

# ATLAS *of the* WISCONSIN PRAIRIE *and* SAVANNA FLORA

THEODORE S. COCHRANE AND HUGH H. ILTIS



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Cover: *Tallgrass prairie cross section, showing principal grasses and forbs, and extent of root development. Original drawing by Bobbie Lively Diebold.*

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## ABSTRACT

This *Atlas of the Wisconsin Prairie and Savanna Flora* treats most of the native vascular plants of Wisconsin grassland and savanna communities from the standpoints of floristics and phytogeography. Included are 341 species and 73 additional subspecies, varieties, and hybrids (discussed and mapped) as well as 103 species and 50 infraspecific taxa and hybrids (discussed or casually mentioned). Part I discusses the physical geography and climate of Wisconsin; the composition of its prairie, barrens, and savanna communities; and the history of its flora. Part II consists of 354 dot maps showing the exact distributions of the taxa as based on herbarium specimens, each accompanied by a statement describing the plant's habitats, abundance, overall distribution, and geo-floristic affinities. One of the practical uses of this work is to help guide ecologists and conservationists in the planning of prairie restorations.

**Key Words:**

Wisconsin, prairie, savanna, grassland, plant distribution, restoration, conservation.



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## PRESENTATION

It is with much pleasure that I see this prairie and savanna atlas come to fruition. This project has developed well beyond its original scope, and the result is a work that will be widely consulted by the many persons and agencies interested in prairie restoration and the Wisconsin flora in general.

This is a notable accomplishment of the University of Wisconsin–Madison Herbarium, officially designated the Wisconsin State Herbarium in 1995. We are now embarking on an era of electronic dissemination of information on the Wisconsin flora. *The Checklist of the Vascular Plants of Wisconsin* (DNR Technical Bulletin 192) was placed online in late summer, 1998 ([www.ies.wisc.edu/herbarium/](http://www.ies.wisc.edu/herbarium/)), and this will form the backbone of multiple additions to follow, such as detailed plant distribution maps (including the maps in this publication), photographs of Wisconsin plant species, plant description data, and access to the growing database of the more than 400,000 herbarium specimens housed in different Wisconsin herbaria. This initiative is being coordinated with other universities and museums, the Wisconsin Department of Natural Resources (DNR), and other interested parties. This kind of collaborative effort will provide much valuable information on key aspects of our state's flora.

**Paul E. Berry**

Director, University of Wisconsin–Madison Herbarium  
(The Wisconsin State Herbarium)

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## FOREWORD

Since the first Midwest Prairie Conference was held in 1968 (which has since evolved into the biennial North American Prairie Conference), there has been a gradual, but steady, increase in the interest of both the general public and government agencies in tallgrass prairie ecology, conservation and restoration. In recent years, this enthusiasm for prairie has spilled over into oak savanna ecosystems as well. The development and popularity of new conferences—the biennial Midwest Oak Savanna Conference, which was first held in Chicago, IL, in 1993, and the North American Savannas and Barrens Conference held in Normal, IL, in 1994—are evidence of this, as is the significant upsurge of interest in private conservation groups and enthusiasm for gardening and landscaping with native plants. Because of the endangered status of both of these ecosystems, many local private conservation groups, as well as state and federal agencies, have made prairie and savanna communities high priority for protection and restoration.

This *Atlas of the Wisconsin Prairie and Savanna Flora* is designed to be an information resource for those planning native prairie and oak savanna restorations and plantings in Wisconsin. The dot range maps provided show the known distributions of native plants in our state and will guide you in selecting species most appropriate for given locations. For best results in matching species to a specific site's characteristics, this atlas should be used in conjunction with its companion publication, *Plant Species Composition of Wisconsin Prairies: an Aid to Selecting Species for Plantings and Restorations* (Henderson 1995a, DNR Technical Bulletin No.188).

Restorations (simply “plantings” in most cases) of these communities have become very popular among private landowners for backyards and rural properties, and among public agencies for parks, wildlife areas, roadsides, and school grounds. Over a half-dozen private companies within or very near to Wisconsin's borders are now specializing in prairie and savanna planting, and are doing well. In addition, a state-sponsored prairie seed farm has been established in Illinois, and one is currently being developed in Wisconsin.

Unfortunately, the availability of information on prairies and savannas in Wisconsin has not kept pace with the upwelling of interest and activity in plantings and restorations. One example is the absence of an atlas of Wisconsin Flora. Without readily available distribution information, prairie and savanna species are frequently being planted outside their natural or historic ranges within Wisconsin. The primary purpose of this atlas project, therefore, is to provide the information needed to begin correcting this problem.

Some individuals planning prairie and savanna plantings may not consider the planting of native species outside their natural/historic ranges to be a problem worth worrying about, given that species ranges are not static in nature. We, however, believe it to be a very important consideration that should not be lightly dismissed.

In the absence of major climatic change or dramatic environmental changes, ranges of plant species tend to be rather stable in the context of human lifespans. (Noted exceptions are recent weedy, mostly Eurasian invaders.) Given the relatively stable climate of Wisconsin, prairie and savanna species have had 6,000 or more years following the last glaciation to recolonize and stabilize their distributions in the state. It is unlikely that any of these species would be significantly expanding their ranges in the state in the next 100 years without direct human assistance. Therefore, the distribution data represented here, which cover the past 150 years, are still very pertinent as to the “natural” ranges of these species, and they should not be ignored in planning native prairie and savanna plantings or restorations. To do otherwise will threaten the long-term integrity of the rich regional variation in prairie and savanna community composition that currently exists across Wisconsin, as well as the unique genetic composition of local populations. Ignoring these geographical ranges also increases the risk of future range distribution data becoming contaminated with artificial range expansions, which will compromise the data’s usefulness to our attempts at understanding the ecology of these species and the prairie/savanna communities, and also in detecting natural range extensions that may occur with future climatic change.

These range maps were produced by the University of Wisconsin–Madison Herbarium with long-term funding from the UW–Madison Department of Botany, and since 1992 from the DNR’s Bureau of Research (now Integrated Science Services), and assistance from the DNR’s Bureau of Endangered Resources. They are in the public domain and may be reproduced as long as credit is given to the authors, the UW–Madison Herbarium, and the DNR.

Of course, no atlas is ever complete. Should you find what appears to be a natural population of any of the species covered in this publication that lies outside the distribution shown, please contact the UW–Madison Herbarium so that the range maps can be updated in the future.

**Richard A. Henderson**

Terrestrial Ecologist and Wildlife and Forestry Researcher, DNR

*Prairie is composed of many different species of native American plants. It appears as an inextricable mass of endlessly variable vegetation. One glories in its beauty, its diversity, and the ever changing pattern of its floral arrangements. But he is awed by its immensity, its complexity, and the seeming impossibility of understanding and describing it. After certain principles and facts become clear, however, one comes not only to know and understand the grasslands but also to delight in them and to love them.*

J. E. Weaver, 1954

*North American Prairie*

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## AUTHORS AND ACKNOWLEDGMENTS

**Theodore S. Cochrane** has been Herbarium Curator at the University of Wisconsin–Madison since 1970, and received his M.S. in botany there in 1983. His research has focused on the identification and distribution of the Wisconsin flora, especially Cyperaceae and Juncaceae, Neotropical Capparidaceae, and selected series of North American *Carex*. For the past 15 years he has been working with Hugh Iltis and Mexican colleagues of the University of Guadalajara on the flora of the Sierra de Manantlán Biosphere Reserve.

**Hugh H. Iltis**, born in Brno, Czechoslovakia, has resided in the U.S. since 1939, receiving his Ph.D. from the Missouri Botanical Garden–Washington University, St. Louis, in 1952. Botanist and environmentalist, he has devoted his life to the study of the flora of Wisconsin, the Neotropical species of Capparidaceae, and is co-describer of the fourth known species of *Zea*, namely *Z. diploperennis*, of the Sierra de Manantlán. He thus became godfather to the establishment of the Manantlán Biosphere Reserve, and has long been a strong advocate of what is now known as Biophilia, the gene-based need for contact with nature and natural patterns. A well-known fighter for nature preservation and population control, Dr. Iltis was a Professor of Botany at the University of Wisconsin–Madison and Director of the Herbarium from 1955 to 1993, where he is now emeritus.

This *Atlas of the Wisconsin Prairie and Savanna Flora* was compiled and produced at the University of Wisconsin–Madison Herbarium. It is part of a long-term project to map all the plant species of Wisconsin, a goal supported for some 75 years by the University of Wisconsin–Madison, Department of Botany. The prairie and savanna atlas, specifically, has been supported since its inception in 1992 by the University of Wisconsin–Madison Department of Botany and the Wisconsin Department of Natural Resources, Bureau of Research (now Integrated Science Services). Richard A. Henderson, terrestrial ecologist and wildlife and forestry researcher, conceived the idea of an atlas, provided the impetus by supplying the initial list of species to be included, and arranged for funding to hire mappers. We are most thankful for the assistance of the Department of Botany, its Herbarium, and its Multimedia Facility, in furnishing facilities and work time for the authors and illustrator, Kandis Elliot.

Several Wisconsin herbaria and associated botanists have provided considerable assistance over an extended period of time. We are most grateful to the directors, curators, and staff of the various herbaria for permission to survey their collections. Gary A. Fewless, Robert W. Freckmann, Susan Garrity, Neil A. Harriman, the late Rudy G. Koch, Neil T. Luebke, Katherine D. Rill, Joseph R. Rohrer, and Peter J. Salamun were at all times most gracious in permitting us to invade their respective herbaria while we were working on atlas projects, as was Anita F. Cholewa of the University of Minnesota Herbarium. Some herbaria, especially those of the Milwaukee Public Museum, University of Wisconsin–Eau Claire, and University of Wisconsin–Green Bay, were most accommodating in sending large loans of specimens. Other individuals have contributed significantly to different aspects of the atlas. These include Neil Luebke and Kevin J. Lyman (Milwaukee Public Museum), Gary A. Fewless (University of Wisconsin–Green Bay), Thomas A. Meyer (Wisconsin DNR), and William J. Hess and Kim A. Allen (Morton Arboretum), all of whom cooperated by making data available in electronic form. We thank Freckmann for access to his unpublished distribution maps for *Panicum* and Kelly Kearns for furnishing the list of native plant nurseries reproduced in Appendix B. Kandis Elliot, Department of Botany Senior Artist, redrew the base map, prepared the plant drawings from color transparencies, and electronically designed this book. She and James W. Jaeger converted the original pencil working maps to electronic format.

The maps themselves represent the cumulative efforts of numerous individuals, not all of whom can be mentioned here. The earliest mapping was done by N. C. Fassett and his colleagues and students, who during the period 1929 to 1952 published 37 *Preliminary Reports* and four books on Wisconsin plant families (see Appendix C). These works may be thought of as having an atlas function, for each species within them was accompanied by a dot distribution map based on herbarium specimens, a major innovation for a state flora. Unfortunately, scarcely any of Fassett's Wisconsin manuscript maps have survived. The majority of the maps on hand were made by various undergraduate and graduate students and staff (between 1955 and 1970 under the supervision of Hugh H. Iltis), especially by Stephen Gilson in 1964 and 1965, and (since 1970 under the supervision of Theodore S. Cochrane), especially by Christine Williams, Barbara A. Warnes, and Robert H. Read during 1971 and 1972, and by Cochrane from 1970 to the present, in an attempt to map all Wisconsin specimens at the University of Wisconsin–Madison Herbarium. Intensified mapping, both updating earlier maps and completing new maps, was undertaken during the period 1992 to 1994 specifically for this project by Andrew H. Williams, Quentin J. Carpenter, Kristin E. Westad, Joseph P. LeBouton, and Nicholas I. Hill.

Although we have assumed authorship of this book, we are well aware of the large number of people who have contributed in one way or another to this work, especially those former graduate students and colleagues who are cited as authors in Appendix C, Reports on the Flora of Wisconsin. Their original papers have added immeasurably to the foundation upon which this work rests, as have unpublished studies on Wisconsin Heliantheae by T. Melchert, *Rosa* by W. H. Lewis, Scrophulariaceae by F. S. Crosswhite, and Apiaceae by L. Constance and M. E. Mathias. To them we are indebted, as we are to the many colleagues who have provided or verified identifications for specific families or genera. As with any floristic work, the value of the product is wholly dependent upon accurate determination of the specimens. Both authors are intimately acquainted with the flora of Wisconsin, and one of their major concerns has always been the time-consuming task of verifying the identity of each specimen. Probably the majority of the plants mapped were checked by the authors, but we were fortunate to have had the cooperation of numerous colleagues who, having identified specimens for previous studies, contributed to the accuracy of the atlas. Specialists in certain difficult groups, including G. W. Argus (*Salix*), R. J. Bayer (*Antennaria*), H. E. Ballard, Jr. (*Viola*), W. Dietrich (*Oenothera*), A. G. Jones (*Aster*), R. R. Kowal (*Senecio*), A. F. Cholewa (*Sisyrinchium*), and R. W. Freckmann (*Panicum*), have been consulted specifically for this book.

Other people who worked part-time or volunteered to assist on the project include Mark A. Wetter, who double-checked the authorities for plant names, and Merel R. Black, who helped in the search for common names and the compilation of the index. Paul E. Berry read and commented on the introductory text, and Richard A. Henderson reviewed the entire manuscript. Bobbie Lively Diebold granted permission to use the prairie cross section reproduced on the cover. Nancy R. Halliday granted permission to reproduce the prairie gradient illustration (Figure 4). All other illustrations were electronically painted by Kandis Elliot, using 35 mm slides of Wisconsin plants and habitats as reference images. Some of the slides were our own; others were loaned by Kenneth J. Sytsma and Robert R. Kowal. The Part I and Part II openers, which depict two favorite prairies, are by Thomas A. Meyer (Snapper Prairie) and Mark K. Leach (Avoca Prairie and Savanna). Finally, we wish to thank the editorial staff of the Wisconsin DNR, especially Dreux J. Watermolen, Managing Editor at the DNR Bureau of Integrated Science Services, for his assistance in guiding the book through the publication process.

This atlas is based in part upon work supported since 1992 by the Wisconsin Department of Natural Resources. The DNR provided funding for much of the final map production comprising the heart of this volume and helped fund some of the electronic formatting of this book. However, any opinions, conclusions, or recommendations are those of the authors and do not necessarily reflect the views of the Wisconsin DNR.

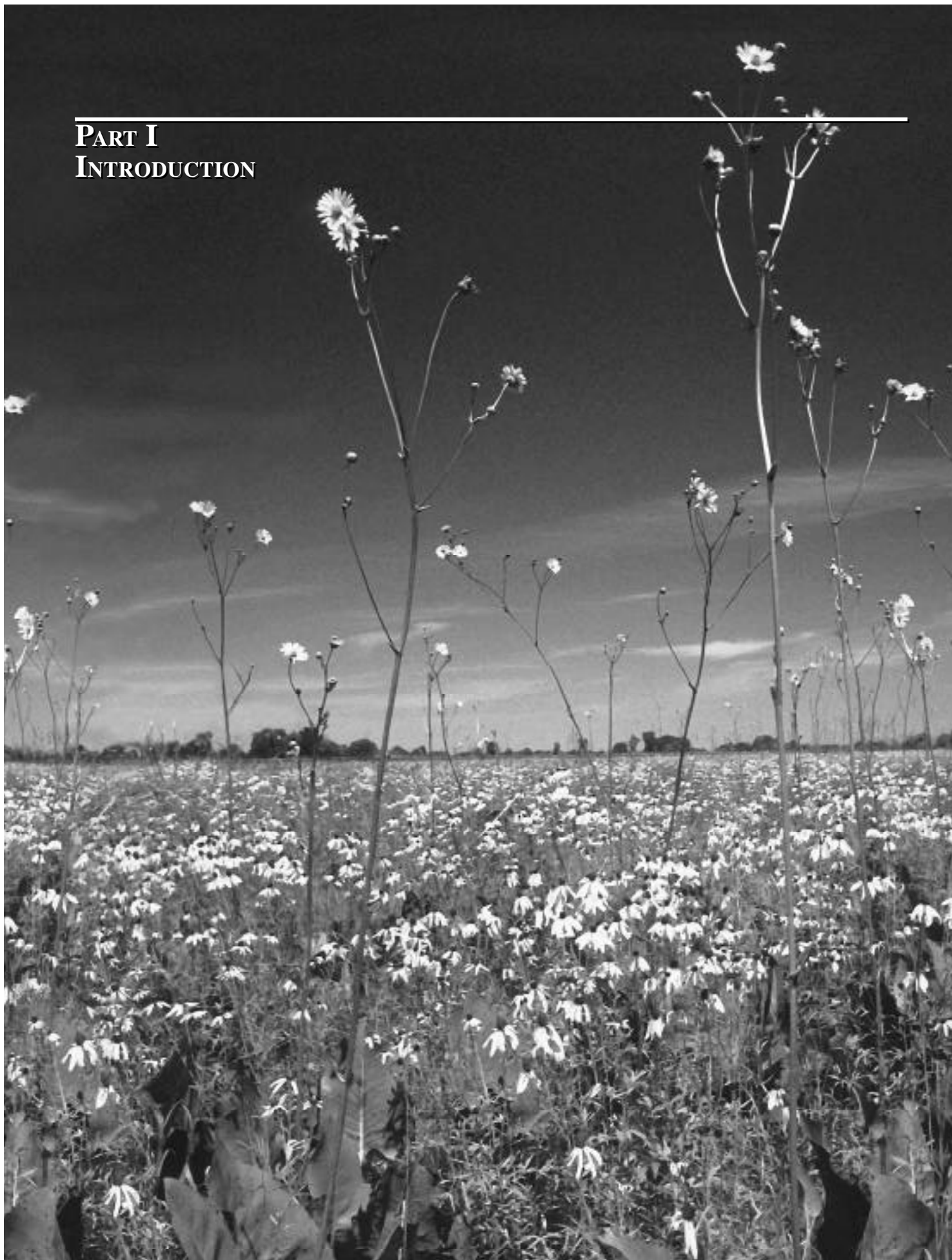
**Snapper (Miller) Prairie State Natural Area**, a high-quality lowland remnant in Jefferson County, Wisconsin, is dominated by Big Bluestem, Little Bluestem, and Northern Dropseed grasses. Subordinate to the grasses are many showy prairie forbs, including asters, blazing-stars, and the Yellow Coneflower (drooping rays) and Prairie-dock (very large basal leaves and tall naked stems) evident in this picture. Our Wisconsin deep-soil prairies consist chiefly of tall grasses and tall herbs like these, intermingled with shorter plants that bloom earlier in the season.

*Photo by Thomas A. Meyer*



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**PART I**  
**INTRODUCTION**



## INTRODUCTION

This *Atlas of the Wisconsin Prairie and Savanna Flora* is intended to serve anyone interested in the prairies, oak savannas, and oak woodlands of Wisconsin, whether an expert ecologist undertaking the restoration or recovery of a large-scale site, a novice prairie enthusiast contemplating a backyard garden, a professional biogeographer studying plant distributions, or a natural history amateur charmed by prairie flowers. Any one of these should expect to find help in answering two questions: where in Wisconsin does a particular species now grow (or where did it once grow, or did it occur at all?); and what kind of habitat does it prefer? Although the book may assist in the identification of plants, it is not a flora as such; and for that, the user will need to consult other works to confirm identifications (see Appendix C). Its major purpose is to provide distribution maps and habitat descriptions for grassland and savanna plants of the state. The atlas also provides an introduction to the ecology of these communities and supplementary information pertaining to the taxonomy and geography of individual species.

Richard A. Henderson, an authority in the field of prairie and savanna restoration, compiled a list of 289 species that were potential candidates for this book. His approach was entirely restoration oriented, and his choices were influenced by the lists of species presented in Curtis (1959) and plant material offered by wildflower nurseries. Catalogues of native landscapers and nurserymen in the Upper Midwest were also studied. We have excluded eight and added 60 species to make the coverage more comprehensive, and to alert a wide audience to the presence and diversity of the many species contributing to Wisconsin's

natural environment. A still larger number of infrequent species, not used by restorationists or of less ecological importance, were omitted. In the transition from savanna to forest there are numerous forest species, as for example Downy Wild-rye (*Elymus villosus*) and Zigzag Goldenrod (*Solidago flexicaulis*) that were not included because they bear little relation to either grasslands or oak openings.

### Scope of the Atlas

This work covers vascular plant species that are members of the Wisconsin prairie and savanna biota, including distribution maps and notes on their habitat and frequency. From the standpoint of the Wisconsin DNR, the original purpose was to map only native plant species used by people who protect and/or design and restore prairies and savannas. It follows that the most striking and characteristic wildflowers and grasses of prairie and savanna communities are the ones covered in this book. However, because these richly integrated communities contained many subordinate grass and non-grass species, the atlas also treats some common, though less characteristic species, even if they are not usually planted or sown during a prairie restoration. Not all members of our grassland and savanna flora are covered; many others occur in prairies, savannas, barrens, glades, and other native communities (Table 1). Some of these species are listed in Table 2. Additional lists of characteristic herbaceous and shrubby species associated with prairies and savannas may be found in Curtis (1959), Curtis and Greene (1949), Green (1950),

**TABLE 1. Acronyms to native plant communities**

The acronyms in this table indicate native plant communities in which each species was found during Curtis's Plant Ecology Laboratory studies and are compatible with the symbols in his "Species List" (Curtis 1959) and in Table 2.

AQE	Aquatic, Emergent	NDM	Northern Dry-mesic Forest	PW	Prairie, Wet
BF	Boreal Forest	NM	Northern Mesic Forest	PWM	Prairie, Wet-mesic
BG	Bracken Grassland	NS	Northern Sedge Meadow	SB	Sand Barrens
BOG	Open Bog	NWM	Northern Wet-mesic Forest	SC	Shrub Carr
CG	Cedar Glade	OB	Oak Barrens	SD	Southern Dry Forest
CLE	Cliff, Exposed	OO	Oak Opening	SDM	Southern Dry-mesic Forest
CLS	Cliff, Shaded	PB	Pine Barrens	SM	Southern Mesic Forest
DUN	Dune, Lake	PD	Prairie, Dry	SS	Southern Sedge Meadow
FN	Fen	PDM	Prairie, Dry-mesic	SW	Southern Wet Forest
ND	Northern Dry Forest	PM	Prairie, Mesic	SWM	Southern Wet-mesic Forest

**TABLE 2. Wisconsin prairie and savanna plants not mapped in this book**

Each of the species has been placed in one or more native communities according to Curtis's (1959) acronyms presented in Table 1. Acronyms are in approximate order by percent of stands in which each species occurs. Sources for determining inclusion and assigning habitats were Curtis (1959), Pruka (1995), specimen labels, and field experience of the authors. This list does not include many additional species that might be encountered, nor all habitats in which they might occur. Maps for many of these species may be found in the *Preliminary Reports on Flora of Wisconsin* and the books listed in Appendix C.

<i>Agastache foeniculum</i> (PB, OB, PDM)	<i>Liparis loeselii</i> (FN, BOG, PW, CLS)
<i>Agastache nepetoides</i> (SDM, SM, SD, OO, SWM, PWM)	<i>Lycopus americanus</i> (FN, SS, SW, PW, PWM, PM, CLS)
<i>Agalinis gattingeri</i> (PM)	<i>Lycopus uniflorus</i> (NS, SS, FN, PW, AQE, BOG, SW, NWM)
<i>Anemone quinquefolia</i> (SDM, NDM, PM, PWM, PW)	<i>Mollugo verticillata</i> (SB)
<i>Anemone virginiana</i> (SDM, SM, CLS, PM, OO, NDM)	<i>Onoclea sensibilis</i> (AT, SS, SW, NW, BOG, NWM, NM, PW)
<i>Apios americana</i> (SW, PW, PWM)	<i>Ophioglossum vulgatum</i> (FN, PW, SS)
<i>Arenaria lateriflora</i> (SWM, SDM, SD, PM)	<i>Opuntia fragilis</i> (CLE, CG)
<i>Astragalus neglectus</i> (PM)	<i>Orobanche fasciculata</i> (DUN, PDM)
<i>Betula pumila</i> (BOG, PW)	<i>Orobanche uniflora</i> (OO, SM, SD, DUN, PD)
<i>Cacalia muehlenbergii</i> (SM, SW, OO, CLS)	<i>Panicum lanuginosum</i> var. <i>implicatum</i> (SB, SD, OO, CG, PD, DUN)
<i>Calystegia spithamea</i> (ND, PB, OO, PDM, PM)	<i>Panicum linearifolium</i> (PD, OO)
<i>Campanula aparinoides</i> (FN, NS, PW)	<i>Parthenocissus vitacea</i> (SD, OO, CG, PDM, PWM, PM)
<i>Carex brevior</i> (SB, PDM, OO)	<i>Pentaphylloides (Potentilla) floribunda</i> (FN, PW)
<i>Carex muhlenbergii</i> (SB)	<i>Phryma leptostachya</i> (SDM, SM, OO, NDM, NM)
<i>Carex siccata</i> (OB, PD)	<i>Physalis longifolia</i> var. <i>subglabrata</i> (SB, PD, PDM)
<i>Celastrus scandens</i> (SDM, CG, PDM, PD)	<i>Plantago patagonica</i> (SB)
<i>Cenchrus longispinus</i> (SB)	<i>Platanthera flava</i> (PW, PWM)
<i>Cirsium altissimum</i> (SDM, OO, PM, SM)	<i>Platanthera lacera</i> (BOG, PW)
<i>Cornus racemosa</i> (SD, OO, PWM, PM, PW, PDM)	<i>Polygonella articulata</i> (SB, OB, DUN)
<i>Cornus stolonifera</i> (SC, FN, AT, SS, PW)	<i>Polygonum amphibium</i> (AQE, PW, SW, BOG)
<i>Corylus americana</i> (SD, OB, PWM, PM, PW, PDM)	<i>Polygonum tenue</i> (PDM, PD)
<i>Croton glandulosus</i> var. <i>septentrionalis</i> (SB)	<i>Prunus serotina</i> (SD, SDM, NDM, OO, CG, PM, BF)
<i>Cypripedium candidum</i> (FN, PW)	<i>Pteridium aquilinum</i> var. <i>latiusculum</i> (BG, PB, OB, OO, PM, PWM, PDM)
<i>Desmodium canescens</i> (OO)	<i>Quercus bicolor</i> (SW, OO)
<i>Desmodium cuspidatum</i> (SD, OO, SDM)	<i>Quercus rubra</i> (SDM, SM)
<i>Desmodium nudiflorum</i> (SDM, OO, SM, NDM)	<i>Rhus aromatica</i> (SB)
<i>Draba reptans</i> (PD, PDM, CLE, SB)	<i>Rhus copallina</i> (SB)
<i>Elymus villosus</i> (SDM, OO)	<i>Rosa carolina</i> (OO, PDM, PM, PWM)
<i>Equisetum hyemale</i> (DUN, PDM, PD)	<i>Rubus allegheniensis</i> (PD)
<i>Eriophorum angustifolium</i> (BOG, FN, PW)	<i>Rubus flagellaris</i> (PD, OO, PM)
<i>Eupatorium sessilifolium</i> (SDM, OO)	<i>Rubus occidentalis</i> (OO, PDM, PD)
<i>Euphorbia maculata</i> (SB)	<i>Selaginella rupestris</i> (SB, PDM)
<i>Froelichia floridana</i> (SB)	<i>Silene antirrhina</i> (CLE, SB, PD, PDM)
<i>Glyceria striata</i> (FN, SWM, SW, PW)	<i>Sium suave</i> (AQE, SC, PWM)
<i>Helianthemum bicknellii</i> (SB, PD, PDM, OB)	<i>Solidago ulmifolia</i> (SDM, OO, SM, CLS, NDM)
<i>Hudsonia tomentosa</i> (SB)	<i>Stachys palustris</i> (SS, PWM, PW, SW, SC)
<i>Hypericum punctatum</i> (SWM, PWM)	<i>Strophostyles helvula</i> (SDM, OO, CLE, CG)
<i>Hypericum sphaerocarpum</i> (PWM)	<i>Symphoricarpos occidentalis</i> (OO, PD, PWM, PM)
<i>Isanthus brachiatus</i> (PD)	<i>Talinum rugospermum</i> (SB, CLE)
<i>Juncus greenei</i> (SB)	<i>Teucrium canadense</i> (SW, PWM, PM)
<i>Juncus interior</i> (PD, PM)	<i>Triodanis perfoliata</i> (SB, OB, PDM, CLE)
<i>Juncus torreyi</i> (PWM)	<i>Viola cucullata</i> (NM, NW, BF, OO, SDM, PW, PWM, PM)
<i>Krigia virginica</i> (SB)	<i>Vitis riparia</i> (OO, CG, OB, PDM, PWM, PM, PD)
<i>Lechea intermedia</i> (SB, PDM, PD, PB, OB, CLE)	
<i>Lechea tenuifolia</i> (SB, PDM, PD)	
<i>Linaria canadensis</i> (SB)	

**Table 3. Endangered, threatened, and extirpated vascular plants of Wisconsin prairies, oak barrens, and oak savannas**  
Modified after Bureau of Endangered Resources (1993).

Wet prairies	Wet-mesic prairies	Mesic prairies	Dry-mesic prairies
<i>Hypericum sphaerocarpum</i> <i>Tofieldia glutinosa</i>	<i>Asclepias purpurascens</i> <i>Asclepias sullivantii</i> <i>Cacalia plantaginea</i> <i>Camassia scilloides</i> <i>Cypripedium candidum</i> <sup>2</sup> <i>Fimbristylis puberula</i> <i>Parthenium integrifolium</i> <i>Phlox glaberrima</i> ssp. <i>interior</i> <i>Platanthera flava</i> var. <i>herbiola</i> <i>Platanthera leucophaea</i> <sup>1</sup> <i>Polytaenia nuttallii</i> <i>Tomanthera auriculata</i>	<i>Agalinis skinneriana</i> <sup>2</sup> <i>Asclepias meadii</i> <sup>2,3</sup> <i>Asclepias ovalifolia</i> <i>Asclepias sullivantii</i> <i>Astragalus neglectus</i> <i>Cacalia plantaginea</i> <i>Camassia scilloides</i> <i>Echinacea pallida</i> <i>Gentiana alba</i> <i>Lespedeza leptostachya</i> <i>Parthenium integrifolium</i> <i>Platanthera leucophaea</i> <sup>1</sup> <i>Viola sagittata</i> var. <i>ovata</i>	<i>Besseyia bullii</i> <i>Cirsium hillii</i> <i>Echinacea pallida</i> <i>Gentiana alba</i> <i>Lespedeza leptostachya</i> <i>Liatris punctata</i> var. <i>nebraskana</i> <i>Parthenium integrifolium</i> <i>Polygala incarnata</i> <i>Prenanthes aspera</i> <i>Ruellia humilis</i>
Dry prairies	Sand prairies	Oak barrens	Oak savannas
<i>Agalinis gattingeri</i> <i>Agalinis skinneriana</i> <sup>2</sup> <i>Anemone caroliniana</i> <i>Anemone multifida</i> var. <i>hudsoniana</i> <i>Asclepias lanuginosa</i> <i>Astragalus crassicaarpus</i> <i>Besseyia bullii</i> <i>Cacalia plantaginea</i> <i>Cirsium hillii</i> <i>Echinacea pallida</i> <i>Lespedeza leptostachya</i> <i>Lespedeza virginica</i> <i>Lesquerella ludoviciana</i> <i>Liatris punctata</i> var. <i>nebraskana</i> <i>Orobancha fasciculata</i> <i>Prenanthes aspera</i> <i>Scutellaria parvula</i> var. <i>parvula</i>	<i>Asclepias lanuginosa</i> <i>Besseyia bullii</i> <i>Cirsium hillii</i> <i>Lespedeza leptostachya</i> <sup>1</sup> <i>Opuntia fragilis</i> <i>Orobancha fasciculata</i> <i>Orobancha ludoviciana</i> <i>Prenanthes aspera</i>	<i>Asclepias lanuginosa</i> <i>Liatris punctata</i> var. <i>nebraskana</i> <i>Opuntia fragilis</i>	<i>Agastache nepetoides</i> <i>Asclepias purpurascens</i> <i>Astragalus crassicaarpus</i> <i>Besseyia bullii</i> <i>Camassia scilloides</i> <i>Gentiana alba</i> <i>Polytaenia nuttallii</i> <i>Prenanthes crepidinea</i> <i>Ruellia humilis</i> <i>Viola sagittata</i> var. <i>ovata</i>
Oak woodlands	Bedrock glades		
<i>Agastache nepetoides</i> <i>Asclepias purpurascens</i> <i>Camassia scilloides</i> <i>Thaspium barbinode</i>	<i>Agalinis gattingeri</i> <i>Lespedeza virginica</i> <i>Opuntia fragilis</i>		

<sup>1</sup>Threatened at federal level<sup>2</sup>Concern at federal level<sup>3</sup>Extirpated at state level

Haney and Apfelbaum (1997), Henderson (1995a), Hujik (1995), Pruksa (1995), Whitford and Whitford (1971), Will-Wolf and Stearns (1998), and other references.

In ecological terms (Curtis 1959), the majority of species that appear in this book are either *prevalent* species or *modal* species. Prevalent species are those most likely to be present in any stand of a particular community type as well as being the ones with the highest densities. A species is modal in the one plant community in which it exhibits its maximum presence value. Some modal species are also prevalent ones, but many are infrequent or rare. There are 204 species of native vascular plants listed by Curtis (1959) as prevalent or modal within the prairie communities of Wisconsin. Of these, 193 are mapped in this atlas.

In recent years, especially since Earth Day 1970 and the passage of the Federal Endangered Species Act of 1973, there has been increasing concern over the identity, distribution, status, and preservation of rare species of plants and animals in Wisconsin (Bureau of Endangered Resources 1993, Read 1976). Although state or federally listed threatened or endangered species are not emphasized in this publication, many of them are indeed imperiled. Of the 1,702 species of vascular plants native to Wisconsin (Wetter et al. 1998), the DNR's Natural Heritage Inventory (1998) considers 73 endangered, 65 threatened, 4 extirpated, and 179 of significant conservation concern. Thus, 321 species, or about 19% of the native flora, have been or are in danger of local extinction or extirpation and hence candidates for listing in Wisconsin.

In this atlas in appropriate cases, following the name of the species, a status is given to indicate its listing by the Natural Heritage Inventory (1998) and Bureau of Endangered Resources (1993) as **Endangered**, **Threatened**, **Extirpated**, or of **Special Concern**, the latter term relating to those possibly in jeopardy but of uncertain status and not yet afforded legal protection. Altogether, about 28% of the endangered and threatened plant species occur primarily in prairie and oak-ecosystem habitats (Table 3). Additional species assigned to the advisory Special Concern category may, in fact, be extirpated (e.g., *Pedimelum argophyllum*) or may deserve legal status as Endangered (e.g., *Desmodium canescens*) or Threatened (e.g., *Comelina erecta* var. *deamiana*). No other natural communities in Wisconsin have been so profoundly decimated by the hand of man. Some impression of the extent of loss may be gained from Table 7 in Henderson and Sample (1995), which lists 65 extirpated, rare, and declining Wisconsin

grassland plants. (Twenty-two additional species can be considered to belong on the Henderson and Sample list, because they commonly occur in prairies as well as savannas, and because the official state lists of rare vascular plants were revised since the time of that publication.) Furthermore, many of these species are rare or infrequent throughout their range, and some are innately conservative, that is, they rarely occur anywhere except in little-disturbed vegetation remnants. As a result, prairie species like Pink Milkwort (*Polygala incarnata*), Silvery Scurf-pea (*Pedimelum argophyllum*), and the white-lettuces (*Prenanthes* spp.) are among the rarest and most elusive native plants in Wisconsin, and at least one, Mead's Milkweed (*Asclepias meadii*), is thought to have been extirpated from our flora (Table 3). Many once-common species, for example, the rosinweeds (*Silphium* spp.), of widespread but economically valuable habitats such as dry-mesic to wet-mesic prairies, may now be more in danger of extirpation than rarer species of specialized, economically unimportant habitats.

### Methods and Sources of Data

A distribution map is only as good as the data and identifications of the specimens on which it is based. In general, only records vouchered by actual pressed plant specimens deposited in an herbarium are the factual basis of the dots on our maps. Thus, the distribution of our native grassland and woodland species is indicated on outline maps by dots, each representing from one to several herbarium collections. A triangle is used in rare cases where all that is known from a county are specimens without specific location. In several instances, sight records (indicated on the maps by a +) by professional botanists were utilized, those in Lincoln County by F. C. Seymour (ms. cards), in central Wisconsin by J. W. Thomson (1940) or, less often, T. G. Hartley (1962) or P. D. Sørensen (ms. cards). Those from other areas are mostly from records of the DNR's Natural Heritage Inventory.

The distribution maps were generated by manually placing symbols at exact localities cited on specimen labels or shown on manuscript maps; thus, each dot is site-specific to within a few miles and specimen-vouchered by one or more herbarium specimens. The only map records from the literature to have been incorporated are some from older *Preliminary Reports* and from Hartley's dissertation on the "Flora of the Driftless Area" (1962). Because Wis-



**Figure 1.** Base maps of Wisconsin showing the boundaries of various features of glacial (A) and bedrock geology (D, E), selected geographical provinces (F, G) and soil types (H, I), and the Tension Zone (B) and floristic provinces (C). A, redrawn after Little (1971); B and C, from Curtis (1959); D, drawn by following the line of contact between the Prairie du Chien Dolomite and the Upper Cambrian Sandstone; E (Niagara Dolomite), F, and G, from Martin (1965); E (Cambrian Sandstone) from Wisconsin Geological and Natural History Survey (1995); H, redrawn after Whitson (1927); I, redrawn after Johnson and Iltis (1964).

consin herbarium collections range from the late 1850s to the present, the maps present collection information accumulated over the course of almost 150 years. Given the destructive role of man in changing the face of the land, it hardly needs to be said that many dots represent populations that are no longer extant. By the same token, the absence of a dot in an area does not necessarily mean that the plant does not occur there.

A line enclosing the famous **Driftless Area** of Wisconsin and adjoining Minnesota, Iowa, and Illinois appears on every distribution map (Figure 1A). It indicates a hilly region never covered by ice and drift (glacial gravel), at least during the most recent glacial advances. Other features of Wisconsin physical geography such as the **Region of Limestones** (Figure 1D), the limits of the **Cambrian Sandstone** and **Niagara (Silurian) Dolomite** (Figure 1E) and the extent of **Prairie, Sandy, and Sandy Loam Soils** (Figure 1H and I) are sometimes shown, as are the boundaries of the **Northern Highlands** (Figure 1F) and **Central Plain** (Figure 1G). Running across the middle of the state from northwest to southeast is a narrow band or zone that marks major changes in the climate, and hence the vegetation, in relation to plant distribution (Figure 1B). Because the southern range limits of many northern species and the northern range limits of many southern and western species are contained within this climatic and floristic **Tension Zone** (see Curtis 1959), which also separates the **Prairie-Southern Forest** from the **Mixed Conifer-Northern Hardwoods** biogeographic provinces (Figure 1C), it also appears on many of the distribution maps.

The distribution of the species in Wisconsin, habitat information, and dates of flowering and fruiting were obtained chiefly from collections in the herbaria of the University of Wisconsin System: Madison (WIS), Milwaukee (UWM), Green Bay, Eau Claire (UWEC), La Crosse (UWL), Oshkosh (OSH), and Stevens Point (UWSP). Our maps also include records of Wisconsin material contained in such important herbaria as the Milwaukee Public Museum (MIL), the University of Minnesota (MIN), and the Morton Arboretum (MOR). In addition, records have been incorporated based on specimens in the herbaria of the University of Wisconsin–River Falls (RIVE), University of Wisconsin–Platteville, University of Iowa (IA), Beloit College (BELC), Iowa State University (ISC), Field Museum of Natural History (F), Northland College (Ashland, Wisconsin), St. Norbert College (SNC), and the private herbarium of Mrs. K. Rill

(Oshkosh, Wisconsin). We wish to express our thanks to all the curators and directors for their cooperation.

### **Botanical Information**

The core of the atlas comprises Part II, 354 sequentially numbered maps and accompanying habitat and distributional captions. The 52 plant families represented are first divided according to the three major groupings of vascular plants to which they belong, namely the pteridophytes, representing Ferns and Fern Allies, and the monocotyledons and dicotyledons, the two subclasses of angiosperms, or flowering plants. The families are then arranged alphabetically. Under each family are the genera and species, also alphabetically. The nomenclature generally follows the second edition of Gleason and Cronquist's *Manual of Vascular Plants* (1991), occasionally Kartesz's *Synonymized Checklist* (1994), and in a few cases, different floras or monographs. Having a more intimate knowledge of the flora of Wisconsin, we have sometimes chosen to list infra-specific taxa not recognized by these authorities.

The habitat descriptions were derived primarily from information given on specimen labels and our own field experience. Geographical, biological, and other information is based on floras and available monographs and revisions, supplemented by herbarium label data.

The text accompanying each map includes the **scientific name** of the species, the **common name** or names, its **status** (if rare), the **total range** outside of Wisconsin with an attempt to identify or imply the floristic element to which it belongs and its post-glacial migrational origin, the **general range** within the state, a description of its **habitat**, and **flowering and/or fruiting** times. The names and/or abbreviations immediately after each Latin name are those of the botanist(s) responsible for originally describing the species. Taxonomic synonyms—scientific names once commonly used in other floras but now considered to apply to the same taxon—appear in brackets. Habitats printed in boldface indicate according to Curtis (1959, p. 633) "...the native community in which the species achieved maximum presence," that is, the community of modality. *Presence* is high for species occurring in most or nearly all sample stands of the community. The highest presence may occur in rare communities with few species, hence the oft-reported "cedar glade" in Curtis's (1959) Species List. The number in parentheses is the number of plant communities in which Curtis' Plant Ecology Laboratory (PEL) studies found the

species to occur, that is, the *fidelity* of that species. The smaller the number, the rarer the species and the more it is restricted to a particular habitat. Because not all the species listed in this atlas were quantitatively analyzed during the PEL studies, a number of them lack this information.

Common or vernacular names are listed for each mapped species even though some are not well established by usage. Regional source books were surveyed for common names, and a few were added based on our own experience. Many common names cited in popular references are included even if they appear to have been invented for the sake of giving each species a common name.

The range statement attempts to identify or imply the floristic element to which a species belongs and its post-glacial migrational origin. In all pertinent major floras covering Wisconsin (Fernald 1950, Gleason 1952, Gleason & Cronquist 1991) the plants are described as ranging from north to south, then from east to west—a biogeographically illogical sequence, because almost 100% of the species ranges developed in the recent past moved from south to north, and in Wisconsin, considering the whole flora, almost as often from west to east as vice-versa. Therefore, we have turned most of the range statements upside down to reflect the probable direction of migration.

Information on **Excluded Species** (Appendix A) and **Native Plant Nurseries** (Appendix B) follows the map section. Critical literature, mostly Wisconsin oriented, is cited under each family and sometimes also under individual species. Appendix C contains the *Preliminary Reports on the Flora of Wisconsin* (1929–1988), a series of some 70 treatments of selected Wisconsin families and genera, as well as the four book-length treatments for Wisconsin families, and other articles listed alphabetically, along with supplementary references to provide expanded coverage for our flora.

All interested parties, botanists and amateurs alike, are encouraged to correct records and report new finds to the authors for the purpose of keeping information on the Wisconsin flora current.

## North American Grasslands

The vast central North American grasslands lie between the woodlands at the base of the Rocky Mountains and the western margins of the eastern deciduous forest and extends from southern Alberta and Saskatchewan to south-central

Texas (Figure 2). Going from west to east, it can be divided into three geographically parallel climax associations: the **shortgrass plains**, the **mixedgrass prairies**, and the **tallgrass prairies** (Carpenter 1940, Risser et al. 1981, Weaver 1954, Weaver & Albertson 1956). Superimposed over this pattern of continuous and interdigitating grassland types are gradients of annual precipitation and soil depth (generally declining from east to west), temperature (rising from north to south), and floristic diversity (i.e., species richness, increasing from north to south and decreasing from east to west).

Prairies vary greatly in character and composition from place to place. Generally, with enough moisture, the Tallgrass Prairie Association, also known as the true or eastern prairie, predominates in Wisconsin; although on dry, southwest-facing hillsides, shortgrass communities not unlike the mixedgrass or even shortgrass prairies from farther west are found. The tallgrass prairie receives more rainfall, is more ecologically diverse, and contains a greater number of major dominants than either the mixedgrass prairies or shortgrass plains. Originally, the tallgrass prairie stretched in an arc from south-central Manitoba to Texas and extended eastward from a transition zone with the Mixedgrass Prairie Association near the 97th Meridian to the borders of the deciduous forest biome. In the Midwest it projected eastward as the triangular-shaped “Prairie Peninsula” (Figure 2, inset), crossing southwestern Wisconsin and most of Illinois and reaching into Indiana and eastern Ohio, with scattered outliers in Kentucky, southern Michigan and southern Ontario (Gleason 1913, Langendoen & Maycock 1983, Transeau 1935). Along its eastern edge, major portions of the tallgrass prairie, including Wisconsin’s grassland communities and the entire Prairie Peninsula, constitute a variant facies within the tallgrass association that has been termed subclimax prairie (McComb & Loomis 1944) or the prairie-forest ecotone (Anderson 1983, Carpenter 1940, Davis 1977). This broad ecotone comprised a mosaic of plant community types that formed a continuum from prairie to forest. The transition with the boreal forest in the far north and west was an aspen parkland, and that with the deciduous forest farther south, as in Wisconsin, was an oak savanna. Boundaries between these ecosystems varied from gradual to abrupt owing to local environmental and topographic conditions and other factors. Peninsula-like prolongations and island-like relicts of prairie and forest communities passed into one another on both uplands and lowlands, with much of the boundary

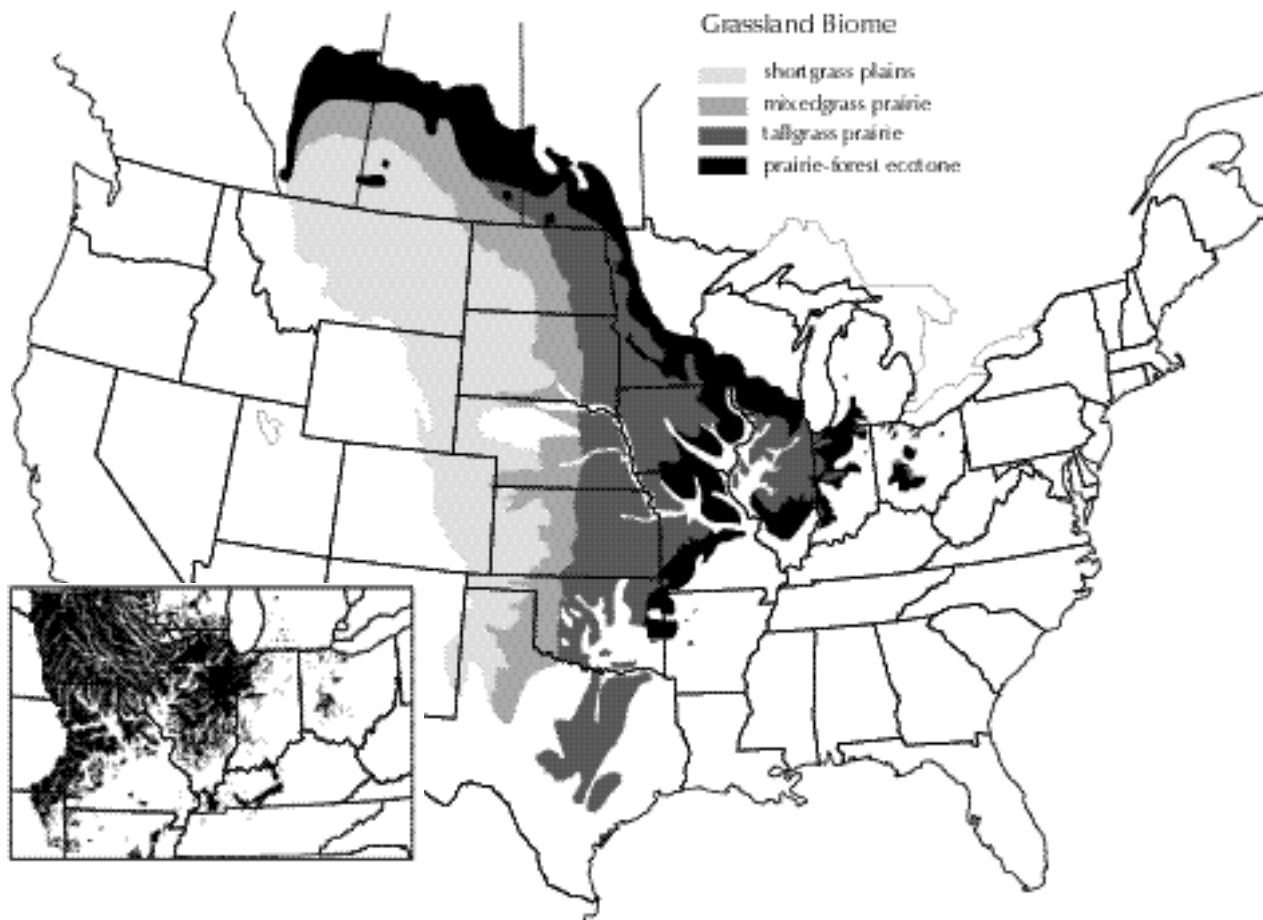


between the two formations taking on an open, park-like character now all but lost to cow and plow.

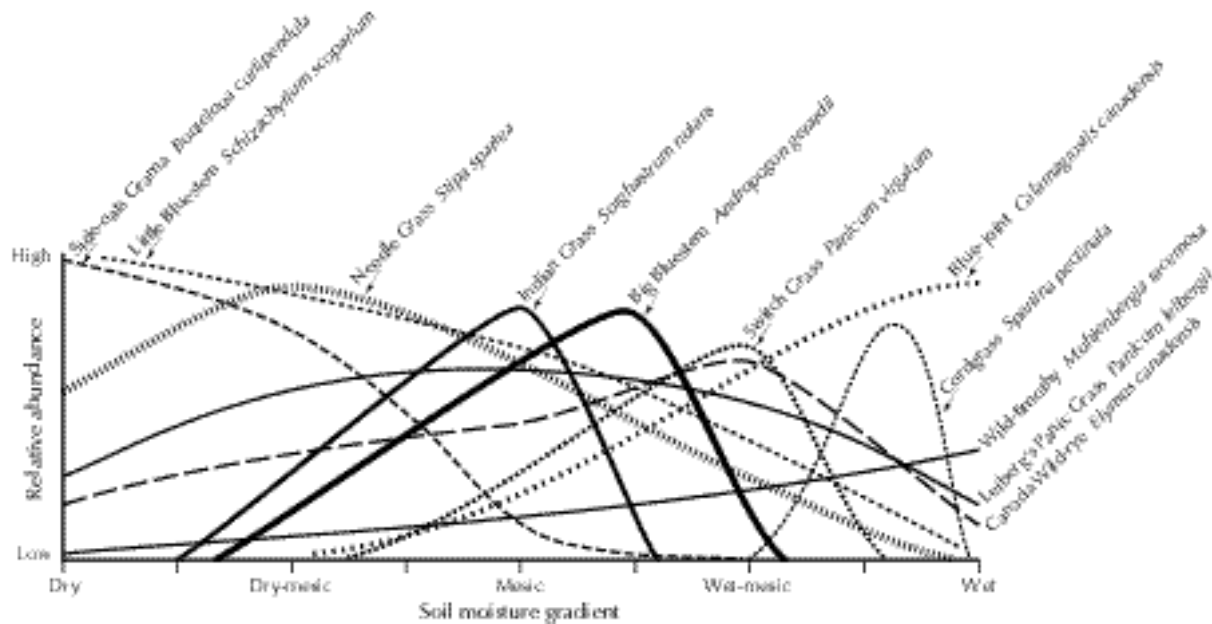
### Composition

Although grasses comprise less than 10% of the plant species (in the case of Wisconsin, 17 of Curtis's 204 prevalent and modal species), in terms of individuals and plant biomass, they are the dominant plants of the prairies. Grass species, like the communities they represent (Curtis 1955, 1959), sort themselves out in a more or less definite ordination in relation to soil moisture (Figure 3). In Wisconsin, on upland sites, or steep, calcareous slopes, short (0.5 to 1.5 feet) to mid-sized (2 to 4 feet), non-rhizomatous,

bunch- or less often sod-forming grasses predominate and often present a floristic composition and visual aspect more closely resembling the shortgrass plains and mixedgrass prairies hundreds of miles to the west: Little Bluestem (*Schizachyrium scoparium*), Side-oats Grama (*Bouteloua curtipendula*), and June Grass (*Koeleria macrantha*) on the driest prairies, Prairie Dropseed (*Sporobolus heterolepis*), Indian Grass (*Sorghastrum nutans*), and Needle Grass (*Stipa spartea*) on dry-mesic or sandy prairies. Proceeding along this idealized moisture gradient to still well-drained, typical tallgrass mesic prairies, the major dominant becomes the tall (5 to 8 feet), rhizomatous, sod-forming Big Bluestem (*Andropogon gerardii*); then, on still moister, wet-mesic prairies, Big Bluestem, Switch Grass



**Figure 2.** The grassland biome of Midwestern North America, showing the general ranges of the tallgrass and mixedgrass prairies, shortgrass plains, and prairie-forest ecotone. The white oval in west-central Nebraska is the chief sandhill region. Not shown are the Atlantic and Gulf of Mexico coastal plain grasslands and pine savannas; the intermountain grasslands that extend from western Wyoming to eastern Oregon and the Palouse area; the desert grasslands that reach from Mexico into western Texas, New Mexico, and Arizona; or the central California grasslands. Depending on local conditions, topographic exposure, moisture-holding capacity of the soil, and other factors, all these Midwestern grassland ecosystems may be found in Wisconsin. Redrawn after Carpenter (1940). Inset depicts the Prairie Peninsula, an eastward extension of the tallgrass prairie, and its outliers. Reproduced from Transeau (1935).

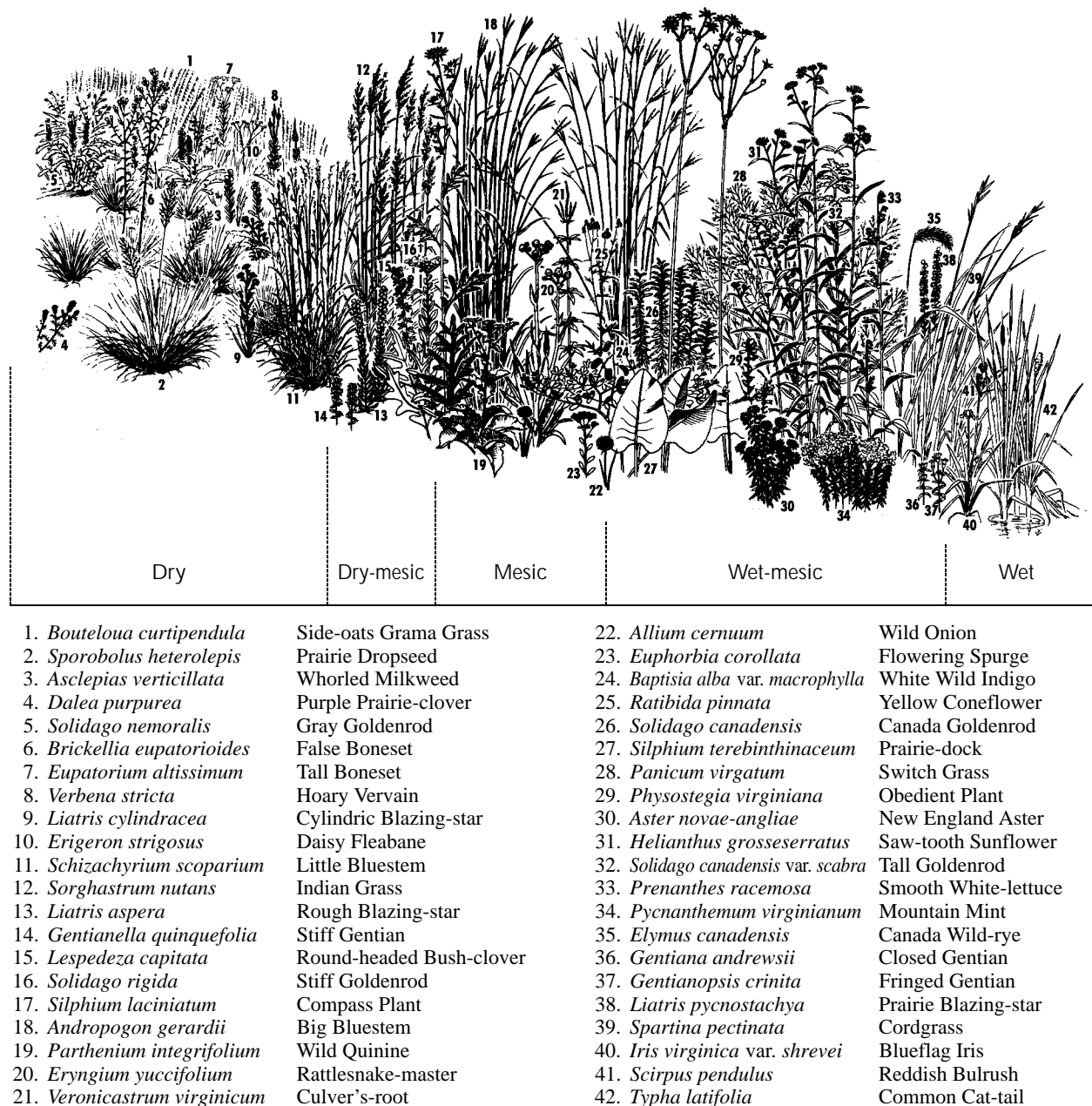


**Figure 3.** Generalized behavior of 11 important prairie grasses in relation to a soil moisture gradient. Each curve is unique, suggesting that the species respond in an individualistic manner to the conditions of the environment. Adapted from Bazzaz and Parrish (1982) and Curtis (1959).

(*Panicum virgatum*), and Canada Wild-rye (*Elymus canadensis*); and in wet prairies, Blue-joint (*Calamagrostis canadensis*) and Cordgrass (*Spartina pectinata*). Upland Wild-timothy (*Muhlenbergia racemosa*) and Leiberg's Panic Grass (*Panicum leibergii*) occur across a wide variety of sites. Nowadays, of course, the list of dominants often includes naturalized grasses even in some well-preserved prairie remnants. Native communities utilized as pastures or otherwise artificially disturbed quickly deteriorate as the original grasses and forbs are replaced by almost wholly non-native, mostly European species. Depending on the type of habitat and degree of disturbance, the following occur in or even dominate native and surrogate grassland habitats: Canada Bluegrass (*Poa compressa*), Smooth Brome (*Bromus inermis*), Quack Grass (*Elytrigia [Agropyron] repens*), Timothy (*Phleum pratense*), and Orchard Grass (*Dactylis glomerata*) on uplands, Redtop (*Agrostis gigantea*) and Reed Canary Grass (*Phalaris arundinacea*) in lowlands, and Kentucky Bluegrass (*Poa pratensis*) everywhere across the continuum except at the wettest end. Especially difficult to eradicate are perennial Smooth Brome, which forms luxuriant sods on roadsides, pastures, and prairies; the rhizomatous perennials Canada Bluegrass and Kentucky Bluegrass,

both ubiquitous in Wisconsin's grassland and savanna communities; and the terrible Reed Canary Grass, which, deliberately planted for hay, pasturage and erosion control, has become the dominant grass cover in marshes, sedge meadows, wet prairies, low fields, and other moist habitats throughout Wisconsin.

This ordination of the major grass dominants can be replicated in the associated herbaceous species, or forbs, which, very much an integral part of the structure of prairie vegetation, contribute seasonally conspicuous color, texture, and variety (Figure 4). Except for a very few pristine, relic "virgin prairies" untouched by plowing or cattle grazing, the original character of the forb flora has changed depending on the degree of disturbance a particular remnant has suffered. Wisconsin prairies are chiefly "degraded prairies," the quality of which is often judged by the degree of replacement of the native species by introduced weedy ones. Besides floristic composition, community physiognomy and seasonal aspects like blooming and color can be used in evaluating the natural quality of a stand. Environmental attributes such as soil profile and color, microclimate, and degree and type of artificial disturbance may also serve to delineate original prairies that have been either excessively degraded or destroyed.

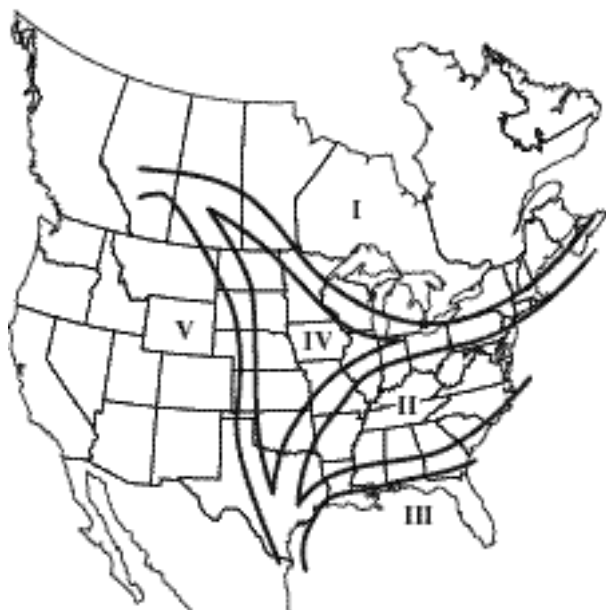


**Figure 4.** Generalized behavior of grass and forb species along a compositional gradient. The figure illustrates major dominants and secondary species that make up most of the vegetation in some prairies. Original drawing by Nancy R. Halliday.

### Climate

Climate is generally recognized as the chief factor shaping the Great Plains environment (Borchert 1950, Weaver 1954, Weaver & Albertson 1956). The extensive plains of North America lie in the eastern rain shadow of the Rocky Mountains, which intercept humid air masses moving eastward

from the Pacific Ocean. These Pacific air masses appear to force their way like a wedge between the southward-flowing, cold Arctic and the northward-moving, warm Maritime Tropical air masses (Borchert 1950, Bryson 1966, Bryson & Hare 1974). The mean positions of these air mass boundaries or fronts are correlated with the mid-continental location of the main body of plains and prairie vegetation (Figure 5),



**Figure 5.** Climatic regions of eastern North America at the present time. Redrawn after Borchert (1950). The maps identify climatic regions dominated by the Arctic and Pacific air masses in winter and summer, respectively (I), Pacific air mass (IV, V), and Maritime Tropical air mass (II, III). The transition zone between regions I and IV corresponds with the Polar Frontal Zone. Regions are climatically the same as those shown in Figure 6.



**Figure 6.** Paleoclimatic regions of eastern North America during a late postglacial, prehistoric period of relatively strong mean easterly circulation. During this period of relatively warm and dry summers a wedge of prairie vegetation extended eastward to Ohio or farther east as the Prairie Peninsula. Redrawn after Borchert (1950). I, the northeastern region with snowy winters; II, southeastern states and eastern seaboard with rainy winters; III, south Atlantic and Gulf Coast states with sub-tropical summers; IV, prairie region with usually dry winters and occasionally low summer rainfall; V, Great Plains with relatively dry winters and dry summers.



**Figure 7.** Isoclimatic lines of precipitation-evaporation ratios for the United States, which correspond closely to the distribution of the Prairie Peninsula flora. From Jenny (1941).



**Figure 8.** Isoclimatic lines of average relative humidity for July for the United States. The evaporating power of the air is more efficacious than precipitation amounts alone in explaining the distribution of climax communities. From USDA (1941).

which had developed by 10,000 years before present (yr B.P.) in response to late glacial climatic warming and melting of the continental ice sheet (Borchert 1950, Bryson et al. 1970, Delcourt & Delcourt 1993). During a late post-glacial, prehistoric period of shifting air mass boundaries, warming climate, and more frequent drought than at present (Figure 6), prairie vegetation spread eastward as the Prairie Peninsula, reaching its easternmost extent during the Hypsithermal Interval, generally dated between 9,000 and 4,000 yr B.P. (Delcourt & Delcourt 1993, Sears 1942, Wright 1968). Climatic conditions then changed again, with global cooling during the last 3,000 years resulting in the westward withdrawal of the Prairie Peninsula to its present-day position (Delcourt & Delcourt 1993).

The central North American grassland region experiences great and erratic variability in weather from year to year, depending on the location and duration of fronts and the frequency of their shifts (Coupland 1958, Risser 1985, Sims et al. 1978). There is less rain, higher temperatures, lower humidity, higher evapotranspiration rates, and more frequent droughts than in the mixed northern and deciduous hardwood forest regions to the east (Looman 1983, Risser et al. 1981, Transeau 1935). Other factors also correlate with the distribution of these biomes, and many of them are mutually or reciprocally related, making it difficult or impossible to rank their relative importance with respect to vegetation. The relationship between precipitation and evaporation was used by Transeau (1905, 1930, 1935) to help explain the existence of the Prairie Peninsula. More than any single meteorological variable (e.g., the total amount of precipitation), isoclimatic lines of precipitation-evaporation ratios match remarkably well on a gross scale the distribution of the Grassland Formation and other vegetation types in the eastern United States (Figure 7). Transeau (1935) also indicated that midsummer relative humidity (Figure 8) is among the more important factors in relation to the Prairie Peninsula.

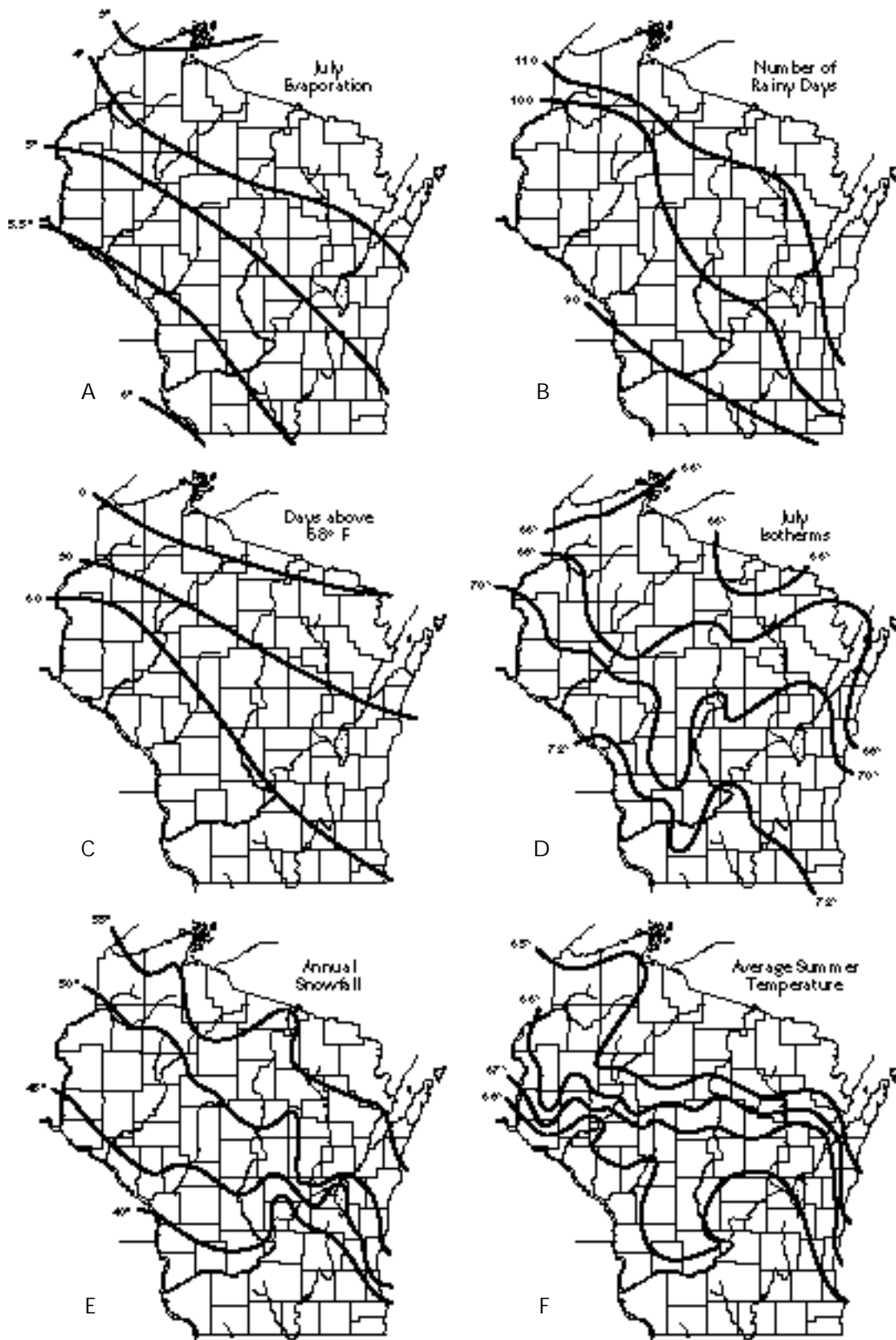
The prevailing westerly winds moderate the climate of Wisconsin, the southwestern half of which lies partly within Borchert's Region IV, the prairie region, and mostly within the transitional zone between Region IV and Region I, the northeastern region (Figure 5). Many (but not all) climatic factors show good correlation with the Tension Zone (see Curtis 1959). Six of the more important factors for the vegetation are shown in Figure 9. Within the Prairie-Southern Forest Province, there are higher levels of **July evaporation** (Figure 9A), fewer **rainy days** (Figure 9B), more

days with average **temperature above 68°F** (Figure 9C), higher **July temperatures** (Figure 9D), less average **annual snowfall** (Figure 9E), and higher **average summer temperatures** (Figure 9F). Annual mean temperature, January mean temperature, and length of growing season also have a corresponding relation with the floristic provinces.

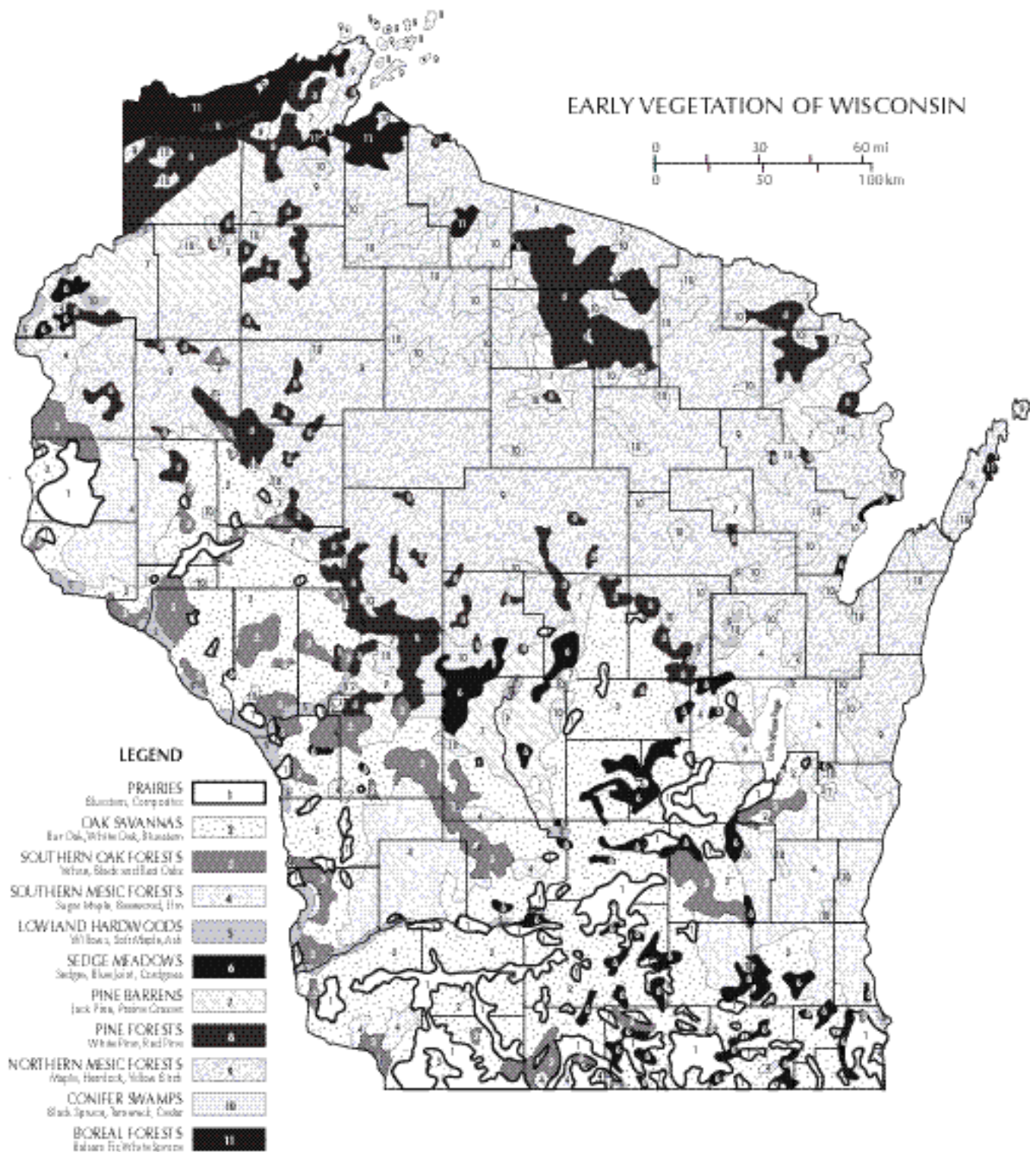
High temperatures and limited, more erratic precipitation are the most significant climatic factors in maintaining grassland climax against the invasion of forest. The seasonal distribution of precipitation and its range of fluctuation from year to year are probably more important than the actual total rainfall; in other words, periodic drought is critical in affecting plant growth on the prairies. With the appearance of hot dry summers and long cold winters the climate of the prairies and plains became unsuitable for the wide-ranging deciduous forests they previously supported and led to the development of the grassland ecosystem, which probably arose during the Miocene-Pliocene transition, about 7–5 million yr B.P. (Axelrod 1985), or earlier. During intervening epochs, grassland areas have been occupied alternately for varying periods of time by different vegetation types that were largely controlled by fluctuating glacial and interglacial regimes. The specific composition of the contemporary grassland biome, especially in the glaciated regions, is post-Pleistocene in age, having developed during the warmer and/or drier climates of the Holocene (Axelrod 1985, Wells 1970a, Wright 1970).

### Ecology

Climate alone does not explain the distribution of prairie along the borders of the grassland ecosystem or in regions farther east that support both forests and grasslands. It is well established through historic accounts (see Curtis 1959, Pyne 1982) and research studies (e.g., Bragg & Hulbert 1976, Vogl 1964) that forest can invade prairie and prairie can invade forest. To understand the persistence of grasslands in the Prairie Peninsula, the interrelated roles of three major determinants, namely climate, fire, and grazing animals, must be taken into account (Anderson 1982, 1990; Owen & Wiegert 1981; Vinton et al. 1993). Extremes of climate such as the impact of periodic summer droughts (Anderson 1970; Stewart 1951, 1956; Tomanek & Hulett 1970; Transeau 1935; Weaver 1954; Wells 1970a, b) are probably more important to the existence of the prairies than are temperature regime and average annual precipitation. Fire frequency and intensity are related to landscape



**Figure 9.** Climate maps, showing factors that correlate with the vegetation of Wisconsin. From Curtis (1950).



**Figure 10.** The presettlement distribution of plant communities based on General Land Office Survey records. Adapted from the UW–Extension Geological and Natural History Survey map (1965). Original color version available from Map Sales, GNHS, 3817 Mineral Point Road, Madison, WI, 53705-5100. Map interpretation on next page.



**Figure 10.** Continued.

### **Interpretation of the Vegetation of Wisconsin**

This map is based on the original land survey conducted about the middle of the last century. Surveyors were required to place a stake each half mile, identified by notation of nearby trees, and to note briefly the general plant cover of each quarter section. These records have been used to reconstruct the presettlement distribution patterns of plant communities shown on the map.

The plant communities recognized, however, are based on systematic studies of present-day vegetation. The results of these studies are summarized in *The Vegetation of Wisconsin* (J. T. Curtis 1959), in which each community, with its history, location, and relationship to other communities and to the environment, is considered in detail. Since some of the factors determining vegetation vary gradually, the vegetation itself varies gradually, and boundaries on the map are somewhat arbitrary.

The vegetation of the state is divided into northern and southern floristic provinces by a line that runs in an S-curve northwest from Milwaukee to Hudson. North of this line the vegetation is a broadleaf forest containing conifers—pines, hemlock, spruces, and fir. Southwest of the line, conifers are much less important and are replaced by forests with several species of oaks, and by the prairies—areas dominated by grasses and tall herbs.

Fire has been important in determining almost all of the plant communities and their location. Before the coming of Europeans, the prairies (1) and the open woodlands burned almost every year. Thus most of the southern part of the state was covered with prairies or oak savannas (2), an orchard-like community with a few large bur or white oaks growing in fields of grass. Only in the more protected places did forests survive. Some of these were oak (3), but many were sugar maple-basswood-slippery elm forests (4). The lowlands were occupied by river bottom forests (5), and sedge meadows (6). With settlement, the fires were stopped, and the oak savannas grew up to the dense white oak-black oak forests found today. Most of the prairies have been cultivated, and at present, with the oak savannas, are among the rarest of our plant communities.

In the northern part of the state, a combination of fire and poor soil resulted in the development of pine barrens (7) on the sandy soils, and pine forests (8) on somewhat better soils. In the absence of fire, the white pine forests gradually changed to the northern equivalent of the sugar maple-basswood forests, a community containing sugar maple, yellow birch, and hemlock, with beech added in the eastern counties (9). Also present in the north were large tracts of lowland, with tamarack and black spruce bogs in the wetter areas, and white cedar swamps in drier, but still very moist habitats (10). In the extreme north are local occurrences of the northern conifer forests (11) dominated by fir and spruce.

A comparison of this map with maps of climate, soil, and glacial deposits shows many correspondences, indicating many relationships between vegetation and the environment. The original vegetation was thus determined by the distribution of both climatic and soil factors, modified by fire (J. T. Curtis, G. Cottam & O. L. Loucks, 1965).



features. Level to undulating topography with a thick stand of tallgrass biomass over which a hot fire could spread unchecked (Anderson 1982; Axelrod 1985; Wells 1970a, b) appears to be a determining factor affecting the distribution of grassland communities versus savannas or forests in the central Great Plains and may be especially significant in ecotonal regions (Anderson 1972, 1990, 1991; Ebinger 1991; Gleason 1913; Rodgers & Anderson 1979). The scattered bur oaks on glacial hills versus the treeless plains were proof of the killing power of hot fires. Grazing by herds of ungulates has modified grassland communities by selectively removing plant material (and perhaps destroying scattered trees and shrubs), trampling, influencing decomposition, and concentrating nutrients (Dyer et al. 1982, McNaughton et al. 1982).

Besides climate, fire, and grazing, other factors affect the vegetation. The local distribution of plant species, and as a result, plant communities, is directly related to complexities of physiography, substrate, biota, and history. In his inventory of hill prairies of Illinois, Evers (1955) concluded that on a single hillside there is much variation in plant distributions as a result of edaphic factors. It might be indicated that today, the chief factor affecting vegetation is the diverse anthropocentric uses to which the land is being put, which in prairie states primarily means conversion to agricultural fields, mowing meadows, or cattle pastures, or other purposes, especially development, that have degraded or eliminated much native habitat.

### *Effects of Fire*

The prairie is a product of many factors, but it was the prairie fires set by lightning and, locally, the nearly annual burning by Native Americans that maintained the prairies and savannas in the face of forest succession in the Middle West (Axelrod 1985; Curtis 1959; Malin 1953; Pyne et al. 1996; Sauer 1950; Stewart 1951, 1956; Vogl 1964, 1974; and various other authors). The widespread nature of fire was emphasized in the frontier journals and diaries, its importance was well documented in the early scientific literature, and its use as a management tool has been the subject of a tremendous amount of scientific research (for reviews see Collins & Wallace 1990; Henderson & Statz 1995; Kozlowski & Ahlgren 1974; Pemble et al. 1975; Wright & Bailey 1980, 1982). Besides hindering the development of competitive grasses and invading woody species, burning reduces accumulated vegetative litter, indirectly

stimulating below-ground decomposition (Curtis & Partch 1950, Henderson 1982). The Curtis Prairie in the University of Wisconsin Arboretum in Madison presents a classic case of the importance of prescribed burning in maintaining a tallgrass prairie community (Anderson 1973, Cottam & Wilson 1966, Curtis & Partch 1948).

Prior to European settlement, fires were undoubtedly widespread and frequent and certainly played a major role in suppressing woody growth. Shrubs and trees may have been restricted by droughts, fires, and biotic factors, but they were not eliminated (Curtis 1959, Malin 1953). The tallgrass prairie zone, dominated as it is by warm-season perennial grasses, is quickly invaded by woody vegetation in the absence of fire. Tree and brush densities have increased tremendously in postsettlement time. In presettlement times, prairies occurred most commonly on level to gently sloping ground and south- and west-facing steep slopes; savannas and woodlands on slopes; and forests on the eastern side of natural firebreaks, in ravines, or on north- and east-facing slopes. Apparently, this segregation of vegetation types was determined largely by firebreaks, which controlled the frequency, and topography, the denseness of vegetation (biomass) and hence the intensity of fire (Gleason 1913, Wells 1970b, Grimm 1984, Anderson 1991). Thus, it appears probable that in the prairie-forest border region the presence or absence of tallgrass prairie on any particular site was determined by the incidence of fire (Curtis 1959, Will-Wolf & Montague 1994).

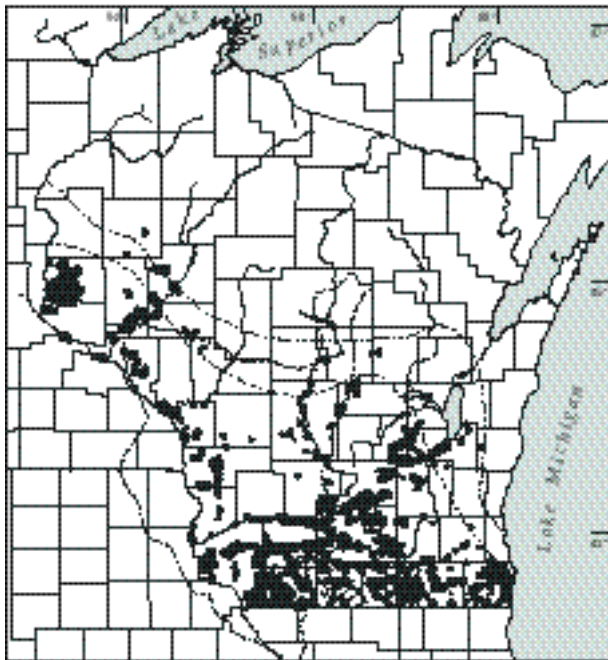
### **Wisconsin Grasslands and Savannas**

The continental glaciers of the last ice age had for the most part melted from Wisconsin by 10,000 yr B.P., leaving behind the drift, moraines, outwash, and lake deposits that cover the Glaciated Region today. One extensive area escaped at least the later glacial advances, namely the hilly Driftless Area (King 1981, Knox 1982, Knox & Mickelson 1974), which largely occupies southwestern Wisconsin and only barely overlaps the boundaries of Minnesota, Iowa, and Illinois (Figure 1A). At the time of European settlement, about one-third of the Driftless Area was covered in prairies that were essentially treeless or were dotted with groves and oak openings and interspersed with forests. Such significant relief features as stream valleys, floodplains, terraces, and bluffs furnish much of the topography upon which the present prairie remnants survive.

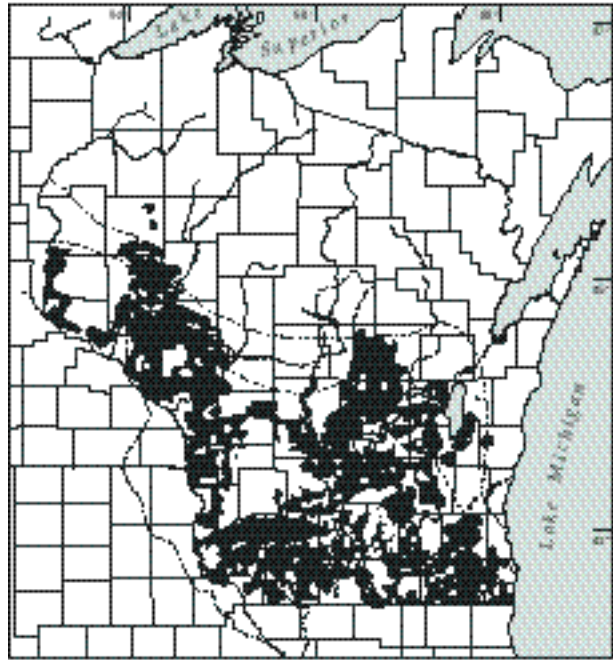
The vegetation of Wisconsin developed after the demise of the last glacial ice, with prairies slowly replacing deciduous forest in response to a drying and warming trend and reaching their greatest extent during the height of the Hypsithermal Interval 8,000–6,000 yr B.P. (Axelrod 1985, Deevey & Flint 1957, Wright 1976). At its close, the climate of the Prairie Peninsula became cooler and moister, and the seasonal contrast in temperature was reduced. These changes decreased the frequency and intensity of wildfires and summer droughts and created conditions more consistent with the physiological tolerances of trees. By around 3,000 yr B.P., grasslands were being replaced by eastern forests from Minnesota to Illinois (Gleason 1923, Grimm 1983, Jacobson et al. 1987). Thus, it appears that for the past 5,000 years the Prairie Peninsula has been a shifting mosaic of prairie, savanna, and forest under climatic conditions that allowed all of these vegetation types to thrive in this region.

The presettlement distribution of the major vegetation types in Wisconsin is shown in Figure 10. The prairies (Figure 11) and savannas (Figure 12) lie within the Prairie-South-

ern Forest floristic province, which occupies the region south and west of the climatic-floristic Tension Zone. At the time of settlement, the total acreage of grasslands, that is, prairies, sand barrens, bracken grasslands, fens, and sedge meadows combined, was 3.1 million acres (Curtis 1959). The prairies themselves originally covered approximately 2.1 million acres and formed the northeastern periphery of the great mid-continental grasslands of North America. The large islands of prairie such as the mesic Arlington, Rock, Military Ridge, and Walworth prairies or the low prairies in southeastern Wisconsin that existed on surrounding glaciated lands have been almost totally obliterated. According to the State Natural Heritage Inventory, only 2,000 acres of native prairie, or 0.1% of the original acreage, remains (Henderson & Sample 1995). Northward and eastward, the prairies became smaller and more scattered until they reached the Tension Zone. Here, along both north-south and east-west transition zones, forests and grasslands merged. Savannas were present throughout this same region, and one savanna type, the pine barrens (Figure 13), reappeared north of the Tension Zone in areas of very



**Figure 11.** Original tallgrass prairies. Within Wisconsin, prairies are located southwest of the Tension Zone, occupying their greatest area in the southern third of the state. Redrawn after Curtis (1959).



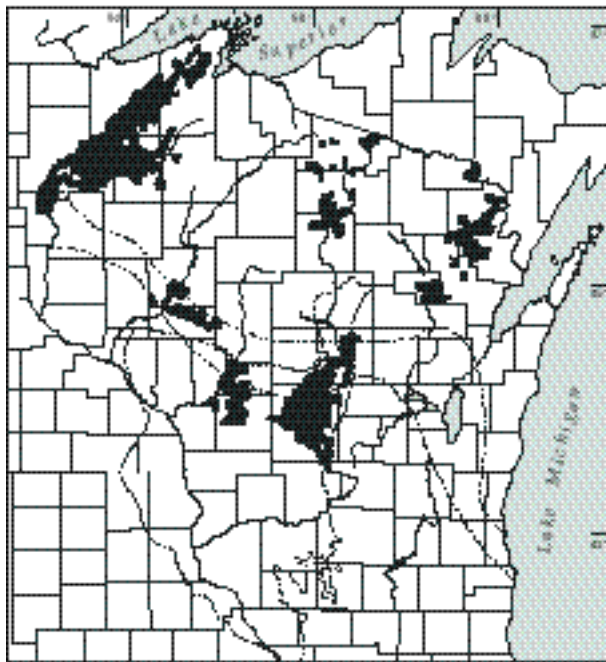
**Figure 12.** Original oak savannas. Oak openings were present throughout the region southwest of the Tension Zone. Oak barrens are restricted to areas of very sandy soil, especially the sand plains of central Wisconsin and terraces along major rivers. Redrawn after Curtis (1959).

sandy soil. Native prairie vegetation occurred on outwash sands at numerous smaller sites within the Tension Zone in central counties (Whitford 1972) and on nearly level heavy clays in southeastern counties (Whitford 1958). A remarkable diversity of prairie plants occurred northward well into the Mixed Conifer-Northern Hardwoods floristic province, particularly in large sandy tracts of pine barrens and bracken grasslands in northeastern Wisconsin and in areas of pine barrens and brush prairies in northwestern Wisconsin. Northern records for various prairie species may indicate 1) plants with range limits that naturally extend farther than others, 2) plants with at least some ability to spread and establish themselves beyond their native range, or 3) adventive species native farther south or west and not well established. Even in southern Wisconsin, most prairie species that are still common have become established on non-prairie soils (Gould 1941).

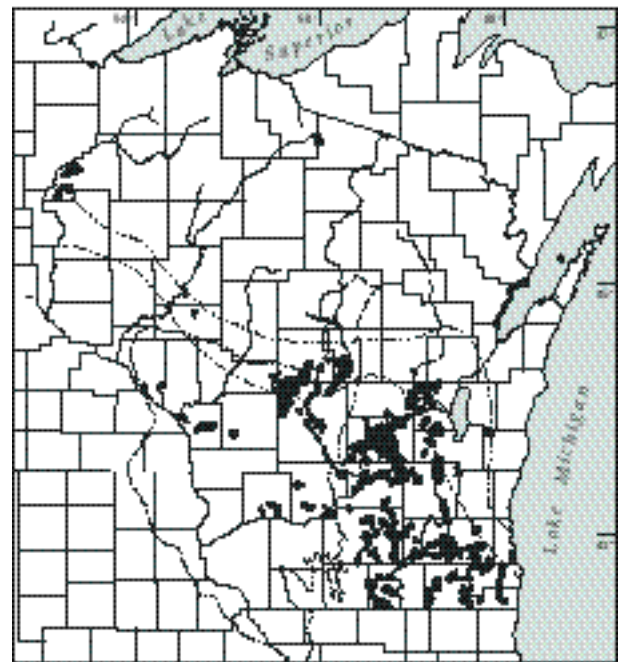
Prairie plants still occur in many habitats. Permanently wet communities like sedge meadows (Figure 14), shrub thickets, and fens resemble prairies in ecology and composition. Oak openings, oak and pine barrens, and related com-

munities contain large numbers of prairie plants. Dunes, old fields, roadsides, railroad corridors, and other minor or weed communities may also sustain prairie species, as do rock ledges, bluffs, and cliffs, summits of which usually support savanna, woodland, or glade vegetation with ground layers very similar to the dry prairies. Thin-soil borders adjoining outcrops support lichens, mosses, and small flowering plants such as Rock Cress (*Arabis lyrata*), Rock Spike-moss (*Selaginella rupestris*), pinweeds (*Lechea* spp.), and pussy-toes (*Antennaria* spp.), while shadier borders are favorite haunts of Wild Columbine (*Aquilegia canadensis*), Alum-root (*Heuchera richardsonii*), and Harebell (*Campanula rotundifolia*).

The major plant communities of Wisconsin have been treated in detail by Curtis (1959) in his monumental synthesis, *The Vegetation of Wisconsin*, in which the vegetational continuum provides the means to arrange natural assortments of dominant species or communities according to ecological similarity along environmental gradients. The apparent differences in species composition associated with



**Figure 13.** Original pine barrens. North of the Tension Zone, the oak barrens yield to a true savanna (locally known as barrens) in which the major dominant is usually Jack Pine and the understory often prairie-like. Most regions of former barrens are now forested, except for tracts maintained as savannas or brush prairies through prescribed burning. Redrawn after Curtis (1959).



**Figure 14.** Original sedge meadows. Sedge meadows are present in all parts of Wisconsin, but are concentrated in areas of extinct lake beds and along shores in the south. They are closely related to fens and wet prairies, but are dominated by sedges instead of grasses. Redrawn after Curtis (1959).

Table 4. Indicator species for five segments of the prairie gradient. From Curtis (1959).

Wet prairie species	Wet-mesic species	Mesic species	Dry-mesic species	Dry species
<i>Aster novae-angliae</i>	<i>Cicuta maculata</i>	<i>Aster laevis</i>	<i>Anemone cylindrica</i>	<i>Arenaria stricta</i>
<i>Calamagrostis canadensis</i>	<i>Desmodium canadense</i>	<i>Ceanothus americanus</i>	<i>Asclepias verticillata</i>	<i>Artemisia caudata</i>
<i>Hypoxis hirsuta</i>	<i>Dodecatheon meadia</i>	<i>Cirsium discolor</i>	<i>Dalea candida</i>	<i>Aster sericeus</i>
<i>Oxypolis rigidior</i>	<i>Fragaria virginiana</i>	<i>Desmodium illinoense</i>	<i>Helianthus occidentalis</i>	<i>Bouteloua curtipendula</i>
<i>Pycnanthemum virginianum</i>	<i>Galium boreale</i>	<i>Eryngium yuccifolium</i>	<i>Linum sulcatum</i>	<i>Dalea purpurea</i>
<i>Solidago gigantea</i>	<i>Helianthus grosseserratus</i>	<i>Helianthus pauciflorus</i>	<i>Panicum oligosanthos</i>	<i>Panicum perlongum</i>
<i>Spartina pectinata</i>	<i>Heuchera richardsonii</i>	<i>Liatris aspera</i>	<i>Potentilla arguta</i>	<i>Pulsatilla patens</i>
<i>Thalictrum dasycarpum</i>	<i>Lathyrus venosus</i>	<i>Panicum leibergii</i>	<i>Scutellaria leonardii</i>	<i>Schizachyrium scoparium</i>
<i>Veronicastrum virginicum</i>	<i>Phlox pilosa</i>	<i>Ratibida pinnata</i>	<i>Sporobolus heterolepis</i>	<i>Solidago nemoralis</i>
<i>Zizia aurea</i>	<i>Rudbeckia hirta</i>	<i>Solidago missouriensis</i>	<i>Stipa spartea</i>	<i>Solidago ptarmicoides</i>

topography led Curtis and Greene (1949) to select groups of indicator species that attained peaks of optimum growth for five segments of the prairie continuum (Table 4). Individual stands of prairie are placed along the gradient according to a site index calculated by means of these indicator species (Curtis 1955, 1959). The fundamental outline of the following discussion is based on the communities as designated in Curtis (1959). Henderson (1995a) has summarized available knowledge on species presence, density, and frequency for each of the five prairie types and sand barrens.

### ***Prairie Communities***

Once the European settlers arrived, the prairies of Wisconsin disappeared quickly. Prior to 1830, the prairies stretched for miles on level outwash plains, undulating glaciated terrain, and rolling surfaces or steep slopes of dolomitic bedrock. Smaller, more scattered prairies occurred on hillsides, bluff tops, and other uneven land forms, as well as on inundated lowlands, sites where extant remnants are more likely still to be found. Because most of the prairie soils of Wisconsin are predisposed to agricultural use, only a few large natural prairies remain, most notably Avoca Prairie and Savanna State Natural Area in Iowa County, which contains the largest tallgrass prairie east of the Mississippi River, and the rather unique, fen-like Chiwaukee Prairie on top of the Niagara dolomite in Kenosha County. Otherwise, what remains of the original prairies are relics on sites unsuitable

or unavailable for agricultural purposes, most often very dry prairies on steep topography, rarely mesic prairies along railroad and highway rights-of-way and in corners of neglected cemeteries, or wet prairies on lowlands subject to flooding. These remnants continue to suffer or disappear because of overgrazing, invasion by trees and shrubs due to long periods without burning, drainage changes, soil disturbances, and herbicide use. Even on protected prairies, populations have declined and species have died out entirely. (See Leach & Givnish 1996; but because most stands they studied have rarely been burned, it is unclear whether habitat fragmentation and edge effects, or lack of management, is more responsible for the gradual dilution of biodiversity.) Today, not surprisingly, considering their agricultural value, the tall-grass deep-soil prairies and the related oak savannas are the two most endangered ecosystems in the Midwest, and are, in fact, among the most decimated in the whole world (Wisconsin Department of Natural Resources 1995).

#### **• Dry Prairies**

Of all the different Wisconsin prairies, the most frequently surviving are the various dry prairies. Distinctive grassland communities have developed on deposits of sand along rivers, on glacial gravels (kames, eskers, drumlins, outwash terraces), and most commonly on dolomitic bedrock that may be exposed on bluffs and hillsides. These have become known, respectively, as sand prairies, gravel-hill prairies, and dry lime prairies (which, on steep rocky

hillsides, have been dubbed “goat prairies,” because it requires the agility of a goat to scramble up them). Sand prairies are also found on inland dunes, old lake beds, and sandstone cliffs. In the presence of fire, these climax communities displace barrens (desert-like associations of *Opuntia* and *Hudsonia*—southwestern and Atlantic Coastal Plain floristic elements, respectively—with ground lichens and annuals like Coastal Joint-weed, *Polygonella articulata*). In the absence of fire these communities succumb to shading by Jack Pine (*Pinus banksiana*) and scrub oaks. According to Curtis (1959), sand prairies cannot be subdivided into different types on the basis of species composition; neither were they recognized as a distinct community by him. However, when reanalyzing Wisconsin Plant Ecology Laboratory (PEL) data augmented by information from additional stands, Umbanhowar (1992, 1993) found a compositional difference between dry prairies on sandy substrates and those on limestone substrates. In Illinois (White & Madany 1978), sand prairies have been kept apart as a separate subclass of communities on the basis of soil structure and moisture levels.

Judging from their species composition (Anderson 1954), limy prairies have affinities with the Cordilleran, Great Plains, and Ozarkian prairies to the far west, southwest, and south of Wisconsin. Little Bluestem, perhaps the most characteristic plant, is accompanied by a long list of other graminoids such as grama grasses (*Bouteloua* spp.), June Grass, drop-seed grasses (*Sporobolus* spp.), panic grasses (*Panicum* spp.), Plains “Muhly” (*Muhlenbergia cuspidata*), and sedges (*Carex* spp.); forbs, including Short Green Milkweed (*Asclepias viridiflora*), Silky Aster (*Aster sericeus*), Purple Prairie-clover (*Dalea [Petalostemon] purpurea*), False Boneset (*Brickellia [Kuhnia] eupatorioides*), etc., on the driest ridges and slopes, Heath Aster (*A. ericoides*), Rough Blazing-star (*Liatris aspera*), Old-field Goldenrod (*Solidago nemoralis*), Prairie Violet (*Viola pedatifida*), Downy Gentian (*Gentiana puberulenta*), etc., in more mesic places; and shrubs such as Lead-plant (*Amorpha canescens*), New Jersey Tea (*Ceanothus americanus*), sumacs (*Rhus* spp.), and roses (*Rosa* spp.). Prairies found on gravel hills and dolomitic bedrock resist both tree growth and grazing pressure, but like those on sand are subject to invasion by weeds and grasses and such trees as Quaking Aspen (*Populus tremuloides*), Black Cherry (*Prunus serotina*), and especially Eastern Red-cedar (*Juniperus virginiana*). However, if grazing pressure by cattle is low, the dry prairie flora for the most part is able to persist under disturbance.

#### • Mesic Prairies

Prairies on deep mineral soils range from dry-mesic and well drained to wet and very poorly drained, with these segments, like all others of the compositional gradient, passing imperceptibly into one another. The mesic prairies thus differ from sedge meadows and fens, which are developed on sedge peat or marl, and from cat-tail marshes, which are permanently inundated. Mesic prairies once occupied perhaps 40%, or approximately 840,500 acres (Curtis 1959), of the prairie-forest border region of Wisconsin. They evolved on flat to gently rolling topography where there had been some accumulation of well-developed soil, and their great biomass insured hot fires, eliminating shrubs and trees. Because of their deep dark soils, these prairies have been all but eliminated due to direct destruction for agricultural purposes. Plowing, over-grazing, mowing, fencerow clearing, Multiflora Rose (*Rosa multiflora*) planting during the 1950s, herbicide spraying especially since the 1960s, and pesticide application, as well as draining and irrigating, have favored exotic weeds at the expense of the natives and have made many once-common species, along with their pollinating insects and their seed-dispersing birds, locally rare or often extinct. Thus, the left-over remnants are minute, fragmented, and very scattered, pathetic monuments to human shortsightedness, greed, and need.

The mesic prairies exhibit the deepest soils, the highest plant species diversity, and the tallest grasses and forbs, Big Bluestem being the leading dominant. The other major dominants, Little Bluestem, Needle Grass, Prairie Dropseed, and Leiberg’s Panic Grass, are essentially equal in importance to one another (Curtis 1959). As for the forbs, Illinois Tick-trefoil (*Desmodium illinoense*), Stiff Sunflower (*Helianthus pauciflorus*), Rough Blazing-star, Compassplant (*Silphium laciniatum*), Prairie-dock (*Silphium terebinthinaceum*), and Prairie Violet, all have ranges coinciding with that of the mesic tallgrass prairie. These, together with the more wide-ranging White Wild False-indigo (*Baptisia alba*), Pasture Thistle (*Cirsium discolor*), and Yellow Coneflower (*Ratibida pinnata*), are among the long list of most prevalent mesic prairie species.

Composition is sometimes not as uniform as might be expected, however, due to the regional geographical relations of the component species. For example, suites of often rare species to be found only in the southeastern corner of Wisconsin include the Chestnut Sedge (*Fimbristylis puberula*), Nodding Wild Onion (*Allium cernuum*), Stout Blue-eyed-grass (*Sisyrinchium angustifolium*), Marsh Gay-feather

(*Liatris spicata*), and Smooth Phlox (*Phlox glaberrima*). These are all southern or southeastern elements at the very northern or northwestern edge of their range. Conversely, in our far western counties on or near the bluffs of the Mississippi and St. Croix rivers, Ground-plum (*Astragalus crassius*), Downy Prairie-clover (*Dalea [Petalostemon] villosa*), Silvery Scurf-pea, Prairie Sagewort (*Artemisia frigida*), and Dotted Blazing-star (*Liatris punctata*)—all northern Great Plains elements—reach the easternmost edge of their range. All have generally similar distributions that, like the preceding group, do not correspond with the general range of the prairies in Wisconsin. Other important forbs such as Prairie-dock, which is restricted to an area south and east of Wood County, and Pale Purple Coneflower (*Echinacea pallida*), which is local in the southern two tiers of counties, also have clearly defined distribution patterns related to their southern Midwestern origins.

Several common agricultural crops and weeds are terrible pests in prairies as well: White Campion (*Silene latifolia* [*Lychnis alba*]), sweet-clovers (*Melilotus alba* and *M. officinalis*), Red Clover (*Trifolium pratense*), Leafy Spurge (*Euphorbia esula*), Wild Parsnip (*Pastinaca sativa*), and Common Dandelion (*Taraxacum officinale*) routinely invade prairies, as do the all-too-familiar forage grasses, especially the two common bluegrasses (*Poa pratensis* and *P. compressa*), Smooth Brome, Orchard Grass, and Quack Grass. In many mesic and lowland prairies, the native flora is scarcely able to compete against invasion by such ecologically aggressive exotics (Curtis 1959).

#### • Lowland Prairies

Lowland prairies are found in river valleys or lake basins where the soil is nearly always wet from surface water in winter and spring, or from floodwaters at any time of the year. The cold-air drainage to which some such sites are subject produces summer fogs and late spring and early autumn frosts.

The overwhelming dominants of the wettest prairies are Blue-joint and Cordgrass. The other leading dominants include Big Bluestem, Upland Wild-timothy, and many species of sedges (*Carex* spp., *Schoenoplectus* spp. [*Scirpus*, in part]). Wet prairies merge into marshes in even wetter conditions, and into the much more frequent and floristically richer wet-mesic prairies on the drier side of the continuum. The wide-ranging grasses that peak as dominants of wet-mesic prairies include Big Bluestem, Blue-joint, Cordgrass, Canada Wild-rye, and Leiberg's Panic Grass. As for

forbs, in the water and along the margins of ponds, sloughs, and swales Marsh-marigold (*Caltha palustris*), Bottle Gentian (*Gentiana andrewsii*), and Blue Flag (*Iris virginica*) lend color to the dense vegetation, as do Common Milkweed (*Asclepias syriaca*), False-toadflax (*Comandra umbellata*), Canadian Tick-trefoil (*Desmodium canadense*), Prairie Phlox (*Phlox pilosa*), and Black-eyed Susan (*Rudbeckia hirta*) on the hummocks and swells. Such characteristic sedge meadow plants as Blue-joint, Meadow Anemone (*Anemone canadensis*), water-hemlocks (*Cicuta* spp.), Field Horsetail (*Equisetum arvense*), bedstraws (*Galium* spp., including *G. obtusum*), Marsh Pea (*Lathyrus palustris*), and Purple Meadow-rue (*Thalictrum dasycarpum*) are also prevalent. Fens contain many prairie and sedge meadow species as well as some uniquely their own, especially delicate, open-habitat specialists with Atlantic Coastal Plain affinities such as One-flowered Satin Grass (*Muhlenbergia uniflora*) or Low Nut-rush (*Scleria verticillata*), a minute annual that is known from here all the way to Brazil.

#### Sand Barrens

The sand barrens of southern Wisconsin actually consist of a mixture of mostly naturally disturbed habitats, including active and stabilized blowouts and dunes and sand flats, and also once-plowed, now-abandoned fields too dry to support a crop. Originally, some were probably thinly vegetated with dry-mesic to dry sand prairies, but most have by now become excessively degraded, as along the lower Wisconsin River Valley, where dunes were flattened in the 1930s in preparation for turning them into pine plantations. Nonetheless, abandoned fields and roadsides in such regions still possess interesting mixtures of native pioneer species from nearby prairies, and introduced pioneers—species which in Eurasia long ago played an analogous ecological role. The latter, of course, are now our weeds, and thus mature sand-barrens vegetation reflects the development of a grassland community that is very different from, albeit closely related to, dry-mesic prairies and oak openings (Curtis 1959). Many important widespread bunch grasses of sandy habitats grow here, including June Grass and the two pink tumble grasses, Fall Witch Grass (*Digitaria [Leptoloma] cognata*) and Purple Love Grass (*Eragrostis spectabilis*), as well as the (with us, rare) pioneering Sand-reed (*Calamovilfa longifolia* var. *longifolia*) and Sand Dropseed (*Sporobolus cryptandrus*), both widespread western elements. A whole suite of species that came to Wisconsin from various directions are essen-

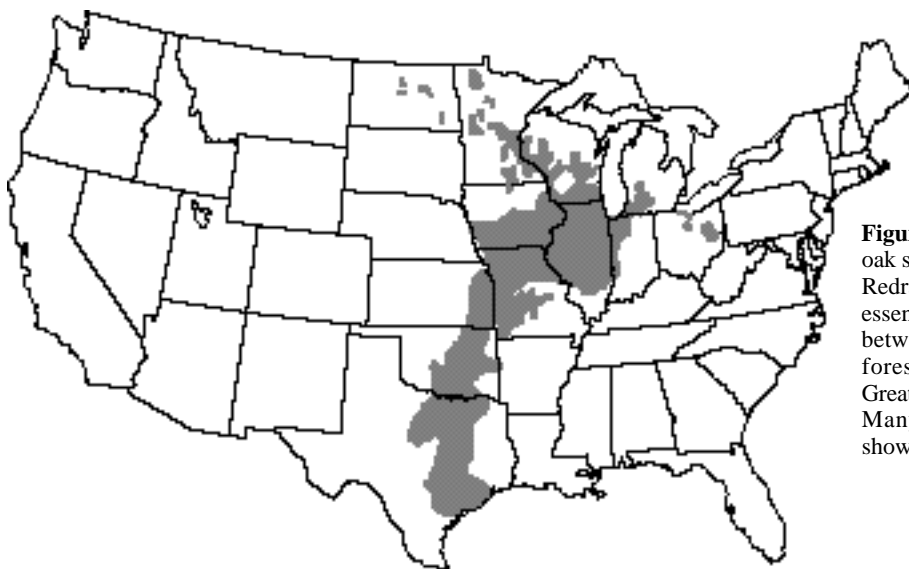
tially confined to this community, including Rock Spike-moss (Appalachian; see below), Sand Bracted Sedge (*Carex muhlenbergii*—eastern states), Sand Croton (*Croton glaudulosus* var. *septentrionalis*—subtropical and tropical America), Rough Sand Sedge (*Cyperus schweinitzii*—Nebraska sandhills, see below), Blue Toadflax (*Linaria canadensis*—southern states), Western Ragweed (*Ambrosia psilostachya*—Great Plains), Virginia Dwarf-dandelion (*Krigia virginica*—eastern states), and, locally, the charming Fame-flower (*Talinum rugospermum*—central Great Plains sandhills). The principal species occupying blowouts include three-awn grasses (*Aristida basiramea*—Great Plains, and the beautiful *A. tuberculosa*—Atlantic Coastal Plain dunes), Large Cotton-weed (*Froelichia floridana* var. *campestris*—southeastern states), and Coastal Joint-weed (Atlantic Coastal Plain dunes). The only woody species encountered frequently is the diminutive, evergreen False Heather (*Hudsonia tomentosa*), still another element of the Atlantic Coastal Plain and an important source of ecologically specialized swale and sand prairie components.

### Savanna Communities

The original vegetation pattern of the Midwestern prairie-forest border was a landscape characterized by a mosaic of prairies on hills, bluffs, and flat to gently rolling plains, oak forests in the river valleys and on their east- and north-facing slopes, and, alternating with these, savannas and woodlands (Anderson 1991, Ebinger 1991). Certainly, Wisconsin's

Prairie-Southern Forest Province at the time of European settlement was dominated by oak savannas and open oak woodlands (Figure 15; see also Figures 2, 10, & 12). Oak savannas had a very open canopy and were either oak openings (of pure Bur Oak, *Quercus macrocarpa*, pure White Oak, *Q. alba*, or a mixture of the two) or oak barrens (of Black Oak, *Q. velutina*, and/or Northern Pin Oak, *Q. ellipsoidalis*) (Curtis 1959). Oak woodlands and forests had a more or less closed canopy and were of several types: Bur Oak-Swamp White Oak (*Q. bicolor*), White Oak-Bur Oak-Red Oak (*Q. rubra*), Chinquapin Oak (*Q. muhlenbergii*), or Northern Pin Oak (Faber-Langendoen 1995). These oaks are both fire resistant and shade intolerant. All the oaks occurred in both savannas and forests/woodlands, together with Shagbark Hickory (*Carya ovata*), Large-toothed Aspen (*Populus grandidentata*), Black Cherry (*Prunus serotina*), Iowa Crab (*Malus ioensis*), and other tree species of lesser importance. The distributions of six major tree species of the Wisconsin savannas are shown in Figure 16.

According to Curtis (1959), the presettlement oak savannas occupied 5.5 million acres in southern Wisconsin, making them the most common community in the Prairie-Southern Forest Province. Oak and pine barrens occupied 4.1 million acres, and oak forests, many of which may have been open woodland depending on their fire history, another 1.4 million acres. Intact stands of oak savanna are now so rare that less than 500 acres, or less than 0.01 percent of the original acreage, are listed in the Natural Heritage Inventory as having a plant assemblage similar to that of the origi-



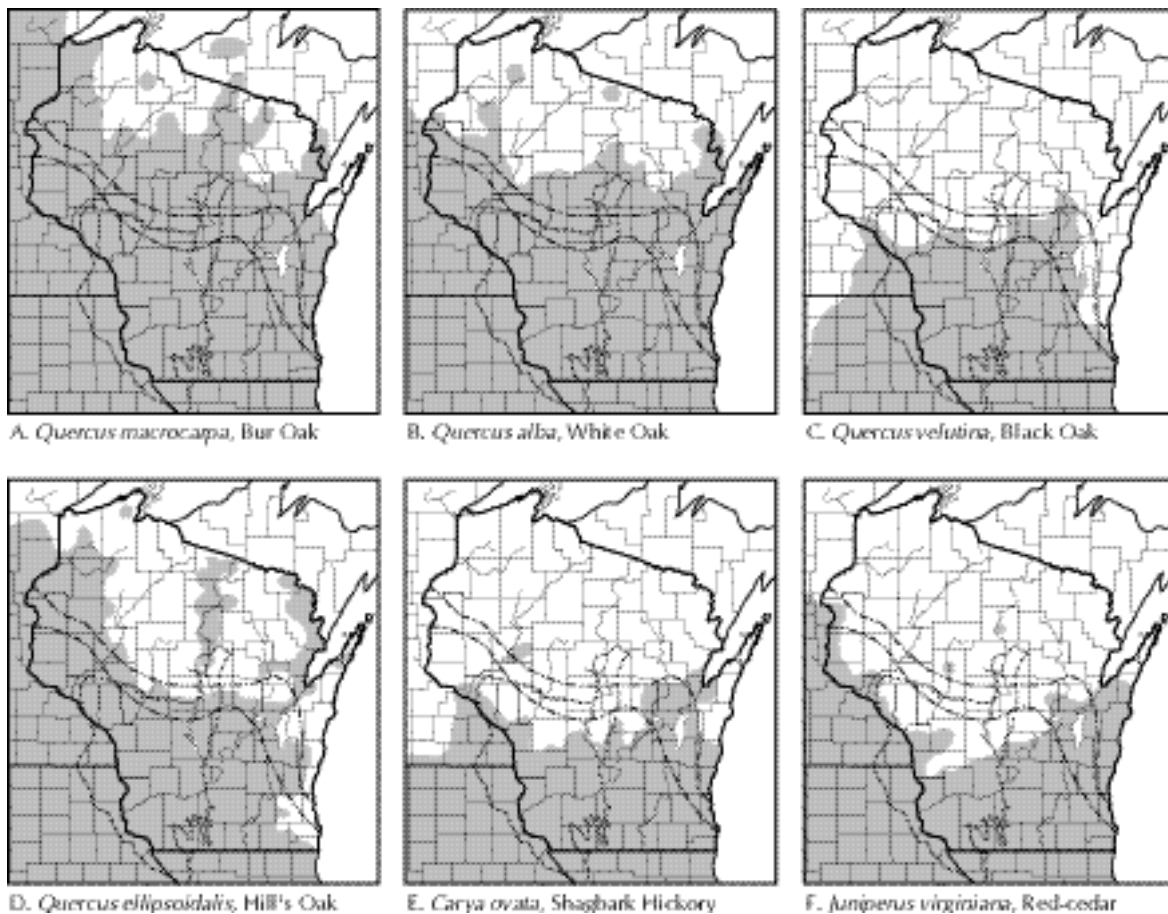
**Figure 15.** The presettlement distribution of oak savanna and woodlands in the Midwest. Redrawn from Nuzzo (1994). Savannas are essentially transitional communities located between and arbitrarily separated from the forests of the East and the prairies of the Great Plains (compare with Figures 2 & 12). Many outlying areas are too small to be shown on a map of this scale.



nal oak savanna (Henderson & Sample 1995). Very rarely, scattered and stately open-grown bur oaks, with an understory totally devastated by grazing, did survive to bear witness to the majestic, park-like oak opening. In the Midwest as a whole, oak savannas now occupy 0.02 percent of their estimated presettlement area (Nuzzo 1986, 1994).

Ecologists have always struggled with the definition of the term *savanna*, particularly in North America (Dyksterhus 1957, Penfound 1962). The oak savanna, a term often used interchangeably with oak opening, was defined arbitrarily by Curtis (1959) as stands of open-grown oaks with densities ranging from one tree per acre up to a maximum of 50% canopy cover, and having a predominantly herbaceous ground layer of native forbs and grasses. However, the image of a savanna being a prairie dotted with trees, or scattered trees or groves with a prairie understory, is far too narrow. Contemporary ecologists now define oak savannas as communities dominated by oaks, having an average tree

canopy of more than 10% but less than 80%, with or without a sparse shrub layer, but with a predominantly grassy ground layer rich in forbs associated with both prairie and forest communities (Haney & Apfelbaum 1990, Nuzzo 1986, White & Madany 1978). The once ubiquitous savannas of Minnesota, Iowa, and Wisconsin ranged from very open, prairie-like oak openings (grasses as an understory to trees), through close-growing or chaparral-like scrub forests, to dense shrub thickets (grasses intermixed with woody plants). These occurred on sites varying from wet to dry and flat to hilly, and developed on soils varying from thin and sandy or rocky to deep and loamy or clayey. Modern terminology for a comprehensive classification of these habitat types is still evolving (several classifications are summarized by Leach & Ross 1995). For example, Curtis (1959) recognized only four types of savanna communities in Wisconsin, namely oak barrens, oak opening, pine barrens, and cedar glade, whereas Haney and Apfelbaum



**Figure 16.** Distribution of major tree species in Wisconsin grassland and savanna communities. Modified after Little (1971).



(1997) recognized six oak savanna types in the Upper Midwest: eastern sand savanna, northern sand savanna (including oak and pine barrens), mesic loam savanna, floodplain savanna, clay-loam savanna, and southern oak savanna. Meanwhile, the Illinois Natural Areas Inventory (White & Madany 1978) divided the savanna community class into three subclasses separated by soil type: savanna, sand savanna, and barren; and seven natural communities based on soil moisture: dry-mesic savanna, mesic savanna, dry sand savanna, dry-mesic sand savanna, dry barren, dry-mesic barren, and mesic barren. Identical savannas probably occurred in Wisconsin, at least in terms of their canopies if not their understories. Almost unknown but deserving of attention are wet and wet-mesic savannas, rare and unusual communities that were mentioned by Bray (1955) and Curtis (1959), but which remain unrecognized in community classification systems for Wisconsin and Illinois.

Once definitions are taken into account, the next interesting problem is to construct with fair accuracy a picture of savanna understories and groundlayers in the absence of surviving savannas, quantitative data, or even any extensive list of savanna species. Little accurate information has been available to help answer the cutting-edge question of whether Midwestern savannas had a characteristic flora or even a few species restricted to them (Bray 1955; Leach 1996; Packard 1988b, 1993; Pruksa 1994a, b, 1995). The species listed by early observers, and those present in relics and successful in modern restorations, reveal, not surprisingly, that savannas present differences in species composition on both regional and geographic scales comparable to the situation found in the prairies or in the deciduous forests to the east and south. Upland savannas were studied in Wisconsin in the 1950s by Curtis (1959) and his student Bray (1955, 1958, 1960), whose published species lists for the oak savannas may be misleading, because according to the observations of restoration practitioners, the flora of oak ecosystems may have been, in fact, more diverse (DeLong & Hooper 1996; Leach 1994, 1996; Leach & Givnish 1999; Packard 1988a, b; Pruksa 1994a, b; Henderson 1995b). Closed savannas or savanna woodlands (i.e., overgrown savannas with 50–100% canopy cover) in the recent terminology were lumped by Curtis (1959) with the southern dry and southern dry-mesic forests, despite their original distinctness from oak forest (Henderson 1995b). Recent floristic summaries of the ground layer plants of open savannas indicate that the species in the dry stands (Will-Wolf & Stearns 1998) were very different from those of either mesic

(Leach 1994, 1996; Packard 1988b, 1993) or wet stands (Hujik 1995), and presumably the floristic composition of closed savannas behaved in a similar fashion.

Oak savannas thrived on the same kind of balance between climatic regime and natural disturbance as did the prairies or the forests. Historically, these disturbances included herbivory, drought, exceptionally wet seasons, and fire. Although not every acre burned every year, the historical and scientific evidence indicates that the frequency, intensity, and extent of wildfires had an enormous impact on the ecology of oak forests and oak savannas (Abrams 1992). Just as frequent fires maintained the treeless structure and affected the species composition within the prairie biome, reduced fire frequency and intensity encouraged the abundance of oaks and the establishment of fire-tolerant tree species within the prairie-forest transition zone (Anderson 1970, 1998; Anderson & Brown 1986; Cooper 1961; Dorney 1981; Grimm 1983). Bur oaks needed only a brief period of protection from fire to flourish, their thick bark, especially evident on young trees, conferring resistance to fire and allowing them to grow to tree size. Fires resulted from both lightning strikes and human activities, and in either case spread accidentally on their own or were intentionally set for diverse purposes (Abrams 1992, Curtis 1959, Komarek 1968, Pyne 1982, Stewart 1956). Abrams (1992) estimated that fires occurred at 1- to 10-year intervals in oak savannas.

The arrival of European settlers to the Midwest in about 1830 immediately overturned the regional fire ecology. The oak woodlands, oak openings, and oak-pine forests experienced irrevocable alteration due to fire suppression, clearing of trees, removal of native animals, introduction of domestic livestock, invasion of weedy native and aggressive exotic species, and very soon, habitat fragmentation. Unfarmed savannas, except very dry or very wet ones, were changed into closed-canopy forests within two to three decades, owing to successional replacement of any one of the dominant oaks by other shade tolerant/fire intolerant trees and shrubs (Beilmann & Brenner 1951, Bray 1960, Curtis 1959, Grimm 1983, Nuzzo 1986, Stout 1944). Oak openings and oak barrens used for agricultural purposes may have retained their original tree cover, but overgrazing by domestic livestock, augmented by the rapid spread of many weedy species, eliminated the shrub and herb strata. Having been effectively exterminated, the savanna communities will continue to exist only to the extent that programs of active restoration are carried out.

### • Typical Savannas

Very little concrete knowledge is available concerning the composition and dynamics of the more or less distinct subtypes of savannas that might be recognized for Wisconsin. The typical savannas occurred on soils ranging from shallow to deep and from dry to wet, but were probably most extensive on the fine-textured soils of level ground (White & Madany 1978). Typical dry to dry-mesic savannas were found on soils comparable to those of dry to dry-mesic upland forests, and their dominants were derived from the southern Ozarkian and Appalachian dry forests (Bur, Black, and White oaks in the overstory) and from the dry-mesic prairies (Big Bluestem, Little Bluestem, and Needle Grass in the ground layer; Curtis 1959, White & Madany 1978). The ground layer species were probably a mixture of prairie plants, e.g., Lead-plant, Prairie Tickseed (*Coreopsis palmata*), Purple Prairie-clover, and Flowering Spurge (*Euphorbia corollata*), forest and forest-border species such as Hog-peanut (*Amphicarpa bracteata*), Wild Sarsaparilla (*Aralia nudicaulis*), Pennsylvania Sedge (*Carex pensylvanica*), and Pointed Tick-trefoil (*Desmodium glutinosum*), and savanna specialists that thrived in a combination of shade and sun. According to Bray's study (1960), oak savannas showed a decrease in grasses and an increase in forbs and shrubs compared to prairies, but a corresponding increase in grasses and decrease in forbs as compared with forests, with the prairie species predominant in open savannas (Curtis 1959). This conclusion simply verifies the continuum from sun-loving prairie species that can tolerate only light shade, to forest species that can tolerate but do not thrive in moderate sunlight.

Less is known about the mesic and lowland savannas of deeper mineral soils. Mesic savannas were dominated by White and Bur oaks, lowland savannas by Swamp White, Bur, or White oaks with River Birch (*Betula nigra*) and Silver Maple (*Acer saccharinum*) in spots. The canopy dominants of mesic savannas remained the same as in dry savannas, and their more favorable moisture conditions presumably resulted in ground layer vegetation that was similar to that of mesic prairies (but see Leach 1996). Tallgrass Formation species listed as probable savanna specialists (Packard 1988a, b, 1993) include some that today reach their highest levels of presence in prairies, e.g., Purple Milkweed (*Asclepias purpurascens*), Veiny Pea (*Lathyrus venosus*), Pale Indian-plantain (*Cacalia [Arnoglossum] atriplicifolia*), and Cream Gentian (*Gentiana alba*), as well as some that peak in woodlands, e.g., Woodland Brome (*Bro-*

*mus pubescens*), Rye grasses (*Elymus* spp.), Bottlebrush Grass (*E. hystrix*), and Elm-leaved Goldenrod. Some of these may have been characteristic savanna species that have survived successional shifts to more or less closed forests by moving into drier microsites (Pruka 1994a, b) in the same way that lowland prairie species invade drier savannas (Bray 1958, Hujik 1995). The whole argument about whether there are savanna specialists loses credibility when considering on the one hand the continuous floristic change of species replacing one another from the Atlantic shores to the foothills of the western mountains, and the probability that among the 1,000 or so species of the Midwestern tallgrass prairies (Ladd 1997), there will be some that fall in the middle of the continuum, or that grow well in semishade. In fact, but rarely, climax mesic deciduous forest species have been found occasionally in mesic prairies, for example, Nodding Trillium, Bloodroot, etc., near Juda, Green County—a nearly unbelievable situation, explained by a hot fire destroying a maple forest canopy in late fall, with the surviving herbaceous layer soon invaded by the sun-loving prairie plants.

Lowland savannas were situated at the interface of lowland forests with wet prairies or sedge meadows. The ground layers of the few remnants at Avoca Prairie and Savanna and Chiwaukee Prairie studied by Hujik (1995) were more complex than those of lowland prairies. Spatial patterning of groundlayer vegetation varied simultaneously along light and microtopographical gradients, with prairie species, e.g., Meadowsweet (*Spiraea alba*), White Wild Indigo, Common Yarrow (*Achillea millefolium*), and Common Mountain Mint (*Pycnanthemum virginianum*) being most abundant in the mostly open areas; supposed savanna specialists such as Sensitive Fern (*Onoclea sensibilis*), Meadow Anemone, and Wood Nettle (*Laportea canadensis*) in partial shade; and species characteristic of both savannas and forests such as Common Carrion-flower (*Smilax herbacea*), River-bank Grape (*Vitis riparia*), Wild Yam (*Dioscorea villosa*), and Wild Goldenglow (*Rudbeckia laciniata*) in the mostly shady areas.

### • Sand Savannas

In sandy areas, the Bur oaks and White oaks of the heavy-soil savannas or oak openings are replaced by Black Oak or Northern Pin (Hill's) Oak (oak barrens) or Jack Pine (pine barrens), species that, even if burned again and again, keep coming up from underground "grubs" in the case of the oaks (Curtis 1959), or seeds in the case of Jack Pine.

These canopy dominants may occur in nearly pure stands of a single species, or in mixtures of two or all three. Systems for classifying vegetation call these communities by different names. *Oak barrens* and *pine barrens* have long been used in Wisconsin, whereas *sand savanna* is widely used in Indiana, Illinois, and Michigan. The use of terms like brush prairie, scrub oak savanna, oak barrens, oak grove, and woodland imply that sand savannas form a continuum from prairie to forest, and that savanna consisting of solitary scattered trees was not the most characteristic type (Heikens & Robertson 1994, Leach & Ross 1995, Will-Wolf & Stearns 1998). In presettlement times, the extent to which sand savannas developed in place of sand prairies depended upon topography, soil moisture, and the presence of Native Americans, and the extent to which these limited or encouraged the severity or frequency of fires.

### Origin of the Prairie and Savanna Flora

Ecological plant geography, or ecology, describes the distribution of plant communities and their interactions with the environment. Historical plant geography attempts to reconstruct the history of a flora and of its species, where its elements came from, and how it was assembled, by using fossil evidence as well as characteristics of the species themselves, their ecology, morphology, physiology, genetics, and cytology.

In regions of high endemism such as California or Texas—never glaciated nor covered by ocean for tens of millions of years—this is a daunting task indeed. However, for oceanic islands like Hawaii, rising *de novo* out of the sea, or land-locked areas such as Wisconsin that until geologically recent times were largely covered by mile-thick, slowly moving ice, floristic analysis is relatively easy. Thus, reconstructing the postglacial migrational history of Wisconsin's flora, in broad strokes to be sure, is a subject that has long occupied our interest.

### Glacial Setting

Glacial maps of North America all show that—except for the Driftless Area—the northern portions of the Prairie Province, including the whole of the Great Lakes region, were glaciated during the Pleistocene epoch. Earth's climate had become locally cold enough that more snow fell than melted, and huge masses of ice gradually accumulated. Complexes of massive ice sheets spread southward

many times from northern centers in North America, Greenland, and Europe, then largely melted, only to reform in response to climatic oscillations. For many tens of thousands of years the climate fluctuated markedly, so that there were alternating periods of general advance and withdrawal by the ice. Full-glacial conditions last peaked about 20,000 yr B.P., when continental ice sheets surged southward from Cordilleran and Hudson Bay centers, at which time the eastern, or Laurentide, Ice Sheet reached the Ohio River, Mississippi River Valley to central Illinois, and northern Great Plains (Figure 17). The maximum extent of ice advance during the last, or Wisconsin, glacial interval from 15,000 to 12,000 yr B.P. is shown in Figure 18.

All plant and animal life was ostensibly eliminated from ice-covered territory. Thus, the present flora of the region is quite recent, derived from, and still developing as the result of, dispersal and migration into newly exposed glaciated land during and following the northward retraction of the Wisconsin ice sheet. To understand the present-day distribution of individual species and whole floras, biogeographers must take into account where these organisms might have been living in past times. Species or plant associations do not migrate readily except into open habitats, and the last glaciation occurred very recently—about 13,000 years ago in southern Wisconsin and about 10,000 years ago in the north (Mickelson et al. 1983).

#### • *Survivia*

There are next to no endemics in Wisconsin, only Cliff Goldenrod (*Solidago sciaphila*), Cliff Cudweed (*Gnaphalium saxicola*), and a unique hybrid or two. Nor, except for Glade Mallow (*Napaea dioica*) and Saw-leaf Mugwort (*Artemisia serrata*), are there any to speak of in the Middle West—some barely differentiated microspecies mostly of questionable validity (see Johnson & Iltis 1964, Mickelson & Iltis 1967). With these minor exceptions, all our prairie species, as well as all others in Wisconsin's flora, have at least some populations growing south of the last (Wisconsin) maximum glacial advance. We can thus assign our plants to one or another of the various, rather arbitrarily delimited *survivia* (or refugia, as these have been called) from whence we hypothesize they migrated east, north, and west, as the case may be, after the glaciers finally melted. For wide-ranging species with relatively broad tolerances such as Tall Anemone (*Anemone virginiana*), the *survivia* may well have extended across most of the southern states; conversely, for species such as Sand Cyperus (*Cyperus*



**Figure 17.** Maximum extent of all glacial advances in the Pleistocene epoch. The Laurentide Ice Sheet, spreading from two centers in the vicinity of Hudson Bay, left the Driftless Area in southwestern Wisconsin and northern Illinois. The illustration is a historical composite; in reality, the Driftless Area was never completely surrounded by ice at any one time. From Farb (1963).



**Figure 18.** Maximum extent of glaciation in the most recent or Late Wisconsin stage (Pleistocene epoch). Modified after Farb (1963).

*lupulinus* ssp. *macilentus*—see below) that survived in the relatively narrow mountain chains of the southern Appalachian region with limited southern habitats, survivia can be much more sharply delimited.

Because populations, now often only relictual, of almost all species did survive somewhere south of the ice, we may assume that the vegetation and climate in eastern North America, a region with pronounced topography, high moisture, and equable climate, was not too different from now. Conversely, cooling effects were more pronounced in the central United States, where the climate was much more continental. Along the Mississippi River, with its raging torrents of ice-cold melt water, and in the Midwest as a whole, climate must have been much cooler and wetter than now, and the periglacial effects, including the width of the permafrost zone, more extensive (Péwé 1983). Nonetheless, in many areas in the East, direct climatic effects of the glaciers were strongly marked for only ca. 50–125 miles to the south of the ice margin (Péwé 1983) and had little effect on the “mixed mesophytic forest” (Braun 1950, 1955). The high endemism from Maryland, Kentucky, and southern Missouri southward—sharply delimited by the margin of the Wisconsin ice advance, both of animals such as fish, salamanders, snails, and crawfish, and of many species of plants—speaks volumes about the relative mildness of the glacial climate in those areas (Braun 1950, 1955).

Such evidence suggests that the concept of survivia, which often can still be identified, and of the outward migration postglacially of their floristic elements in equiformal progressive areas (see Cain 1944, Hultén 1937), especially in the case of many Appalachian elements, is a reasonable hypothesis. (It has not escaped our attention that this is a still controversial issue, for there are those who are compelled to apply the frigid European Pleistocene model to the quite different, milder situation in North America. Reports of glaciers in North Carolina, Jack Pine in Georgia, or musk ox in Texas are all based on mistakes or taxonomic misidentifications.)

#### • Migrations

The landscape that was left behind after deglaciation was one vast, sparsely vegetated, gravelly, sandy, or muddy seed bed—an ecologically open habitat just waiting to be invaded by a rain of seeds and propagules. From the four corners of the compass, from these floristic survivia, came our flora: the periglacial belt of tundra and conifers, the northern Great Plains and the arid southwest, the Ozarks

and the Cumberlands, the hot Mississippi Embayment and the Gulf and Atlantic dunes and coastal plains, the cool and moist Appalachian deciduous forest, and even arctic and subarctic Alaska.

Revegetation of soilless, sterile glaciated areas took time. The migration of propagules and ensuing invasion of rich flora had to necessarily follow the development of soil, mycorrhizae incursion, and shade for mesophytes. These building stages were followed by an incongruous, helter-skelter floristic mixture of periglacial conifers and tundra plants, deciduous trees and shrubs, and heliophytic prairie plants. These soon sorted themselves out under the dictates of competition and succession into plant communities reflecting the regional climate. Eventually, in the climatic wedge of the Prairie Peninsula, those species that liked a prairie climate flourished—no matter what their region of origin. Many other species became extinct, while a vast number survived elsewhere, for example in the forests to the north or in specialized habitats in the Driftless Area. It is thus not surprising that our prairie flora is now composed of a large number of broadly adapted, widespread species that had their roots in diverse habitats.

The story is, of course, much more complex. There must have been tallgrass prairie communities in favorable places south of the Prairie Peninsula during the Wisconsin Ice Age, and in the Prairie Peninsula periodically during the past million years. Natural selection for plants favoring a tallgrass climate in the same general geographic region as today must have occurred at least three separate times during the substages of the Wisconsin glaciation (and probably more frequently, in view of the evidence today of eight or so substages during the Late Wisconsin, and at least 20 glacial-interglacial cycles during the late Quaternary). During this epoch of more than a million years, the speciation that resulted in some 300 or more regional prairie endemics must have occurred, a winnowing and sifting of floristic candidates preadapted to such a climate, all contributed (then as now) by surrounding ecosystems to the ecological melting pot.

An interesting aspect of the hypothesis of glacial survival, one that indirectly supports the whole concept, is the evolutionary divergence of many phylads into species pairs, one eastern and mesophytic, one more western and either xerophytic or cordilleran (montane/subalpine meadow examples include *Dodecatheon*, *Polemonium*, and *Camassia*). The two ranges, once separated by huge distances plus climate, glaciers, dry grasslands, and other factors for tens

of millenia, reexpanded west and east, as the case may be, and in some cases overlapped in the deglaciaded regions. Where sympatric in similar habitats, the species hybridized.

This east-west pairing includes forest species as well as prairie species, and is of great evolutionary interest. Among the most striking examples are our two species of fringed gentian, in the segregate genus *Gentianopsis*: the mesophytic, acidophilic, Appalachian *G. crinita*, and the relatively xerophytic, calciphilic *G. procera* of the High Plains. Although separated by different ecologies and flowering periods (*G. procera* blooms earlier, as befits a species coming from a shorter growing season), the two do hybridize in the calcareous fen-like Chiwaukee Prairie and in northern Indiana (Iltis 1965, Mason & Iltis, 1966). A similar, but even more remarkable case involves the highly distinct, sand-loving species of *Cyperus* sect. *Laxiglu-mi*, the western Schweinitz's *Cyperus* (*C. schweinitzii*), native to the Great Plains sand prairies and the Nebraska Sand Hills and beyond, with openly branched inflorescences, and the more specialized, tight-headed Sand *Cyperus* (*C. lupulinus* ssp. *macilentus*) of rocky or sandy, sunny "islands" within the Appalachian forests (Marcks & Iltis 1967, Marcks 1974). When they eventually flowed together in the Upper Middle West early on after the final glacial retreat ( $\pm 6,000$  yr B.P.), they hybridized to produce a widespread introgressed population (basically *C. schweinitzii* introgressed with *C. lupulinus* ssp. *macilentus*), one that because of its morphological stability has earned recognition as a full-fledged species, Houghton's Flat Sedge, *C. houghtonii*. But within the last 150 years, with the drastic increase in disturbance due to agriculture, lumbering, and other human activities, the extensive sympatric populations of the parental species have undergone a second cycle of hybridization, producing especially on the sand terraces along the lower Wisconsin River Valley extensive hybrid swarms of enormous variability, a variability that confounds the taxonomic amateur and delights the evolutionary-oriented systematist.

Many other such east-west pairs could be mentioned (e.g., the white and red baneberries, *Actaea* spp.), all of which overlap their ranges and hybridize only in once-glaciaded regions, but the two cited cases of prairie plants exemplify the dynamic interaction of biogeography, ecology, systematics, and history that make even our rather depauperate flora a fascinating subject for study.

It should be emphasized that assignment to this or that glacial survival region is not always clear or easy, certainly

not in the many widespread forest species of the southern states that may occur from North Carolina clear to Arkansas and the prairie border. But even in these cases, new molecular techniques, cytotaxonomic insights (polyploidy), and center(s) of a species' variability can usually identify the general area of survival (i.e., origin). Norman Fassett (1944a; see Iltis & Shaughnessy 1960), Wisconsin's great taxonomist, made an intensive study of Eastern Shooting-star, *Dodecatheon meadia*, and was able to show that its center was in the Ozarks and west-central southern states. There, the plants within any population were much alike, either all white or all pink or purple, this due presumably to inbreeding, whereas in Wisconsin such as along the railroad west of Madison or on the Chiwaukee Prairie, they were a riotous mixture of all shades of purple to white, suggesting a post-glacial mass immigration and intermingling of the various southern types.

A splendid example of tracing migration from the southern Appalachians involves the Rock Spike-moss (*Selaginella rupestris*), a species sufficiently widespread—from the eastern mountains north to Wisconsin and also in the Ozarks—that its area of survival was an open question. Tryon (1955) was able to show that the Appalachian plants regularly produced spores by sexual means, the original and therefore primitive condition. On the other hand, plants in populations to the north, then west to Wisconsin and again south to the Ozarks, were increasingly apomictic (i.e., producing spores asexually without benefit of fertilization), a highly specialized condition. Ozarkian plants were 100% apomictic, establishing the direction of migration. Other cytotaxonomic examples show similar patterns, with the primitive diploids restricted to the southern states and the polyploids widespread in the glaciated northern areas.

### *Affinities of the Flora*

The contemporary flora of Wisconsin's Prairie-Southern Forest Province may be young, but it is diverse. This territory includes both the unglaciated Driftless Area, with its great variety of habitats including cool moist gorges, dry sunny hilltops, and exposed bedrock, and glaciated topography, with its monotonous cover of undulating drift left by the melting ice sheets. All this constituted available surfaces for immediate or eventual occupation by plant life. A full range of floristic elements expanded into Wisconsin's developing landscape, albeit within limits exerted by local environmental conditions. At the present time, the southern region of

Wisconsin has favorable environmental conditions for both prairies and eastern forests, because it contains practically the full complement of our Prairie and Alleghenian elements.

Existing stands of a particular community type probably do not exactly or even closely resemble those that once existed either here or elsewhere in North America prior to the Pleistocene. Each community in general, and any given stand in particular, is the result of diverse historical happenings and environmental factors that were in operation while species naturally organized themselves into different assemblages or communities. "The expansion of prairies in Wisconsin was not a single, unified movement of a homogeneous plant formation" (Curtis 1959, p. 290). Instead, species of each floristic element, whether Alleghenian and entering directly from the east, Coastal Plain from the east and south, Ozarkian and Prairie from the south and west, or Arctic and Cordilleran elements from the west and north, migrated or dispersed by various routes and at different times, in different ways, to different habitats. New England Aster (*Aster novae-angliae*), Canadian Tick-trefoil, Early Buttercup (*Ranunculus fascicularis*), and Eastern Figwort (*Scrophularia marilandica*), deciduous forest elements that spread westward to the grasslands, must have entered Wisconsin from the east; species of the interior like Heath Aster, Illinois Tick-trefoil, and Prairie Buttercup (*R. rhomboideus*) could have dispersed from the south; and western elements like American Figwort (*S. lanceolata*), directly from the west. The southwestern or Mexican element Plains Prickly-pear (*Opuntia macrorhiza*), adapted to the hot, dry climate of the arid Southwest, occurs today on open sandy bluffs in southwestern Wisconsin alongside Paper Birch (*Betula papyrifera*), a species characteristic of the Boreal Forest Region and adapted to long cold winters and cool moist summers. However, many bluffs in the area have only one species or the other, or neither, illustrating that while the flora of a particular place consists of species of diverse origins and histories, each differs from that of other places because of the way species react to local microclimates.

### *Basic Patterns of Distribution*

The Wisconsin flora is made up of numerous temperate American species and smaller numbers of Eurasian, Mexican, and South American immigrants. Most of these species were members either of the world-wide Arcto-Tertiary and Boreo-tropical geofloras or the southwestern Madro-Ter-

tiary geoflora. There are rare cases of plants that seem clearly to have originated on other continents. Besides these elements, there are disjunct populations and endemic taxa of more limited occurrence, the distributions of which are difficult or seemingly impossible to interpret.

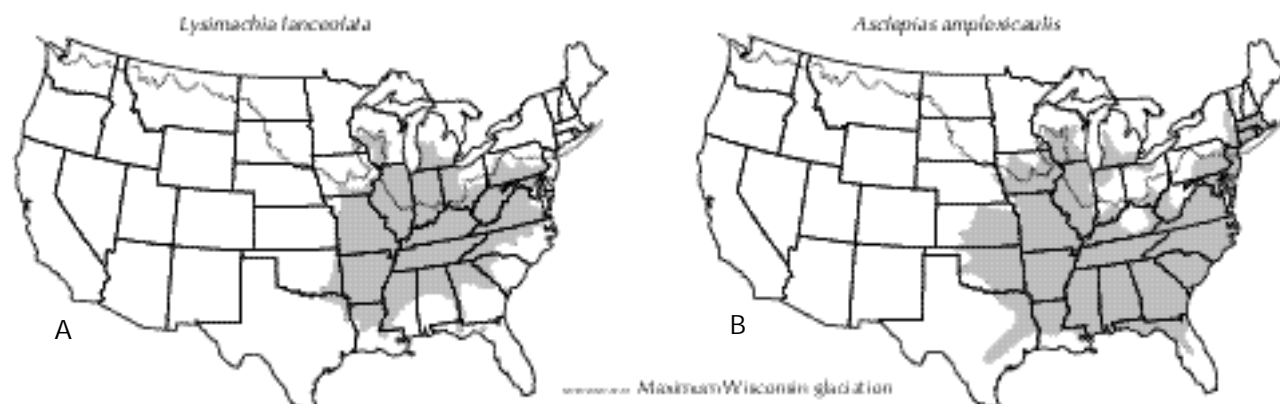
In general, the majority of prairie and savanna species are wide-ranging plants of north-temperate to subarctic regions, including not only those endemic to North America, but also circumboreal and Arctic-alpine species. A large number have an essentially transcontinental or least a very wide range, e.g., Nodding Wild Onion, Meadow Anemone, Smooth Aster (*Aster laevis*), Canada Wild-rye, Tall Sunflower (*Helianthus giganteus*), False Dandelion (*Krigia biflora*), Wild Lettuce (*Lactuca canadensis*), Fringed Loosestrife (*Lysimachia ciliata*), Purple Meadow-rue, Blue Vervain (*Verbena hastata*), etc. Other taxa are restricted to the eastern half of the continent, but often with sister species in the West, e.g., Marsh Fern (*Thelypteris palustris* var. *pubescens*), Wild Columbine, Calico Aster (*Aster lateri-florus*), Pasture Thistle, Bottle Gentian, Wood-betony (*Pedicularis canadensis*), Prairie Phlox, Culver's-root, (*Veronicastrum virginicum*), or the western half, e.g., White Sage (*Artemisia ludoviciana*), Wild Licorice (*Glycyrrhiza lepidota*), and American Figwort. Other temperate endemics are interior Midwest species with diverse relationships like Wild-hyacinth, *Camassia scilloides* (to the Pacific Northwest); White Prairie-clover, *Dalea candida* (to Mexico); Mullein-foxglove, *Dasistoma macrophylla* (to the eastern United States); Carolina Larkspur, *Delphinium carolinianum* (to the southwestern mountains); and Common Ironweed, *Vernonia fasciculata* (to tropical America). Finally, there is a rather heterogeneous group comprising disjunct populations and regional endemics. These taxa generally are confined to the Driftless Area or the Great Lakes.

### Outline of Floristic Elements

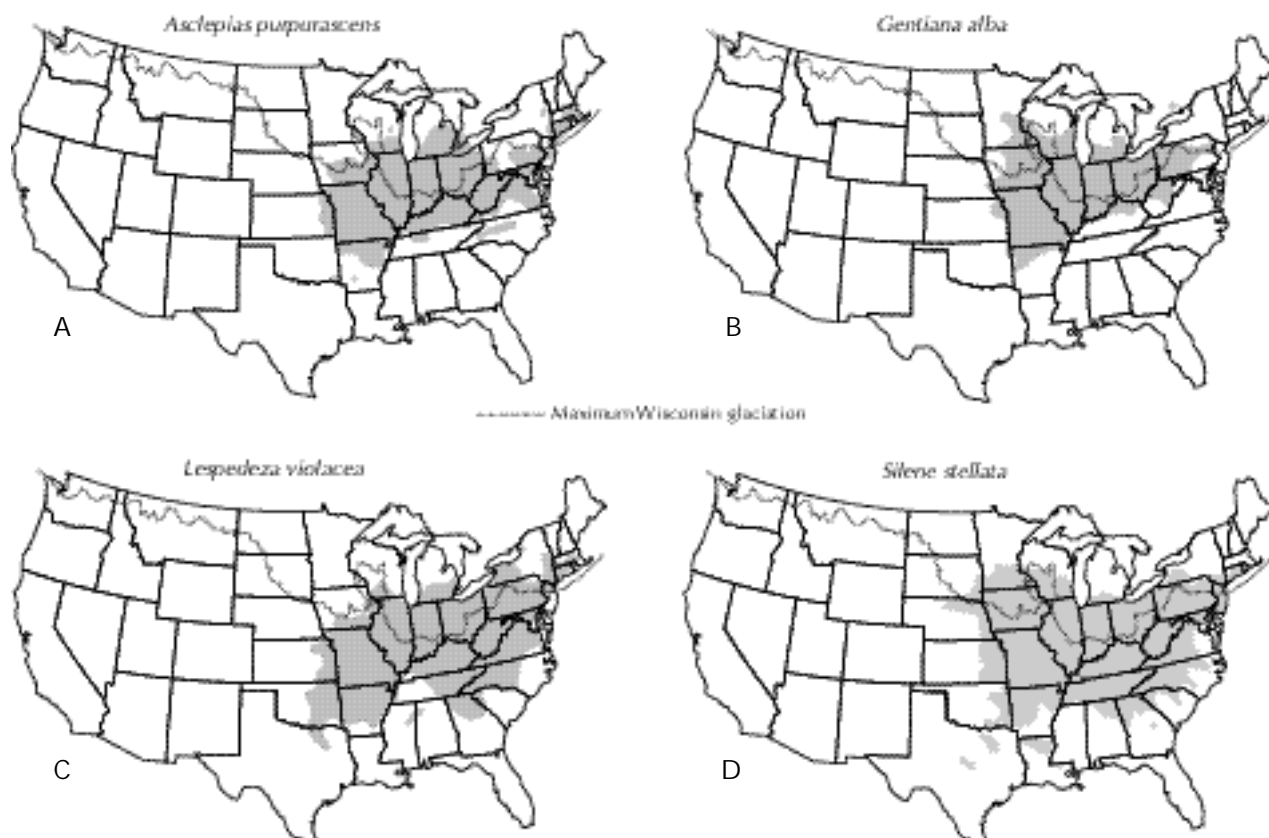
Each floristic element is comprised of species that share the same pattern of geographical distribution and by implication a common historical background. Of the several major elements, the Alleghenian, Ozarkian, and Prairie and Great Plains are the ones contributing the greatest number of species to the prairies and savannas of Wisconsin (see Figures 19–22). Two other elements well represented in the state, the Boreal Forest and Coastal Plain, are less significant contributors. Members of the former group occur primarily in the Mixed Conifer-Northern Hardwoods Province but are

nonetheless represented in prairies (e.g., Slender Wheat Grass [*Elymus trachycaulus*]) and savannas (e.g., Starry False Solomon's-seal [*Smilacina stellata*]), whereas on the whole, those of the Coastal Plain, although substantial in number, are often of local occurrence or are associated with sandy shores, swales, and fens. However, several species of this element occur in grassland habitats, usually in oak and sand barrens: Dune Three-awn Grass (*Aristida tuberculosa*), Hoary Frostweed (*Helianthemum bicknellii*), Common Rock-rose (*H. canadense*), Greene's Rush (*Juncus greenei*), Wild Lupine (*Lupinus perennis*), Joint-weed, Steeplebush (*Spiraea tomentosa*), and Grass-leaved Goldenrod (*Euthamia graminifolia*). Comparatively few species of Mexican or South American affinity and of Cordilleran (western mountain) or Arctic-alpine relationships have reached Wisconsin.

The Alleghenian-Ozarkian Element (that group of species centering on the southern Appalachians, ranging from Alabama to southeastern Quebec, and often throughout the Eastern Deciduous Forest Region all the way to the Ozarks) is composed of a large group of temperate forest species, many common and widely distributed. American groups with this relationship are represented in prairies by Bush-clover (*Lespedeza capitata*) (most *Lespedeza* species are southeastern, but some occur in Asia and Australia), Lance-leaved Loosestrife (*Lysimachia lanceolata*; Figure 19A) (*Lysimachia* section *Steironema* is a small group endemic to the Southeast), Clasping Milkweed (*Asclepias amplexicaulis*; Figure 19B) (many *Asclepias* species are southeastern, many also southwestern and Mexican, a few South American and African), and New England Aster (*Aster* section *Aster*, like the genus *Solidago*, the golden-rods, is a very large, actively evolving, taxonomically difficult group with its center of diversity in the East). This element is well represented in Wisconsin's woods, savannas, and barrens: Hog-peanut, Prairie Red-root (*Ceanothus herbaceus*), Upland Boneset (*Eupatorium sessilifolium*), Hairy Puccoon (*Lithospermum carolinense*), Wood-betony, Hairy Beard-tongue (*Penstemon hirsutus*), Lopseed (*Phytolacca leptostachya*), Red-stalked Plantain (*Plantago rugelii*), Black Cherry, and Yellow Pimpernel (*Taenidia integrifolia*). Many savanna species have as their immediate region of origin the lower Midwest and Southeast. Forest-border species having this basic pattern include Purple Milkweed (Figure 20A), Pale Indian-plantain, Bottlebrush Grass, Cream Gentian (Figure 20B), Veiny Pea, Violet Bush-clover (*Lespedeza violacea*; Figure 20C), Broad-leaved Panic Grass (*Panicum latifolium*), Starry Campion (*Silene stellata* -

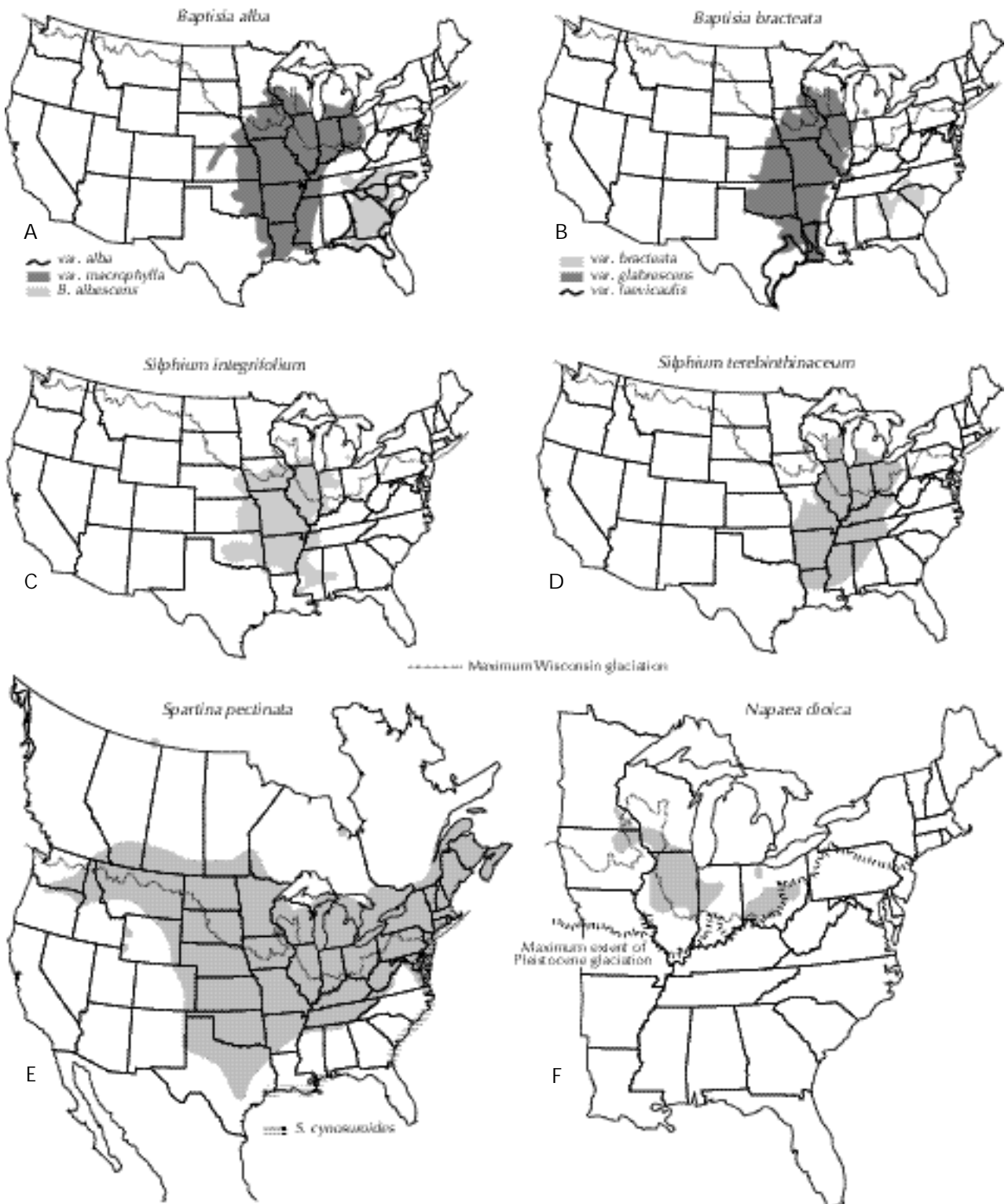


**Figure 19.** Distribution of Alleghenian-Ozarkian elements of the Wisconsin grasslands. **A.** *Lysimachia lanceolata*, Lance-leaved Loosestrife. Redrawn in part after Ray (1944). **B.** *Asclepias amplexicaulis*, Claspng Milkweed. Modified after Woodson (1954).

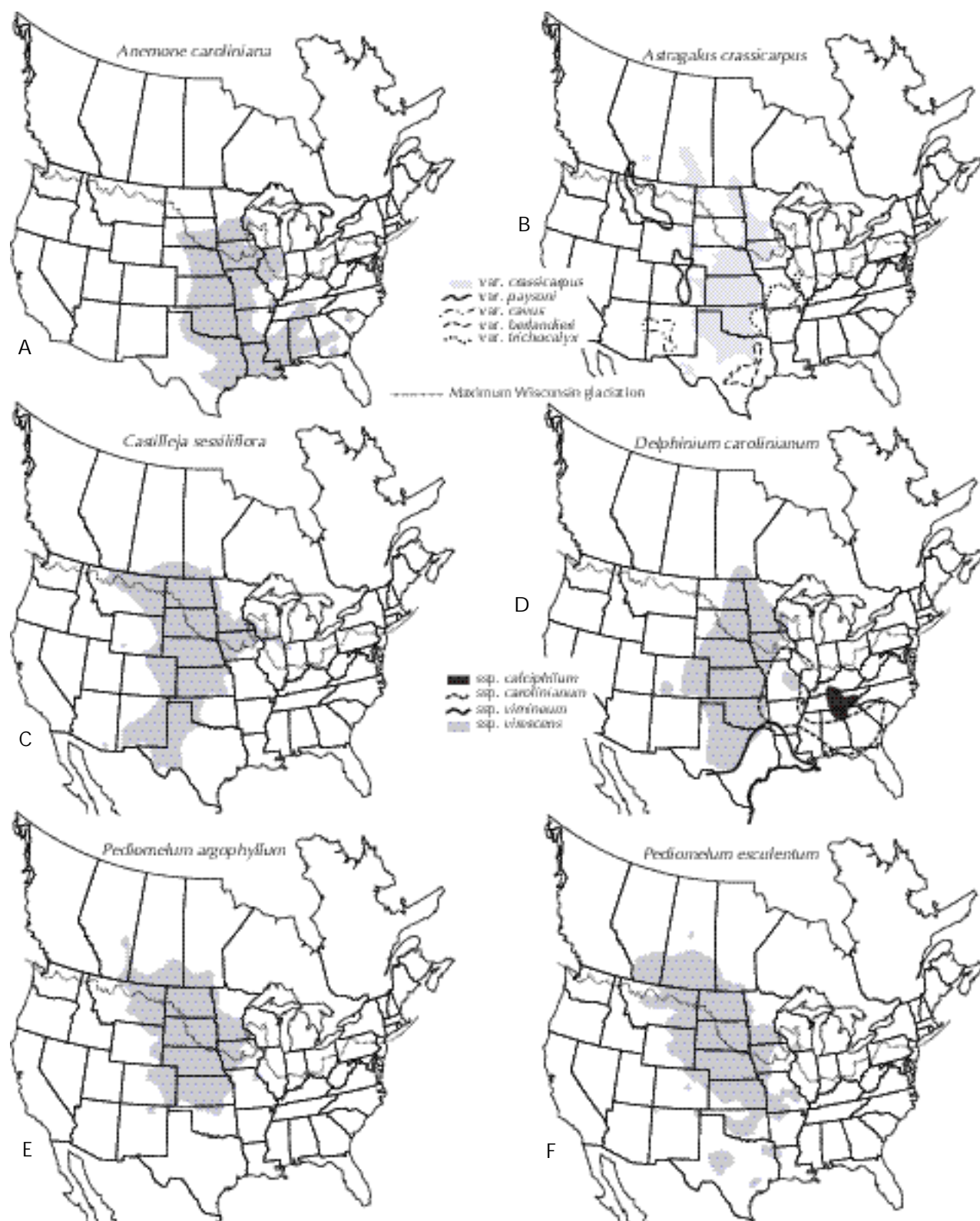


**Figure 20.** Distribution of Alleghenian (and/or Ozarkian) elements of Wisconsin savannas and prairies. **A.** *Asclepias purpurascens*, Purple Milkweed. Redrawn after class term paper by S. Kroken (1989). **B.** *Gentiana alba*, Cream Gentian. Modified slightly after Pringle (1967). **C.** *Lespedeza violacea*, Violet Bush-clover. Modified slightly after Clewell (1966). **D.** *Silene stellata*, Starry Campion. Compiled from various sources, including Hitchcock and Maguire (1947).





**Figure 21.** Distribution of Prairie elements of the Wisconsin grasslands. **A.** The two varieties of *Baptisia alba*, Milky Wild Indigo, and a related species. Compiled from various sources. **B.** The three varieties of *Baptisia bracteata*, Cream Wild Indigo. Compiled from various sources. **C.** *Silphium integrifolium*, Prairie Rosinweed. Modified after Settle and Fisher (1970). **D.** *Silphium terebinthinaceum*, Prairie-dock (generalized). Most species of *Silphium* are southeastern. **E.** *Spartina pectinata*, Prairie Cordgrass, probably derived from *S. cynosuroides*. Redrawn after Mobberley (1956). **F.** *Napaea dioica*, Glade Mallow, a monotypic genus and our only Midwestern endemic genus. Redrawn after Iltis (1963).



**Figure 22.** Distribution of Prairie-Great Plains elements reaching their eastern range limit in Wisconsin. **A.** *Anemone caroliniana*, Carolina Anemone. Redrawn after Dutton et al. (1997). **B.** The five varieties of *Astragalus crassicaulis*, Ground-plum. Redrawn after Barneby (1964). **C.** *Castilleja sessiliflora*, Downy Painted-cup. Modified after Pennell (1935). Its closest relatives (four species) are in the western United States and Mexico. **D.** The four subspecies of *Delphinium carolinianum*, Plains Larkspur. Redrawn after Warnock (1997). **E.** *Pedicularis argophyllum*, Silvery Scurf-pea. Modified after Fassett (1939). **F.** *Pedicularis esculentum*, Breadroot Scurf-pea. Modified after Fassett (1939).

ta; Figure 20D), and Late Horse-gentian (*Triosteum perfoliatum*), most of which are listed by Packard (1988b, 1993) in his summaries of restoration work on savannas in Illinois.

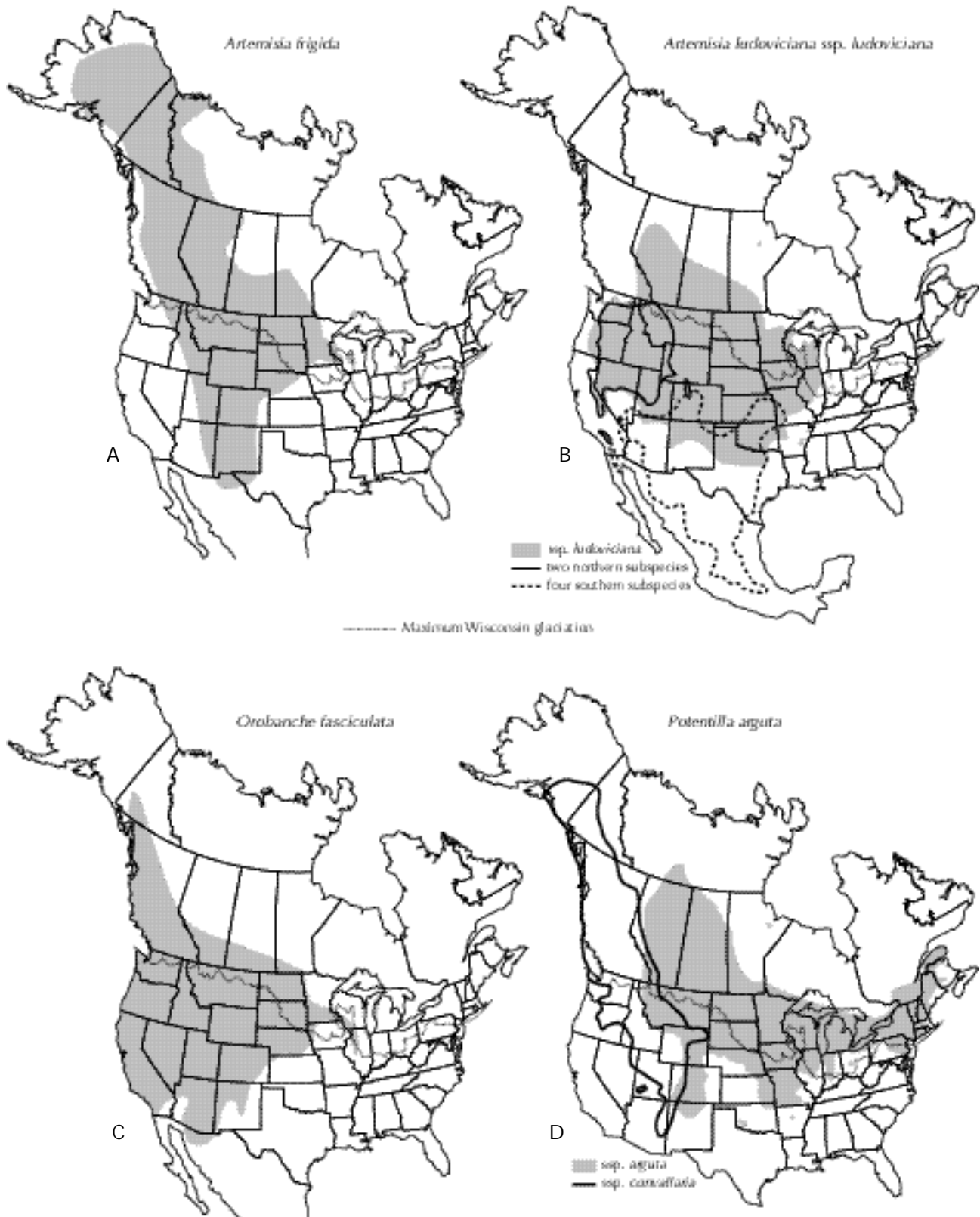
The prairie flora, that group of species having an overall range that covers part or all of the existing prairies, may be classified among several elements. One element involves plants of the true prairie, which generally range from the southern Great Plains northward toward or into the Prairie Provinces of Canada and eastward into the Prairie Peninsula. A large percentage of species belonging to the Prairie element are derived from the southeastern deciduous forest region and have geographical distributions that center on the Ozark Mountains, from which they radiate in all directions—east to the deciduous forest, west to the plains, and north into the Prairie Peninsula. Plants of the true prairie in Wisconsin include two *Baptisia* (Figures 21A& B) and four *Silphium* species (the geographical distributions of Rosinweed, *S. integrifolium*, and Prairie-dock are shown in Figures 21C & D, respectively), Prairie Indian-plantain (*Cacalia* [*Arnoglossum*] *plantaginea*), Purple Prairie-clover, Missouri Goldenrod (*Solidago missouriensis*), Stiff Goldenrod (*S. rigida*), Prairie Cordgrass (Figure 21E), and Porcupine Grass (*Stipa spartea*), as well as Glade Mallow (Figure 21F).

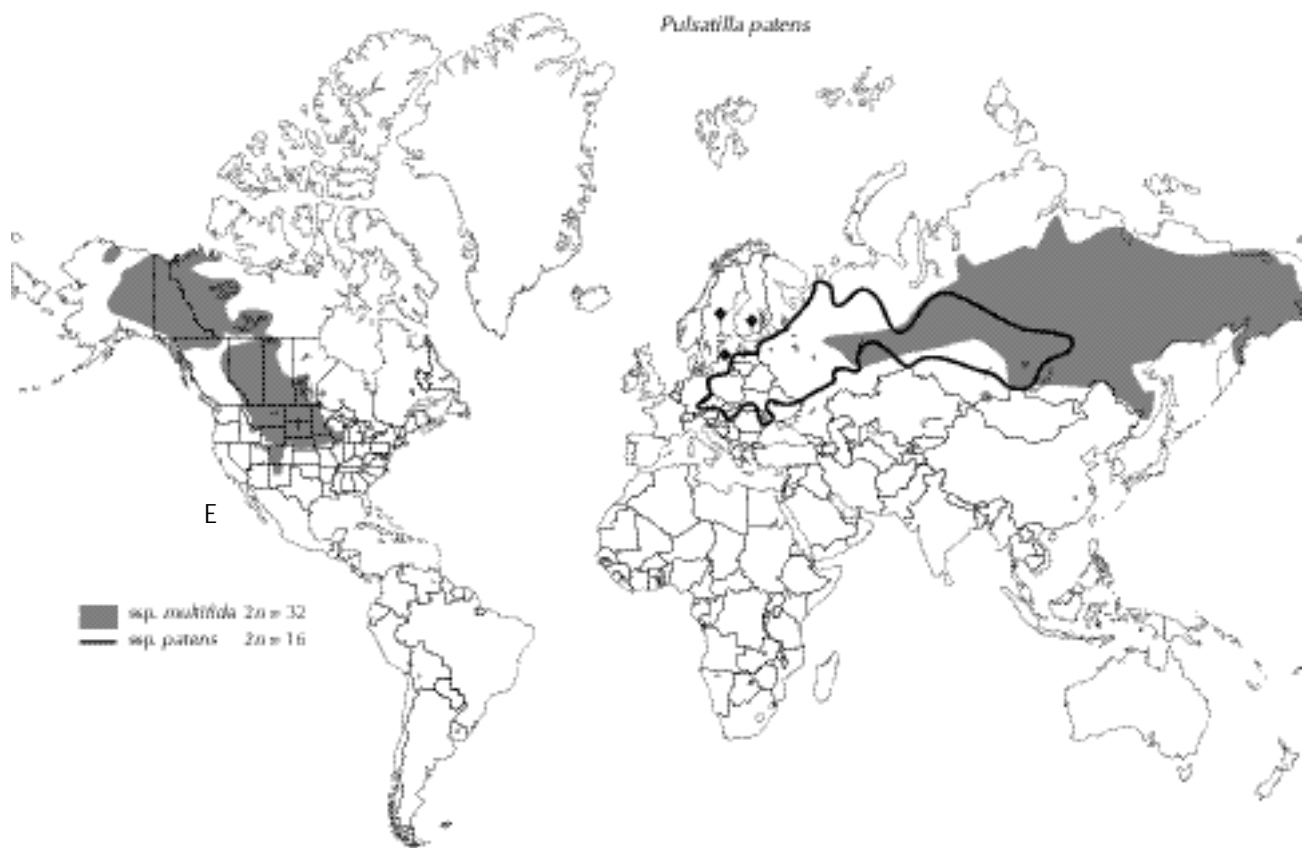
A second natural subdivision of the prairie flora in Wisconsin includes the Great Plains elements that reach their eastern limits in Wisconsin. Presumably, climatic conditions explain why some species of Great Plains affinity have only barely reached Wisconsin, because many others extend southward and eastward into the Prairie Peninsula or beyond. Most of these genera are Arcto-Tertiary in origin. *Anemone*, *Astragalus*, and *Stipa* are large genera of northern grasslands; *Besseyia*, *Castilleja*, and *Penstemon* are endemic, mainly Cordilleran genera with Eurasian relatives; only *Pedimelum* has Southern Hemisphere relationships. The total ranges of Carolina Anemone (*Anemone caroliniana*), Ground-plum, Downy Yellow Painted-cup (*C. sessiliflora*), Carolina Larkspur, Silvery Scurf-pea, and Prairie-turnip (*Pedimelum esculentum*), are shown in Figure 22. The following species all have the same basic distribution pattern: Autumn Onion (*Allium stellatum*), Short Green Milkweed, Prairie Sand-reed, Alum-root, Northern Plains Blazing-star (*Liatris ligulistylis*), Dotted Blazing-star, Prairie Dandelion (*Microseris cuspidata*), Slender Beard-tongue (*Penstemon gracilis*), Early Buttercup, and Prairie Dropseed. Kitten's-tail, *Besseyia bullii*, is much more restricted, being limited to seven Midwestern states.

In the third element belong those plants occurring throughout a much larger region of the West and, in the northern Great Plains, reaching their eastern and southern limits in America. These Arcto-Tertiary elements often have their generic relationships to arid, cool-temperate Eurasia and often have centers of diversity in the West. They include Prairie Sagewort (Figure 23A), Louisiana Sagewort (Figure 23B), Fleabane (*Erigeron glabellus*), June Grass, Clustered Broom-rape (*Orobanche fasciculata*, Figure 23C), Tall Cinquefoil (*Potentilla arguta*, Figure 23D), and Pasqueflower (*Pulsatilla* [*Anemone*] *patens*, Figure 23E).

The Western or Cordilleran element constitutes a large group of alpine, plateau, and foothill species that on the whole has a range centering in the western mountains of Canada and the United States, but has a surprisingly large contingent that migrated east once the ice melted. Some of these species are disjunct from the Arctic and are considered part of the Arctic or Arctic-Alpine Element. In Wisconsin, this is a significant group, members of which often reach their eastern limits in the western Great Lakes region. Typical species include Richardson's Sedge (*Carex richardsonii*), Prairie-smoke (*Geum triflorum*), Edible Valerian (*Valeriana edulis*), and White Camass (*Zigadenus elegans*), and such shrubs as Red Osier Dogwood (*Cornus stolonifera*) and Wolfberry (*Symphoricarpos occidentalis*).

The Arctic Element, sometimes called the Arctic-alpine Element, comprises a rather small group in the flora of Wisconsin; its representatives often have no close affinity to other species or groups in our flora. We even have one tundra species, the exceedingly rare Lapland Azalea (*Rhododendron lapponicum*), but a number of subarctic plants endemic to North America such as Spreading Dogbane (*Apocynum androsaemifolium*), Fringed Brome (*Bromus ciliatus*), Blue-joint, Common Water-hemlock (*Cicuta maculata*), Bog Lobelia (*Lobelia kalmii*), and Golden Ragwort (*Senecio* [*Packera*] *aureus*) are common in our prairies, fens, and sedge meadows. The group is usually defined broadly enough to contain the Arctic-circumpolar species, those occurring in Europe and/or Asia as well as North America: Common Horsetail (*Equisetum arvense*), Cut-leaved Anemone (*Anemone multifida*) (also bipolar; very rare in Wisconsin), Lyrate Rock Cress, Grove Sandwort (*Arenaria lateriflora*), Rock Sandwort (*Arenaria stricta* ssp. *dawsonensis*, a Wisconsin rarity), Harebell, Northern Bedstraw (*Galium boreale*), Sweet Grass (*Hierochloe hirta*), Marsh Pea, and Shrubby Cinquefoil (*Pentaphylloides* [*Potentilla*] *floribunda*).

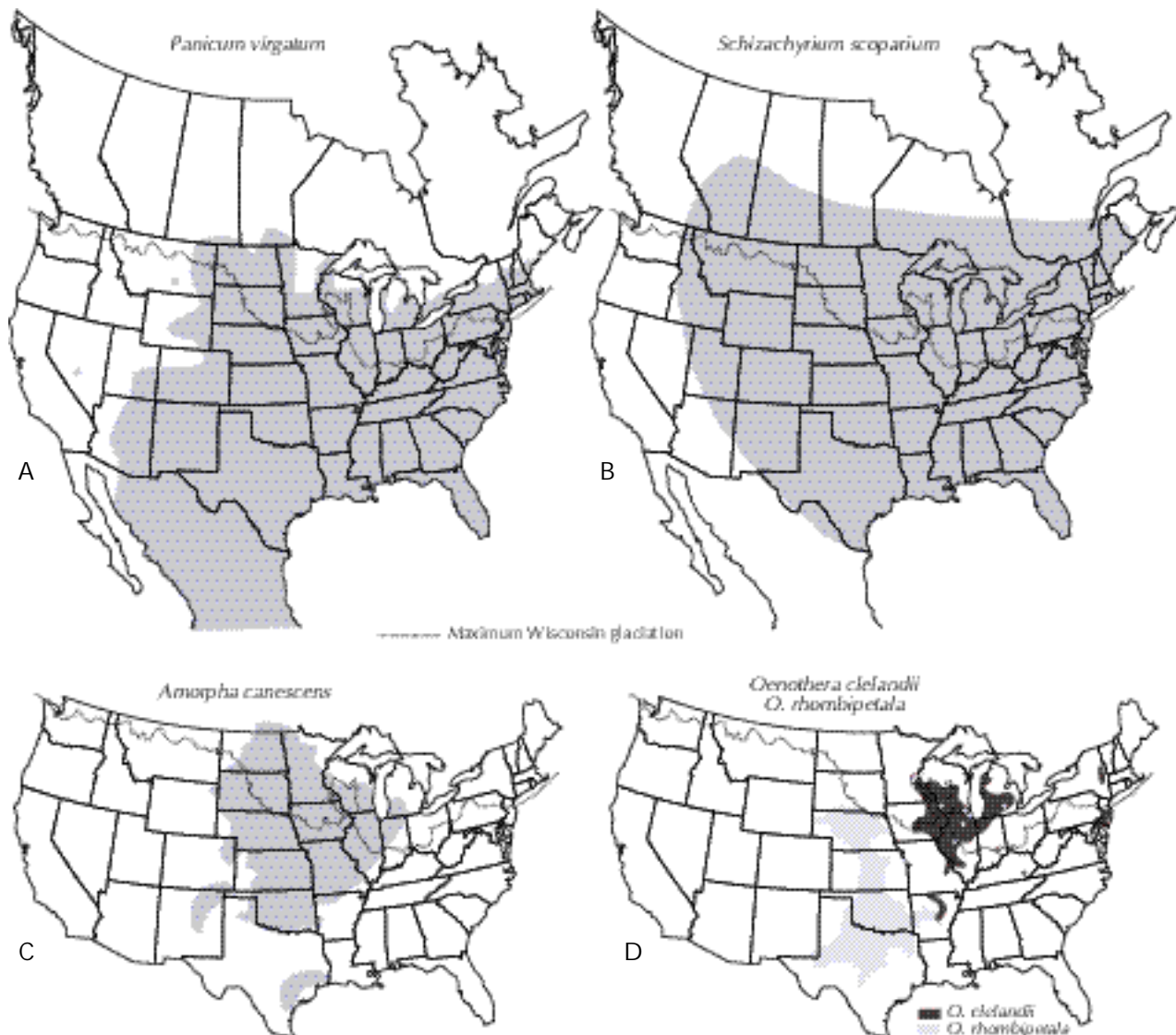




**Figure 23.** Facing page and above. Distribution of Arcto-Tertiary elements of the Wisconsin grasslands. **A.** *Artemisia frigida*, Prairie Sagewort. Native eastward to the Mississippi River, and occasionally adventive beyond (distribution in part generalized). **B.** *Artemisia ludoviciana* ssp. *ludoviciana*, Louisiana Sagewort, and the combined ranges of two northern and four southern subspecies. Modified after Keck (1946). Native eastward to Illinois and Wisconsin, and naturalized beyond to New England. **C.** *Orobancha fasciculata*, Clustered Broom-rape. United States range redrawn after class term paper by B. C. Reuter (1985). **D.** The two subspecies of *Potentilla arguta*, Tall Cinquefoil. Modified after class term paper by W. Shaeffer, undated. Two related species of *Potentilla* section *Drymocallis* are not shown. **E.** The two subspecies of *Pulsatilla patens*, Pasqueflower. American distribution redrawn after Dutton et al. (1997); Eurasian distribution redrawn after Hultén and Fries (1986).

Many of the heliophytic species with southern and southwestern affinities belong to genera with probable subtropical or even tropical origins. Among them are such well-known grasses as Switch Grass (Figure 24A), Little Bluestem (Figure 24B), and Big Bluestem, together with Lead-plant (*Amorpha canescens*, Figure 24C), evening-primroses, e.g., *Oenothera villosa* and *O. clelandii* (Figure 24D), tick-trefoils, e.g., *Desmodium canescens* and *D. illinoense*, Wild Licorice, and Yellow Star-grass (*Hypoxis hirsuta*), the latter of a large, basically Southern Hemisphere (Gondwanaland) genus. The 15 species of *Amorpha* are mostly eastern North American, but their relationship is to the southwestern Madro-Tertiary flora.

Species of dry or dry-mesic prairies that center in the arid Great Plains are mainly Madro-Tertiary Elements, an autochthonous (locally self-developed) flora that evolved during the last 30 million years out of partly neotropical (Andes, South American deserts) and partly northern groups. The center of origin and diversity of the genera lies in the deserts and semiarid areas of Mexico and adjoining southwestern United States (hence the name, from the Sierra Madre Mountains). There is no direct, recent relationship to the Arcto-Tertiary Flora. Madro-Tertiary groups include many species of *Asclepias* such as *A. verticillata* (Figure 25A), of *Bouteloua* such as *B. curtipendula* (Figure 25B) and *B. gracilis*, of *Dalea* such as *D. candida*, *D. purpurea*

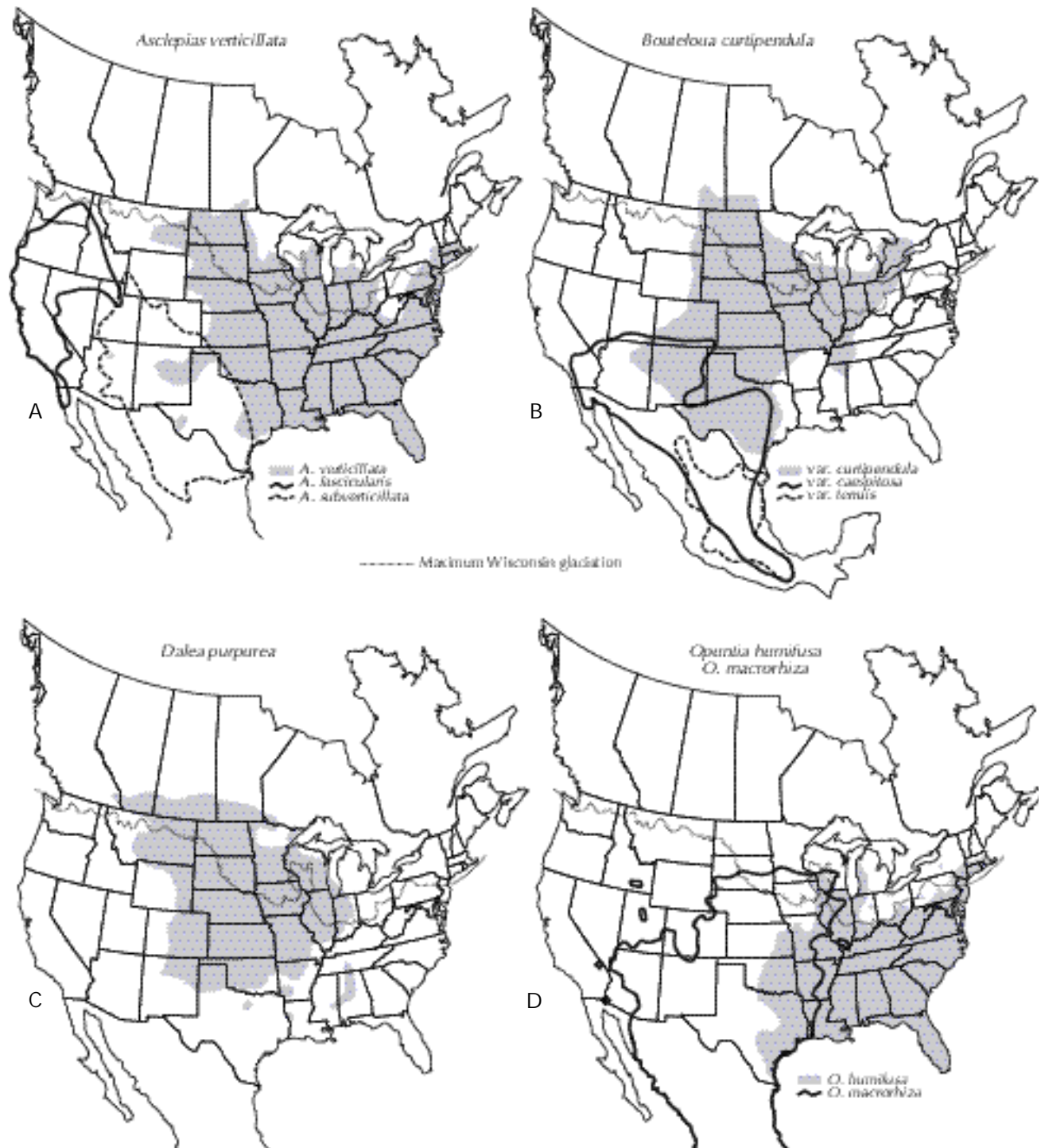


**Figure 24.** Distribution of Southwestern elements of the Wisconsin grasslands. **A.** *Panicum virgatum*, Switch Grass (generalized). **B.** *Schizachyrium scoparium*, Little Bluestem (generalized). **C.** *Amorpha canescens*, Lead-plant. Redrawn after Wilbur (1975). **D.** *Oenothera clelandii*, Cleland's Evening-primrose, and the closely related *O. rhombipetala*, Long-spike Evening-primrose, the latter adventive in Wisconsin. Redrawn after Dietrich and Wagner (1988).

(Figure 25C), and *D. villosa*, and as most characteristic, the 1,000 plus members of Cactaceae, with three *Opuntia* species our only representatives. Two, the locally common Plains Prickly-pear and the rare Eastern Prickly-pear (*O. humifusa*), are mapped in Figure 25D. The rare Fragile Prickly-pear (*O. fragilis*), reputedly once distributed on the fur of bison, is widely scattered as minute populations on granite or quartzite outcrops and sandstone ridges.

An additional small element not always recognized by floristic workers, the so-called Great Lakes Element, is most interesting because it contains a heterogeneous mixture of species that are more or less confined to the Great Lakes region, that is, they are endemic. Among them are certain dune and beach taxa; a few plants of fens such as Kalm's St. John's-wort (*Hypericum kalmianum*) (derived from Ozarkian relatives; for maps, see Utech & Iltis 1970) and





**Figure 25.** Distribution of Madro-Tertiary Elements of the Wisconsin grasslands. **A.** *Asclepias verticillata*, Whorled Milkweed, and two related species. Modified slightly after Woodson (1954). **B.** The three varieties of *Bouteloua curtipendula*, Side-oats Grama. Redrawn after Gould and Kapadia (1964). **C.** *Dalea purpurea*, Purple Prairie-clover. Redrawn after Fassett (1939). **D.** *Opuntia humifusa*, Eastern Prickly-pear, and *O. macrorhiza*, Plains Prickly-pear. Both modified slightly after Benson (1982).

Ohio Goldenrod (*Solidago ohioensis*) (related to southeastern taxa; for a map of its total range, see Pringle 1982); and several forbs of deep-soil prairies, e.g., Saw-leaf Mugwort, Kitten's-tail, Hill's Thistle (*Cirsium hillii*), and Prairie Bush-clover (*Lespedeza leptostachya*), an offshoot of the southern Atlantic Coastal Plain Narrow-leaved Lespedeza (*L. angustifolia*). Finally, we must mention the Glade Mallow, a tall and rank, locally occurring but not particularly rare perennial herb of wooded floodplains and moist prairies (Iltis 1963, Mickelson & Iltis 1967). The only endemic genus in the Upper Midwest, it is segregated as such because of, among other characters, its numerous, small, unisexual flowers (plants dioecious, that is, male and female flowers on different plants). It has an enigmatic history that probably involves long-distance dispersal from far-away lands, possibly California or South America (nobody knows).

The five special prairie examples are mapped in Mickelson and Iltis (1967), who hypothesize that each of them must have had either an ancient, pre-Wisconsin or even pre-glacial origin with subsequent survival either in unglaciated or in once-glaciated territory between differentially advancing glacial lobes, where they evolved into new taxa; or a recent, post-glacial origin from a more wide-spread Great Plains, western, or southern species.

In summary, the history of these special prairie and fen species, and others found entirely or mainly on the sand dunes of the Great Lakes (e.g., Sand-reed Grass, *Calamovilfa longifolia* var. *magna*, and Dune Thistle, *Cirsium pitcheri*, both derived from prairie taxa from farther west), is of particular interest, because the geographical ranges of these plants are restricted to glaciated territory. As the Midwest's only endemics, they are treasured by taxonomists and evolutionists alike.

## Management of Prairies and Savannas

Southwestern Wisconsin lies within the wide ecotonal belt that separates the central North American grasslands from the eastern deciduous forests, and most any environmental change will shift the balance toward one ecosystem or the other. Because civilization has now shifted this balance more in the direction of forest, we must manage remnants of prairie or savanna if their biological diversity is to be maintained.

Today, the active management of landscapes for biodiversity, rather than for agriculture or other utilitarian rewards, has become an unwelcome responsibility for a

reluctant, often impoverished humanity the world over. Indeed, managing even perfectly preserved or carefully restored prairie remnants has become a problematic endeavor. Fragmented, isolated, highly susceptible to edge effects and the vagaries of island biogeographical principles (MacArthur & Wilson 1967)—namely the gradual, automatic, chance depletion of localized biodiversity (Leach & Givnish 1996) with little hope of renewal from now mostly distant seed sources—prairie and savanna communities, whether in public or private ownership (Houle 1996), will require the best of our knowledge and the most prudent care if their rich biodiversity is to survive.

Many complex problems need consideration. Contending with such invasive weeds as the bluegrasses (*Poa* spp.), sweet-clovers (*Melilotus* spp.), Leafy Spurge, and Wild Parsnip is bad enough. Likewise, the use of fire and grazing may at times involve difficulties—the road to mismanagement is usually paved with the best of intentions. A tallgrass prairie is, after all, an elaborate ecosystem of dynamic parts with multifactorial environmental relationships: a hundred or more species of vascular plants, myriad insects and nematodes, ground lichens and soil fungi, animal and plant parasites, all interacting with rainfall and sunlight, and above all with the rich black prairie soil. Almost any human activity could have unpredictable consequences.

Take fire, for example, a powerful management tool. Fire is essential to restore and maintain prairie and savanna vegetation within our ecotonal climate by suppressing the growth of invading trees and shrubs. But fire must be used judiciously. Some entomologists believe that it reduces long-term arthropod abundance and diversity, and that even controlled burns may damage or endanger prairie-restricted insects. Scientists who undertook experimental burning of prairies realized long ago that fire may temporarily set back insect and spider populations, and as recent research has demonstrated, at least temporarily reduce numbers of certain prairie insect "specialists" (Swengel 1996, 1997; Swengel & Swengel 1997). Of the insect species characteristically found in prairies, about 10 to 20 percent are restricted to native prairie habitat (R. Panzer, pers. comm.). Studies of the effects of fire on insects show that only a small subset of the restricted species are apt to be harmed (R. Panzer, pers. comm.). For the vast majority of insects, prescribed burning does not seem to hinder survival (Reed 1997, Siemann et al. 1997). For example, in Illinois, Dietrich et al. (1998) found "no significant differences" in diversity between burned and unburned units within enclosed and



unenclosed plots; and Panzer (1988, p. 87), noting that “Small remnant insect populations...are much more susceptible to environmental stresses such as fires than were massive unfragmented presettlement populations,” nonetheless concluded that most prairie insects, even butterflies, have the ability to rebound quickly following partial burns on managed sites. These findings, however, are still preliminary. For the majority of prairie insect species, we still know little or nothing about their responses to fire or the factors that determine post-burn recovery rates. There is a great need for more detailed study with proper experimental controls of fire effects on insects.

Insects play many roles in the ecology of prairies, not the least of which is the pollination of flowers (Buchmann & Nabhan 1996, Graenicher 1900–1935, Robertson 1928). Because populations of some prairie-obligates require more than one year to recover from a fire, in particular those that overwinter in litter or exclusively inside the stems of grasses or forbs as pupae or eggs, the most prudent course would be *never to burn all of a remnant prairie at the same time*, or even in the same year. In the case of very small and isolated remnants, especially, significant parts of each should be protected from fire in any given year. Burn-sensitive species then have a better chance of survival at least somewhere on that prairie.

An alternative to fire for woody plant control is mowing, which, partially mimicking the effects of fire, may thus be an appropriate alternative for increasing survival rates of some prairie butterfly species (McCabe 1981, Swengel 1996). But whether, when, and how much mowing, like whether, when, and how much burning or grazing, are questions in need of scientific research. In any case, fire is necessary in the management of most prairies, and indispensable during the early years of a prairie or savanna restoration. Depending on the topography of the individual site, burning may have to be carried out several years in succession.

Grazing by cattle has been proposed as a panacea for prairie restoration (Williams 1996, 1997, 1999a, 1999b; but see Harrington et al. 1998). Although it is true that survival of certain otherwise uncommon species is favored by cattle grazing, sometimes dramatically so (e.g., Marbleseed, *Onosmodium bejariense*), many other native species, especially forbs in mesic and wet-mesic habitats, are selectively eliminated (Dix 1959). Bison have been shown to be much more appropriate as grazers of the western prairies (Collins et al. 1998, Hartnett et al. 1997, Kaiser 1998, Steuter 1997), especially in their preference, unlike that of cattle, for the coarse,

tall grasses (Knapp et al. 1999). After all, native herbivores were once the principal biotic factor that helped shape the Great Plains grasslands (Risser 1988, Van Dyne et al. 1980).

Conversely, Bison probably were not major players in Wisconsin's tallgrass prairies. Historical and archaeological records suggest that in Wisconsin (Schorger 1937), Illinois (Griffin & Wray 1946), and probably all of the eastern extension of the tallgrass prairie (McDonald 1981, Roe 1970, Schorger 1944), Bison were absent or rare prior to 1500 AD, as they were apparently during the entire 10,000 years or more that prairies and savannas were developing in the Upper Midwest. Bison did not appear east of the Mississippi River in large numbers until the seventeenth and eighteenth centuries, to be eliminated first by Native American hunters and soon thereafter by pioneers. In Wisconsin, Bison were always rare; the last two were killed in 1832 (Jackson 1961). Although Elk and White-tailed Deer were more common, they also suffered reduction by hunting both before and after European settlement.

For us in the Midwest, any long-term vision of prairie conservation must include first increasing preservation and restoration efforts to a biologically more realistic scope; for until preserved areas are expanded to the *minimal viable size of several thousand acres or more*, “It is unlikely that we will ever again be able to accommodate mega-fauna such as bison, elk, and wolves in a naturally functioning grassland ecosystem in Wisconsin” (Henderson 1995b, p. 123). The proposal to re-create the extensive Sauk Prairie on the lands of the former Badger Army Ammunition Plant should thus include among its grazers not only Elk and White-tailed Deer, but also, in deference to the wishes of the Ho-Chunk Nation, a small herd of Bison as well. Ultimately, the public and their politicians must learn to accept the fact that for the tallgrass prairie to survive, *very large areas need to be removed from the economy of man and returned to the economy of nature*. Meanwhile, we need to preserve every surviving bit of virgin prairie, restore every as-yet-unplowed remnant, reconnect fragmented landscapes by environmental corridors, and thus rescue as many endangered species as we can. For as Aldo Leopold admonished us in *Round River* (L. Leopold 1953, pp. 146–147), “The outstanding scientific discovery of the 20th century is not television or radio, but rather the complexity of the land organism,” and therefore “to keep every cog and wheel is the first precaution of intelligent tinkering.” A major restoration on what once was the Sauk Prairie is Wisconsin's, and the Midwest's, last best chance to pass on to our children a viable prairie and savanna landscape.

## What of the Future?

*Postscript by Theodore S. Cochrane*

The need to conserve Wisconsin's natural beauty and diverse flora and fauna, its ecosystems and landscapes, is much more urgent than ever in view of four basic concerns:

- Man's need for nature (Iltis 1966, 1967, 1969; Iltis, Loucks & Andrews 1970), what E. O. Wilson (1984), America's foremost evolutionary biologist, has called *biophilia*, the human organism's innate affinity with wild nature and those plants and animals that, the world over, we bring into our homes and gardens, all a reflection of our humanity and the inextricable link between green plants and living animals with the evolution of our human mind;
- Our preoccupation with technological progress and economic growth (Samson & Knopf 1994), both of which are, after all, still largely dependent on continuing and unsustainable destruction of the natural environment and the correlated and ever-increasing elimination of its species, communities, and ecosystems (Myers 1993);
- Our need for wilderness and many more natural areas as benchmarks in understanding, through research, the workings of nature (Iltis 1959), an understanding we neglect at our peril;
- Lastly, of particular importance to Wisconsin, the natural landscape as an economic resource second only to agriculture, the green wild goose that lays the golden egg of tourism.

Untamed lands are desperately needed for education, research, recreation, and aesthetics; for maintaining a balanced, stable environment (that grasslands are superior carbon sinks in comparison to forests is only one specific relationship to current environmental issues); for serving as living models for ecological restoration, for only undisturbed ecosystems such as virgin prairies retain all their vast ecological complexities; for reminding us of our history and linking us to the land; and for experiencing ourselves and passing on to future generations a beautiful and healthy, livable world.

Alas, it is almost all over for Wisconsin's prairies and savannas, communities that are recognized as important reservoirs for biological diversity (Samson & Knopf 1996),

yet are very nearly absent or nonfunctionally represented on the living landscape. A number of prairie and savanna plant and animal species are rare or endangered, with their surviving numbers so small and the individual plants of these micropopulations so isolated that, from the standpoint of their genetic future, they may no longer constitute viable populations, what with inbreeding taking its toll. Many existing vegetation remnants are very small and often so degraded that they scarcely comprise recognizable communities. Unless the recognition, protection, preservation, management, and as a last resort *restoration* (returning a site to its original condition) of existing prairie and savanna remnants is stepped up, the permanent extinction of these characteristic Midwestern plant communities from Wisconsin is only a matter of time. Once destroyed, the only recourse will be *reconstruction*—reestablishing through guidelines of the newly emerging ecological science of restoration a broad range of prairie organisms on a former prairie site. Restoration is a slow process requiring one to several decades; however, reconstruction requires several centuries (Schramm 1992)—if re-creation of the prairie ecosystem in all its complexity is indeed possible at all.

Up to a point, regaining and keeping indefinitely native biodiversity is feasible for most but probably not all components of grassland and savanna ecosystems, especially at the dry and wet ends of the vegetational continuum. Mesic communities will require more work and time to restore (Henderson 1995b; Henderson & Sample 1995; Packard 1988a). Substantial opportunities also exist for the restoration of oak and pine barrens in Wisconsin (Eckstein & Moss 1995). Although it is important that landscape regions, large and small, be restored and maintained to promote the biodiversity once supported by our prairie and savanna ecosystems, it is equally important that neither small sites in relatively natural condition nor degraded larger remnants be ignored. Good-quality small sites are the last refuge for many species of plants, insects, and the million microorganisms in a handful of soil. Even degraded sites, being more common and often larger, represent opportunities for restoration of the prairie and savanna flora (Henderson & Sample 1995; see also the Wisconsin Department of Natural Resources 1995, Packard & Mutel 1997, Sample & Mossman 1997). We dare not let these accidentally preserved areas slide into oblivion, for they are the invaluable seed banks of the future. Whether of whole species or of locally adapted populations, *extinction is forever*.

## Humans and Mother Nature, the Unbreakable Bond

*Postscript by Hugh H. Illis*

May this study, with all its imperfections and omissions, serve as a stimulus to invigorate prairie appreciation and prairie preservation and restoration, for in these activities there is more involved than just beautiful flowers, or a lovely landscape, or even the satisfaction of “doing the right thing.” It was the prairie ecosystem, after all, that over the millenia produced the prairie soils, including the dark-colored, humus-rich chernozems, the most fertile soils in the whole world. And it was these prairie soils, half of which now sit on the bottom of the Gulf of Mexico, the other half, once structured and crumbly, now more often than not compacted and eroded, that made Wisconsin rich, a fact realized by every farmer and a few politicians. To this day we barely understand how these soils were made to be so rich by the prairie ecosystems. Plant- and animal-soil relationships have been studied for decades, as have the effects of drought, grazing, and many other aspects of the prairie’s enormous complexity; nonetheless, how to keep this prairie soil sustainably productive in the long, long run for our grandchildren and far beyond into the dark, ominous future, is a loaded question rarely considered, and as yet unanswered.

There is now hardly a single large piece of prairie ecosystem left to study or to experiment with, to learn how it renews its fertility. But why worry? May we not rely on science and technology to find the answers in the laboratory? May we not continue to count on economic credit, machinery, and chemicals—fertilizers, herbicides, and pesticides, massively applied—to produce bumper crops? Have there not regularly been agricultural surpluses?

But dare we neglect to appreciate the roles of animals, from protozoa to nematodes, millipedes, earthworms, insects, and ground squirrels, or of prairie vegetation, from *Andropogon* to *Tradescantia*, *Baptisia*, and *Silphium*, and the incorporation of plant materials, functions that are barely understood if they are considered at all?

Cornfields alone will not do, for monocultures, even if periodically interspersed with leguminous crops, can not, in their simplicity, give us all the answers. To truly understand prairies, be it the evolution of their flowers or the genesis of their soils, we need samples of unplowed, unsprayed, naturally functioning ecosystems, and an ecologically educated public who will support their preservation. Questions of human population growth and of our insatiable, unsus-

tainable hunger for the world’s limited resources (Daily & Ehrlich 1992)—in short, of *Living Within Limits* (Hardin 1993), all come into play, even if all that we may wish for on a personal level is to preserve from cow and plow a dry hillside with a dozen pasqueflowers.

From a purely biological standpoint, it is our human fate, like that of all living things on this Earth, to do but one simple thing, and that is to *be a good ancestor*: certainly to our own children, and yes, even to the many generations yet to come. This is the biological imperative of life, which we cannot escape, except by misguided and seductive dreams of intellectual and technological superiority. This is our evolutionarily dictated responsibility, our duty—which we must assume (whether we like it or not), because we are living, reproducing beings, the result of evolution by natural selection—as it will be from now on and evermore.

Our crowning glory, the human brain, is a double-edged sword. On the one hand, it has deluded us by giving us God-like powers to destroy thoughtlessly our very own environment and that of future generations—the only species ever that deliberately has so tempted the fate of its own survival. On the other hand, it has empowered us to understand evolution and ecology, and with this the ability to direct our own destiny. And that imposes on us an everlasting new imperative, unheard of before in the history of life, and that is to consciously preserve, as all good ancestors must do, or restore if that is what is needed, the biological habitat that selected us, and to which we are bound by the dictates of evolution. Whether tropical rainforests or Wisconsin prairies, we must shield them from the instinctual fury of destruction wrought by our high but uninformed intelligence. Prairies, as much as tropical rainforests, are part of our holy Mother Nature, and we neglect her protection from humanity at our very own peril. Think globally, but act locally, if not for the sake of our prairie flowers, at least for the sake of our own children.

May this atlas, then, packed with geographical and ecological information, be a useful tool in fulfilling these noble endeavors, for nothing we do can ever be more important. If we succeed, we can have hope that children all over the world, ours and yours, today, tomorrow, and for millenia to come, will have a Mother Nature they can call their own, and that in Wisconsin they will be able to lie quietly in the grass on a sunny prairie hillside filled with flowers, watch bumblebees visit shooting-stars and pasqueflowers, hear dickcissels and meadowlarks call in the sky, and be ever enchanted and empowered by that great symphony we call life.

## APPENDIX A

### Excluded Prairie and Savanna Species

Eight species are excluded from this atlas. Six (•) are apparently spontaneous but non-native introductions, and two (§) are not known to occur in Wisconsin. Some of these plants are being used in landscape plantings, along with cultivars of Black-eyed Susan (*Rudbeckia hirta*) and Lance-leaf Tickseed (*Coreopsis lanceolata*).

- *Cirsium undulatum* (Nutt.) Spreng., WAVY-LEAVED THISTLE, is a Great Plains species, the natural range of which is usually reported as being from Minnesota to Missouri and westward. Rarely adventive farther east, it was reported from five Wisconsin counties by Johnson and Iltis (1963).
- *Echinacea purpurea* (L.) Moench, PURPLE CONEFLOWER, is native in the Midwest but to the south of Wisconsin. An all-time favorite of wildflower gardeners, it was first collected as an escape in 1951 in Dane County, and other Wisconsin records all seem to represent rare escapes from cultivation or wildflower plantings, as is the case in the Curtis Prairie at the U. W. Arboretum, Madison, where it is common.
- *Filipendula rubra* (Hill) Robinson, QUEEN-OF-THE-PRAIRIE, has been found in widely scattered locations in Wisconsin, but with one exception all Wisconsin collections are recent and certainly represent escapes from cultivation. There are no confirming specimens from southeastern Wisconsin, where its fen habitat occurs. The lack of information on the label of one old specimen, collected at Mazomanie, Dane County, in 1865, possibly by T. J. Hale, make it doubtful that this record should be accepted even as an escape, let alone a natural population (cf. Mason & Iltis 1958).
- § *Gentiana saponaria* L., SOAPWORT GENTIAN, is a widespread eastern species that has sometimes been reported as occurring in Wisconsin in standard floristic manuals. Such reports were based upon misidentifications of plants resulting from *G. andrewsii* × *G. puberulenta* crosses (Mason 1959). We have seen no specimen apart from these hybrids, and the distribution of this gentian as given by Gleason and Cronquist (1991) or Pringle's revision (1967; cf. also Pringle 1964, Mason & Iltis 1965) does not suggest that it ranges as far north as Wisconsin.
- *Grindelia squarrosa* (Pursh) Dunal, GUMWEED, represented with us by var. *squarrosa* and var. *serrulata* (Rydb.) Steyerl., is quite clearly introduced in Wisconsin as elsewhere in this region, its natural distribution ranging from Minnesota to Texas and westward (Fernald 1950; Wetter pers. comm.). Fairly well naturalized in Wisconsin, it almost always occurs in ruderal habitats but rarely also in ecologically open, dry, gravelly prairies.
- *Helianthus mollis* Lam., SOFT or DOWNY SUNFLOWER, is a southern and southeastern species that should no doubt be regarded as adventive. Our few herbarium collections were made along railroads and roadsides in four eastern and northern counties in the early decades of this century.
- § *Lilium superbum* L., TURK'S-CAP LILY, is native well south of our region. The Wisconsin *Lilium* is usually recognized at the rank of species as *L. michiganense* Farw. Although it was once considered a subspecies of *L. canadense* L., Gleason combined *L. michiganense* with *L. superbum* under the latter name, and Curtis (1959) also called our plants *L. superbum*. The three taxa are certainly closely related.
- *Ratibida columnifera* (Nutt.) Wooton & Standl., LONG-HEADED CONEFLOWER, is abundant on prairies and open ground throughout the Great Plains. Native from Minnesota to Alberta and south into Mexico (Fernald 1950, Gleason & Cronquist 1991), it is here adventive in abandoned fields, gravel pits, railroad yards, and waste ground generally, but also rarely in ecologically open, dry sand prairies.

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## APPENDIX B

### Native Plant Nurseries

The following companies, organizations, and individuals may be able to provide seeds or plants native to Wisconsin or the Midwest. Except as noted, seeds and plants are generally nursery grown. Some companies may also provide consultation, design, landscape installation, and/or maintenance services.

There are several arguments for buying seed and stock from reputable suppliers, as opposed to indulging in the destructive practice of native plant exploitation and collection. Haphazardly moving plants from one location to another contaminates geographical distribution data with artificial range extensions. Moreover, much debate and controversy hinges on the genetic implications of using local ecotypes versus plants of different provenance in plantings and restorations. Genes of the introduced populations may pollute local gene pools and can lead to the phenomenon called “genetic swamping.” To protect local gene pools when restoring or re-creating a natural area, be it a large-scale restoration or backyard garden, or to control erosion or enhance forage, it is best to obtain seeds or plants from within or as close as possible to the project site. Furthermore, local sources often possess genotypes that are adapted to the local environment, leading to higher short-term and long-term success rates. To prevent the local extinction of marketable species, native plants should be bought, not dug, and if possible, these plants should be derived from sources that are within a 50-mile radius of the site. If a nursery cannot state that its plants are “nursery propagated,” then they may have been collected in the wild. Always ask about their origin when purchasing nursery-propagated plants and seeds. Stocks originating from outside Wisconsin, say from Texas, Nebraska, or North Dakota, generally should not be used, except that Minnesota or northern Illinois populations may be more closely related to those in the project area than populations from farther away in Wisconsin. Landscapers and restorationists have a responsibility to help preserve the genetic structure of the different wild ecotypes or “ecovars” by having knowledge of where, precisely, their plants and seeds originate—and to keep records of major outplantings.

This list was compiled by the Bureau of Endangered Resources, Wisconsin Department of Natural Resources (DNR), and does not imply any endorsement or recommendation by the DNR, or by the Department of Botany, University of Wisconsin. Revisions or additions should be sent to BER, DNR, P.O. Box 7921, Madison WI 53707 (Attn: Kelly Kearns).

### Nurseries That Primarily Carry Plant Material Native to Wisconsin

**Agrecol** wholesales seeds and plants of more than 100 species of prairie, wetland, and savanna species. Their nursery stock is from native Wisconsin genotypes. They are continually adding new species. Contact: Steve Banovetz, 1984 Berlin Road, Sun Prairie, WI 53590. 608-825-9765.

**Applied Ecological Services, Inc./TaylorCreek Nursery** has prairie, woodland, and wetland plants for use in restoration projects. They do ecological research and consulting, site design preparation, planting, and management. Contact: Steve Apfelbaum, Route 3, Smith Road, P.O. Box 256, Brodhead, WI 53520. 608-897-8547.

**Bluestem Farm** provides consultation, plants, and services primarily in Baraboo area, no mail order. We specialize in custom propagation of difficult species, including orchids. Contact: Martha Barrett and Scott Weber, S5920 Lehman Road, Baraboo, WI 53913. 608-356-0179.

**Boehlke's Woodland Gardens** supplies prairie grasses and forbs, also wetland and woodland plants. Contact: Boehlke's Woodland Gardens, 5890 Wausaukee Road, West Bend, WI 53095. 262-876-2598.

**Country Road Greenhouse** is a wholesale grower specializing in containerized prairie and wetland forbs, grasses, and sedges. Contact: 19561 East Twombly, Rochelle, IL 61068. 815-384-3311.

**Enders Greenhouse** propagates over 200 species of native woodland, prairie, and wetland plants for retail or large contracts. Plant list available. Contact: Anne Meyer, 104 Enders Drive, Cherry Valley, IL 61016. 815-332-5255, FAX: 815-332-5255.

- Genesis Nursery** carries seeds (and some plants) for over 400 prairie, wetland, and savanna species and containerized plants for about 100 species. Northwest Illinois ecotypes. Also provides consultation, restoration, and planting. Contact: Dennis Lubbs, 23200 Hurd Road, Tampico, IL 61283. 815-438-2220, FAX: 815-438-2222.
- Inn Exchange** specializes in selling prairie, wetland, and savanna seeds and plants native to Wisconsin, Illinois, Iowa, and the general Driftless Area. Contact: Howard and Donna Bright, 1878 Old Mission Drive, Harpers Ferry, IA52146. 319-535-7231, FAX: 319-535-7362.
- Kettle Moraine Natural Landscaping** specializes in locally gathered prairie seeds from east-central Wisconsin. They do consulting, provide custom seed mixes, and have experience with residential, school, and commercial sites. Contact: Connie Ramthun, W996 Birchwood Drive, Campbellsport, WI 53010. 920-533-8939.
- Landscape Alternatives** offers 150 species of prairie, wetland, and woodland plants (no seeds). Catalog is \$2.00. Contact: Roy Robinson, 1705 Albans Street, Roseville, MN 55113. 612-488-3142.
- Little Valley Farm** carries both seeds and plants of many native species of grasses, forbs, shrubs, trees, and vines. Contact: Barbara Glass, Route 3, Box 544, Snead Creek Road, Spring Green, WI 53588. 608-935-3324.
- Midwest Wildflowers** can supply over 100 species of wildflower seeds. Catalog \$1.00. Contact: Leroy Busker, Box 64, Rockton, IL 60172.
- Murn Environmental, Inc.** carries a wide range of seeds and plants for wetland, woodland, and prairie species. They also do restoration, design, planting, management, and research. Contact: Tom Murn, 11643 East Minkey Road, Darien, WI 53114. 262-676-4709, FAX: 262-676-5744.
- Native Plants** fills a unique niche in the native plant industry. They work with local highway departments, developers, and others to salvage native plants from areas where they would otherwise be destroyed. Plants are then used at the site or are available for other projects. Persons interested in purchasing plants can call to place an order for desired plant species or to check on what is currently in stock. Contact: Brad Mrzlak, 22 Langdon Street, Madison, WI 53703. 608-259-0995.
- Oak Prairie Farm** produces Wisconsin Crop Improvement Association certified native prairie seeds and also performs consultation and installation services. Contact: Jim Heinrich, W4642 Highway 33, Pardeeville, WI 53954. 608-429-3882.
- Prairie Future Seed Co.** can supply a wide range of prairie seeds native to Wisconsin. They also do consultation and restoration projects. Contact: Randy R. Powers, P.O. Box 644, Menomonee Falls, WI 53052. 262-246-4019.
- Prairie Moon Nursery** carries seeds and plants of over 400 prairie, wetland, and woodland plant species native to Wisconsin, Minnesota, Illinois, and Iowa. Contact: Alan Wade, Route 3, Box 163, Winona, MN 55987. 507-452-1362, FAX: 507-454-5238.
- Prairie Nursery** has both seeds and plants of many native prairie species as well as some wetland and woodland seeds and plants. They provide an array of consulting services, including: site evaluation, planting design, site preparation, planting, and post-planting management for sites of all sizes. Contact: Neil Diboll, P.O. Box 306, Westfield, WI 53964. 608-296-3679.
- Prairie Restorations, Inc.** specializes in restoration and maintenance of prairies. Retail sale of prairie plants is done mail order or at their nursery northwest of Minneapolis. Contact: Ron Bowen, P.O. Box 327, Princeton, MN 55371. 612-389-4342 (office), 612-389-5733 (nursery).
- Prairie Ridge Nursery/CRM Ecosystems, Inc.** has prairie, wetland, and woodland seeds and plants. They are also available for consulting, planning, planting, and management services for projects of all sizes. Contact: Joyce Powers, RR 2 9738 Overland Road, Mt. Horeb, WI 53572. 608-437-5245.

**Prairie Seed Source** sells local southeast Wisconsin seeds of more than 150 prairie and savanna species, including mixes suited to the soil moisture regime of your project. They can also give slide presentations and provide consulting services. Contact: Robert Ahrenhoerster, P.O. Box 83, North Lake, WI 53064-0083. 262-673-7166.

**Reeseville Ridge Nursery** deals mainly with native trees and shrubs, and specializes in custom propagation of woody plants. Contact: Darrell J. Kromm, P.O. Box 171, 309 South Main Street, Reeseville, WI 53579. 920-927-3291.

**Retzer Nature Center**, as a service of Waukesha County Parks, supplies native prairie, woodland, and wetland plants and seeds for sites within 50 miles from the Waukesha County line. They specialize in prairie mixes and can provide technical assistance on restoration projects. Contact: Jerry Schwarzmeier, W284 S1530 Road DT, Waukesha, WI 53188. 262-521-5407.

**Rohde's Nursery** supplies woodland, wetland, and prairie plants; also provides a complete design service along with the ability to install/build any size project, and help with consultation and restoration. Contact: Lenn Rohde, N8098 Duck Creek Avenue, Neshkoro, WI 54960. 920-293-4373.

**WehrNature Center** can provide persons in southeast Wisconsin with prairie seeds and instructions for small scale prairie gardening. Contact: Wehr Nature Center, 9107 West College Avenue, Franklin, WI 53132. 414-425-8550.

**Wood's Edge** sells woodland wildflowers grown from seeds from Grant County. We prefer to sell plants or bareroot stock. Contact: Bernie Galgoci or Martha Peterson, 532 Stanek Road, Muscoda, WI 53573. 608-739-3527, E-mail: woodedge@mwt.net.

## Nurseries That Carry Native Midwestern Plants, Non-Native, and/or Wild-dug Plants

The following companies sell plants native to the Midwest but not specifically from Wisconsin or the surrounding region. People who want only native species when creating their very own piece of prairie, woodland, or wetland should be aware that many of these nurseries and seed farms also sell non-native species. So-called "native" grasses, e.g., Sheep Fescue (*Festuca ovina*) and Sand Lovegrass (*Eragrostis trichodes*), and "native" wildflowers, e.g., Blanket-flower (*Gaillardia* spp.), Purple Coneflower (*Echinacea purpurea*), Blue Wild-indigo (*Baptisia australis*), Blue Flax (*Linum lewisii*), etc., may not be native to Wisconsin at all, even though they may occur naturally in other parts of the Midwest or North America. Even if they are attractive in gardens, they should not be used if you want to create a true prairie setting or add authentic native prairie plants to a traditional perennial garden. Use discretion when selecting plants from these nurseries, or ask for plants that came from your area. Several of the following companies sell plants collected from the wild. This is indicated in the nursery description where known.

**Allendan Seed** is an Iowa-based company that offers seeds for a variety of landscaping projects. Contact: Allendan Seed, Route 4 Box 625, Winterset, IA 50273. 515-462-1241.

**Aquatic Resources and Glacial Pond Farms** is a source of both grasses and forbs for prairie plantings, as well as vegetation for wetland landscaping. Contact: Aquatic Resources and Glacial Pond Farms, P.O. Box 2221, Wausau, WI 54402. 715-845-2099.

**Bauer's Garden Center** carries a complete line of garden supplies, as well as a wide selection of wildflowers, all available for sale in 4 1/2 inch pots. Contact: Bauer's Garden Center, 1559 West Forest Home Avenue, Milwaukee, WI 53204. 414-384-7995.

**Bayside Garden Center** is a source for both grasses and forbs of the prairies, as well as wetland and woodland plants. Contact Bayside Garden Center, 400 East Brown Deer Road, Milwaukee, WI 53217. 414-352-6159.

**Berthold Nursery** has a variety of native trees and shrubs. Contact: Rick Repenning, 4510 Dean Street, Woodstock, IL 60098. 815-338-4914, 708-439-2600.

**Cascade Forest Nursery** carries woodland plant species. Contact: Cascade Forest Nursery, Route 1, Cascade, IA 52033. 319-852-3042.

**Cold Stream Farm** can provide both wetland and woodland plants. Contact: Cold Stream Farm, 2030 Free Soil Road, Free Soil, MI 49411-9752. 616-464-5809.

**Deltor Tree Farm** carries woodland species. Contact: Deltor Tree Farm, Box 6 County P, Plainfield, WI 54966. 715-335-4444.

**Evergreen Nursery Co., Inc.** specializes in woodland plants. Contact: Evergreen Nursery Co., Inc., 5027 County TT, Sturgeon Bay, WI 54235. 920-743-4464.

**The Flower Factory** has an extensive selection of native, non-native, and ornamental plants. Contact: David or Nancy Nedveck, 4062 Highway A, Stoughton, WI 53589. 608-873-8329.

**Glen Flora Nursery** can provide prairie forbs and wetland and woodland plants. Contact: Glen Flora Nursery, 8407 Glen Flora Road, Kiel, WI 53042. 920-773-2493.

**Great Lakes Nursery Co.** grows select native seedlings and transplants of northern trees, shrubs, and some herbaceous plants, non-natives, and cultivars. Contact: Tim Gutsch, 1002 Hamilton Street, Wausau, WI 54403. 715-845-7752.

**A Growing Concern** is a source for seeds and plants of woodlands. Contact: AGrowing Concern, 4990 West Donna Drive, Brown Deer, WI 53223. 414-354-1638.

**H & R Nursery, Inc.** carries woodland wild flowers and ferns in addition to horticultural species. They do not sell seeds or mail order their plants. Contact: Dale Rickert, 6520 West Silver Spring Drive, Milwaukee, WI 53218. 414-466-6289.

**Hauser's Superior View Farm** has a large selection of northern-grown perennials and biennials, a few of which are species native to Wisconsin. They have a minimum order of \$25.00. Contact: Jim Hauser, Route 1, Box 199, Bayfield, WI 54814. 715-779-5404.

**Hild & Associates** offers seeds and bareroot material propagated in their nursery from nearby seed sources. They do some consultation and installation and are members of the MN Erosion Control Association, The Vegetation Management Association of MN, and the MN Native Seed and Plant Producers Association. Contact Hild & Associates, 326 Glover Road South, River Falls, WI 54022. 715-426-5131 or 1-800-790-9495, FAX: 715-426-9887, E-mail: ghild@skypoint.com / Website: www.hildnatives.com.

**Itasca Greenhouse, Inc.** grows tree seedlings. Most species are grown to plantable size in less than one year. Custom and contract growing services are available to our customers who want specific trees grown. Contact: Itasca Greenhouse, Inc., P.O. Box 273, Cohasset, MN 55721. 218-328-6261 or 1-800-538-TREE, E-mail: igtrees@northernnet.com.

**J and J Tranzplant** specializes in nursery propagated native as well as non-native aquatic plant material. Available bareroot, 2" plugs to one gallon pots. They also carry a large selection of aquatic seeds native to central WI. 65% of material is nursery-propagated and 35% is collected from the wild. Consulting and planting on a limited basis, 42-page catalog available. Contact: James and Kristine Malchow, P.O. Box 227, Wild Rose, WI 54984-0227. 920-622-3552 or 1-800-622-5055, FAX: 920-622-3660.



- Johnson's Nursery Inc.** are growers of a wide selection of balled and burlapped landscape plants. This diverse selection includes many native trees, shrubs, and vines. Contact: Bill Reichenbach, W180 N6275 Marcy Road, Menomonee Falls, WI 53051. 262-252-4988.
- Jung Seeds Co.** has a brochure which pictures all the prairie grasses and wildflowers they carry. Most seeds and plants sold without regard to genetic source. Contact: L. L. Olds Seed Co., P.O. Box 77990, Madison, WI 53707. 608-249-9291.
- Kester's Wild Game Food Nurseries, Inc.** carries native wetland species as well as non-native species for wildlife plantings. They carry both wild-collected and nursery-grown stock. Contact: Dave and Patricia Kester, P.O. Box 516, Omro, WI 54963. 920-685-2929.
- Laura's Lane Nursery** is a supplier of woodland plants. Contact: Laura's Lane Nursery, Box 232, Plainfield, WI 54966. 715-366-2477.
- Lodholz North Star Acres, Inc.** specializes in woodland plants. Contact: Lodholz North Star Acres, Inc., 420 Highway A, Tomahawk, WI 54487. 715-453-2976.
- Marshland Transplant Aquatic and Woodland Nursery** sells plants and seeds of aquatic, woodland, and prairie species. Some plants and seeds are wild collected. Contact: Tom Traxler, P.O. Box 1, Berlin, WI 54923. 920-361-4200.
- Midwest Aquatics** specializes in propagated and wild-collected native wetland and aquatic species and custom harvest of seeds. Contact: Douglas Nelson, Route 360-5, Wautoma, WI 54982. 920-787-3282.
- Milaeger's Gardens** carries some prairie grasses and wildflowers in addition to ornamentals. Contact: Milaeger's Gardens, 4838 Douglas Avenue, Racine, WI 53402-2498. 262-639-2371.
- Miller Nurseries** has both prairie forbs and woodland plant species. Contact: Miller Nurseries, P.O. Box 66, Germantown, WI 53022. 262-628-9588.
- Mohn Frontier Seed Company** is a family-owned business in southwestern Minnesota offering wildflower seeds and plants as well as a variety of prairie grasses. Products are suited to prairies, woodlands, and/or wetlands, and are native to Minnesota. Contact: Mohn Frontier Seed Company, Route 1 Box 152, Cottonwood, MN 56229. 507-423-6482, FAX: 507-423-5552.
- The Natural Garden** carries many varieties of native and non-native wetland, prairie, and woodland plants and has landscape design and construction services available. Contact: The Natural Garden, 38W443 Highway 64, St. Charles, IL 60174. 708-584-0150.
- Oasis WaterGardens** sells aquatic plants and supplies for water gardens and aquariums. Contact: Jerry Ray, 2968 Pine Tree Road, Oneida, WI 54155. 414-869-1085.
- Orchid Gardens** has wildflowers, ferns, and shrubs indigenous to northern Minnesota. There is a fee for consultation. Contact: Carl A. Phillips, 2232 139th Avenue NW, Andover, MN 55304.
- Osenbaugh Grass Seeds** is a seed supplier for grasses and forbs of the prairie. Contact: Osenbaugh Grass Seeds, RR #1 Box 44, Lucas, IA 50151. 515-766-6476 or 1-800-LUCAS88.
- Prairie Frontier** carries over 100 different native and naturalized wildflower and prairie grass seeds, and specializes in large planting projects. Native prairie, meadow, and butterfly mixes as well as 10 other mixes containing some non-native species are available. Mixes and individual species can be purchased in bulk; seeds are generally sold wholesale to developers, landscapers, nurseries, and garden centers or retail through outlet stores or our website at <http://www.prairiefrontier.com>. Contact Jim and Deb Edlhuber, W281 S3606 Pheasant Run, Waukesha, WI 53188. 262-544-0159, FAX: 262-544-6708, E-mail: [wildflower@prairiefrontier.com](mailto:wildflower@prairiefrontier.com).
- Prairie Grass Unlimited** can provide both prairie and wetland plants. Contact: Prairie Grass Unlimited, P.O. Box 59, Burlington, IA 52601.

**Shady Acres Nursery** offers an extensive line of perennials and grasses, some of which are native. Contact: Jim Garbe, 5725 S. Martin Road, New Berlin, WI 53146. Catalog available for \$3.00. 262-679-1610.

**Smith Nursery Co.** sells wholesale native and non-native shrubs, vines, and trees in multiples of 5 and 10. Seeds are also available. Extensive selection in catalog. Contact: Bill Smith, P.O. Box 515, Charles City, IA 50616. 515-228-3239.

**Sound Solutions** provides plants, trees, and seeds for the restoration needs of its clients. It has 70 acres of land devoted to propagating native wetland, prairie, and woodland species, providing customers with seeds, plugs, and bareroot stock to aid in the completion of successful projects. Contact: Daniel Zay, 708 Roosevelt Road, Walkerton, Indiana 46574. 219-586-3400, FAX: 219-586-3446.

**Specialty Seeds** sells wholesale bulk and mixed seeds. They carry mostly prairie species and some woodland wildflowers and can customize orders for genotype. Contact: Margit Sandor or Frank Nechvatal, 210 Grell Lane, P.O. Box 400, Johnson Creek, WI 53038. 1-800-824-4668.

**Wali Nursery** specializes in woodland plant species. Contact: Wali Nursery, Route 9 Box 9080, Hayward, WI 54843. 715-462-3565.

**Westfork Walnut Nursery** is a supplier of woodland plants. Contact: Westfork Walnut Nursery, Route 3 Box 145, Viroqua, WI 54665. 608-637-2528.

**Wildflowers from Nature's Way** specializes in prairie wildflower and grass seed mixes all from Iowa source plants. They also sell some woodland wildflowers. Contact: Dorothy Baringer, RR 1, Box 62, Woodburn, IA 50275. 515-342-6246.

**Wildlife Habitat** carries prairie grass seeds. Contact: Wildlife Habitat, RR #3 Box 178, Owatonna, MN 55060. 507-451-6771.

**Wildlife Nursery** specializes in wild-collected wetland and non-native plants that attract wildlife. They also do consulting on a limited basis. Contact: John J. Lemberger, P.O. Box 2724, Oshkosh, WI 54901. 920-231-3780.

## Restoration Consultants

The following companies and individuals operate as consultants in Wisconsin and the surrounding areas. Although most simply do consultation, some will provide planting and management services.

**Robert Abernathy** is a consultant who does botanical inventories and restoration consultation and management in wetlands, woodlands, and prairies. Contact: Robert Abernathy, W 8507 Meadow Brook Road, Argyle, WI 53504. 608-543-3865.

**Brian Bader** provides consulting services for prairie, savanna, and woodland restoration. He develops comprehensive management plans and coordinates planting plans, site preparation, planting, and management, and advises on propagation needs. Contact: Brian Bader, 1913 Sachtjen Road, Madison, WI. 608-243-7871.

**Robert Baller** is a botanist/ecologist available for consultation and native plant surveys. Contact: Robert Baller, P.O. Box 533, Beloit, WI 53512. 608-365-2065.

**BioLogic Environmental Consulting, LLC** specializes in the inventory, assessment, restoration, planning, and management of forests, grasslands, wetlands, and other ecosystems. Restoration services include site evaluation, species selection, site preparation, and planting and management guidelines. Contact: Michael Anderson, 122 Nygard Street, Madison, WI 53713. 608-256-4401.

**Biophilia** specializes in butterfly gardening and native plants that attract butterflies. Contact: Randall Korb, 1903 North Whitney Drive, Appleton, WI 54914. 920-734-1744.

**Bison Belly Futures** serves Wisconsin's Driftless Area with a range of land stewardship services, including consulting, land management, native landscaping, and education. Specific services include site evaluation, brush and invasive species control, installation of small-scale prairie and woodland plantings, prescribed burns, and the development of self-guided nature trails. Contact: Gigi La Budde, S11793 Hazelnut Road, Spring Green, WI 53588. 608-588-2048, E-mail: spikey@mhtc.net / Website: <http://www.mhtc.net/~spikey/bison.html>.

**The Blue Mounds Project** provides landowners in western Dane and Iowa counties with an ecological extension program. Staff consult with landowners interested in restoring any native vegetation, assist with planning, restoration, and management, and train landowners in restoration techniques. Contact: Brian Pruka, P.O. Box 332, Mount Horeb, WI 53572. 608-244-2181.

**Clark Forestry Consulting** is active in conserving, restoring, and protecting native habitats. Specialties: timber sales and services, the development of landscape management plans, and fully insured prescribed burns, including site assessment, firebreak construction and preparation, and post-fire monitoring and mop-up. Contact: Fred Clark, P.O. Box 572, Poynette, WI 53955. 608-356-2801.

**Creative Landscapes** does design and installation of native landscapes. Contact: Charles and Karen Koehler, 3412 Superior Avenue, Sheboygan, WI 53081.

**Sean Dalton of Natural Re-creation!** is a native-landscapes consultant specializing in prairies and savannas. He is available for consultation and site planning, and will do restoration work in the greater La Crosse area. Visit his website at <http://www.paradisenow.com>, e-mail him at [sean@win.bright.net](mailto:sean@win.bright.net), or contact him at Sean Dalton, W20531 Gilbo Lane, Galesville, WI 54630. 608-582-2675.

**Jerry Davis** is available for consultation, either informal or formal, with emphasis on use of trees and shrubs. Contact: Jerry Davis, Biology Department, UW-La Crosse, La Crosse, WI 54601. 608-785-6963.

**Roy Diblik** specializes in utilizing native plants in urban settings. Contact: Roy Diblik, Box 95, Springfield, WI 53176. 262-248-8229.

**Donald L. Vorpahl Associates** provides site evaluation and design, seed and plant selection, planting and management services for restoring and developing native plant communities on commercial and residential sites of all sizes. Contact: Don Vorpahl, N6143 Hilbert Road, Hilbert, WI 54129. 920-853-3729.

**Earthkeepers** provides alternative lawn care and wildflower plantings. Contact: Randy Mueller, N8635 County Hwy E, Watertown, WI 53094. 920-262-9095 or 1-800-261-9095.

**Foth and Van Dyke** has a staff including a biologist, a botanist, and several landscape architects at your disposal. Services include planning of reclamation and restoration of native plant communities. Contact: Bruce Woods, Foth and Van Dyke, Park West, Suite 400, 406 Science Drive, Madison, WI 53711. 608-238-4761, FAX: 608-238-4633.

**Graef, Anhalt, Schloemer, and Associates. Inc.** specializes in evaluating wetlands delineation and functional values as well as planning the restoration and creation of wetland communities. Contact: Eric C. Parker, Environmental Specialist, 345 North 95th Street, Milwaukee, WI 53226-4441. 414-259-1500, FAX: 414-259-0037.

**Inner-Coastal Ecological Services (ICES)** conducts natural area and right-of-way inventories of flora specifically, and fauna as required. ICES utilizes GIS and CAD software to map this information, enabling large scale tracking and planning. ICES designs, installs, and maintains native plant community restorations and manages other natural areas. ICES also contracts for seeds and plant materials and conducts ecological research. Contact: Michael Ulrich, 1935 Winneba-

go Street, Madison, WI 53704. 608-246-8020.

**Invasive Plant Control, Inc.** offers a variety of services, including workshops, help in developing grants, and plant removal. Contact: Steven Manning, 2713 Larmon Dr., Nashville, TN. 1-800-449-6339, FAX: 615-385-4124, E-mail: info@invasiveplantcontrol.com / Website: www.invasiveplantcontrol.com.

**Babette Kis** does consultation work and leads workshops on native and invasive species. She also raises wildflowers from seeds collected in Racine County, specializing in propagating more difficult species and working with the pH needs of plants. Contact: Babette Kis, 6048 North 114th Street, Milwaukee, WI 53225-1210. 414-286-3147.

**Mick Kennedy** is a consultant, designing and building native landscapes and restoring and managing both prairies and woodlands. Contact: Mike Kennedy, Wisconsin Landscapes, Inc., 10921 Spring Creek Road, Blue Mounds, WI 53517. 608-437-3662, FAX: 608-437-8472.

**Landscape Lady, Ltd.** will do design, installation, and maintenance of natural landscapes. Contact: Gloy Jacobson, 3312 North Weil Street, Milwaukee, WI 53212. 414-933-0540.

**Landscapes, Naturally...** provides native landscape design services for residential, municipal, commercial, and rural properties, pre- and post-construction land use consultation, plant inventories, landscaping for wildlife, and environmental education services. Contact: Lynn M. White, 2417 Marathon Avenue, Neenah, WI 54956. 920-751-8335.

**Mead and Hunt, Inc.** does planning, analysis, and construction supervision on wetlands, floodplains, and shores. Contact: Perry Rossa, Environmental Scientist/Wetlands, Mead and Hunt, Inc., 6501 Watts Road, Suite 101, Madison, WI 53719. 608-273-6380.

**Midwest Land and Culture, Inc.** specializes in consultation on landscape development, management plans, and site evaluation. Contact: Cathie Bruner, 216 N. Dickinson St., Madison, WI 53703. 608-250-2545.

**Gail Moede** is a landscape architect specializing in prairie and wetland restorations. She will help with residential landscaping incorporating native plant species. Contact: Gail Moede, N 6240 Stonewood Drive, Watertown, WI 53094. 920-699-3737.

**Susan B. Murray** is available for landscape and environmental design site planning, developing management plans and landscaping plans, and doing consultations on native landscapes. Contact: Susan Murray, Landscape Architect, ASLA, 1230 Bowen Court, Madison, WI 53715. 608-255-9006, FAX: 608-255-8661.

**Native Landscapes** specializes in the assessment, design, management, and restoration of natural areas and research of rare plant and management-related issues. Contact: Vicki Nuzzo, 1947 Madron Road, Rockford, IL 61107. 815-637-6622.

**Natural Lawn and Landscape Service** will aid in care of your property, including native plantings, prairie and path mowing, and buckthorn removal. Contact: Gene Haack at 414-344-0131.

**North American Butterfly Association** advises on constructing butterfly-friendly gardens and habitats. Contact: Program for Butterfly Gardens and Habitat, 909 Birch Street, Baraboo, WI 53913.

**Oak Woodland Services** consults on safe use of herbicides in forests and prairies in southwestern Wisconsin. Contact: Pat Schroeder, 7385 Timberline Trail, Arena, WI 53503. 608-753-2674.

**The Prairie Enthusiasts** is a non-profit membership organization of persons interested in identifying, protecting, and managing native prairies. They can provide consultation and management services, including prescribed burning. Members may become active in a wide range of prairie surveys, management, restoration, and education projects. Contact: Gary Eldred, 4192 Sleepy Hollow Trail, Boscobel, WI 54805. 608-375-5271.

**Prairie Sun Consultants** has a botanist/restoration ecologist who will do site assessments and inventories and provide consultation on weed control in and restoration/natural landscaping of prairies, savannas, and woodlands. Contact: Patricia K. Armstrong, 612 Stauton Road, Naperville, IL 60565. 630-983-8404.

**R-8 Landscape Design and Consultation** specializes in native, natural, and traditional landscapes, providing customers with a range of options from perennial to theme gardens. Contact: Carol M. Fuchs, 1337 South 114th Street, West Allis, WI 53214-2235. 414-771-3392, FAX: 414-771-8898.

**Red Buffalo Prairie Restorations** provides prairie and savanna seeds for plants of the Wisconsin Driftless Area, as well as consultation, land management, and brush and tree clearing for restorations or remnants, always with an eye for aesthetics. Experience in controlled burning. Contact: Greg Nessler, RR 1 Box 133A, Viola, WI 54664. 608-627-1376.

**Jim Riemer** does consultation work, most of his experience being in small prairie restorations. Contact: Jim Riemer, Cths Building, Barron, WI 54818. 715-537-6317 or 715-822-3879.

**Kay Rill** specializes in plant inventories. Contact: Kay Rill, 1505 East Nevada Avenue, Oshkosh, WI 54901. 920-233-5527.

**Jim Sime** works mainly in restoring prairies and savannas which are now fading or are on the verge of disappearing in favor of other vegetation. Contact: Jim Sime, 6327 Elmwood Avenue, Middleton, WI 53562. 608-831-9297.

**STS Consultants, LTD.** is a geotechnical and environmental engineering firm that is experienced in large and small scale wetland identification/delineation, assessment, creation, and restoration design and construction management. Contact: Jan Tesch, 1035 Kepler Drive, Green Bay, WI 54313, 414-468-1978; or Chuck Bartelt, 11425 West Lake Park Drive, Milwaukee, WI 53224, 414-359-3030.

**Thompson and Associates Wetland Services** is experienced in all aspects of wetland mitigation and management, including: wetland delineation, wetland mitigation site search, site design, vegetation and hydrological monitoring, as well as native plant surveys and management of wetlands. Contact: Alice Thompson, Wetland Ecologist, 1320 Manitowoc Ave., South Milwaukee, WI 53172. 414-571-8383, FAX: 414-571-8384, E-mail: thompal@execpc.com.

**Robert Wernerehl** does botanical inventories and restoration consultation, especially on lowland forests and sedge meadows. Contact: Robert Wernerehl, 8237 Sweeney Road, Barneveld, WI 53507. 608-795-4244.

**Andrew Williams** can help conduct prairie plant inventories. Contact: Andrew Williams, P.O. Box 1646, Madison, WI 53701. 608-284-1731.

**Windy Oaks Aquatics** sells various waterlilies and marginals, as well as accessories. Consultation, installation, and landscaping services are available. Retail catalog for \$1.00. Contact: Windy Oaks Aquatics, W377 S10677 Betts Road, Eagle, WI 53119. Phone/FAX: 262-594-3033.

**Witness Tree Native Landscapes, Inc.** specializes in analysis, design, and restoration of landscapes. Contact: June Keibler, 121 Ford Street, Geneva, IL 60134.

**Elizabeth Zimmerman** conducts botanical and bird inventories and advises on ecological restoration. She specializes in wetlands statewide and also does botanical illustrations. Contact: Elizabeth Zimmerman, N 3485 Highway A, Fort Atkinson, WI 53538. 920-423-4074.

## APPENDIX C

### Reports on the Flora of Wisconsin

As the result of intensive field work that has been carried out in Wisconsin over the years, and the numerous taxonomic publications that have appeared dealing with the occurrence of plants in the state, Wisconsin is floristically one of the better known states in some ways. One series of papers in particular is important as a source of information on the vascular plants of Wisconsin: the *Preliminary Reports on the Flora of Wisconsin*. These include some 70 studies of selected families and genera, the more recent ones being submonographic in scope, which have appeared at irregular intervals since 1929 in the *Transactions of the Wisconsin Academy of Sciences, Arts and Letters*. Many of these treatments, which emphasize the detailed geographic distributions of each species within Wisconsin, were written by, or edited by, either the late Norman C. Fassett, Hugh H. Iltis, or Theodore S. Cochrane, and their students or cooperating associates who contributed treatments for plant groups for which they are specialists.

This appendix consists primarily of a comprehensive listing of the *Preliminary Reports*, but also includes other articles or book-length treatments that have been published for a few Wisconsin families. Families for which no references are listed have not been so treated. For the sake of simplicity, "Ferns and Fern Allies" and "Spring Flora" have been treated as though they were family names. For ease of use with this atlas, the families are listed alphabetically, but numbers preceeding entries refer to the old-fashioned but eminently useful system of Engler and Prantl. Herbaria, including that of the University of Wisconsin–Madison, and standard identification manuals such as *Gray's Manual of Botany*, 8th ed. (Fernald 1950) are generally arranged according to this classification, in which supposed levels of phylogenetic development are summarized by ranking families in a numerical sequence. Following the *Preliminary Reports* is a cursory list of texts and articles useful to those wanting to consult additional references pertinent to Wisconsin or the Midwest.

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|--|---|
| 266 ACANTHACEAE: (No treatment)  | 74 ARISTOLOCHIACEAE: (No treatment)   |
| 163 ACERACEAE: Fassett, N. C. 1930. Prel. Rpt. 8. Trans. Wisconsin Acad. 25:195–197.   | 248 ASCLEPIADACEAE: Noamesi, G. K. and H. H. Iltis. 1958 ["1957"]. Prel. Rpt. 40. Trans. Wisconsin Acad. 46:107–114.  |
| 272 ADOXACEAE: Wade, D. E. and D. R. Wade. 1940. Prel. Rpt. 28. Trans. Wisconsin Acad. 32:92–101.                                  | 280 ASTERACEAE: Shinnars, L. H. 1941. The genus <i>Aster</i> in Wisconsin. Amer. Midl. Naturalist 26:398–420.   |
| Cochrane, T. S. and P. J. Salamun. 1974. Prel. Rpt. 64. Trans. Wisconsin Acad. 62:247–252.   | Melchert, T. E. 1960. Heliantheae of Wisconsin. M.S. Thesis, Univ. Wisconsin–Madison. 74 pp. + 46 maps.   |
| 84 AIZOACEAE: (No treatment)   | Johnson, M. F. and H. H. Iltis. 1964 ["1963"]. Prel. Rpt. 48. Compositae I (Tribes Eupatorieae, Veronieae, Cynarieae, and Cichorieae). Trans. Wisconsin Acad. 52:255–342. |
| 15 ALISMACEAE: Fassett, N. C. 1929. Prel. Rpt. 1. Trans. Wisconsin Acad. 24:250–256.   | Barkley, T. M. 1964 ["1963"]. Prel. Rpt. 49. Compositae II (the genus <i>Senecio</i> ). Trans. Wisconsin Acad. 52:343–352.  |
| 79 AMARANTHACEAE: Sauer, J. D. and R. Davidson. 1962. Prel. Rpt. 45. Trans. Wisconsin Acad. 50:75–87.                              | Salamun, P. J. 1964 ["1963"]. Prel. Rpt. 50. Compositae III (the genus <i>Solidago</i> ). Trans. Wisconsin Acad. 52:353–382.  |
| 40 AMARYLLIDACEAE: McIntosh, J. M. 1950. Prel. Rpt. 34. Trans. Wisconsin Acad. 40(1):230, 236.                                     | Mickelson, C. J. and H. H. Iltis. 1967 ["1966"]. Prel. Rpt. 55. Compositae IV (Tribes Helenieae and Anthemideae). Trans. Wisconsin Acad. 55:187–222.                      |
| 153 ANACARDIACEAE: Fassett, N. C. 1940. Prel. Rpt. 29. Trans. Wisconsin Acad. 32:103–106.  | Beals, E. W. and R. F. Peters. 1967 ["1966"]. Prel. Rpt. 56. Compositae V (Tribe Inuleae). Trans. Wisconsin Acad. 55:223–242.   |
| 157 AQUIFOLIACEAE: (No treatment)  | Payne, W. W. 1970. Prel. Rpt. 62. Compositae VI (the genus <i>Ambrosia</i> ). Trans. Wisconsin Acad. 58:353–371.  |
| 228 APIACEAE: Fassett, N. C. 1941. Wisconsin Plant Ranges No. 1. Dept. Botany, Univ. Wisconsin–Madison. 10 pp. (mimeo), maps 1–20. | 168 BALSAMINACEAE: (No treatment)   |
| 247 APOCYNACEAE: (No treatment)  | 93 BERBERIDACEAE: Fassett, N. C. 1946. Prel. Rpt. 33. Trans. Wisconsin Acad. 38:206–208.  |
| 23 ARACEAE: Fassett, N. C. 1937. Prel. Rpt. 25. Trans. Wisconsin Acad. 30:17, 19.  | 61 BETULACEAE: Fassett, N. C. 1930. Prel. Rpt. 7. Trans. Wisconsin Acad. 25:189–194.  |
| 227 ARALIACEAE: Fassett, N. C. and H. J. Elser. 1950. Prel. Rpt. 35. Trans. Wisconsin Acad. 40(1): 83–85.                          |   |

- 258 BIGNONIACEAE: (No treatment)
- 52 BORAGINACEAE: Kruschke, E. P. 1946 ["1944"]. Prel. Rpt. 32. Trans. Wisconsin Acad. 36:273–290.
- 105 BRASSICACEAE: Patman, J. P. and H. H. Iltis. 1962 ["1961"]. Prel. Rpt. 44. Trans. Wisconsin Acad. 50:17–72.
- 16 BUTOMACEAE: (No treatment)
- 210 CACTACEAE: Ugent, D. 1963 ["1962"]. Prel. Rpt. 47. Trans. Wisconsin Acad. 51:128–134.
- 128.1 CAESALPINIACEAE: (see Fabaceae, Caesalpinaceae)
- 148 CALLITRICHACEAE: Fassett, N. C. 1933. Prel. Rpt. 21. Trans. Wisconsin Acad. 28:184–186.
- 276 CAMPANULACEAE, LOBELIACEAE: Mahony, K. L. 1929. Prel. Rpt. 3. Trans. Wisconsin Acad. 24:357–361.
- 107 CAPPARACEAE: (No treatment)
- 271 CAPRIFOLIACEAE: Wade, D. E. and D. R. Wade. 1940. Prel. Rpt. 28. Trans. Wisconsin Acad. 32:91–101.
- Salamun, P. J. 1980. Prel. Rpt. 68. Trans. Wisconsin Acad. 67:103–129.
- 87 CARYOPHYLLACEAE: Schlising, R. A. and H. H. Iltis. 1962 ["1961"]. Prel. Rpt. 46. Trans. Wisconsin Acad. 50:89–139.
- 158 CELASTRACEAE: (No treatment)
- 89 CERATOPHYLLACEAE: Fassett, N. C. 1946. Prel. Rpt. 33. Trans. Wisconsin Acad. 38:192–194.
- 78 CHENOPODIACEAE: (No treatment)
- 193 CISTACEAE: (No treatment)
- 33 COMMELINACEAE: Fassett, N. C. 1932. Prel. Rpt. 16. Trans. Wisconsin Acad. 27:228, 229.
- 280 COMPOSITAE: (see Asteraceae)
- 249 CONVOLVULACEAE: Fogelberg, S. O. 1937. Prel. Rpt. 26. Trans. Wisconsin Acad. 30:21–25.
- 229 CORNACEAE: Drescher, A. A. 1933. Prel. Rpt. 22. Trans. Wisconsin Acad. 28:187–190.
- 115 CRASSULACEAE: (No treatment)
- 105 CRUCIFERAE: (see Brassicaceae)
- 275 CUCURBITACEAE: Mahony, K. L. 1929. Prel. Rpt. 3. Trans. Wisconsin Acad. 24:360–361.
- 20 CYPERACEAE: Greene, H. C. 1953. Prel. Rpt. 37. Cyperaceae, Part I (all genera except *Carex*). Trans. Wisconsin Acad. 42:47–67.
- Marcks, B. G. 1974. Prel. Rpt. 66. Cyperaceae, Part II (only the genus *Cyperus*). Trans. Wisconsin Acad. 62:261–284.
- 43 DIOSCOREACEAE: McIntosh, J. M. 1950. Prel. Rpt. 34. Trans. Wisconsin Acad. 40(1): 230, 236.
- 274 DIPSAKACEAE: Salamun, P. J. and T. S. Cochrane. 1974. Prel. Rpt. 65. Trans. Wisconsin Acad. 62:253–260.
- 112 DROSERACEAE: Livergood, F. B. 1932. Prel. Rpt. 18. Trans. Wisconsin Acad. 27:235–236.
- 189 ELATINACEAE: Fassett, N. C. 1930. Prel. Rpt. 9. Trans. Wisconsin Acad. 25:199–200.
- 215 ELAEAGNACEAE: Ugent, D. 1963 ["1962"]. Prel. Rpt. 47. Trans. Wisconsin Acad. 51:86–87, 89.
- EQUISETACEAE: Hauke, R. L. 1965. Prel. Rpt. 54. Trans. Wisconsin Acad. 54:331–346.
- 233 ERICACEAE: Fassett, N. C. 1929. Prel. Rpt. 2. Trans. Wisconsin Acad. 24:257–268.
- 30 ERIOCAULACEAE: Fassett, N. C. 1932. Prel. Rpt. 16. Trans. Wisconsin Acad. 27:227, 229.
- 147 EUPHORBIACEAE: Fassett, N. C. 1933. Prel. Rpt. 21. Trans. Wisconsin Acad. 28:178, 180–185.
- Richardson, J. W., D. Burch and T. S. Cochrane. 1988 ["1987"]. Prel. Rpt. 69. Trans. Wisconsin Acad. 75:97–129.
- 128 FABACEAE, CAESALPINIACEAE: Fassett, N. C. 1939. The Leguminous Plants of Wisconsin. Univ. Wisconsin Press, Madison. 1–157 pp., figs. 1–60, maps, plates I–XXIV.
- Gillett, J. M. and T. S. Cochrane. 1973. Prel. Rpt. 63 (only the genus *Trifolium*). Trans. Wisconsin Acad. 61:59–74.
- 62 FAGACEAE: Costello, D. F. 1931. Prel. Rpt. 13. Trans. Wisconsin Acad. 26:275–279.
- FERNS AND FERN ALLIES: Tryon, R. M., N. C. Fassett, D. W. Dunlop and M. E. Diemer. 1940. The Ferns and Fern Allies of Wisconsin. Dept. Bot., Univ. Wisconsin–Madison. 158 pp., figs. 1–215, maps 1–76.
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- 246 GENTIANACEAE, MENYANTHACEAE: Mason, C. T., Jr. and H. H. Iltis. 1966 ["1965"]. Prel. Rpt. 53. Trans. Wisconsin Acad. 54:295–329.
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- 129 GERANIACEAE: Fassett, N. C. 1933. Prel. Rpt. 21. Trans. Wisconsin Acad. 28:175–176.
- 19 GRAMINEAE: (see Poaceae)
- 225 HALORAGACEAE: Fassett, N. C. 1930. Prel. Rpt. 10. Trans. Wisconsin Acad. 25:201–203.
- 123 HAMAMELIDACEAE: (No treatment)
- 225.1 HIPPURIDACEAE: Fassett, N. C. 1930. Prel. Rpt. 10. Trans. Wisconsin Acad. 25:202–203.
- Ugent, D. 1962. Prel. Rpt. 47. Trans. Wisconsin Acad. 51:128.
- 17 HYDROCHARITACEAE: (No treatment)
- 251 HYDROPHYLLACEAE: Shields, J. W. 1967. Prel. Rpt. 58. Trans. Wisconsin Acad. 55:255–259.
- 187 HYPERICACEAE: McLaughlin, W. T. 1931. Prel. Rpt. 14. Trans. Wisconsin Acad. 26:281–288.
- Utech, F. H. and H. H. Iltis. 1970. Prel. Rpt. 61. Trans. Wisconsin Acad. 58:325–351.
- 44 IRIDACEAE: McIntosh, J. M. 1950. Prel. Rpt. 34. Trans. Wisconsin Acad. 40(1): 230–231, 236–238.

- 60 JUGLANDACEAE: Fassett, N. C. 1932. Prel. Rpt. 17. Trans. Wisconsin Acad. 27:231–234.
- 36 JUNCACEAE: McIntosh, J. M. 1950. Prel. Rpt. 34. Trans. Wisconsin Acad. 40(1): 231–234, 238–242.
- 14 JUNCAGINACEAE: Fassett, N. C. 1929. Prel. Rpt. 1. Trans. Wisconsin Acad. Sci. 24:249–250.
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