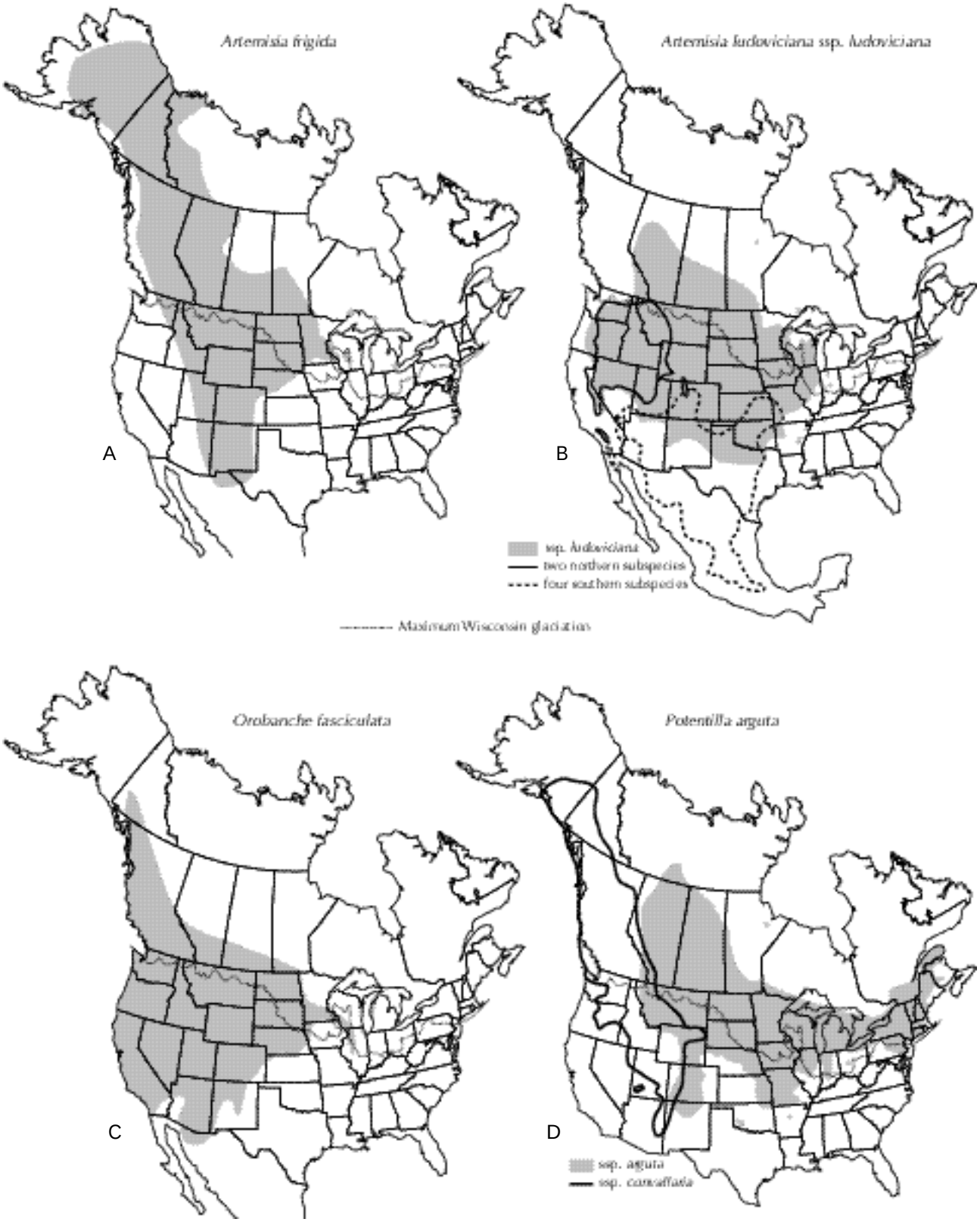
Artemisia frigida
A
Artemisia ludoviciana ssp. ludoviciana
B
ssp. ludoviciana
two northern subspecies
four southern subspecies
Maximum Wisconsin glaciation
Orobanche fasciculata
C
Potentilla arguta
D
ssp. arguta
ssp. convaffata

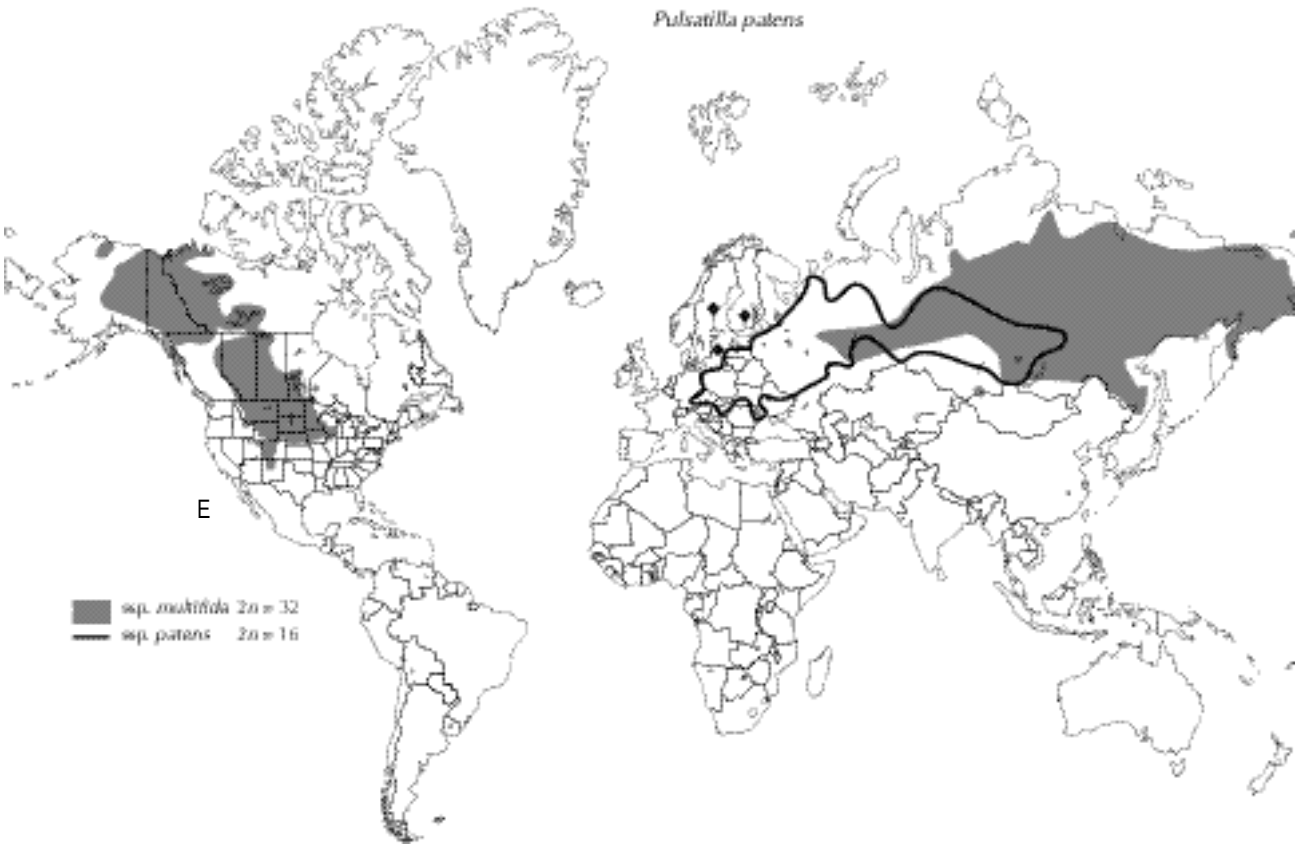

Figure 23. Facing page and above. Distribution of Arcto-Tertiary elements of the Wisconsin grasslands. **A.** *Artemisia frigida,* Prairie Sagewort. Native eastward to the Mississippi River, and occasionally adventive beyond (distribution in part generalized). **B.** *Artemisia ludoviciana* ssp. *ludoviciana,*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

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

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

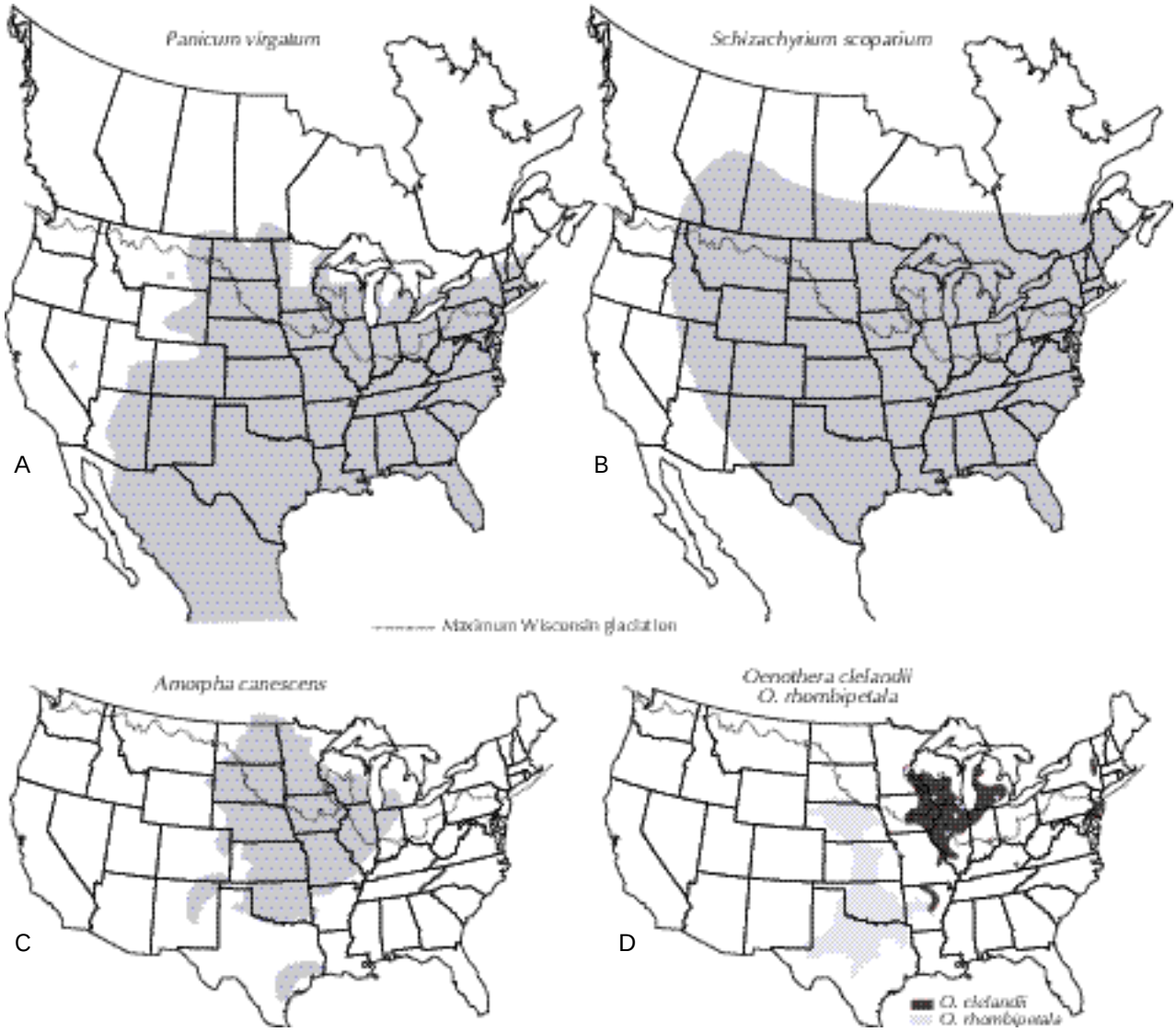

Figure 24. Distribution of Southwestern elements of the Wisconsin grasslands. **A.** *Panicum virgatum,* Switch Grass (generalized). **B.** *Schizachyrium scoparium,* Little Bluestem (generalized). **C.** *Amorpha canescens,* Lead-plant. Redrawn after Wilbur (1975). **D.** *Oenothera clelandii,* Cleland's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

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

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

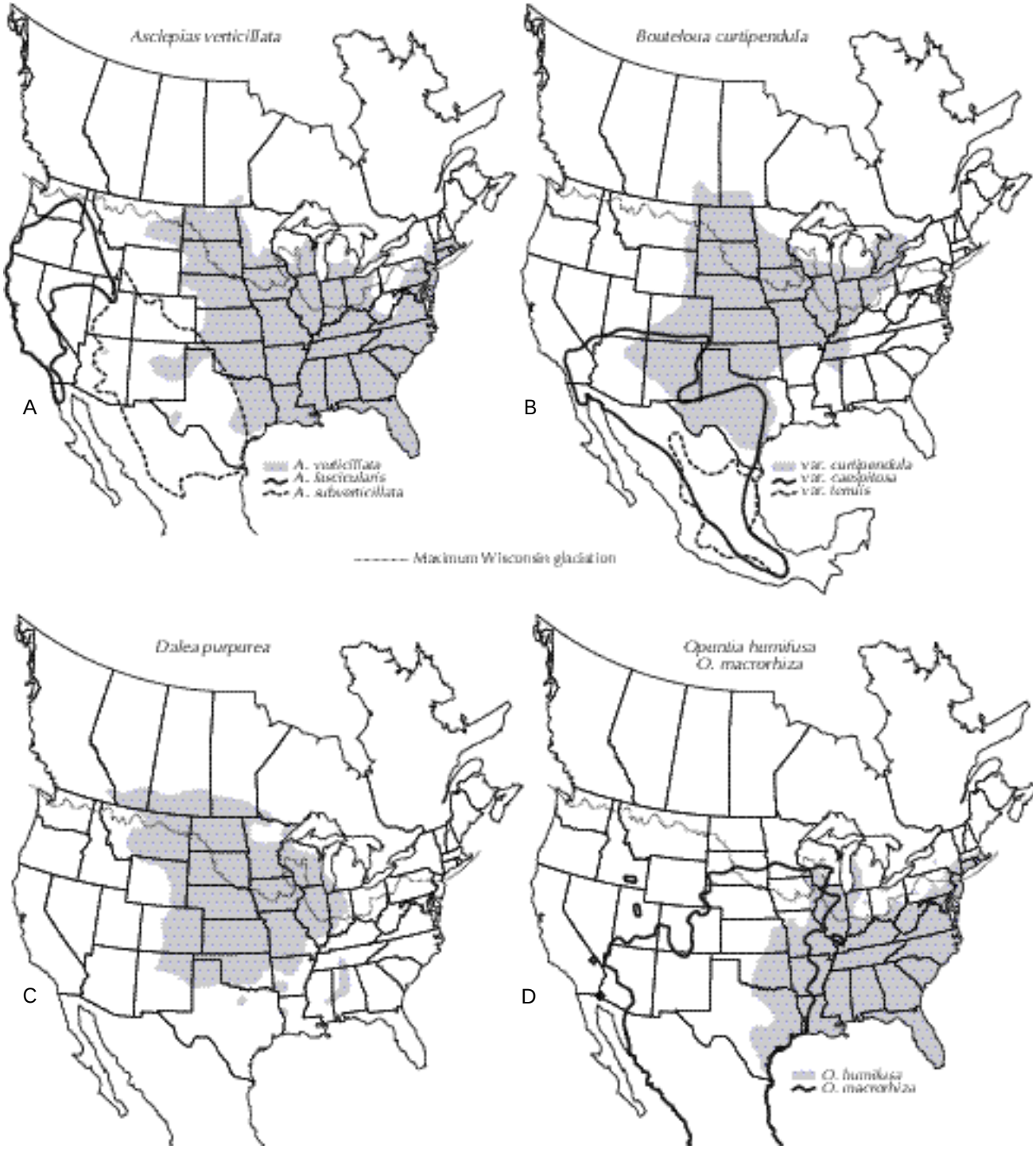

Figure 25. Distribution of Madro-Tertiary Elements of the Wisconsin grasslands. **A.** *Asclepias verticillata,* Whorled Milkweed, and two related species. Modified slightly after Woodson (1954). **B.** The three varieties of *Bouteloua curtipendula,* Side-oats Grama. Redrawn after Gould and Kapadia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

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

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

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

Management of Prairies and Savannas

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

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

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

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

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

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

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

Grazing by cattle has been proposed as a panacea for prairie restoration (Williams 1996, 1997, 1999a, 1999b; but see Harrington et al. 1998). Although it is true that survival of certain otherwise uncommon species is favored by cattle grazing, sometimes dramatically so (e.g., Marbleseed, *Onosmodium bejariense)*, many other native species, especially forbs in mesic and wet-mesic habitats, are selectively eliminated (Dix 1959). Bison have been shown to be much more appropriate as grazers of the western prairies (Collins et al. 1998, Hartnett et al. 1997, Kaiser 1998, Steuter 1997), especially in their preference, unlike that of cattle, for the coarse, tall grasses (Knapp et al. 1999). After all, native herbivores were once the principal biotic factor that helped shape the Great Plains grasslands (Risser 1988, Van Dyne et al. 1980).

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

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

What of the Future?

Postscript by Theodore S. Cochrane

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

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

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

Alas, it is almost all over for Wisconsin's prairies and savannas, communities that are recognized as important reservoirs for biological diversity (Samson & Knopf 1996), yet are very nearly absent or nonfunctionally represented on the living landscape. A number of prairie and savanna plant and animal species are rare or endangered, with their surviving numbers so small and the individual plants of these micropopulations so isolated that, from the standpoint of their genetic future, they may no longer constitute viable populations, what with inbreeding taking its toll. Many existing vegetation remnants are very small and often so degraded that they scarcely comprise recognizable communities. Unless the recognition, protection, preservation, management, and as a last resort *restoration* (returning a site to its original condition) of existing prairie and savanna remnants is stepped up, the permanent extinction of these characteristic Midwestern plant communities from Wisconsin is only a matter of time. Once destroyed, the only recourse will be *reconstruction*—reestablishing through guidelines of the newly emerging ecological science of restoration a broad range of prairie organisms on a former prairie site. Restoration is a slow process requiring one to several decades; however, reconstruction requires several centuries (Schramm 1992)—if re-creation of the prairie ecosystem in all its complexity is indeed possible at all.

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

Humans and Mother Nature, the Unbreakable Bond

Postscipt by Hugh H. Iltis

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

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

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

Cornfields alone will not do, for monocultures, even if periodically interspersed with leguminous crops, can not, in their simplicity, give us all the answers. To truly understand prairies, be it the evolution of their flowers or the genesis of their soils, we need samples of unplowed, unsprayed, naturally functioning ecosystems, and an ecologically educated public who will support their preservation. Questions of human population growth and of our insatiable, unsustainable hunger for the world's limited resources (Daily & Ehrlich 1992)—in short, of *Living Within Limits* (Hardin 1993), all come into play, even if all that we may wish for on a personal level is to preserve from cow and plow a dry hillside with a dozen pasqueflowers.

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

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

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