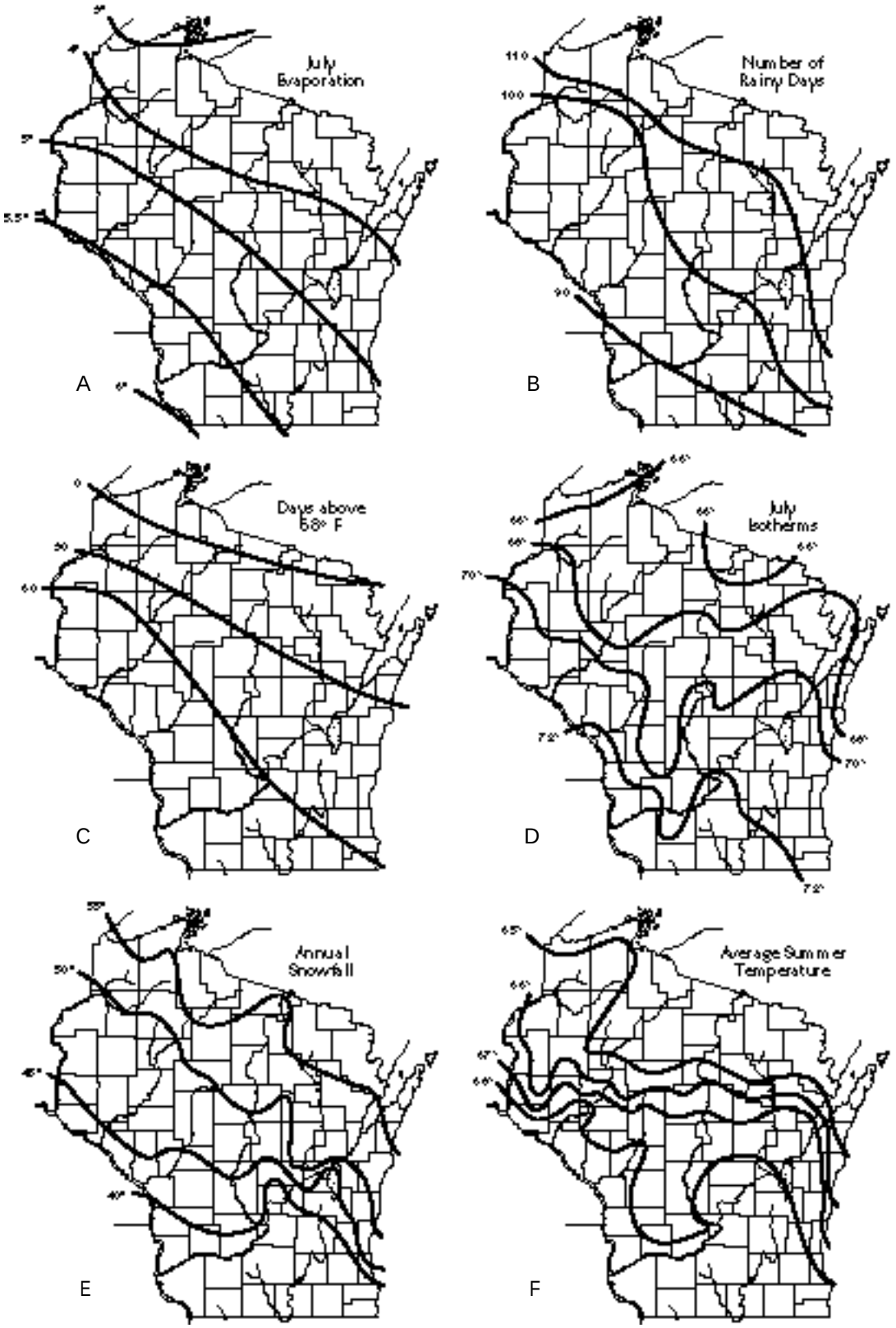

Figure 9. Climate maps, showing factors that correlate with the vegetation of Wisconsin. From Curtis (1950).

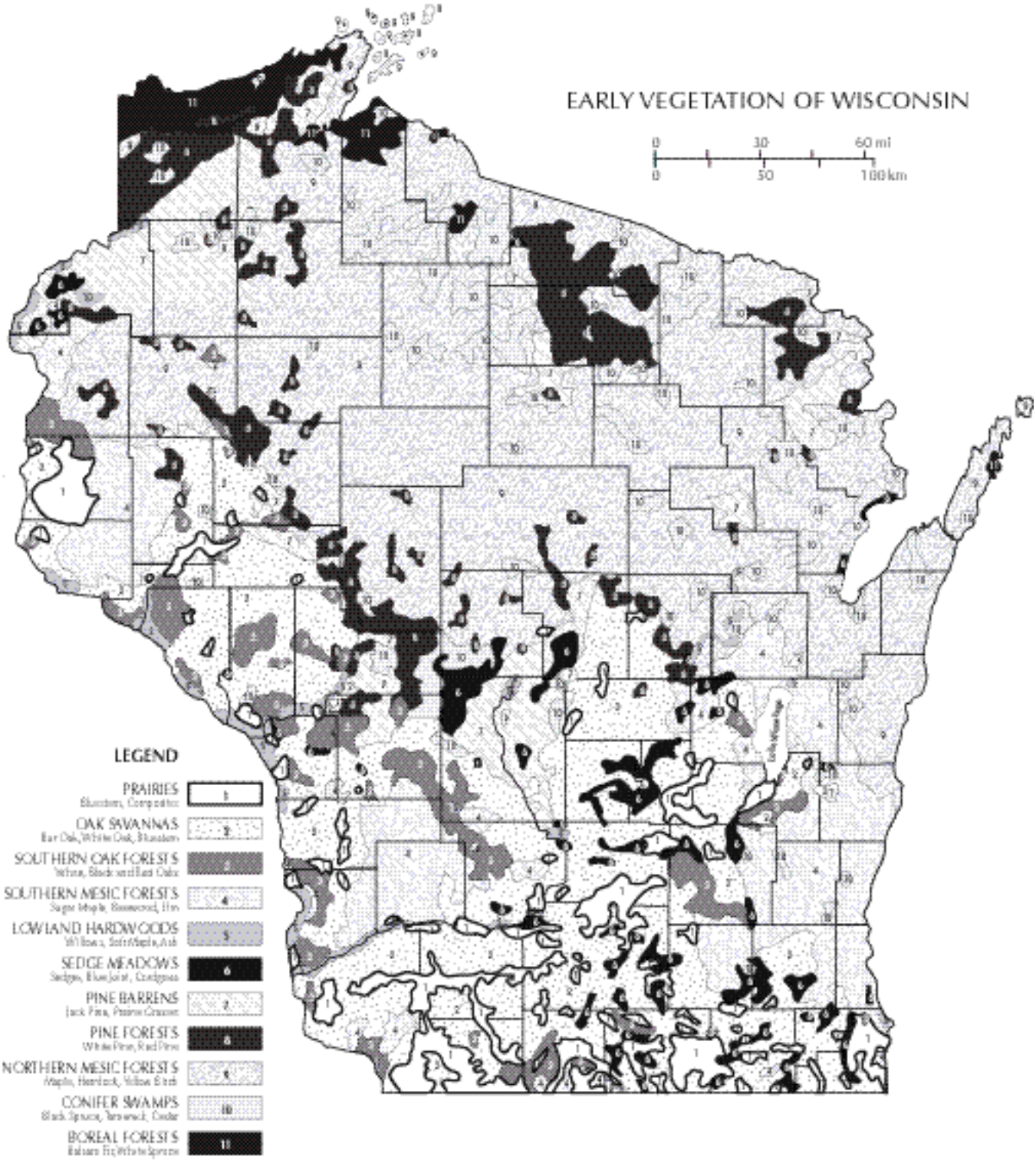

Figure 10. The presettlement distribution of plant communities based on General Land Office Survey records. Adapted from the UW–Extension Geological and Natural History Survey map (1965). Original color version available from Map Sales, GNHS, 3817 Mineral Point Road, Madison, WI, 53705-5100. Map interpretation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

Acomparison 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-Southern 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

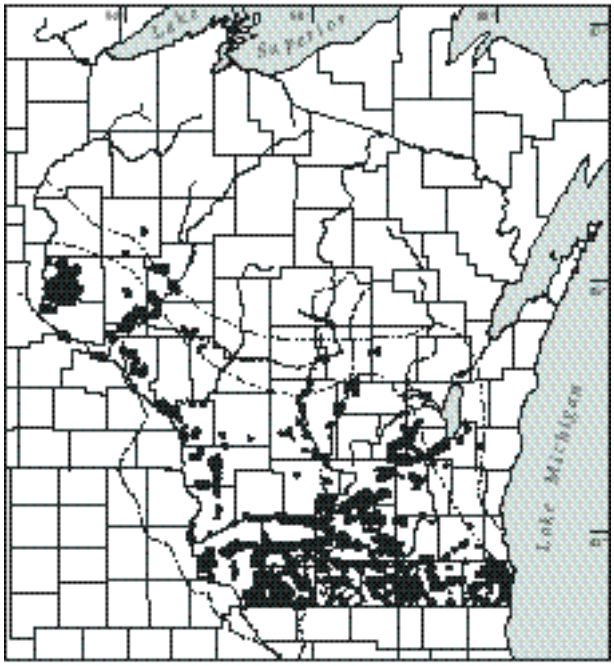

Figure 11. Original tallgrass prairies. Within Wisconsin, prairies are located southwest of the Tension Zone, occupying their greatest area in the southern third of the state. Redrawn after Curtis (1959).

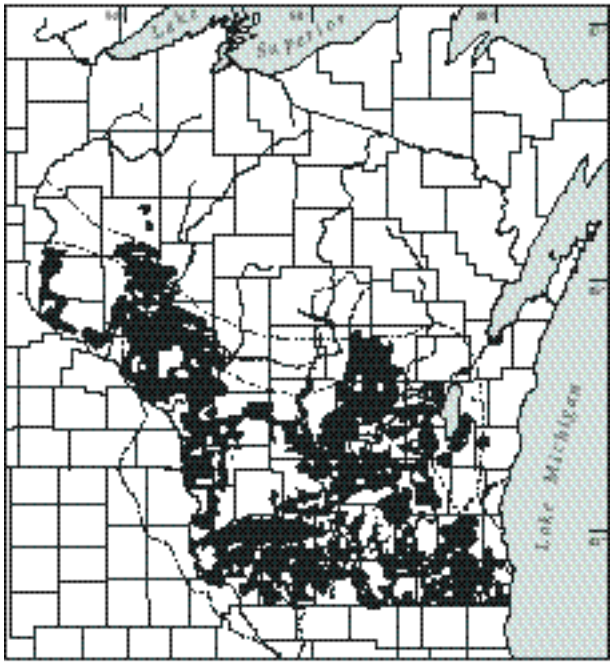

Figure 12. Original oak savannas. Oak openings were present throughout the region southwest of the Tension Zone. Oak barrens are restricted to areas of very sandy soil, especially the sand plains of central Wisconsin and terraces along major rivers. Redrawn after Curtis (1959).

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 communities 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 pussytoes *(Antennaria* spp.), while shadier borders are favorite haunts of Wild Columbine *(Aquilegia canadensis)*, Alumroot *(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

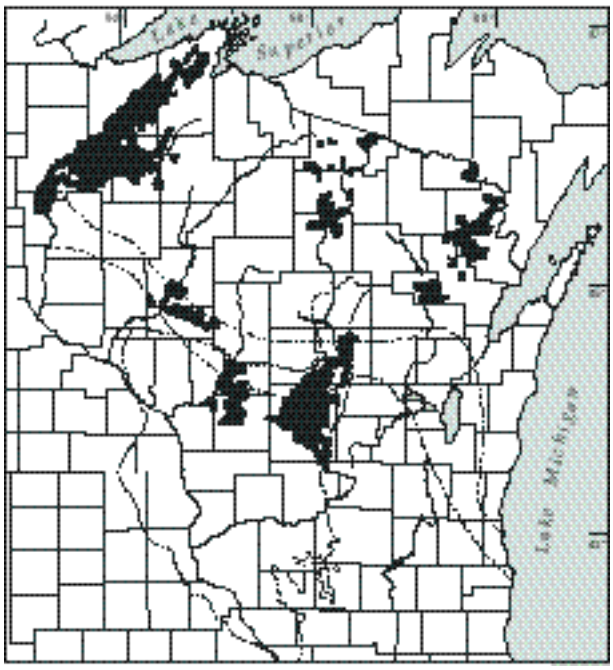

Figure 13. Original pine barrens. North of the Tension Zone, the oak barrens yield to a true savanna (locally known as barrens) in which the major dominant is usually Jack Pine and the understory often prairie-like. Most regions of former barrens are now forested, except for tracts maintained as savannas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

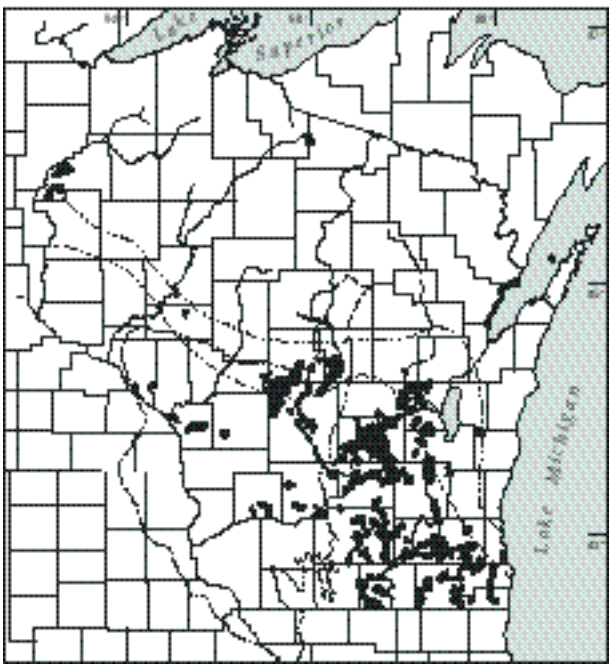

Figure 14. Original sedge meadows. Sedge meadows are present in all parts of Wisconsin, but are concentrated in areas of extinct lake beds and along shores in the south. They are closely related to fens and wet prairies, but are dominated by sedges instead of grasses. Redrawn after Curtis (1959).

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

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 tallgrass 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 virginana).* 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 crassicarpus),* 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 analagous 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. Awhole suite of species that came to Wisconsin from various directions are essen-

tially confined to this community, including Rock Spikemoss (Appalachian; see below), Sand Bracted Sedge *(Carex muhlenbergii*—eastern states), Sand Croton *(Croton glandulosus* 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-

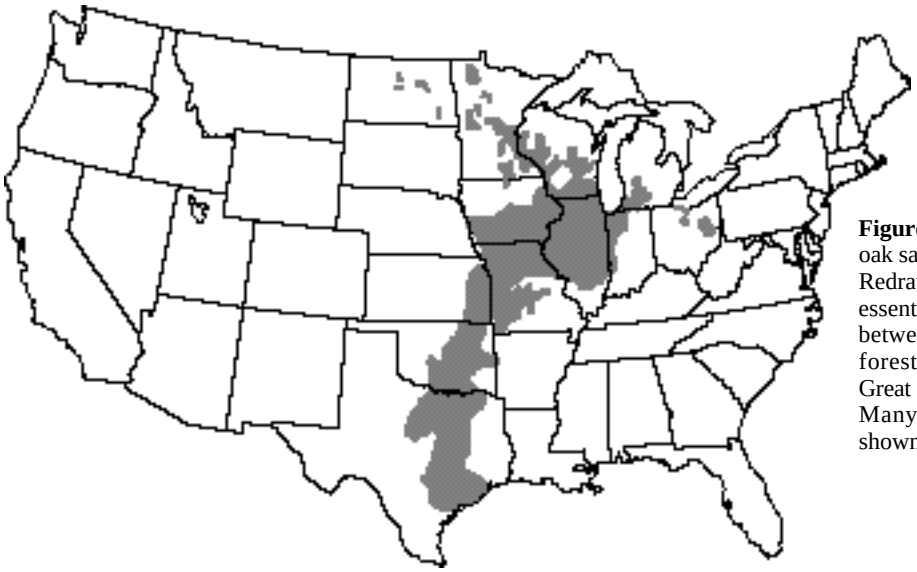

Figure 15. The presettlement distribution of oak savanna and woodlands in the Midwest. Redrawn from Nuzzo (1994). Savannas are essentially transitional communities located between and arbitrarily separated from the forests of the East and the prairies of the Great Plains (compare with Figures 2 & 12). 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 (Dyksterhius 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

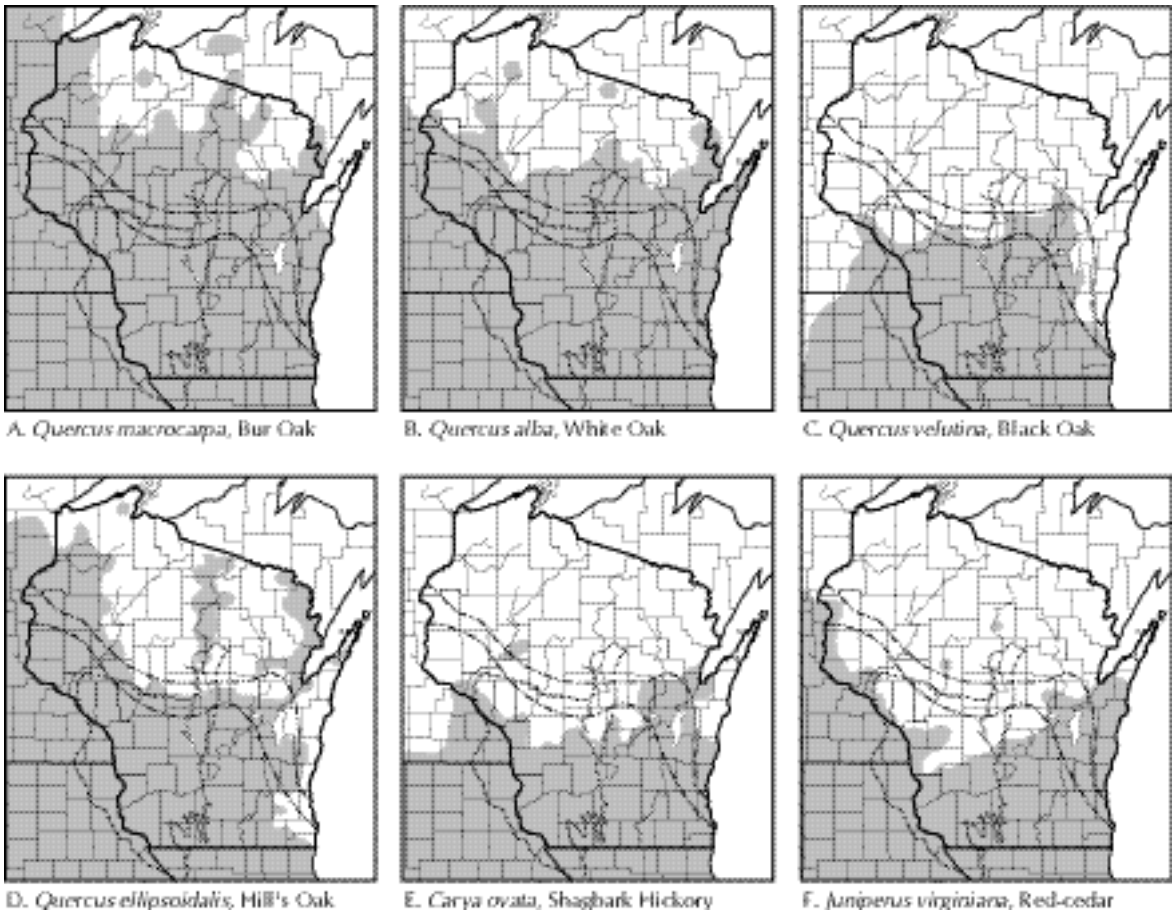

Figure 16. Distribution of major tree species in Wisconsin grassland and savanna communities. Modified after Little (1971).

(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; Pruka 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; Pruka 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 *(Amphicarpaea 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 *(Bromus 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