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.

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

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
Hypericum sphaerocarpum	*Asclepias purpurascens*	*Agalinis skinneriana*[2]	*Besseya bullii*
Tofieldia glutinosa	*Asclepias sullivantii*	*Asclepias meadii*[2,3]	*Cirsium hillii*
	Cacalia plantaginea	*Asclepias ovalifolia*	*Echinacea pallida*
	Camassia scilloides	*Asclepias sullivantii*	*Gentiana alba*
	Cypripedium candidum[2]	*Astragalus neglectus*	*Lespedeza leptostachya*
	Fimbristylis puberula	*Cacalia plantaginea*	*Liatris punctata* var. *nebraskana*
	Parthenium integrifolium	*Camassia scilloides*	*Parthenium integrifolium*
	Phlox glaberrima ssp. *interior*	*Echinacea pallida*	*Polygala incarnata*
	Platanthera flava var. *herbiola*	*Gentiana alba*	*Prenanthes aspera*
	Platanthera leucophaea[1]	*Lespedeza leptostachya*	*Ruellia humilis*
	Polytaenia nuttallii	*Parthenium integrifolium*	
	Tomanthera auriculata	*Platanthera leucophaea*[1]	
		Viola sagittata var. *ovata*	

Dry prairies	Sand prairies	Oak barrens	Oak savannas
Agalinis gattingeri	*Asclepias lanuginosa*	*Asclepias lanuginosa*	*Agastache nepetoides*
Agalinis skinneriana[2]	*Besseya bullii*	*Liatris punctata* var. *nebraskana*	*Asclepias purpurascens*
Anemone caroliniana	*Cirsium hillii*	*Opuntia fragilis*	*Astragalus crassicarpus*
Anemone multifida var. *hudsoniana*	*Lespedeza leptostachya*[1]		*Besseya bullii*
Asclepias lanuginosa	*Opuntia fragilis*		*Camassia scilloides*
Astragalus crassicarpus	*Orobanche fasciculata*		*Gentiana alba*
Besseya bullii	*Orobanche ludoviciana*		*Polytaenia nuttallii*
Cacalia plantaginea	*Prenanthes aspera*		*Prenanthes crepidinea*
Cirsium hillii			*Ruellia humilis*
Echinacea pallida			*Viola sagittata* var. *ovata*
Lespedeza leptostachya			
Lespedeza virginica			
Lesquerella ludoviciana			
Liatris punctata var. *nebraskana*			
Orobanche fasciculata			
Prenanthes aspera			
Scutellaria parvula var. *parvula*			

Oak woodlands	Bedrock glades
Agastache nepetoides	*Agalinis gattingeri*
Asclepias purpurascens	*Lespedeza virginica*
Camassia scilloides	*Opuntia fragilis*
Thaspium barbinode	

[1]Threatened at federal level
[2]Concern at federal level
[3]Extirpated at state level

Haney and Apfelbaum (1997), Henderson (1995a), Hujik (1995), Pruka (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., *Pediomelum argophyllum)* or may deserve legal status as Endangered (e.g., *Desmodium canescens)* or Threatened (e.g., *Commelina 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 *(Pediomelum 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

Adistribution 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. Atriangle 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-

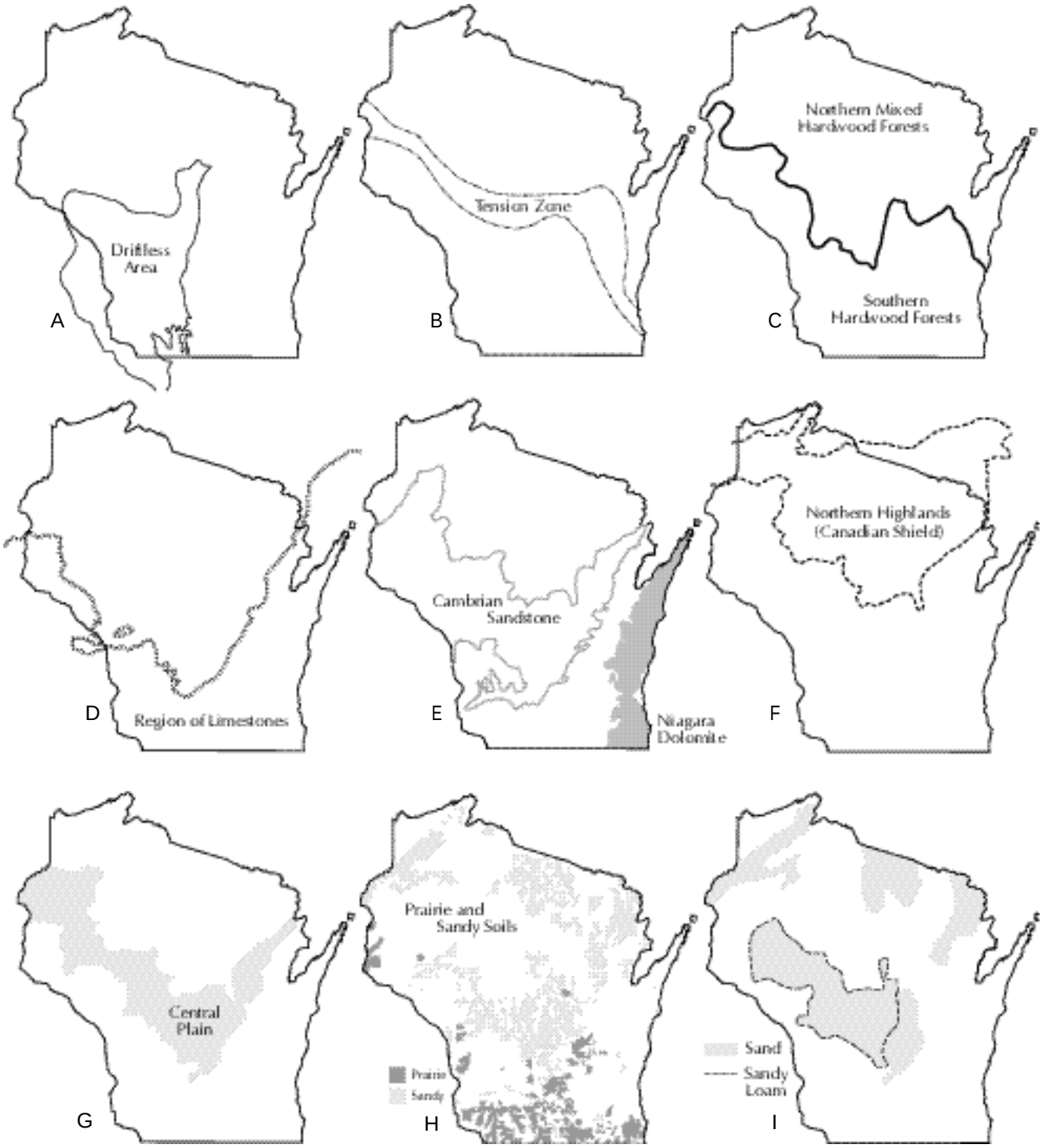


Figure 1. Base maps of Wisconsin showing the boundaries of various features of glacial **(A)** and bedrock geology **(D, E),** selected geographical provinces **(F, G)** and soil types **(H, I)**, and the Tension Zone **(B)** and floristic provinces **(C).** A, redrawn after Little (1971); B and C, from 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 infraspecific 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 postglacial 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

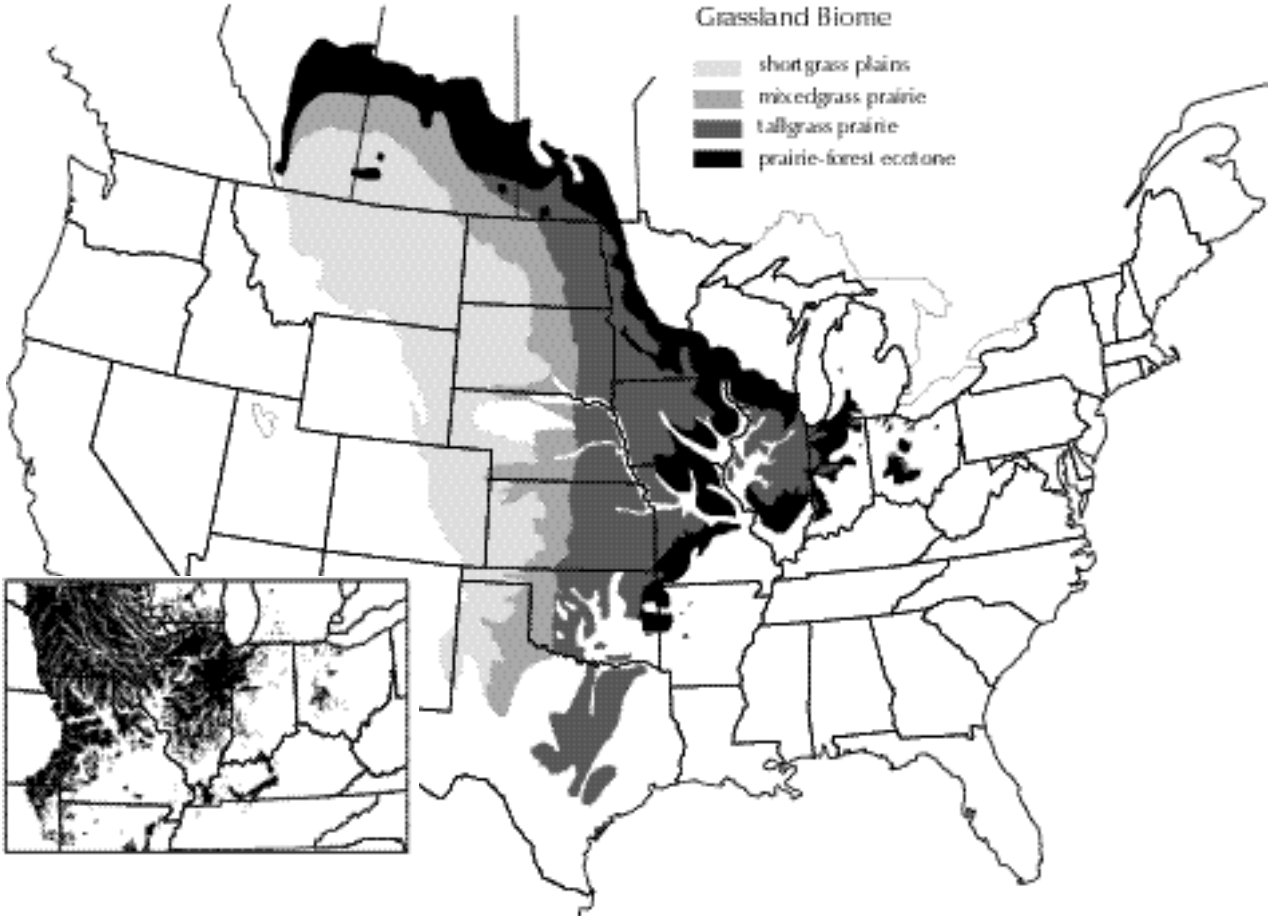


Figure 2. The grassland biome of Midwestern North America, showing the general ranges of the tallgrass and mixedgrass prairies, shortgrass plains, and prairie-forest ecotone. The white oval in west-central Nebraska is the chief sandhill region. Not shown are the Atlantic and Gulf of Mexico coastal plain 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).

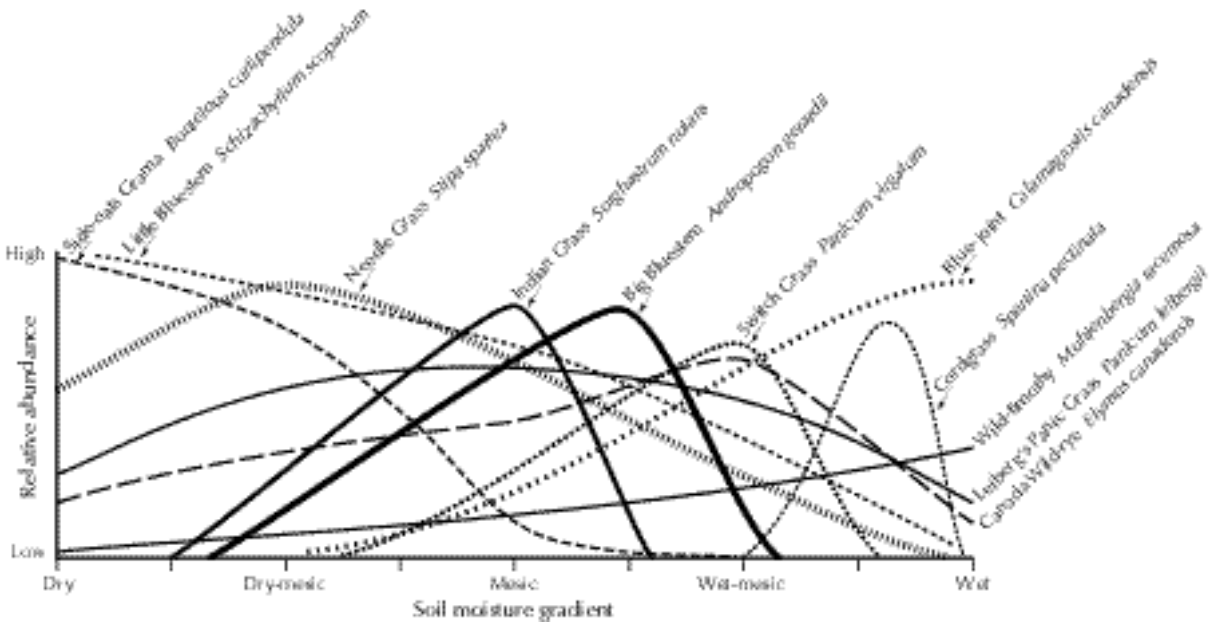
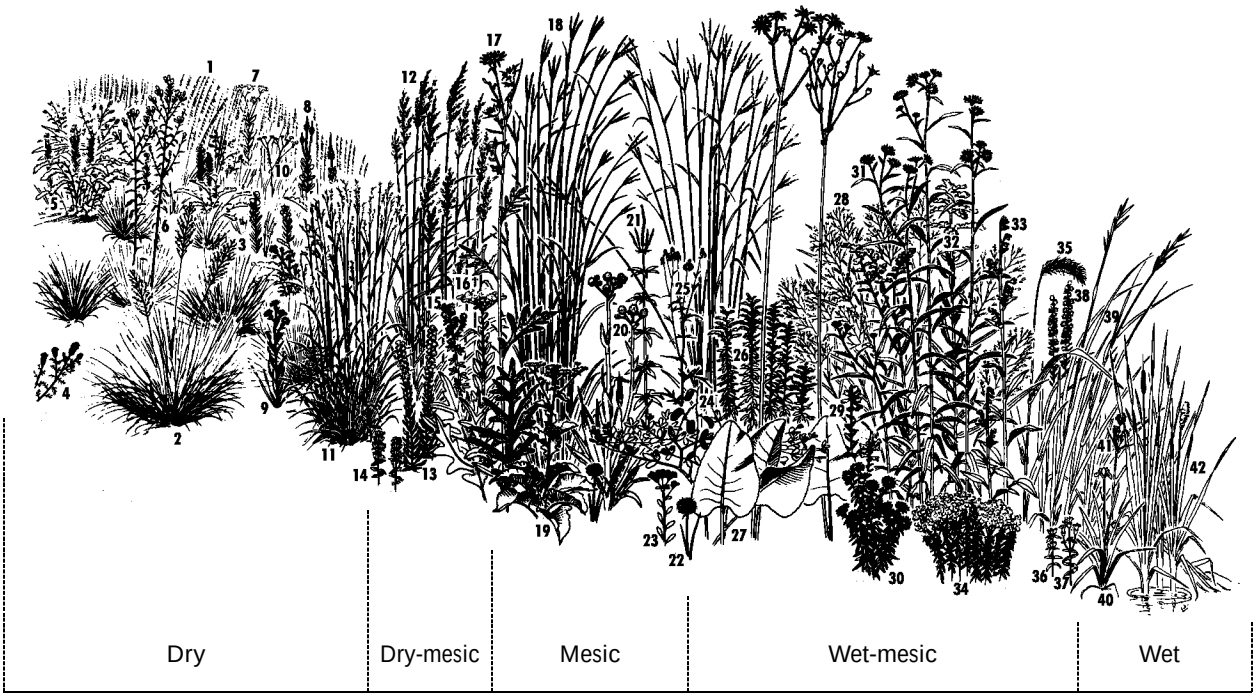


Figure 3. Generalized behavior of 11 important prairie grasses in relation to a soil moisture gradient. Each curve is unique, suggesting that the species respond in an individualistic manner to the conditions of the environment. Adapted from Bazzaz and Parrish (1982) and Curtis (1959).

(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.



1. *Bouteloua curtipendula*	Side-oats Grama Grass	22. *Allium cernuum*	Wild Onion
2. *Sporobolus heterolepis*	Prairie Dropseed	23. *Euphorbia corollata*	Flowering Spurge
3. *Asclepias verticillata*	Whorled Milkweed	24. *Baptisia alba* var. *macrophylla*	White Wild Indigo
4. *Dalea purpurea*	Purple Prairie-clover	25. *Ratibida pinnata*	Yellow Coneflower
5. *Solidago nemoralis*	Gray Goldenrod	26. *Solidago canadensis*	Canada Goldenrod
6. *Brickellia eupatorioides*	False Boneset	27. *Silphium terebinthinaceum*	Prairie-dock
7. *Eupatorium altissimum*	Tall Boneset	28. *Panicum virgatum*	Switch Grass
8. *Verbena stricta*	Hoary Vervain	29. *Physostegia virginiana*	Obedient Plant
9. *Liatris cylindracea*	Cylindric Blazing-star	30. *Aster novae-angliae*	New England Aster
10. *Erigeron strigosus*	Daisy Fleabane	31. *Helianthus grosseserratus*	Saw-tooth Sunflower
11. *Schizachyrium scoparium*	Little Bluestem	32. *Solidago canadensis* var. *scabra*	Tall Goldenrod
12. *Sorghastrum nutans*	Indian Grass	33. *Prenanthes racemosa*	Smooth White-lettuce
13. *Liatris aspera*	Rough Blazing-star	34. *Pycnanthemum virginianum*	Mountain Mint
14. *Gentianella quinquefolia*	Stiff Gentian	35. *Elymus canadensis*	Canada Wild-rye
15. *Lespedeza capitata*	Round-headed Bush-clover	36. *Gentiana andrewsii*	Closed Gentian
16. *Solidago rigida*	Stiff Goldenrod	37. *Gentianopsis crinita*	Fringed Gentian
17. *Silphium laciniatum*	Compass Plant	38. *Liatris pycnostachya*	Prairie Blazing-star
18. *Andropogon gerardii*	Big Bluestem	39. *Spartina pectinata*	Cordgrass
19. *Parthenium integrifolium*	Wild Quinine	40. *Iris virginica* var. *shrevei*	Blueflag Iris
20. *Eryngium yuccifolium*	Rattlesnake-master	41. *Scirpus pendulus*	Reddish Bulrush
21. *Veronicastrum virginicum*	Culver's-root	42. *Typha latifolia*	Common Cat-tail

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),

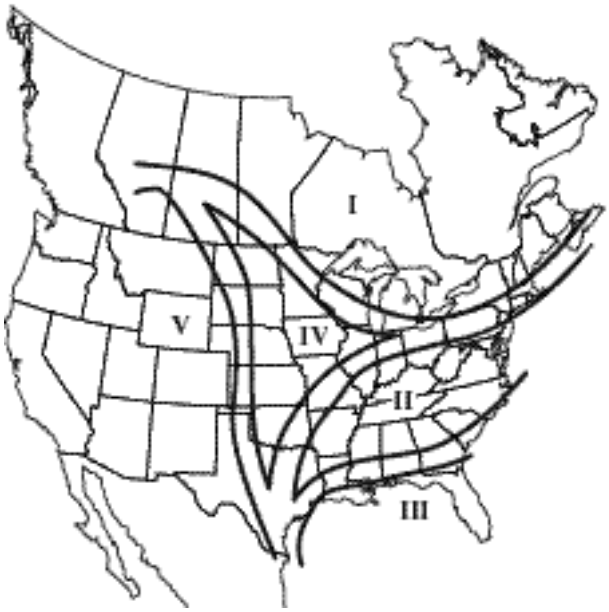


Figure 5. Climatic regions of eastern North America at the present time. Redrawn after Borchert (1950). The maps identify climatic regions dominated by the Arctic and Pacific air masses in winter and summer, respectively **(I),** Pacific air mass **(IV, V),** and Maritime Tropical air mass **(II, III).** The transition zone between regions I and IVcorresponds 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