological records, their examination of numerous historical documents (particularly accounts of early travelers)

lead them to conclude, "Fire, perhaps more than any other factor, maintained the prairie and park-like aspect of the Ozarks." In a "barren-forest mosaic" in southern Indiana, Guyette et al. (2003) obtained dendrochronological results that contrast strongly with those of both Guyette and McGinnes (1982) and Batek et al. (1999). Guyette et al. (2003) summarized their findings as follows: "Fires were more frequent and occurred more regularly in the latter half of the fire chronology (1821 to 1999) where the mean fire interval was 5.3 years [as opposed to 23.0 years from 1650 to 1820] and fire intervals ranged from 1 to 40 years." Results of Guyette et al. (2003) suggest historic fire frequencies vary significantly between areas, and furthermore, that fuel loads, vegetation patterns, weather and climate, topography, and "pyro-cultural influence" profoundly affect fire-return intervals.

Boettcher and Kalisz (1991) used the mass and shape of opal phytoliths in dolomite-derived soils in an attempt to delimit the historical extent of XLPs in the E. Lucy Braun Preserve in Adams County, Ohio. Dumbbell-shaped phytoliths are characteristic of grasses, and therefore large concentrations of these structures are indicative of past and/or present grassland vegetation. Soil samples collected from XLPs and forests both had high concentrations of opal. However, dumbbell-shaped phytoliths were "infrequently encountered" in samples collected from both vegetation types, thus suggesting, " … phytolith-rich forbs as well as grasses may have been important constituents of these forest openings in the past." These data lead the authors to conclude, " … prairie and forest vegetation … naturally alternated over time on these areas," and therefore, " … distinction between 'primary' prairies (natural prairies) and 'secondary' prairies (prairies formed by human disturbance of forests) was judged to be of limited applicability to the study area … ."

CONCLUSIONS

Considerable reductions in the area of many sites over relatively short time periods (< 50 years) support the conclusion that the overwhelming majority of XLPs are quite susceptible to encroachment by woody species, and thus are not primary. Dendrochronological studies conducted in this vegetation type suggest anthropogenically

elevated fire frequencies associated with Native American cultures probably are responsible for maintenance (and possibly the origin) of this vegetation type throughout the majority of eastern United States (Figure 5.4). However, native American burning practices most likely resulted in establishment of XLPs only in areas with extremely shallow (≤ 25 cm), rocky soils and high solar heat loads (moderate to steep slopes with south to west aspects). Prior to periodic anthropogenic disturbance, these areas would have supported relatively open-canopied, xerophytic forests that contained heliophytic herbaceous taxa characteristic of XLPs. Introduction of fire into these habitats would have decreased woody plant cover, resulting in increased insolation and thus in dominance of these heliophytic graminoids and forbs.

In more mesic habitats, XLPs probably originated from clearing of forests for agricultural purposes (grazing, row crop cultivation, and/or timber harvesting). These practices likely promoted soil erosion, especially on moderate to steep slopes, and ensued in abandonment of these marginal agricultural lands. The more xeric conditions of this degraded habitat provided a suitable environment for colonization by the XLP flora (Baskin et al., 1994, 1997), which undoubtedly occurred at a rapid pace in areas adjacent to XLPs or open-canopied xerophytic forests.

In the absence of management (prescribed fire, mowing, cutting, grazing), succession to forested community types occurs in XLPs. Succession rapidly converts XLPs on deeper soils to hardwood forests over periods of a century or less. In more xeric sites, *Juniperus virginia*/hardwood forests are the likely outcome of succession over more prolonged time periods. The pace at which XLPs revert to forested community types via succession may differ between regions as a result of climate. For instance, in habitats of comparable soil depths and plant-available water holding capacities, succession may proceed much faster in sites in the southern Interior Low Plateaus and Ridge and Valley than in those in the Ozark Plateaus due to lower growing season precipitation in the latter.

XLPs in the Cahaba River Valley in Bibb County, Alabama, may be the only examples of this vegetation type that are edaphic climaxes. Although researchers have not studied aerial photographs or dendrochronological records in the Ketona Dolomite

sites, persistence of their open nature suggests they are able to persist in the absence of fire. Furthermore, the considerable number of heliophytic taxa endemic to this community type supports the conclusion that they have persisted over geologic time spans.

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Table 5.1. Summary of the physiographic distribution of xeric limestone prairies in eastern United States organized by state and physiographic province (sensu Fenneman, 1938, [1946] 1949).

State	Physiographic Province	Physiographic/Natural Region	Physiographic Reference	Site Reference(s)
Alabama	Interior Low Plateaus	Little Mountain	Quarterman and Powell, 1978	DeSelm, 1997; Webb et al., 1997
	Interior Low Plateaus	Moulton Valley	Quarterman and Powell, 1978	DeSelm, 1997; Webb et al., 1997
	Interior Low Plateaus	Southern Highland Rim	Quarterman and Powell, 1978	Webb et al., 1997
	Ridge and Valley	Cahaba Valley	Sapp and Emplaincourt, 1975	Allison and Stevens, 2001
	Coastal Plain	Fall Line Hills	Sapp and Emplaincourt, 1975	Webb et al., 1997
	Coastal Plain	Southern Red Hills	Sapp and Emplaincourt, 1975	Harper, 1920
Arkansas	Ozark Plateaus	Springfield Plateau	Fenneman, 1938, [1946] 1949	Keeland, 1978
	Ozark Plateaus	Salem Plateau	Fenneman, 1938, [1946] 1949	Keeland, 1978; Logan, 1992
	Ozark Plateaus	Boston Mountains	Fenneman, 1938, [1946] 1949	Keeland, 1978
Georgia	Ridge and Valley	Chickamauga Valley	Clark and Zisa, 1976	DeSelm, 1993
Illinois	Central Lowland	Chicago Lake Plain	Schwegman, 1973	Kurz, 1981
	Central Lowland	Western Grand Prairie	Schwegman, 1973	Kurz, 1981; McClain and Ebinger, 2002
	Central Lowland	Glaciated Middle Mississippi Border	Schwegman, 1973	Kurz, 1981
	Ozark Plateaus	Northern Section of Ozark Division	Schwegman, 1973	Kurz, 1981; Heikens and Robertson, 1995
	Ozark Plateaus	Southern Section of Ozark Division	Schwegman, 1973	Kurz, 1981; Heikens and Robertson, 1995
	Interior Low Plateaus	Lesser Shawnee Hills	Schwegman, 1973	Kurz, 1981; Heikens and Robertson, 1995
Indiana	Central Lowland	Muscatatuck Flats and Canyons	Homoya et al., 1984	Maxwell, 1987
	Central Lowland	Switzerland Hills	Homoya et al., 1984	Homoya, 1987

Table 5.1 (continued)

	Interior Low Plateaus	Mitchell Plain	Quarterman and Powell, 1978	Aldrich et al., 1982
	Interior Low Plateaus	Mammoth Cave Plateau	Quarterman and Powell, 1978	Bacone and Casebere, 1983
Kentucky	Interior Low Plateaus	Marion [Area]	Quarterman and Powell, 1978	Lawless et al., 2004 [Chapter 2]
	Interior Low Plateaus	Mammoth Cave Plateau	Quarterman and Powell, 1978	Lawless et al., 2004 [Chapter 2]
	Interior Low Plateaus	Ohio River Hills and Lowlands	Quarterman and Powell, 1978	Lawless et al., 2004 [Chapter 2]
	Interior Low Plateaus	Pennyroyal Plain	Fenneman, 1938, [1946] 1949	Lawless et al., 2004 [Chapter 2]
	Interior Low Plateaus	Knobstone Escarpment & Knobs	Quarterman and Powell, 1978	Lawless et al., 2004 [Chapter 2]; Rhoades et al., 2004
	Interior Low Plateaus	Outer Blue Grass	Quarterman and Powell, 1978	Lawless et al., 2004 [Chapter 2]
Missouri	Central Lowland	Osage Plains	Thom and Wilson, 1980	Ladd and Nelson, 1982
	Central Lowland	Eastern Glaciated Plains	Thom and Wilson, 1980	Ladd and Nelson, 1982
	Central Lowland	Lincoln Hills	Thom and Wilson, 1980	Ladd and Nelson, 1982
	Ozark Plateaus	Springfield Plateau	Thom and Wilson, 1980	Ladd and Nelson, 1982
	Ozark Plateaus	Upper Ozark	Thom and Wilson, 1980	Ladd and Nelson, 1982
	Ozark Plateaus	St. Francois Mountains	Thom and Wilson, 1980	Ladd and Nelson, 1982
	Ozark Plateaus	Elk River	Thom and Wilson, 1980	Ladd and Nelson, 1982
	Ozark Plateaus	White River	Thom and Wilson, 1980	Ladd and Nelson, 1982
	Ozark Plateaus	Lower Ozark	Thom and Wilson, 1980	Ladd and Nelson, 1982
	Ozark Plateaus	Ozark Border	Thom and Wilson, 1980	Ladd and Nelson, 1982
Ohio	Interior Low Plateaus	Northeastern Blue Grass	Quarterman and Powell, 1978	Braun, 1928
	Appalachian Plateaus	Marietta Plateau	Brockman, 1988	Rick Gardner, personal communication
Pennsylvania	Ridge and Valley	Appalachian Mountain	Berg et al., 1989	Laughlin and Uhl, 2003
Tennessee	Interior Low Plateaus	Western Higland Rim	Quarterman and Powell, 1978	DeSelm and Chester, 1993
	Interior Low Plateaus	Cumberland River Basin	Quarterman and Powell, 1978	Baskin and Baskin, 1977; DeSelm, 1991
	Ridge and Valley	--[a]	--[a]	DeSelm, 1993

Table 5.1 (continued)

Virginia	Ridge and Valley	Allegheny Mountains	Woodward and Hoffman, 1991	Ludwig, 1999
WestVirginia	Ridge and Valley	-- [a]	-- [a]	Bartgis, 1993

[a] = not reported

Table 5.2. Summary of the geologic substrates upon which xeric limestone prairies occur in eastern United States. Formations and members are organized by physiographic province and geologic system(s), respectively.

Geologic Formation/Member (susbstrate)	System(s)	State(s)	Reference(s)
Ozark Plateaus			
St. Louis Limestone	Mississippian	Illinois	Heikens, 1991
Salem Limestone	Mississippian	Illinois	Heikens, 1991
Burlington Limestone	Mississippian	Illinois	Nelson and Ladd, 1980
Keokuk Limestone	Mississippian	Missouri	Nelson and Ladd, 1980
Kimswick Formation (limestone)	Ordovician	Missouri	George, 1996
Plattin Formation (limestone)	Ordovician	Missouri Arkansas	George, 1996; Logan, 1992
Joachim Dolomite	Ordovician	Missouri	Erickson et al., 1942
Everton Formation (dolomite)	Ordovician	Missouri	Erickson et al., 1942
Powell Dolomite	Ordovician	Missouri	Erickson et al., 1942
Cotter Dolomite	Ordovician	Missouri	Erickson et al., 1942
Jefferson City Dolomite	Ordovician	Missouri	Erickson et al., 1942
Gasconade Dolomite	Ordovician	Missouri	Erickson et al., 1942; Ver Hoef et al., 1993
Eminence Dolomite	Cambrian	Missouri	Ver Hoef et al., 1993
Potosi Dolomite	Cambrian	Missouri	Ver Hoef et al., 1993
Derby-Doerun Dolomite	Cambrian	Missouri	Ladd and Nelson, 1982
Bonneterre Formation (dolomite)	Cambrian	Missouri	Ladd and Nelson, 1982
Central Lowlands			
Keokuk Limestone	Mississippian	Missouri	Ladd and Nelson, 1982
Burlington Limestone	Mississippian	Missouri	Ladd and Nelson, 1982
Chouteau Limestone	Mississippian	Illinois	Willman et al., 1967
Salem Limestone	Mississippian	Illinois	Willman et al., 1967
St. Louis Limestone	Mississippian	Illinois	Willman et al., 1967

Table 5.2 (continued)

Ste. Genevieve Limestone	Mississippian	Illinois	Willman et al., 1967
Kimswick Formation (limestone)	Ordovician	Missouri	Ladd and Nelson, 1982
Plattin Formation (limestone)	Ordovician	Missouri	Ladd and Nelson, 1982
Dillsboro Formation (limestone and shale)	Ordovician	Indiana	Homoya, 1987
Whitewater Formation (limestone and shale)	Ordovician	Indiana	Homoya, 1987

Interior Low Plateaus

Frailey Shale	Mississippian	Illinois	Heikens, 1991
Haney Limestone	Mississippian	Illinois	Heikens, 1991
Renault Limestone	Mississippian	Illinois	Heikens, 1991
Bethel Limestone	Mississippian	Illinois	Heikens, 1991
Ridenhoen formation (limestone)	Mississippian	Illinois	Heikens, 1991
Salem Limestone	Mississippian	Kentucky	Lawless et al., 2004 [Chapter 2]
Glen Dean Limestone	Mississippian	Kentucky	Lawless et al., 2004 [Chapter 2]
Reelsville Limestone	Mississippian	Kentucky	Lawless et al., 2004 [Chapter 2]
Beech Creek Limestone	Mississippian	Kentucky	Lawless et al., 2004 [Chapter 2]
Girkin Limestone	Mississippian	Kentucky	Lawless et al., 2004 [Chapter 2]
Paint Creek Limestone	Mississippian	Kentucky	Lawless et al., 2004 [Chapter 2]
Warsaw Limestone	Mississippian	Tennessee	DeSelm and Chester, 1993
Fort Payne formation (limestone)	Mississippian	Tennessee	DeSelm and Chester, 1993
Tuscumbia Limestone	Mississippian	Alabama	Webb et al., 1997
Bangor Limestone	Mississippian	Alabama	Webb et al., 1997
Louisville Limestone	Silurian	Kentucky	Lawless et al., 2004 [Chapter 2]
Peebles Dolomite	Silurian	Ohio	Swinford, 1985; Gardner and Minnie, 2004
Lilley formation (dolomite)	Silurian	Ohio	Swinford, 1985; Gardner and Minnie, 2004
Bisher formation (dolomite)	Silurian	Ohio	Swinford, 1985; Gardner and Minnie, 2004

Table 5.2 (continued)

Estill Shale	Silurian	Ohio	Swinford ,1985; Gardner and Minnie, 2004

Upper Part of Crab Orchard formation/
    Lower Part of Crab Orchard and
    Brassfield formation (clay shale,
    limestone, and dolomite)
	Silurian	Kentucky	Lawless et al., 2004 [Chapter 2]

Laurel formation (shale and dolomite)	Silurian	Kentucky	Rhoades et al., 2004
Lebanon Limestone	Ordovician	Tennessee	DeSelm 1988, 1991
Ridley Limestone	Ordovician	Tennessee	DeSelm 1988, 1991

Ridge and Valley

Keyser formation/Tonoloway formation (undivided) (limestone)	Devonian, Silurian	Pennsylvania	Steve Grund and John Kunsman, personal communication
Onondoga formation/Old Fort formaton (undivided) (limestone)	Devonian	Pennsylvania	John Kunsman, personal communication
Chambersburg formation (limestone)	Ordovician	Pennsylvania	John Kunsman, personal communication
Coburn formation through Nealmont formation (undivided) (limestone)	Ordovician	Pennsylvania	John Kunsman, personal communication
Reedsville formation (limestone)	Ordovician	Pennsylvania	John Kunsman, personal communication
Tytoona Cave (limestone)	Ordovician	Pennsylvania	Steve Grund, personal communication
Benner formation/Loysburg formation (undivided) (limestone)	Ordovician	Pennsylvania	Steve Grund and John Kunsman, personal communication
Bellefonte formation/Axemann formation (undivided) (limestone and dolomite)	Ordovician	Pennsylvania	Steve Grund, personal communication
Tonoloway Limestone	Ordovician	West Virginia	Bartgis, 1993
Helderberg Limestone	Ordovician	West Virginia	Bartgis, 1993
Ben Hur Limestone	Ordovician	Virginia	Ludwig, 1999
Knox Group Dolomite	Ordovician	Virginia	DeSelm, 1993

Table 5.2 (continued)

Chickamauga Limestone	Ordovician	Alabama, Georgia, Tennessee, Virginia	DeSelm, 1993 DeSelm et al., 1969 Ludwig, 1999
Conasauga formation (limestone)	Ordovician	Alabama	DeSelm, 1993
Mines Limestone	Cambrian	Pennsylvania	Steve Grund, personal communication
Ketona formation (dolomite)	Cambrian	Alabama	Allison and Stevens, 2001
Rome formation (limestone)	Cambrian	Virginia	Ludwig, 1999
Honaker formation (limestone and dolomite)	Cambrian	Virginia	Ludwig, 1999

Coastal Plain

Midway Limestone	Tertiary	Alabama	Harper, 1920

Appalachian Plateaus

Conemaugh formation (limestone)	Pennsylvanian	Ohio	Rick Gardner, personal communication

Table 5.3. Summary of the soil series upon which xeric limestone prairies occur in eastern United States. Series are organized alphabetically by order. Physiographic province(s) and state(s) in which each series occur are provided along with reference(s).

Soil Series	Subgroup	Physiographic Province	State	Reference
Alfisols				
Beasley	Typic Hapludalfs	Interior Low Plateaus	Kentucky	Lawless et al., 2004 [Chapter 2]; Rhoades et al., 2004
Bratton	Typic Hapludalfs	Interior Low Plateaus	Ohio	Gardner and Minnie, 2004
Caneyville	Typic Hapludalfs	Interior Low Plateaus	Kentucky	Lawless et al., 2004 [Chapter 2]; Rhoades et al., 2004; Mann et al., 1999
Colbert	Vertic Hapludalf	Ridge and Valley	Alabama, Georgia, Tennessee, Virginia	DeSelm, 1993
		Interior Low Plateaus	Alabama	Webb et al., 1997
		Interior Low Plateaus	Kentucky	Lawless et al., 2004 [Chapter 2]
Conasauga	Oxyaquic Hapludalfs	Ridge and Valley	Alabama, Georgia, Tennessee, Virginia	DeSelm, 1993
Crider	Typic Paleudalfs	Central Lowland	Indiana	Maxwell, 1987
Cumberland	Rhodic Paleudalfs	Interior Low Plateaus	Kentucky	Lawless et al., 2004 [Chapter 2]
Eden	Typic Hapludalfs	Central Lowland	Indiana	Homoya, 1987
Elba	Typic Hapludalfs	Appalachian Plateaus	Ohio	Rick Gardner, personal communication
Fredonia	Typic Hapludalfs	Interior Low Plateaus	Kentucky	Lawless et al., 2004 [Chapter 2]
Hagerstown	Typic Hapludalfs	Interior Low Plateaus	Indiana	Bacone and Casebere, 1983
		Interior Low Plateaus	Kentucky	Lawless et al., 2004 [Chapter 2]; Mann et al. 1999
		Ridge and Valley	Pennsylvania	Laughlin and Uhl, 2003
Lenberg	Ultic Hapludalfs	Interior Low Plateaus	Kentucky	Lawless et al., 2004 [Chapter 2]
Lowell	Typic Hapludalfs	Appalachian Plateaus	Ohio	Rick Gardner, personal communication
Opequon	Lithic Hapludalfs	Interior Low Plateaus	Ohio	Gardner and Minnie, 2004
		Ridge and Valley	Pennsylvania	Laughlin and Uhl, 2003
Rosine	Ultic Hapludalfs	Interior Low Plateaus	Kentucky	Lawless et al., 2004 [Chapter 2]
Seaton	Typic Hapludalfs	Central Lowland	Illinois	McClain and Ebinger, 2002
Shrouts	Typic Hapludalfs	Interior Low Plateaus	Kentucky	Lawless et al., 2004 [Chapter 2]
Stookey	Typic Hapludalfs	Interior Low Plateaus	Illinois	Heikens, 1991
		Ozark Plateaus	Illinois	Heikens, 1991

154

Table 5.3 (continued)

Talbott	Typic Hapludalfs	Interior Low Plateaus	Tennessee	DeSelm, 1991
Vertrees	Typic Paleudalfs	Interior Low Plateaus	Kentucky	Lawless et al., 2004 [Chapter 2]
Wellston	Ultic Hapludalfs	Interior Low Plateaus	Indiana	Bacone et al., 1983
Zanesville	Oxyaquic Fragiudalfs	Interior Low Plateaus	Indiana	Bacone et al., 1983

Mollisols

Barfield	Lithic Hapludolls	Interior Low Plateaus	Tennessee	DeSelm, 1991
Corydon	Lithic Argiudolls	Interior Low Plateaus	Indiana	Homoya, 1994
			Kentucky	Lawless et al., 2004 [Chapter 2]; Mann et al., 1999
Gasconade	Lithic Hapludolls	Ozark Plateaus	Missouri	Hicks, 1981; George, 1996
		Ozark Plateaus	Arkansas	Keeland, 1978
Gladeville	Lithic Rendolls	Interior Low Plateaus	Tennessee	DeSelm, 1991
		Ridge and Valley	Tennessee	Mann et al., 1999
Sogn	Lithic Haplustolls	Central Lowland	Illinois	McClain and Ebinger, 2002

Ultisols

Bodine	Typic Paleudults	Interior Low Plateaus	Tennessee	DeSelm and Chester, 1993
Elliber	Typic Hapludults	Ridge and Valley	Pennsylvania	Laughlin and Uhl, 2003
Gilpin	Typic Hapludults	Interior Low Plateaus	Indiana	Bacone et al., 1983
			Kentucky	Lawless et al., 2004 [Chapter 2]

Inceptisols

Garmon	Dystric Eutrudepts	Interior Low Plateaus	Kentucky	Lawless et al., 2004 [Chapter 2]; Mann et al., 1999
Muskingum	Typic Dystrudepts	Interior Low Plateaus	Indiana	Bacone et al., 1983
Sulphura	Typic Dystrudepts	Interior Low Plateaus	Tennessee	DeSelm and Chester, 1993

Table 5.3 (continued)

<u>Vertisols</u>

Houston	Oxyaquic Hapluderts	Coastal Plain	Alabama	Harper, 1920

Table 5.4. Summary of the geographic distribution of 13 taxa endemic, or nearly so, to xeric limestone prairies of the eastern United States. (OZMO=Ozark Plateaus of Missouri; OZAR=Ozark Plateaus of Arkansas; RVWV=Ridge and Valley of West Virginia; RVVA=Ridge and Valley of Virginia; RVAL=Ridge and Valley of Alabama)

Endemic Taxa	OZMO	OZAR	RVWV	RVVA	RVAL
Castilleja kraliana					x
Coreopsis grandiflora var. *inclinata*					x
Dalea cahaba					x
Delphinium treleasei	x	x			
Echinacea paradoxa var. *paradoxa*	x	x			
Erigeron strigosus var. *dolomitica*					x
Liatris oligocephala					x
Monarda fistulosa ssp. *brevis*			x	x	
Onosmodium decipiens					x
Scutellaria bushii	x	x			
Silphium glutinosum					x
Spigelia gentianoides					x
Valerianella ozarkana	x	x			
Total	5	5	1	1	8

Table 5.5. Distribution of limestone cedar glade endemic/near endemic taxa in xeric limestone prairies of eastern United States.

Limestone Cedar Glade Endemic Taxa	XLP Distribution	Reference
Astragalus tennesseensis[*]	Tennessee	DeSelm, 1991
Dalea foliosa[*]	Tennessee	DeSelm, 1991
Dalea gattingeri	Alabama	DeSelm, 1993
	Georgia	DeSelm, 1993
	Tennessee	DeSelm, 1993
Echinacea tennesseensis	Tennessee	DeSelm, 1991
Leavenworthia alabamica	Alabama	Webb et al., 1997
Leavenworthia exigua var. *exigua*	Georgia	DeSelm, 1993
	Tennessee	DeSelm and Chester, 1993
Leavenworthia exigua var. *laciniata*	Kentucky	Lawless et al., 2004 [Chapter 2]
Leavenworthia exigua var. *lutea*	Alabama	Allison and Stevens, 2001
Leavenworthia stylosa	Tennessee	Baskin and Baskin, 1977
Lobelia appendiculata var. *gattingeri*	Tennessee	Baskin and Baskin, 1977; DeSelm, 1991
Onosmodium molle	Tennessee	DeSelm, 1991
Pediomelum subacaule	Alabama	Allison and Stevens, 2001
	Georgia	DeSelm, 1993
	Tennessee	DeSelm, 1991, 1993
Talinum calcaricum	Kentucky	Lawless et al., 2004 [Chapter 2]
Trifolium calcaricum	Virginia	Collins and Wieboldt, 1992; Ludwig, 1999

[*] = near endemic

Figure 5.1. Five xeric limestone prairies in eastern United States. Upper left: Hardin County, Kentucky (Interior Low Plateaus) (photo taken by Carol Baskin, July 1982); middle left: Bibb County, Alabama [on Ketona Dolomite] (Ridge and Valley) (photo taken by Patrick Lawless, July 2003); lower left Adams County, Ohio (Interior Low Plateaus) (photo taken by Carol Baskin, August 1978); upper right: Taney County, Missouri (Ozark Plateaus) (photo taken by Carol Baskin, August 1976); lower right: Grant County, West Virginia (Ridge and Valley) (photo taken by Carol Baskin, August 1986).
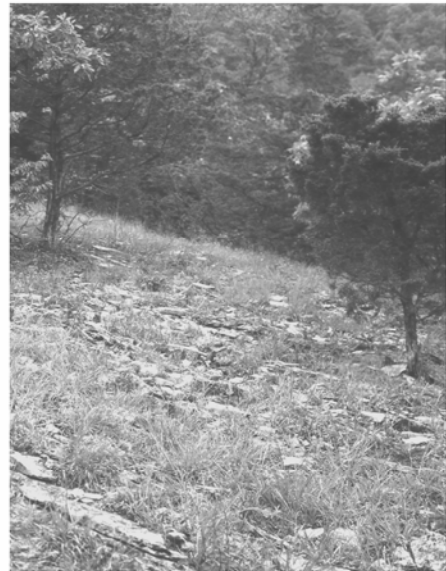
Figure 5.2. County/physiographic province (sensu Fenneman, 1938, [1946] 1949) distribution map of xeric limestone prairies in eastern United States.
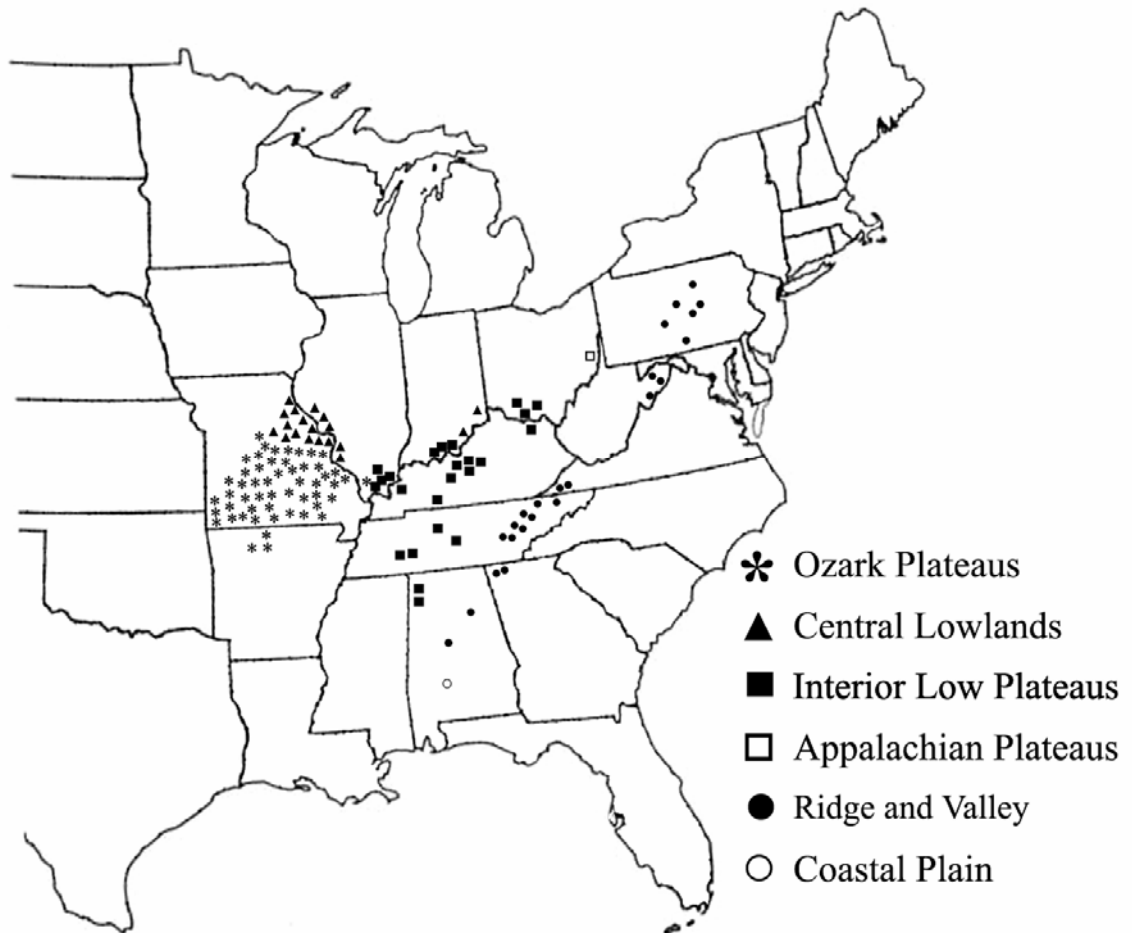
Figure 5.3. Modified Walter-type climatic diagrams for four locations in the geographic range of xeric limestone prairies in eastern United States. Plate a. includes a key to climatological data presented in these diagrams (a = weather service station, b = station elevation, c = mean annual temperature, d = mean annual precipitation, e = number of years for which data were examined, f = latitude and longitude, g = number of growing season days, h = mean low temperature of coldest month, i = lowest recorded temperature). Data were obtained from MCC (2004) (plate a.), NCDC (2004) (b.) and SERCC (2004) (c. and d.).

5.3 a.

5.3 b.

Williamsport, Pennsylvania

Williamsport-Lycoming AP, PA (158 m)

[30] 41° 15' N 76° 55' W

9.9°C 1056 mm

169

-18.3°C
-28.9°C

5.3 c.

Hodgenville, KY

Hodgenville-Lincoln NP, KY [240]   13.7°C 1321 mm
[57] 37° 32' N 85° 44' W   185

Month

-4.2°C
-31.7°C

— Mean Monthly Temperature   — Mean Monthly Precipiation

5.3 d.

Centreville, Alabama

Centreville WSMO, AL (139 m)   16.9°C 1495 mm

[31] 32° 54' N 87° 15' W   227

0.1°C
-21.1°C
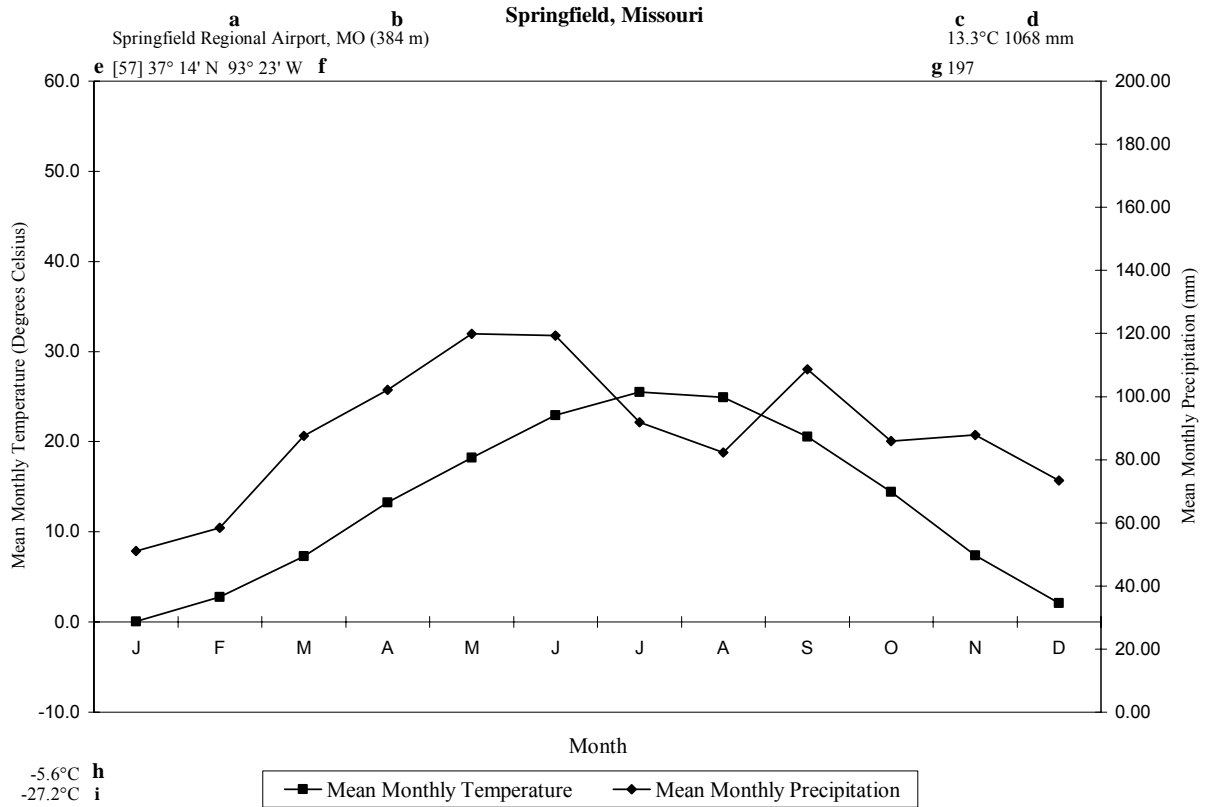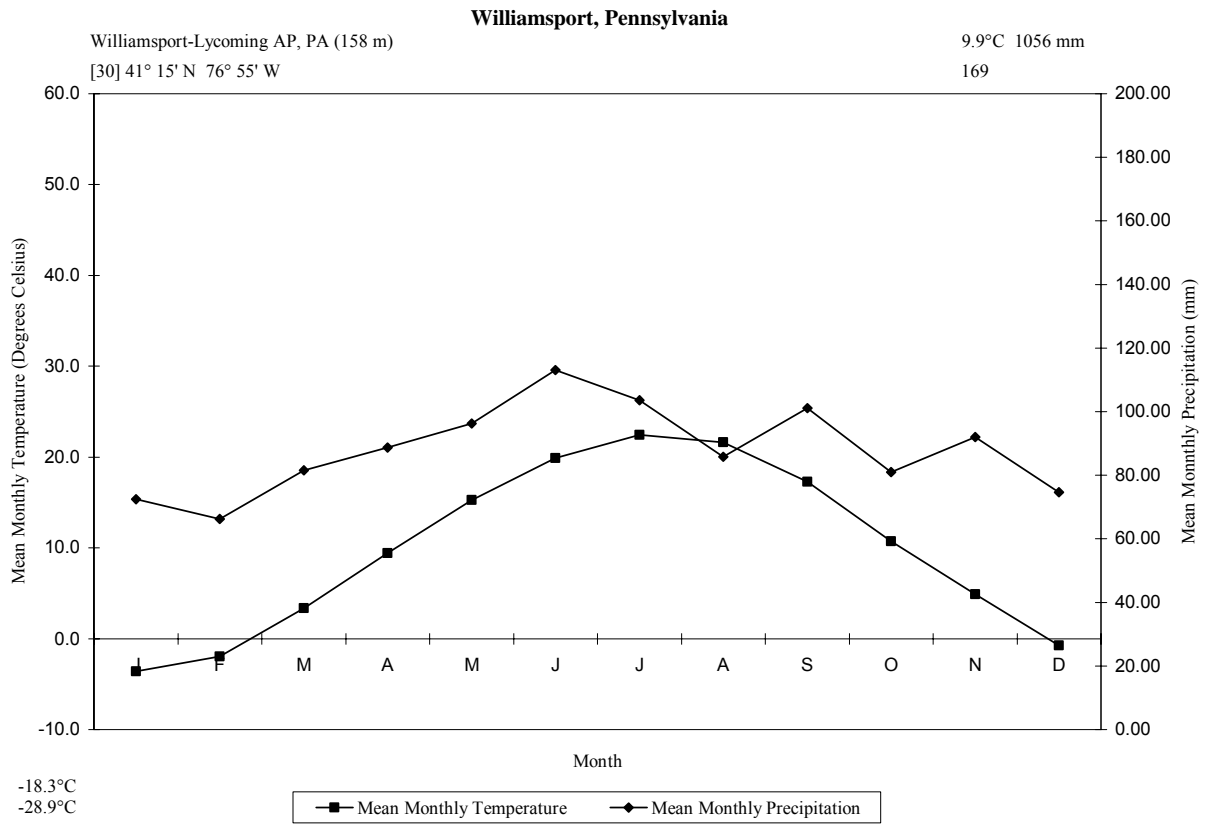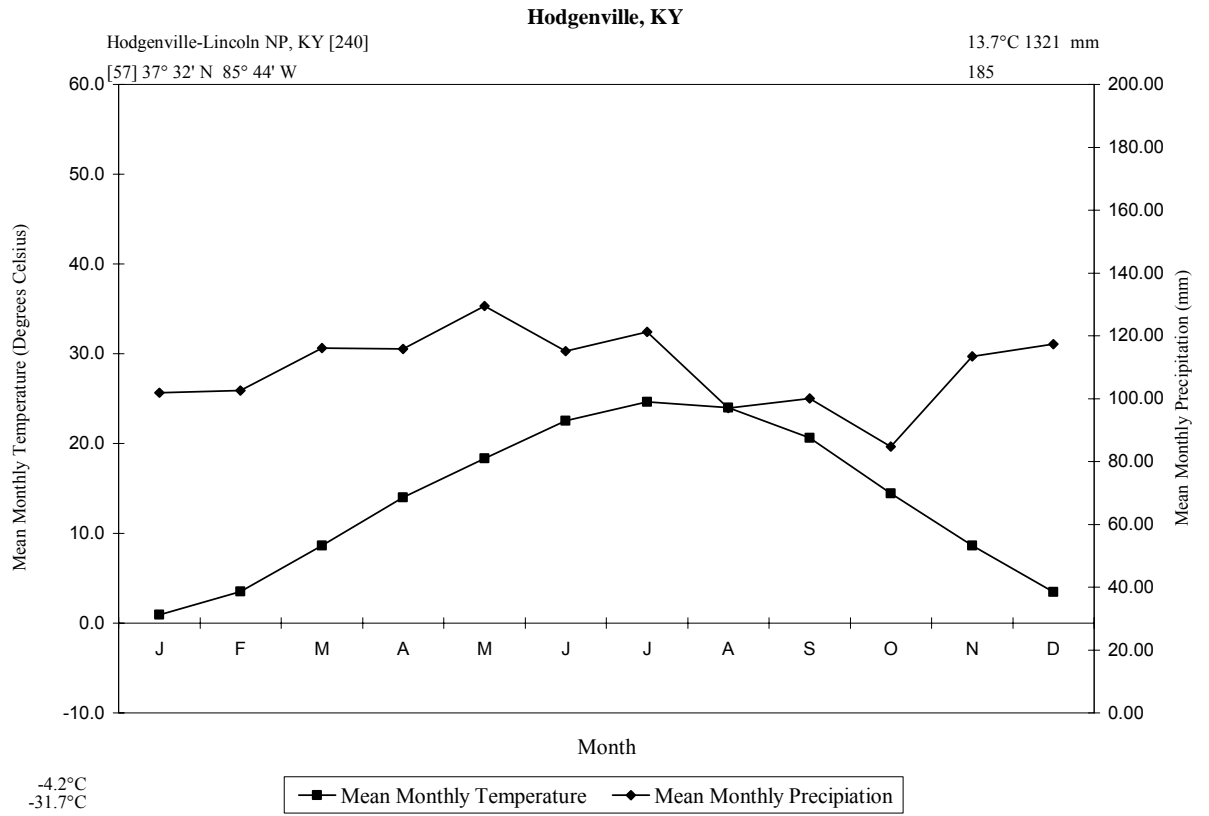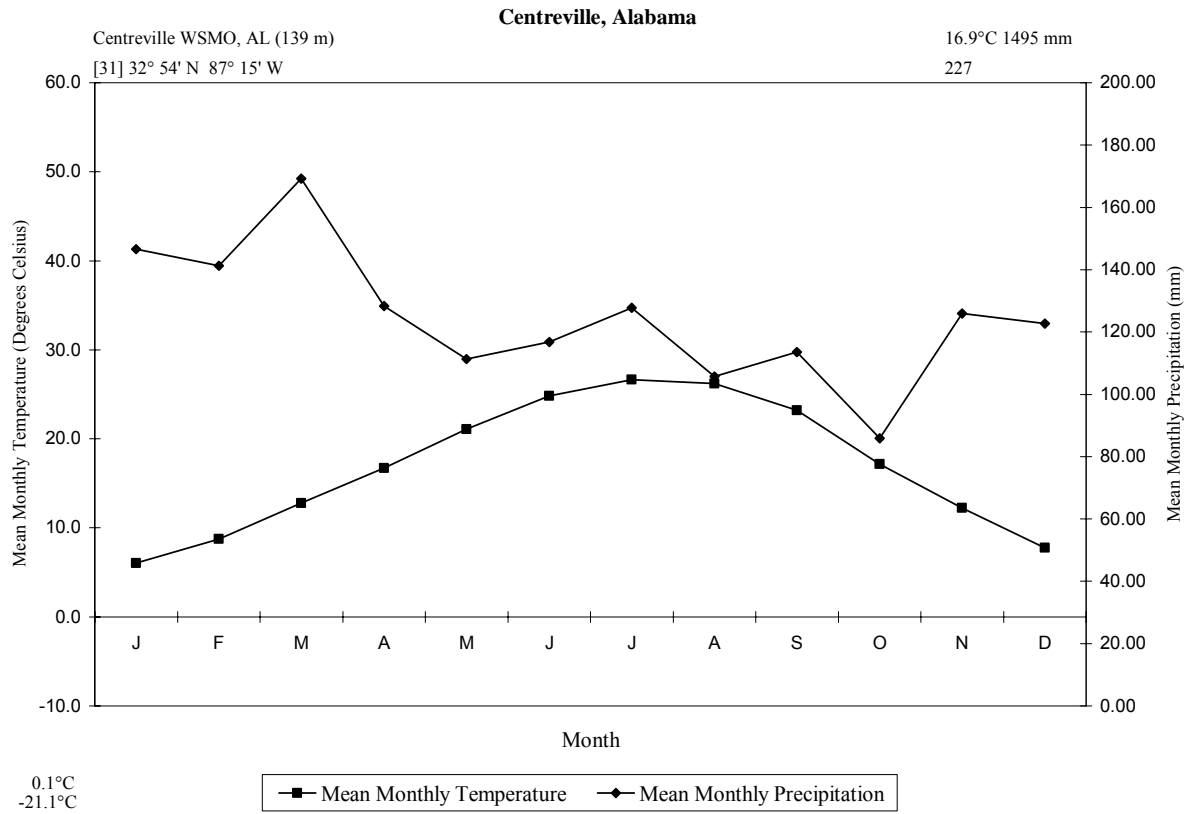
Figure 5.4. A graphical conceptual model of the origin and successional trajectories of xeric limestone prairies of eastern United States.
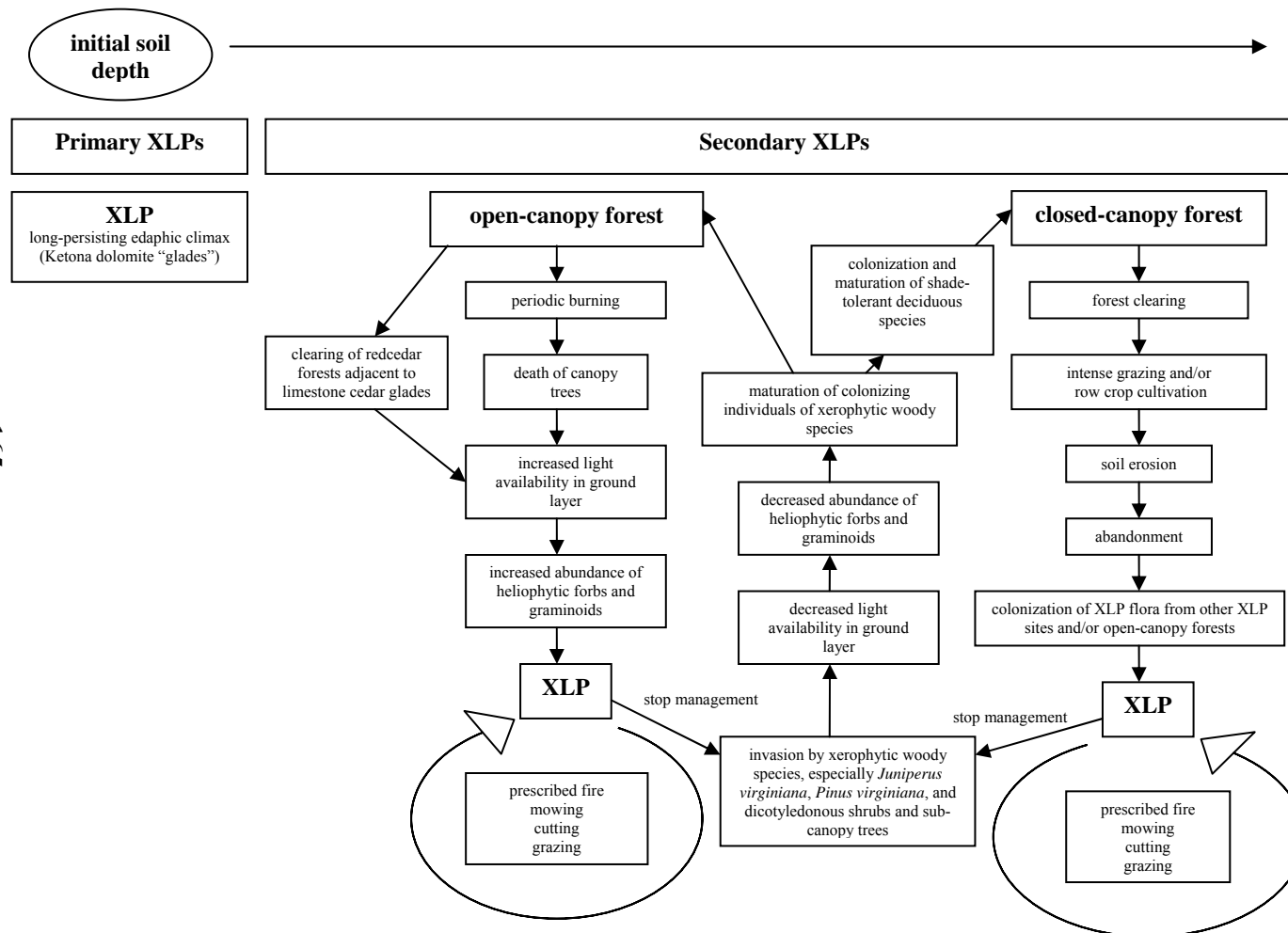
CHAPTER 6

SUMMARY, CONCLUSIONS, AND SYNTHESIS

INTRODUCTION

The purpose of my dissertation research was to collect floristic, vegetation, and physical environmental data from xeric limestone prairies (XLPs) in Kentucky with the ultimate goals of 1) comparing XLPs in Kentucky with those in other regions in eastern United States, 2) gaining further insight into factors affecting composition, structure, and distribution of XLPs, and 3) characterizing XLP vegetation throughout eastern United States. This final chapter 1) summarizes the results of my research, 2) presents conclusions about the classification, distribution, origin, and maintenance of XLPs in eastern United States, and 3) compares various biotic and abiotic characteristics of XLPs, limestone cedar glades, and deep-soil barrens of eastern United States.

VEGETATION

Dominance of native, C_4 perennial grasses in the overwhelming majority of XLPs in eastern United States justifies recognition of only one XLP vegetation type (Table 6.1). *Schizachyrium scoparium* was a dominant taxon (i.e. had the highest cover, frequency, or importance value) in 21 of 23 studies for which quantitative vegetation data were available for eastern United States, including 10 of 12 100-m^2 XLP community types identified in Kentucky (Table 3.5). Thus, ***S. scoparium* is the characteristic dominant of XLPs in Kentucky and in the greater eastern United States**. *Andropogon gerardii* was dominant in one of 12 100-m^2 XLP community types identified in Kentucky (Table 3.5), in the two sites on Monroe Dolomite in Ohio sampled by Braun (1928), in two of 16 plots in the Ridge and Valley in Virginia sampled by Ludwig (1999), and in one (Crowder Cemetery Barren, Roane County, Tennessee) of three sites in the Ridge and Valley in Alabama, Georgia, and Tennessee sampled by DeSelm (1993). *Bouteloua curtipendula* had the highest cover in one of three sites in Illinois sampled by McClain and Ebinger (2002) and in sites ("limestone barrens" and "cedar glades") on Knobly Mountain, West Virginia sampled by Bartgis (1993). *Bouteloua* also had the

166

highest average abundance value (semi-quantitative) in 10 XLPs in the Ridge and Valley in Pennsylvania (Laughlin and Uhl, 2003).

C_4 annual grasses, specifically *Sporobolus neglectus* and *S. vaginiflorus*, were locally dominant in the shallow-soil zones of some sites, particularly those in Kentucky (Chapter 3) and Missouri (Hall, 1955; Skinner, 1979; Ver Hoef et al., 1993). *Sporobolus vaginiflorus* was characteristic of many fine-scale ($\leq$ 1 m^2) community types identified in the Interior Low Plateaus in Kentucky (Tables 3.1, 3.2, and 3.3) and in the Salem Plateau in Missouri (Ver Hoef et al., 1993). In Missouri, *Sporobolus neglectus* had the highest frequency values in quadrats centered around the rare focal species *Penstemon cobaea* var. *purpureus* and *Centaurium texense* [both of which typically occur in shallow soils (< 15 cm)] (Skinner, 1979) and in a glade in the Missouri Botanical Garden Arboretum (Salem Plateau) sampled by Hall (1955). However, **annual grasses are not site dominants (i.e. do not have the highest cover) in any XLPs of eastern United States for which vegetation data are available**.

C_3 perennial forbs (one per site) had the highest average cover value of all taxa in only two of the numerous XLPs in eastern United States for which vegetation data were available. *Hedyotis nigricans* was dominant in a single site in the Central Lowland in Illinois (McClain and Ebinger, 2002) and *Silphium terebinthinaceum* in a single site in the eastern Outer Blue Grass in Kentucky (Table 3.5). In both of these sites, the taxon with the second highest average cover value was a native, C_4 perennial grass [*Bouteloua curtipendula* in the site sampled by McClain and Ebinger (2002) and *Sorghastrum nutans* in Crooked Creek Barrens Site 2 in my study (Table 3.5)]. Bartgis (1993) did not report cover values for sites on Cave Mountain, West Virginia but reported, " … the dominants are typically *Solidago arguta* var. *harrisii*, *Monarda fistulosa* var. *brevis*, and *Paronychia virginica*." These are the only XLPs in eastern United States in which C_4 perennial grasses apparently are not a dominant or subdominant component; however, quantitative vegetation data are needed to accurately assess whether these communities represent a second type of XLP vegetation.

FLORA

Thirteen taxa are endemic/near endemic to XLPs of eastern United Stated.
All of these endemic/near endemic taxa are herbaceous C_3 dicots, and 11 of thirteen are
perennials [*Valerianella ozarkana* (annual) and *Castilleja kraliana* (annual or biennial)].
Eight of these taxa are endemic to sites on Ketona Dolomite in Bibb County, Alabama
(Ridge and Valley), four to sites in the Ozark Plateaus in Missouri and Arkansas, and a
single taxon (*Monarda fistulosa* var. *brevis*) to sites in the Ridge and Valley in West
Virginia and Virginia.

**Many other rare and endangered taxa endemic/near endemic to rock outcrop
plant communities of eastern United States also occur in XLPs.** Fourteen of the 21
taxa endemic/near endemic to limestone cedar glades of southeastern United States
(sensu Baskin and Baskin, 1999, 2003) are present in XLPs (Table 5.5), particularly in
sites adjacent to, or in the vicinity of, limestone cedar glades (i.e. XLPs in Kentucky,
Tennessee, Alabama, Georgia). In addition, Bartgis (1993) reported the occurrence of
eight mid-Appalachian shale barren endemics (sensu Keener, 1983) in XLPs in West
Virginia.

Three hundred and thirty-five taxa were identified in the 18 XLPs sampled in
Kentucky (Appendix 2.1), of which only 20 (6.0%) are nonnative and 24 (7.2%) state-
listed as rare. The majority of taxa in the flora is intraneous C_3 hemicryptophytes.
Detailed phytogeographical and ecological data were not available for the floras of XLPs
in other regions. **However, comparisons between the flora of XLPs in Kentucky and
the floras of XLPs in other regions generally resulted in decreasing similarity
[measured via coefficient of community (CC)] with increasing distance between
sample regions.** For instance, the flora of XLPs in Kentucky and the flora of XLPs in
Ohio (356 taxa; provided by Rick Gardner, Ohio Department of Natural Resources) share
217 taxa (CC = 46.6%). Conversely, 122 taxa occur in XLPs in Kentucky and in XLPs
on Ketona Dolomite in Bibb County, Alabama (331 taxa; Allison and Stevens, 2001) (CC
= 22.4%).

DISTRIBUTION AND PHYSICAL ENVIRONMENTAL CHARACTERISTICS

XLPs are broadly distributed in eastern United States from Missouri and Pennsylvania south to Arkansas and Georgia, where they occur in the Ozark Plateaus, Central Lowland, Interior Low Plateaus, Appalachian Plateaus, Ridge and Valley, and Coastal Plain physiographic provinces (sensu Fenneman 1938, 1946 [1949]) (Figure 5.2). However, within states, XLPs often are restricted to a relatively small number of physiographic regions (e.g. Ozark Plateaus in Arkansas; Ridge and Valley in Pennsylvania, West Virginia, Virginia, and Georgia) or are particularly frequent in only certain regions [Northeastern Bluegrass in Adams County, Ohio; Knobstone Escarpment and Knobs in Kentucky (Table 2.1, Figure 2.2), Ridge and Valley in Bibb County, Alabama].

In many regions, distribution and frequency of XLPs are strongly correlated with the extent and abundance of particular geologic susbstrates. For example, nine of 18 XLPs sampled in Kentucky occurred on Salem Limestone in the Knobstone Escarpment and Knobs; approximately 40 sites on Ketona Dolomite in Bibb County, Alabama (Al Schotz, Alabama Natural Heritage Program, personal communication); and 24 sites on Gasconade Dolomite in the Ozark Scenic Riverways in Missouri (Ver Hoef et al., 1993). In addition, DeSelm, (1993) noted that the distribution of XLPs in the Ridge and Valley in Virginia, Tennessee, Alabama (excluding Bibb County), and Georgia was strongly correlated with the Chickamauga Limestone.

Although XLPs are restricted to shallow, rocky soils derived from calcareous substrates, in general there is not a strong fidelity of XLPs to particular soil series or even orders. Average soil depth was ≤ 1 m in all studies for which data were reported, and soil depths < 10 cm were not uncommon in the rockiest portions of sites (DeSelm, 1991; Ver Hoef et al., 1993; Heikens and Robertson, 1995, George, 1996; Ludwig, 1999; Laughlin and Uhl, 2003; Lawless et al., 2004 [Chapter 2]). Virtually all authors comment on the presence of exposed rock (flagstone, gravel, and/pr talus) at the soil surface. XLPs occur on 33 soils series in five orders (Alfisols, Ultisols, Mollisols, Inceptisols, and Vertisols). Many of the soils upon which XLPs occurred in Kentucky were mapped as rock outcrop complexes (with one or more soils series) and were described as moderately to severely eroded. In studies that included soil chemical analyses, low concentrations of

169

one or more nutrients (typically phosphorus) often were reported (Keeland, 1978; Heikens, 1991; Ludwig, 1999; Allison and Stevens, 2001; Rhoades, 2004).

Throughout their broad geographic distribution in eastern United States, XLPs occur in two relatively distinct environments. In southeastern United States (specifically Kentucky, Tennessee, Alabama, Georgia), they sometimes are associated with limestone cedar glades (Baskin and Baskin, 1977; DeSelm, 1988, 1991, 1993; DeSelm and Webb, 1997), which generally occur on relatively flat to gently rolling terrain (Baskin et al., 1994; Baskin and Baskin, 1999; Baskin and Baskin, 2003). In the Central Basin of Tennessee, XLPs typically occupy the periphery of limestone cedar glades (DeSelm, 1991), where soil depths generally are greater than in the adjacent glade. **The majority of XLPs occur on moderate to steep slopes with south to west aspects** (Braun, 1928; Bartgis, 1993; DeSelm, 1993; Ver Hoef et al., 1993; Heikens and Robertson, 1995; DeSelm and Webb, 1997; Ludwig, 1999; Laughlin and Uhl, 2003; Lawless et al., 2004 [Chapters 2]; Chapter 3). This topographic setting results in high solar heat loads (McCune and Grace, 2002) and can lead to rates of soil erosion that exceed soil genesis (Ware, 2002).

FACTORS AFFECTING COMMUNITY COMPOSITION AND STRUCTURE

Community structure is similar in XLPs throughout eastern United States. In the majority of sites, a small number of C_4 perennial grasses (*Schizachyrium scoparium, Andropogon gerardii, Bouteloua curtipendula, Sorghastrum nutans,* and/or *Sporobolus clandestinus*) make up the majority of plant cover, and a relatively large number of C_3 forbs occur in low abundance (Braun, 1928; Kucera and Martin, 1957; Keeland, 1978; DeSelm, 1988; DeSelm, 1991; Heikens, 1991; Bartgis, 1993; DeSelm, 1993; Ver Hoef et al., 1993; George, 1996; DeSelm and Webb, 1997; Ludwig, 1999; McClain and Ebinger, 2002; Laughlin and Uhl, 2003; Chapter 3). Because the same C_4 perennial graminoids (particularly *Schizachyrium scoparium*) are dominant and/or codominant in the majority of sites in eastern United States (Chapter 5), XLP variability largely is attributable to differences in forb species composition (Chapters 3 and 4).

Geographical trends in both species composition and community type distribution were apparent in Kentucky. Floristic similarity between XLPs in

Kentucky was relatively high (avg. coefficient of community = 0.58 ± 0.07) and exceeded the generally accepted association criterion (0.50, Barbour et al., 1999). However, floristic comparisons including either of the two sites in the eastern Outer Bluegrass (Crooked Creek Barrens Sites 1 and 2), which are geographic outliers of the main concentration of XLPs in Kentucky, typically resulted in low coefficients of community. Low dispersion of coarse-grain ($\geq 10\ m^2$) XLP community types among sites and Level IV ecoregions (sensu Woods et al., 2002) also showed strong effects of geographic distance on similarity between samples (Chapter 4). Strong fidelity of coarse-grain community types to ecoregions suggests regional species pools and coarse-grain environmental conditions often are conserved within ecoregions.

In XLPs and many rock outcrop communities of eastern United States, variability in community composition and structure within sites often is attributable to soil depth. For example, annuals (e.g. *Sporobolus vaginiflorus, Croton capitatus, C. monanthogynus, Heliotropium tenellum*) often were dominant in the most shallow soil regions of many XLPs in Kentucky (see Chapter 3). With increasing soil depth, cover and frequency of perennial graminoids (particularly the dominant C_4 perennial grass *Schizachyrium scoparium*) and forbs (e.g. *Silphium trifoliatum, Liatris* spp., *Solidago nemoralis*) generally increased. Transitions in dominance from annual to perennial taxa with increasing soil depth also has been documented in granite rock outcrop communities (Oosting and Anderson, 1939; Burbanck and Platt, 1971; Shure and Ragsdale, 1977) and in limestone cedar glades (Somers et al., 1987, Rollins, 1997; Baskin et al., 1999). General zonation in community composition and structure (independent of transitions in importance of life cycles) along soil depth gradients is a characteristic feature of most all rock outcrop communities (Oosting and Anderson, 1939; Winterringer and Vestal, 1956; Burbanck and Platt, 1971; Shure and Ragsdale, 1977; Perkins, 1981; Somers et al., 1986; Rollins, 1997; Wiser and White, 1999; Baskin and Baskin, 1999; Catling and Brownell, 1999; Wiser and White, 1999).

XLPs differ from many rock outcrop communities in that they do not contain extensive rock outcrops (pavements or boulders), and they generally do not support the early-stage communities of primary succesion dominated by mosses, lichens, and/or algae. Rock outcrops in XLPs usually exist in the form of flagstone, talus, or

gravel (Braun, 1928; DeSelm, 1988, 1991, 1993; DeSelm and Webb, 1997; Bartgis, 1993; Ver Hoef et al., 1993; Heikens and Robertson, 1995; Ludwig, 1999; Allison and Stevens, 2001; Laughlin and Uhl, 2003). Limestone benches make up the most extensive rock outcrops in XLPs in Kentucky, but they are present in only a limited number of sites, where they are few in number. Although mosses, lichens, blue-green algae (*Nostoc commune*), and macrobiotic crusts are present in some sites, they typically are not frequent (Ver Hoef et al., 1993; personal observation). Conversely, these taxa often make up the first stage in primary succession in rock outcrops, and thus they represent the chief eukaryotic communities initially involved in biological weathering of rocks and corresponding soil genesis (Oosting and Anderson, 1939; Winterringer and Vestal, 1956; Burbanck and Platt, 1971; Shure and Ragsdale, 1977; Perkins, 1981; Somers et al., 1986; Rollins, 1997; Baskin and Baskin, 1999; Catling and Brownell, 1999; Wiser and White, 1999).

ORIGIN AND STABILITY

Aerial photographic and dendrochronological data support the conclusion that the majority of XLPs are not primary. Aerial photographs (taken over short time periods of ~ 20 – 45 years) generally revealed rapid encroachment of woody taxa (especially *Juniperus virginiana*) into openings (Kimmel and Probasco, 1980; Aldrich et al., 1982; Annala et al., 1983; Annala and Kaputska, 1983; Bacone and Casebere, 1983; Ver Hoef et al., 1993; Laughlin, 2004). **Thus, these relatively unstable communities do not represent an edaphic climax.** In fact, Annala and Kaputska (1983) observed that many XLPs in Adams County, Ohio, were established in former agricultural fields subsequent to 1938 (the earliest year for which aerial photographs were available).

Dendrochronological data certainly suggest that anthropogenically elevated fire frequencies were an important factor in maintaining open conditions in some XLPs. Lowell and Astroth (1989) examined both aerial photographic and dendrochronological data for sites in Hercules Glade Wilderness Area (Salem Plateau in Taney County, Missouri) and documented a negative correlation between fire frequency and rates of site enclosure. Dendrochronological studies conducted by Guyette and McGinnes (1982) and Batek et al. (1999) revealed considerable reductions in fire

172

frequencies in XLPs in the Missouri Ozarks subsequent to European settlement, most probably due to cessation of Native American burning practices.

Despite the susceptibility of many XLPs to encroachment by woody species, some sites apparently are quite stable. Comparison of aerial photographs taken of Muldraugh's Barren and Scudder Glade (Hardin County, Kentucky) in 1958 and 1988 do not show dramatic changes in these two sites. However, proximity of old homesteads (circa 1850-1900) to the latter and to Spalding Glade (Larue County, Kentucky) (Lane Linnenkohl, Kentucky State Nature Preserves Commission, personal communication) does not rule out anthropogenic disturbance (e.g. timber harvesting and grazing) as a possible cause of origin for these sites and others in Kentucky. It also is not known whether disturbance is the reason why succession is not evident in these sites between 1958 and 1988. Although researchers have not studied aerial photographs or dendrochronological records in the Ketona Dolomite sites in Bibb County, Alabama, their open nature at present (despite recent discovery; Allison and Stevens, 2001) suggests they are able to persist in the absence of fire. Furthermore, the considerable number of heliophytic taxa endemic to this community type supports the conclusion that they perhaps have persisted over geologic time spans.

COMPARISON OF XLPs, LIMESTONE CEDAR GLADES, AND DEEP-SOIL BARRENS

Baskin et al. (1994) used several biotic and abiotic characteristics to distinguish limestone cedar glades, XLPs, and deep-soil barrens in the Big Barrens and immediately adjacent regions. Subsequently, Baskin and Baskin (1999, 2003) and Baskin et al. (1999) provided comprehensive reviews and syntheses for limestone cedar glades of southeastern United States and for deep-soil barrens in the Big Barrens Region, respectively. My research affords an opportunity for further comparisons of these regionally co-occurring vegetation types based on 1) vegetation, floristic, and physical environmental data I collected from XLPs in Kentucky, and 2) my synthesis of these data for XLPs in greater eastern United States. Thus, I will provide a comparison of XLPs, limestone cedar glades, and deep-soil barrens in eastern United States based on results of my dissertation research and recent work by Baskin and Baskin (1999, 2003) and Baskin

et al. (1999) (Table 6.2). Although some deep-soil barrens exist(ed) outside the Big Barrens Region in Kentucky and Tennessee [e.g. Coastal Plain (Jackson Purchase) in Kentucky (Transeau, 1935; Baskin et al., 1995); Eastern Highland Rim in Kentucky (Baskin et al., 1999), Mitchell Plain in Harrison County, Indiana (Keith, 1983)], detailed floristic, vegetation, geologic, and soils data are not available for the majority of these sites, and thus I include only the deep-soil barrens in the Big Barrens Region in comparisons of this vegetation type with that of XLPs and limestone cedar glades.

In eastern United States, the geographical distribution of XLPs is much greater than that of both limestone cedar glades and deep-soil barrens. XLPs occur in six physiographic provinces in 12 states in both glaciated and unglaciated regions of eastern United States. Conversely, all limestone cedar glades (Interior Low Plateaus and Ridge and Valley) and the majority of deep-soil barrens (Interior Low Plateaus) are restricted to unglaciated north-central southeastern United States (Baskin and Baskin, 1999, 2003, 2004; Baskin et al. 1994). **Anthropogenic origin(s) and relatively low fidelity to particular *geologic systems* and *soil orders* may explain the relatively broad distribution of XLPs in eastern United States** (see Distribution and Physical Environmental Characteristics above)**.**

Life form of dominant graminoids was an important characteristic in distinguishing limestone cedar glades from XLPs and deep-soil barrens in the classification system of Baskin et al. (1994). C_4 annuals (primarily *Sporobolus vaginiflorus, Panicum flexile,* and *P. capillare*) are dominant graminoids in limestone cedar glades (Somers et al., 1986; Rollins, 1997). Conversely, C_4 perennial grasses, (primarily *Schizachyrium scoparium*) are dominant in both XLPs and deep-soil barrens (Table 6.1; Baskin et al., 1999; Chester, 1999). **In my literature review of xeric calcareous grasslands of eastern United States, I did not find any sites outside southeastern United States (Virginia, West Virginia, Kentucky, Tennessee, Alabama, Georgia) in which C_4 annual grasses were dominant. Thus, my research confirms the distribution of limestone cedar glades provided by Baskin and Baskin (1999, 2003, 2004).**

Community structure in XLPs, limestone cedar glades, and deep-soil barrens also differs in other aspects. For example, only limestone cedar glades support communities

in which cryptogams are important (Somers et al., 1986; Baskin et al., 1994; Rollins, 1997; Baskin and Baskin, 1999). Furthermore, forbs, including C_3 annuals, are dominant components of many limestone cedar glade community types. Conversely, forbs are not dominant in any deep-soil barrens (Baskin et al., 1999; Chester, 1999) and are dominant in only a very small proportion of XLPs in eastern United States (Table 6.1).

Results of my dissertation research revealed both similarities and significant differences between the floras of these three vegetation types. Both limestone cedar glades and XLPs support endemic taxa. **However, limestone cedar glades support endemic taxa throughout their range in north-central southeastern United States, and XLP endemic/near endemics occur only in the Ozark Plateaus in Missouri and Arkansas and in the Ridge and Valley in West Virginia, Virginia, and Bibb County, Alabama.** No taxa are known to be endemic to deep-soil barrens.

The majority of taxa in the floras of XLPs in Kentucky, limestone cedar glades of southeastern United States, and deep-soil barrens of the southwestern Pennyroyal Plain (Kentucky and Tennessee) is intraneous C_3 hemicryptophytes. However, the flora of limestone cedar glades contains a higher percentage of therophytes (i.e. annuals) and a lower percentage of woody taxa than the flora of XLPs in Kentucky and of deep-soil barrens in the southwestern Pennyroyal Plain. Furthermore, the flora of XLPs in Kentucky and of deep-soil barrens are characterized by a strong extraneous southern component, whereas taxa with western geographic affinities make up the largest proportion of extraneous taxa in the limestone cedar glade flora of the Central Basin in Tennessee. **In comparison with the deep-soil barrens and limestone cedar glade floras, the percentage (6.0) of nonnative taxa in the flora of XLPs in Kentucky is very low.** Asteraceae and Poaceae contain the largest number of taxa in the floras of all three vegetation types.

Although there is considerable floristic overlap between these regionally co-occurring vegetation types, the flora of XLPs in Kentucky is distinct from that of limestone cedar glades and deep-soil barrens. The flora of XLPs in Kentucky (335 taxa) and the flora of deep-soil barrens in the southwestern Pennyroyal Plain (342) share 161 taxa (coefficient of community = 31.5%). One hundred and sixty-two taxa occur in XLPs in Kentucky and in limestone cedar glades of the Central Basin in Tennessee (411

175

taxa total) (coefficient of community = 27.7%). Of the 24 state-listed taxa (endangered, threatened, or special concern) in the flora of XLPs in Kentucky, 13 also occur in limestone cedar glades of southeastern United States (three of which are limestone cedar glade endemics), five in deep-soil barrens of the southwestern Pennyroyal Plain, three in all three floras, and nine only in XLPs in Kentucky. Thus, **although no taxa are endemic to XLPs in Kentucky, these grasslands provide important habitat for regionally rare taxa.**

Of these three vegetation types, limestone cedar glades are unique in that they are an edaphic climax (i.e. are associated with rock outcrops), are extremely resistant to encroachment by woody species, and do not require management for long-term persistence (Baskin et al., 1994; Baskin and Baskin, 1999, 2003, 2004). Although some sites on Ketona dolomite apparently are edaphic climaxes, the majority of XLPs in eastern United States resulted from anthropogenic disturbance, is susceptible to encroachment by woody species, and requires periodic management (prescribed fire and cutting) to maintain their open nature. **Thus, edaphic conditions in XLPs may retard encroachment of woody species, but soils typically are not shallow enough to prevent recruitment of woody taxa.** Deep-soil barrens in the Pennyroyal Plain in Kentucky and Tennessee generally do not contain exposed rock, originated from Native American burning practices, or perhaps from agricultural practices of Euro-Americans, and quickly revert to forest in the absence of periodic management (Baskin and Baskin, 1981; Baskin et al., 1999).

COMPARISON OF XLPS AND GRASSLANDS IN THE CENTRAL PLAINS AND PRAIRIES FORMATION

XLPs of eastern United States resemble rocky, shallow-soil grasslands in the Central Plains and Prairies Formation (especially those in north-central and west-central Kansas described by Albertson, 1937; Hulett and Tomanek, 1969; Heitschmidt et al., 1970; Hladek et al., 1972). Both of these vegetation types are characterized by xeric conditions and dominance of C_4 perennial grasses (particularly *Schizachyrium scoparium*). **However, the climate in these two regions is quite dissimilar and suggests different origins for these grasslands.**

Mean annual precipitation in XLPs in eastern United States ranges from approximately 100 cm in Missouri (Figure 5.3 a) to approximately 150 cm in Alabama (Figure 5.3 d). **These precipitation regimes generally support forest vegetation in eastern United States (Braun, 1950), and thus existence of nonforested herbaceous communities in this region (including XLPs) is not the result of low precipitation. Rather, these grasslands and rock outcrop communities are either edaphic climaxes (probably sites on Ketona Dolomite in the case of XLPs), or they are the result of disturbance, either anthropogenic (vast majority of XLPs) or natural (e.g. scouring action of water bodies in riparian communities).** Interestingly, the only XLPs that represent an edaphic climax (sites on Ketona Dolomite) also receive the most precipitation annually. However, in accordance with Thornthwaite (1952), it is important to note that these sites also have the highest mean annual temperature of all XLPs in eastern United States, and thus water requirements of vegetation in this area also are higher than that in other areas.

Borchert (1950) attributed both the origin and maintenance of grasslands in the Central Plains and Prairies Formation to low mean annual precipitation and high seasonality in precipitation. Other researchers (e.g. Sauer, 1950; Anderson, 1982; Axelrod, 1985) present cogent arguments for the combined effects of climate, fire, and grazing in establishment and maintenance of these grasslands. However, the rocky, shallow-soil grasslands in western and west-central Kansas (to which XLPs bear the greatest resemblance) are an extraordinary case. **In these sites, unlike the majority of prairies in central North America developed on deep, fertile Mollisols (Weaver, 1954), edaphic conditions are an important factor limiting plant growth (including recruitment, survival, and reproduction of woody taxa).** Combination of these edaphic conditions with the low mean annual precipitation in this region [55 to 65 cm (Hladek et al., 1972; Heitschmidt et al., 1970)] suggests that climate and edaphic conditions interact to produce the xeric conditions responsible for the absence or limited occurrence of woody taxa in these climatic/edaphic climax grasslands. Furthermore, low total plant cover [~ 10 to 25% (Heitschmidt et al., 1970; Hladek et al., 1972)] in these rocky prairies makes it unlikely that they are even capable of supporting a fire.

In summary, XLPs of eastern United States are either edaphic climaxes (Ketona Dolomite sites) or subclimaxes (sensu Weaver and Clements, 1938) that originated from and are perpetuated by anthropogenic disturbance (burning, cutting, and/or agricultural practices).   Conversely, rocky, shallow-soil grasslands in the Central Plains and Prairies Formation originated from interaction of regional climatic and local edaphic condtions. Thus, the primary difference between these two vegetation types is in the importance of climate in the origin and maintenance of rocky, shallow-soil grasslands in the Central Plains and Prairies formation and of anthropogenic disturbance in the origin and maintenance of the vast majority of XLPs in eastern United States.

DIRECTIONS FOR FUTURE RESEARCH

Additional studies are needed to further our understanding of the flora, vegetation, physical environmental characteristics, origin, and maintenance of XLPs in eastern United States. Phytogeographical analysis of the collective flora of this vegetation type in eastern United States would provide insight into the origins of the XLP flora and afford an opportunity for floristic comparisons among regions. Vegetation data are lacking for many regions, including the Central Lowland in Missouri and Indiana, the Interior Low Plateaus in Indiana, the Appalachian Plateaus in Ohio, and the Ridge and Valley in Bibb County, Alabama. Additional dendrochronological studies are necessary for a more complete evaluation of the historical role of fire in the origin and maintenance of XLPs. Soil analyses in XLPs and adjacent habitats could provide insight into the relative importance of edaphic conditions in curbing encroachment of woody taxa into XLPs. Analyses of soil profiles in XLPs may afford inferences about the factors (e.g. erosion) responsible for current edaphic conditions. Aerial photographic studies, particularly for sites in southeastern United States, would allow further assessment of XLP stability under a variety of topographic, edaphic, and climatic conditions. Soil seed bank studies could determine the feasibility of restoring XLPs in areas where considerable forest encroachment has resulted in elimination or reduction of the XLP flora. Finally, further comparisons (via floristic, vegetation, and physical environmental data) of XLPs, "cedar glades" in Wisconsin (sensu Curtis, 1959), and dry lime prairies

(sensu Anderson, 1954) and loess hill prairies (sensu Ugarte, 1987) in the upper Midwest would facilitate development of a comprehensive classification system for xeric grasslands of eastern United States.

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Table 6.1 Summary of dominant taxa in xeric limestone prairies of eastern United States. Data (quantitative and qualitative) are organized by physiographic province (sensu Fenneman 1938, 1946 [1949]).

Physiographic Province	Dominant Taxon	Reference	Data
Ozark Plateaus			
	Sporobolus neglectus	Hall, 1955	frequency
	Schizachyrium scoparium	Kucera and Martin, 1957	avg. cover
	Schizachyrium scoparium	Keeland, 1978	avg. cover
	*Schizachyrium scoparium**	Skinner, 1979	avg. frequency
	Sporobolus neglectus[†]	Skinner, 1979	avg. frequency
	Schizachyrium scoparium	Hicks, 1981	avg. importance value
	Schizachyrium scoparium	Logan, 1992	semi-quantitative
	Schizachyrium scoparium	Ver Hoef et al., 1993	avg. GM
	Panicum virgatum	George, 1996	avg. cover
	Schizachyrium scoparium	George, 1996	avg. cover
Central Lowland			
	Schizachyrium scoparium	Maxwell, 1987	qualitative
	Schizachyrium scoparium	Heikens, 1991	avg. cover
	Schizachyrium scoparium	McClain and Ebinger, 2002	avg. cover
	Bouteloua curtipendula	McClain and Ebinger, 2002	avg. cover
	Hedyotis nigricans	McClain and Ebinger, 2002	avg. cover

Table 6.1 (continued)

Interior Low Plateaus

Schizachyrium scoparium	Braun, 1928	avg. frequency
Andropogon gerardii	Braun, 1928	avg. frequency
Schizachyrium scoparium	Baskin and Baskin, 1977	frequency
Schizachyrium scoparium[‡]	Kurz, 1981	avg. frequency
Schizachyrium scoparium	DeSelm, 1988	importance values
Schizachyrium scoparium	Heikens, 1991	avg. cover
Silphium terebinthinaceum	Heikens, 1991	avg. cover
Schizachyrium scoparium	DeSelm, 1991	avg. cover
Schizachyrium scoparium	DeSelm and Webb, 1997	avg. cover
Sporobolus cryptandrus	DeSelm and Webb, 1997	avg. cover
Schizachyrium scoparium	Table 3.5	avg. cover
Andropogon gerardii	Table 3.5	avg. cover
Silphium terebinthinaceum	Table 3.5	avg. cover

Ridge and Valley

Bouteloua curtipendula	Bartgis, 1993	avg. cover
Solidago arguta var. *harrisii*	Bartgis, 1993	qualitative
Monarda fistulosa var. *brevis*	Bartgis, 1993	qualitative
Paronychia virginica	Bartgis, 1993	qualitative
Schizachyrium scoparium	DeSelm, 1993	avg. cover
Andropogon gerardii	DeSelm, 1993	avg. cover

Table 6.1 (continued)

Schizachyrium scoparium	Ludwig, 1999	avg. cover
Andropogon gerardii	Ludwig, 1999	avg. cover
Schizachyrium scoparium	Allison and Stevens, 2001	qualitative
Bouteloua curtipendula	Laughlin and Uhl, 2003	semi-quantitative

Coastal Plain

Schizachryium scoparium	Harper, 1920	qualitative

* Based on frequency data collected in 0.01 and 0.1-m^2 quadrats centered around the rare focal species *Stenosiphon linifolius*.

[†] Based on frequency data collected in 0.01 and 0.1-m^2 quadrats centered around the rare focal species *Penstemon cobaea* var. *purpureus* and *Centaurium texense*.

[‡] Tweny-three of 32 sample sites were located in the Interior Low Plateaus and nine in the Ozark Plateaus; however, data were not stratified by site.

Table 6.2 Comparison of characteristics of xeric limestone prairies, limestone cedar glades, and deep-soil barrens of eastern United States (modified from Baskin et al., 1994).

Characteristic	Xeric Limestone Prairies	Limestone Cedar Glades	Deep-Soil Barrens*
General Distribution	broadly distributed in eastern United States (primarily unglaciated, but also glaciated)	north-central southeastern United States (unglaciated)	north-central southeastern United States (unglaciated)
States	Missouri, Illinois, Indiana, Ohio, Pennsylvania, West Virginia, Virginia, Kentucky, Tennessee, Georgia, Alabama, Arkansas	Kentucky, Tennessee, Alabama, Georgia, Virginia	Kentucky and Tennessee
Physiographic Provinces	Ozark Plateaus, Central Lowland, Interior Low Plateaus, Appalachian Plateaus, Ridge and Valley, Coastal Plain	Interior Low Plateaus and Ridge and Valley	Interior Low Plateaus
Geologic Substrates	limestone, dolomite, and calcareous shale (Cambrian to Tertiary)	limestone and dolomite (Mississippian, Silurian, and Ordovician)	limestone (some sandstone and shale) (Mississippian)
Soil Orders	Alfisols, Mollisols, Ultisols, Inceptisols, and Vertisols	Alfisols and Mollisols	Alfisols and Ultisols
Soil Depth to Bedrock (m)	≤ 0.1 to ~ 1 m	≤ 0.25 m	≥ 1 m
Exposed Rock	flagstone, gravel, and talus; some benches	pavement, flagstone, and gravel	none

189

Table 6.2 (continued)

Dominant Graminoids	native C_4 perennials	native C_4 annuals	native C_4 perennials
Characteristic Forbs	native C_3 perennials; some C3 summer annuals	native C_3 winter and summer annuals and perennials	native C_3 perennials
Dominance of Forbs	rarely	often	never
Cryptogams Important	no	yes	no
Cover of Woody Taxa	low to moderate	low	moderate to high
Families with Highest Taxonomic Richness in Flora	Asteraceae, Poaceae, Fabaceae, Cyperaceae	Asteraceae, Poaceae, Cyperaceae, Fabaceae	Asteraceae, Poaceae, Fabaceae, Cyperaceae
Majority of Taxa (geographic distribution/ photosynthetic pathway/life form)	intraneous C_3 hemicryptophytes	intraneous C_3 hemicryptophytes	intraneous C_3 hemicryptophytes

Table 6.2 (continued)

Floristic Geographic Affinity	southern	western	southern
Percentage Nonnative Taxa	very low	low to moderate	low
Endemic/Near Endemic Taxa	13 Ozark Plateaus (Missouri and Arkansas) Ridge and Valley (West Virginia, Virginia, Alabama)	21 throughout distribution	none
Origin	primarily anthropogenic; a few may be natural, edaphic climax	natural, edaphic climax	anthropogenic
Stability	high to low	high	low

＊ Contains only data from deep-soil barrens in the southwestern Pennyroyal Plain in Kentucky a

Vascular flora of 18 xeric limestone prairies in the Interior Low Plateaus physiographic province in Kentucky. Taxonomy is in accordance with USDA, NRCS (2004), with the exception of *Elymus glabriflorus* var. *australis*, which is based on the treatment by Campbell (1995). The name and authority for each taxon is followed, in parentheses, by the photosynthetic pathway (C3, C4 or CAM), life form (Ph=phanerophyte, Ch=chamaephyte, H=hemicryptophyte, Cr=cryptophyte, and Th=therophyte; HP=holoparasite), geographic affinity (I=intraneous, EN=extraneous northern, ES=extraneous southern, EE=extraneous eastern, EW=extraneous western, and X=introduced), and conservation status in the state of Kentucky (E=endangered, T=threatened, and S=special concern) (KSNPC 2002) in bold-faced type. Number in bold-faced type following the final parenthesis refers to number of sites in which species was recorded.

Division Pteridophyta, ferns and fern allies

Adiantaceae
Pellaea atropurpurea (L.) Link (C3, H, I) **5**

Aspleniaceae
Asplenium platyneuron (L.) B.S.P. (C3, H, I) **3**

Ophioglossaceae
Ophioglossum englemannii Prantl (C3, Cr, ES) **2**

Division Pinophyta, conifers

Cupressaceae
Juniperus virginiana L. (C3, Ph, I) **18**

Pinaceae
Pinus virginiana Mill. (C3, Ph, I) **5**

Division Magnoliophyta, flowering plants
Class Magnoliopsida (Dicots)

Acanthaceae
Ruellia humilis Nutt. (C3, H, I) **18**

Aceraceae
Acer rubrum L. (C3, Ph, I) **9**
Acer saccharum Marshall (C3, Ph, I) **11**

Anacardiaceae
Rhus aromatica Aiton (C3, Ph, I) **7**

Rhus copallinum L. (C3, Ph, I) **12**
Rhus glabra L. (C3, Ph, I) **2**
Toxicodendron radicans (L.) Kuntze (C3, Ph, I) **9**

Apiaceae
Daucus carota L. (C3, H, X) **1**
Eryngium yuccifolium Michx. (C3, Cr, ES) **10**
Oxypolis rigidior (L.) Raf. (C3, Cr, I) **1**
Sanicula canadensis L. (C3, Cr, I) **7**
Thaspium barbinode (Michx.) Nutt. (C3, Cr, I) **12**
Zizia aptera (Gray) Fernald (C3, H, I) **10**
Zizia aurea (L.) W.D.J. Koch (C3, Cr, I) **6**

Apocynaceae
Apocynum cannabinum L. (C3, H, I) **14**

Aristolochiaceae
Aristolochia serpentaria L. (C3, H, I) **12**

Asclepiadaceae
Asclepias tuberosa L. (C3, H, I) **1**
Asclepias verticillata L. (C3, H, I) **12**
Asclepias viridiflora L. (C3, H, I) **17**
Matelea obliqua (Jacq.) Woodson (C3, I, ES) **4**

Asteraceae
Achillea millefolium L. (C3, H, I) **1**
Ageratina altissima (L.) King & H.E. Robins. (C3, H, I) **1**
Ambrosia artemisiifolia L. (C3, Th, I) **10**
Ambrosia trifida L. (C3, Th, I) **2**
Arnoglossum atriplicifolium (L.) H.E. Robins. (C3, H, I) **2**
Antennaria plantaginifolia (L.) Richards (C3, Ch, I) **2**
Brickellia eupatoriodies (L.) Shinners (C3, H, I) **16**
Centaurea biebersteinii DC. (C3, H, X) **1**
Cirsium discolor (Muhl. ex Willd.) Spreng. (C3, H, I) **6**
Conoclinium coelestinum (L.) DC. (C3, H, ES) **3**
Conyza canadensis (L.) Cronquist (C3, Th, I) **8**
Coreopsis tripteris L. (C3, H, EN) **14**
Echinacea simulata McGregor (C3, H, EW) **14**
Erigeron strigosus Muhl. ex Willd. (C3, H, I) **6**
Eupatorium altissimum L. (C3, H, ES) **13**
Eupatorium hyssopifolium L. (C3, H, ES) **1**
Eupatorium perfoliatum L. (C3, H, I) **2**
Euthamia graminifolia (L.) Nutt. (C3, H, EN) **4**
Helenium autumnale L. (C3, H, I) **7**
Helianthus divaricatus L. (C3, Cr, I) **4**

Helianthus hirsutus Raf. (C3, Cr, I) **18**
Helianthus microcephalus Torr. & Gray (C3, H, ES) **5**
Helianthus mollis Lam. (C3, Cr, I) **4**
Helianthus occidentalis Riddell (C3, Cr, I) **3**
Heliopsis helianthoides (L.) Sweet (C3, Cr, I) **3**
Leucanthemum vulgare Lam. (C3, H, X) **4**
Liatris aspera Michx. (C3, Cr, EW) **10**
Liatris cylindracea Michx. (C3, Cr, EW, **T**) **2**
Liatris spicata (L.) Willd. (C3, Cr, I) **8**
Liatris squarrosa (L.) Michx. var. *squarrosa* (C3, Cr, ES) **15**
Liatris squarrulosa Michx. (C3, Cr, ES) **3**
Lonactis linariifolius (L.) Greene (C3, H, I) **4**
Oligoneuron rigidum (L.) Small var. *glabratum* (E.L. Braun) Nesom (C3, H, EW) **11**
Packera anonyma (Wood) W.A. Weber & A. Löve (C3, H, ES) **5**
Parthenium integrifolium L. (C3, H, I) **12**
Prenanthes aspera Michx. (C3, H, EW, **E**) **1**
Ratibida pinnata (Vent.) Barnhart (C3, H, EW) **10**
Rudbeckia fulgida Aiton (C3, H, I) **12**
Rudbeckia hirta L. (C3, H, I) **1**
Senecio glabellus Poir. (C3, Th, ES) **1**
Sericocarpus asteroides (L.) B.S.P. (C3, H, EE) **1**
Silphium laciniatum L. (C3, H, EW, **E**) **1**
Silphium pinnatifidum Elliott (C3, H, ES, **S**) **3**
Silphium terebinthinaceum Jacq. (C3, H, EW) **5**
Silphium trifoliatum L. var. *trifoliatum* (C3, H, EE) **17**
Solidago bicolor L. (C3, H, I) **1**
Solidago canadensis L. (C3, H, I) **6**
Solidago juncea Aiton (C3, H, I) **1**
Solidago nemoralis Aiton (C3, H, I) **18**
Solidago speciosa Nutt. var. *erecta* (Pursh) MacMill. (C3, H, ES) **3**
Solidago sphacelata Raf. (C3, H, ES) **1**
Solidago ulmifolia Muhl. ex Willd. var. *ulmifolia* (C3, H, I) **11**
Symphyotrichum cordifolium (L.) Nesom (C3, H, I) **2**
Symphyotrichum dumosum (L.) Nesom (C3, H, I) **1**
Symphyotrichum laeve (L.) A. & D. Löve var. *concinum* (Willd.) Nesom (C3, H, I) **2**
Symphyotrichum laeve (L.) A. & D. Löve var. *laeve* (C3, H, I) **12**
Symphyotrichum laterifolium (L.) A. & D. Löve (C3, H, I) **1**
Symphyotrichum novae-angliae (L.) Nesom (C3, H, I) **4**
Symphyotrichum oblongifolium (Nutt.) Nesom (C3, H, I) **2**
Symphyotrichum oolentangiense (Riddell) Nesom (C3, H, EW) **2**
Symphyotrichum patens (Aiton) Nesom var. *patens* (C3, H, I) **12**
Symphyotrichum pilosum (Willd.) Nesom var. *pilosum* (C3, H, I) **4**
Symphyotrichum pilosum (Willd.) Nesom var. *pringlei* (Gray) Nesom (C3, H, EN) **12**
Symphyotrichum sericeum (Vent.) Nesom (C3, H, ES, **S**) **6**
Symphyotrichum shortii (Lindl.) Nesom (C3, H, I) **1**
Symphyotrichum undulatum (L.) Nesom (C3, H, EE) **1**

Symphyotrichum urophyllum (Lindl.) Nesom (C3, H, I) **12**
Taraxacum officinale G. H. Weber ex Wiggers (C3, H, X) **2**
Verbesina virginica L. (C3, H, I) **4**
Vernonia gigantea (Walter) Trel. (C3, H, I) **4**

Betulaceae
Corylus americana Walter (C3, Ph, EN) **2**
Ostrya virginiana (Mill.) Koch (C3, Ph, I) **16**

Bignoniaceae
Bignonia capreolata L. (C3, Ph, I) **1**
Campsis radicans (L.) Seem. ex Bureau (C3, Ph, ES) **1**

Boraginaceae
Heliotropium tenellum (Nutt.) Torr. (C3, Th, ES) **9**
Lithospermum canescens (Michx.) Lehm. (C3, H, I) **16**

Brassicaceae
Arabis laevigata (Muhl. ex Willd.) Poir. var. *laevigata* (C3, H, I) **1**
Cardamine hirsuta L. (C3, Th, X) **1**
Draba verna L. (C3, Th, X) **1**
Leavenworthia exigua Rollins var. *laciniata* Rollins (C3, Th, ES, **T**) **1**
Leavenworthia uniflora (Michx.) Britton (C3, H, I) **2**

Cactaceae
Opuntia humifusa (Raf.) Raf. (CAM, S, ES) **3**

Campanulaceae
Lobelia spicata Lam. (C3, H, I) **18**

Caprifoliaceae
Lonicera japonica Thunb. (C3, Ph, X) **4**
Symphoricarpos orbiculatus Moench (C3, Ph, I) **6**
Viburnum prunifolium L. (C3, Ph, I) **4**
Viburnum rufidulum Raf. (C3, Ph, ES) **6**

Caryophyllaceae
Dianthus armeria L. (C3, Th, X) **1**
Minuartia patula (Michx.) Mattf. (C3, Th, I) **1**

Celastraceae
Celastrus scandens L. (C3, Ph, I) **7**

Clusiaceae
Hypericum denticulatum Ellis (C3, H, EE) **2**
Hypericum dolabriforme Vent. (C3, H, ES) **14**

Hypericum hypericoides (L.) Crantz (C3, H, ES) **2**
Hypericum prolificum L. (C3, Ph, I) **6**
Hypericum punctatum L. (C3, H, I) **5**
Hypericum sphaerocarpum L. (C3, H, EW) **2**

Convolvulaceae
Calystegia spithamaea (L.) Pursh (C3, H, I) **1**
Ipomoea pandurata (L.) G.F. Mey. (C3, Cr, I) **12**

Cornaceae
Cornus drummondii C. A. Mey. (C3, Ph, EW) **4**
Cornus florida L. (C3, Ph, I) **10**

Crassulaceae
Sedum ternatum Michx. (C3, Th, I) **2**

Cuscutaceae
Cuscuta cuspidata Engelm. (HP, Th, EW) **1**

Ebenaceae
Diospyros virginiana L. (C3, Ph, I) **18**

Ericaceae
Vaccinium arboreum Marshall (C3, Ph, ES) **4**
Vaccinium pallidum Aiton (C3, Ph, I) **1**

Euphorbiaceae
Acalypha gracilens Gray (C3, Th, I) **6**
Acalypha virginica L. (C3, Th, I) **1**
Chamaesyce nutans (Lag.) Small (C3, Th, I) **8**
Croton capitatus Michx. (C3, Th, I) **12**
Croton monanthogynus Michx. (C3, Th, ES) **7**
Euphorbia corollata L. (C3, Cr, I) **18**
Euphorbia dentata Michx. (C3, Th, I) **3**

Fabaceae
Cercis canadensis L. (C3, Ph, I) **18**
Chamaecrista fasciculata (Michx.) Greene var. *fasciculata* (C3, Th, I) **11**
Coronilla varia L. (C3, Th, X) **1**
Dalea candida Michx. ex Willd. var. *candida* (C3, H, EW) **1**
Dalea purpurea Vent. var. *purpurea* (C3, H, EW, **S**) **5**
Desmodium canescens (L.) DC. (C3, H, I) **2**
Desmodium ciliare (Muhl. ex Willd.) DC. (C3, H, I) **12**
Desmodium glabellum (Michx.) DC. (C3, H, ES) **4**
Desmodium paniculatum (L.) DC. var. *paniculatum* (C3, H, I) **1**

Desmodium rotundifolium DC. (C3, H, I) **1**
Desmodium sessilifolium (Torr.) Torr. & Gray (C3, H, I) **1**
Desmanthus illinoensis (Michx.) MacMill. ex B.L. Robins. & Fern. (C3, Ph, EW) **1**
Galactia volubilis (L.) Britton (C3, H, I) **15**
Gleditsia triacanthos L. (C3, Ph, I) **3**
Lespedeza capitata Michx. (C3, H, I, **S**) **3**
Lespedeza cuneata (Dum.Cours.) G. Don (C3, H, X) **2**
Lespedeza violacea (L.) Pers. (C3, H, I) **2**
Lespedeza procumbens L. (C3, H, I) **3**
Lespedeza repens (L.) W. Bartram (C3, H, I) **1**
Lespedeza virginica (L.) Britton (C3, H, I) **16**
Melilotus alba Medikus (C3, H, X) **8**
Orbexilum pedunculatum (Mill.) Rydb. var. *psoralioides* (Walt.) Isley (C3, Cr, ES) **1**
Robinia pseudoacacia L. (C3, Ph, I) **2**
Senna marilandica (L.) Link (C3, H, I) **4**
Strophostyles umbellata (Muhl. ex Willd.) Britton (C3, Cr, ES) **3**
Stylosanthes biflora (L.) B.S.P. (C3, H, ES) **6**
Tephrosia virginiana (L.) Pers. (C3, H, I) **8**
Trifolium repens L. (C3, H, X) **1**
Vicia villosa Roth (C3, H, X) 2

Fagaceae
Fagus grandifolia Ehrh. (C3, Ph, I) **5**
Quercus alba L. (C3, Ph, I) **2**
Quercus imbricaria Michx. (C3, Ph, I) **3**
Quercus marilandica Muenchh. (C3, Ph, ES) **13**
Quercus muehlenbergii Engelm. (C3, Ph, I) **13**
Quercus prinus L. (C3, Ph, I) **1**
Quercus rubra L. (C3, Ph, I) **10**
Quercus stellata Wangenh. (C3, Ph, I) **15**
Quercus velutina Lam. (C3, Ph, I) **6**

Gentianaceae
Frasera caroliniensis Walters (C3, H, I) **2**
Gentiana flavida Muhl. ex Nutt. (C3, H, I, **E**) **1**
Gentianella quinquefolia (L.) Small ssp. *occidentalis* (Gray) J. Gillett (C3, H, I) **9**
Sabatia angularis (L.) Pursh (C3, H, I) **15**

Juglandaceae
Carya alba (L.) Nutt. ex Ellis (C3, Ph, I) **3**
Carya tomentosa Nutt. (C3, Ph, I) **3**
Juglans nigra L. (C3, Ph, I) **13**

Lamiaceae
Blephilia ciliata (L.) Benth. (C3, H, I) **13**
Isanthus brachiatus B.S.P. (C3, Th, I) **13**

Lycopus americanus Muhl. ex W. Bartram (C3, H, I) **1**
Monarda fistulosa L. (C3, H, I) **13**
Physostegia virginiana (L.) Benth. (C3, H, I) **18**
Prunella vulgaris L. var. *lanceolata* (Barton) Fernald (C3, H, I) **16**
Pycnanthemum pycnanthemoides (Leavenw.) Fernald (C3, H, ES) **2**
Pycnanthemum tenuifolium Schrad. (C3, H, I) **11**
Salvia lyrata L. (C3, H, I) **5**
Scutellaria elliptica Muhl. (C3, H, I) **3**
Scutellaria parvula Michx. var. *australis* Fassett (C3, Cr, I) **8**
Scutellaria parvula Michx. var. *missouriensis* (Torr.) Goodman & Lawson (C3, Cr, I) **2**
Trichostema dichotomum L. (C3, Th, I) **1**

Lauraceae
Sassafrass albidum (Nutt.) Nees (C3, Ph, I) **11**

Linaceae
Linum medium (Planch.) Britton (C3, H, I) **1**
Linum sulcatum Riddell (C3, Th, EW) **16**
Linum virginianum L. (C3, H, I) **2**

Lythraceae
Cuphea viscosissima Jacq. (C3, Th, ES) **2**

Magnoliaceae
Liriodendron tulipifera L. (C3, Ph, I) **6**

Malvaceae
Malvastrum hispidum (Pursh) Hochr. (C3, Th, EW, **T**) **1**

Oleaceae
Forestiera ligustrina (Michx.) Poir. (C3, Ph, ES, **T**) **1**
Fraxinus americana L. (C3, Ph, I) **18**
Ligustrum sinense Lour. (C3, Ph, X) **1**

Onagraceae
Gaura biennis L. (C3, H, EE) **4**
Gaura filipes Spach (C3, H, ES) **13**
Oenothera biennis L. (C3, H, I) **1**

Oxalidaceae
Oxalis stricta L. (C3, H, I) **1**
Oxalis violacea L. (C3, H, I) **1**

Papaveraceae
Sanguinaria canadensis L. (C3, Cr, I) **1**

Passifloraceae
Passiflora lutea L. (C3, H, I) **2**

Plantaginaceae
Plantago aristata Michx. (C3, Th, I) **1**
Plantago patagonica Jacq. (C3, Th, X) **1**
Plantago virginica L. (C3, Th, I) **4**

Platanaceae
Platanus occidentalis L. (C3, Ph, I) **1**

 Polemoniaceae
Phlox pilosa L. ssp. *pilosa* (C3, H, I) **8**

Polygalaceae
Polygala verticillata L. (C3, Th, I) **13**

Portulacaceae
Talinum calcaricum Ware (C3, H, ES, **E**) **1**

Primulaceae
Anagallis arvensis L. (C3, Th, X) **3**
Dodecatheon meadia L. (C3, H, I) **1**
Lysimachia lanceolata Walter (C3, H, I) **6**

Ranunculaceae
Anemone virginiana L. (C3, H, I) **13**
Clematis pitcheri Torr. & Gray var. *pitcheri* (C3, Ph, EW) **1**
Delphinium carolinianum Walter ssp. *calciphilum* Warnock (C3, H, ES, **T**) **1**
Thalictrum revolutum DC. (C3, H, I) **3**
Thalictrum thalictroides (L.) Eames & Boivin (C3, Cr, I) **2**

Rhamnaceae
Ceanothus americanus L. (C3, Ph, I) **3**
Rhamnus caroliniana Walter (C3, Ph, ES) **18**

Rosaceae
Agrimonia rostellata Wallr. (C3, H, I) **6**
Amelanchier arborea (Michx. f.) Fernald (C3, Ph, I) **6**
Crataegus L. [sp(p).] (C3, Ph) **5**
Fragaria virginiana Duchesne (C3, H, I) **5**
Porteranthus stipulatus (Muhl. ex Willd.) Britton (C3, H, I) **1**
Potentilla simplex Michx. (C3, H, I) **17**
Prunus americana Marshall (C3, Ph, I) **1**
Prunus serotina Ehrh. (C3, Ph, I) **7**
Rosa carolina L. (C3, Ph, I) **16**

Rosa multiflora Thunb. (C3, Ph, X) **4**
Rubus L. [sp(p).] (C3, Ph) **9**

Rubiaceae
Diodia teres Walter (C3, Th, I) **4**
Galium circaezans Michx. (C3, H, I) **11**
Galium pilosum Aiton (C3, H, I) **7**
Galium triflorum Michx. (C3, H, I) **1**
Hedyotis nigricans (Lam.) Fosberg (C3, Th, EW) **11**
Houstonia canadensis Willd. ex Roemer & J.A. Schultes (C3, H, EN) **13**

Salicaceae
Salix humilis Marshall (C3, Ph, I) **1**

Santalaceae
Comandra umbellata (L.) Nutt. (C3, Cr, I) **1**

Scrophulariaceae
Agalinis auriculata (Michx.) Blake (C3, Th, EW, **E**) **1**
Agalinis gattingeri (Small) Small (C3, Th, EW) **4**
Agalinis tenuifolia (Vahl) Raf. (C3, Th, I) **9**
Aureolaria flava (L.) Farw. (C3, Cr, I) **2**
Buchnera americana L. (C3, H, ES) **1**
Castilleja coccinea (L.) Spreng. (C3, Th, I, **E**) **3**
Pedicularis canadensis L. (C3, H, I) **3**
Penstemon digitalis Nutt. ex Sims (C3, H, I) **1**
Penstemon hirsutus (L.) Willd. (C3, H, I) **2**

Simaroubaceae
Ailanthus altissima (Mill.) Swingle (C3, Ph, X) **1**

Solanaceae
Physalis virginiana Mill. (C3, Cr, ES) **12**
Solanum carolinense L. (C3, Cr, I) **1**

Ulmaceae
Celtis occidentalis L. (C3, Ph, I) **1**
Celtis tenuifolia Nutt. (C3, Ph, I) **17**
Ulmus alata Michx. (C3, Ph, ES) **6**
Ulmus rubra Muhl. (C3, Ph, I) **3**

Verbenaceae
Phryma leptostachya L. (C3, H, I) **1**
Verbena simplex Lehm. (C3, H, I) **6**

Violaceae
Hybanthus concolor (T. Forst.) Spreng. (C3, H, I) **3**
Viola egglestonii Brainerd (C3, H, ES, **S**) **9**
Viola palmata L. (C3, H, I) **7**
Viola pedata L. (C3, H, I) **12**
Viola sagittata Aiton (C3, H, I) **2**

Vitaceae
Parthenocissus quinquefolia (L.) Planch. (C3, Ph, I) **9**
Vitis aestivalis Michx. (C3, Ph, I) **11**

Division Magnoliophyta, flowering plants
Class Liliopsida (Monocots)

Agavaceae
Manfreda virginica (L.) Salisb. ex Rose (CAM, H, ES) **16**

Cyperaceae
Carex complanata Torr. & Hook. (C3, Cr, I) **9**
Carex crawei Dewey (C3, Cr, I, **S**) **14**
Carex glaucodea Tuckerman ex Olney (C3, H, I) **8**
Carex juniperorum Catling, Reznicek & Crins (C3, H, EN, **E**) **2**
Carex meadii Dewey (C3, Cr, I) **16**
Carex pensylvanica Lam. (C3, Cr, I) **2**
Carex umbellata Schkuhr ex Willd. (C3, H, I) **12**
Eleocharis compressa Sullivant (C3, Cr, ES) **3**
Eleocharis tenuis (Willd.) J.A. Schultes (C3, Cr, I) **3**
Fimbristylis puberula (Michx.) Vahl var. *puberula* (C4, Cr, I, **T**)
Scirpus pendulus Muhl. (C3, H, I) **8**
Scleria oilgantha Michx. (C3, Cr, I) **13**
Scleria pauciflora Muhl. (C3, Cr, I) **2**

Dioscoreaceae
Dioscorea quaternata J.F. Gmel (C3, Ph, I) **2**

Iridaceae
Hypoxis hirsuta (L.) Coville (C3,Cr, I) **2**
Iris cristata Aiton (C3, Cr, I) **1**
Sisyrinchium albidum Raf. (C3, H, I) **13**

Liliaceae
Allium cernuum Roth (C3, Cr, EN) **8**
Maianthemum stellatum (L.) Link (C3, Cr, I, **E**) **1**
Nothoscordum bivalve (L.) Britton (C3, Cr, I) **1**
Polygonatum biflorum (Walter) Elliott (C3, Cr, I) **10**
Uvularia perfoliata L. (C3, Cr, I) **1**

Orchidaceae
Cypripedium candidum Muhl. ex Willd. (C3, Cr, EN, **E**) **2**
Cypripedium pubescens Willd. var. *pubescens* (C3, Cr, I) **2**
Spiranthes lacera (Raf.) Raf. var. *gracilis* (Bigelow) Leur (C3, H, I) **4**
Spiranthes magnicamporum Sheviak (C3, H, EW, **T**) **9**
Tipularia discolor (Pursh) Nutt. (C3, Cr, I) **1**

Poaceae
Andropogon gerardii Vitman (C4, H, I) **17**
Aristida longispica Poir. (C4, Th, I) **1**
Aristida oligantha Michx. (C4, Th, I) **2**
Aristida purpurascens Poir. var. *purpurascens* (C4, H, I) **13**
Bouteloua curtipendula (Michx.) Torr. (C4, H, I, **S**) **3**
Brachyelytrum erectum (Schreb.) P. Beauv. (C3, H, I) **1**
Bromus pubescens Muhl. ex Willd. (C3, H, I) **1**
Danthonia spicata (L.) P. Beauv. ex Roem. & J.A. Schult. (C3, H, I) **14**
Dichanthelium acuminatum (Sw.) Gould & C.A. Clark var. *fasciculatum* (Torr.)
   Freckmann (C3, H, I) **15**
Dichanthelium boscii (Poir.) Gould & C.A. Clark (C3, H, I) **12**
Dichanthelium commutatum (J.A. Schultes) Gould (C3, H, I) **1**
Dichanthelium dichotomum (L.) Gould var. *dichotomum* (C3, H, I) **6**
Dichanthelium sphaerocarpon (Ellis) Gould (C3, H, I) **3**
Dichanthelium villosissimum (Nash) Freckman (C3, H, I) **1**
Elymus glabriflorus Scribn. & Ball var. *australis* (Scribn. & C.R. Ball) J.J.N. Campbell
(C3, H, I) **5**
Lolium arundinaceum (Schreb.) J.J. Darbyshire (C3, H, X) **3**
Muhlenbergia capillaris (Lam.) Trin. (C4, H, I) **2**
Muhlenbergia cuspidata (Torr. ex Hook.) Rydb. (C4, H, EW, **T**) **2**
Muhlenbergia sylvatica Torr. ex Gray (C4, H, I) **2**
Panicum anceps Michx. (C4, Cr, ES) **2**
Panicum capillare L. (C4, Th, I) **2**
Panicum flexile (Gattinger) Scribn. (C4, Th, I) **14**
Panicum linearifolium (Scribn. ex Nash) Gould (C3, H, I) **13**
Paspalum leave Michx. (C4, H, I) **1**
Schizachyrium scoparium (Michx.) Nash (C4, H, I) **18**
Setaria glauca (L.) P. Beauv. (C4, Th, X) **2**
Sorghastrum nutans (L.) Nash (C4, Cr, I) **16**
Sporobolus compositus (Poir.) Merr. var. *compositus* (C4, H, I) **14**
Sporobolus heterolepis (Gray) Gray (C4, H, EW) **1**
Sporobolus vaginiflorus (Torr. ex Gray) Wood, including
   varieties *ozarkanus* (Fernald) Shinners (C4, Th, I) and *vaginiflorus* (C4, Th, I) **18**
Tridens flavus (L.) Hitchcock (C4, H, I) **12**

Smilacaceae
Smilax bona-nox L. (C3, Ph, ES) **16**

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Lawless, P.J., J.M. Baskin, and C.C. Baskin. Analyses of richness, diversity, and similarity in seven xeric limestone prairies in the Interior Low Plateaus physiographic province in Kentucky. Annual meeting of the Botanical Society of America, July 26-31, 2003, Arthur R. Outlaw Convention Center, Mobile, AL.

Lawless, P.J., J.M. Baskin, and C.C. Baskin. Quantitative vegetation analysis of xeric limestone prairies in the Outer Bluegrass and Mississipian Plateaus physiographic regions of Kentucky: A progress report. The tenth symposium on the natural history of lower Tennessee and Cumberland river valleys, March 21-22, 2003, Brandon Springs Group Camp, Land Between the Lakes, TN.

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