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Getting the Lay of the Land: Introducing North American Native Grasslands

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Section I. Perceptions
Chapter One
Getting the Lay of the Land: Introducing North American Native Grasslands

Anthony Joern and Kathleen H. Keeler

> The expected catastrophic extinction of species (already under way in many places) will alter the planet's biological diversity so profoundly that, at the known rate of extinction, it will take millions of years to recover. Yet few ecologists study extinction. Indeed, very little ecology deals with any processes that last more than a few years, involve more than a handful of species, and cover an area of more than a few hectares. The temporal, spatial and organizational scales of most ecological studies are such that one can read entire issues of major journals and see no hint of impending catastrophe. The problems that ecologists face are so large; how do we contemplate processes that last longer than our research careers and that involve more species than we can count, over areas far too large for conventional experiments? The problems are also complex; understanding ecological processes at these large scales is far more of an intellectual challenge than is the stupefyingly tedious sequence of the human genome. The problems are also more important. With complete certainty, I predict that human genomes will be around in fifty years to sequence; with somewhat less certainty, I predict that there will be ten billion of them, dying from many causes each of which is orders of magnitude more important than the genetic causes the human genome sequencing will uncover. If we do not understand ecological processes better than at present, these ten billion humans will be destroying our planet more rapidly than we are now.
>
> S. L. Pimm, *The Balance of Nature*

On July 6, 1892, Roscoe Pound and Jared Smith set out from Alliance, Nebraska, with a small pony named Moses, a road cart, and field supplies to initiate the Nebraska Sand Hills Botanical Expedition of 1892 (Hill, in press). During this trip, Pound and Smith systematically covered approximately 450 miles in Cherry County over some 30-odd days while carefully recording the vegetation of the region—a first. By the end of their journey, they had collected 286 plant species. Per Rydberg returned to the Sand Hills the following year to continue the quest begun by Pound and Smith (Rydberg 1885). Along with much larger reconnaissance ventures, including that of Lewis and Clark (Cutright 1989), collecting expeditions such as these throughout the Great Plains region typified early grassland study.

While seemingly parochial in nature, the efforts of Pound, Frederik Clements, and other young colleagues, in association with well-established botanists such as Charles Bessey, redirected the course of plant ecology in the United States (Tobey 1981). With Pound at the helm, the *Botanical Survey of Nebraska* culminated in farreaching accomplishments (Tobey 1981), including Pound and Clements's *Phytogeography of Nebraska* (1900). Such pioneering efforts in plant ecology by this group continued, with many critical contributions including Clements's notions of communities (Clements 1916), the development of experimental plant ecology (Clements and Goldsmith 1924), and the lasting contributions of J. E. Weaver, who recorded longterm events critical to our understanding grassland dynamics (Weaver 1968). Grassland study continues to develop and mature. Modem efforts built on the foundations laid by these botanical pioneers now reveal significant new insights on grassland functions while challenging early propositions. Since these early contributions in grassland ecology, many have continued the quest, now offering new critical, significant insights about how grasslands function at a rapidly increasing rate (Coupland 1979; French 1979; Tobey 1981; Risser et al. 1981; Risser 1985, 1988). As a result, many early paradigms have been overturned (Collins and Glenn, Chapter 7; Seastedt, Chapter 8). Our present views represent an evolving synthesis of past and newly uncovered insights. Like the prairie itself, the study of grasslands is dynamic and interactive, with present views likely requiring further modifications in light of future discoveries.

About 100 years has elapsed since these early exploratory events transpired, almost no time at all considering that the generation length of many dominant prairie grasses easily exceeds this period. This short time span, however, has witnessed the virtual extinction of the eastern tallgrass prairie. This potential for rapid human impact was apparent, even in 1892, to the young Pound and Smith. A sense of urgency permeates this prospectus for their inaugural journey of the Survey of Nebraska: "The changes which are taking place in the flora of the state have already been noted.... The rapid settlement of the western portions of the state is undoubtedly accelerating these changes, and requires that those regions be examined at once" (*Botanical Survey of Nebraska* 1892, p. 5).

Compared with the present integrity of most North American grasslands, the setting in 1892 seems, perhaps nostalgically, pristine. Yet the seriousness of the damage caused by human encroachment into the prairie was a strong motivation for considerable botanical exploration in Nebraska even then, and undoubtedly elsewhere as well. As Hill (in press) clearly indicates, "One hundred years ago, Pound and his colleagues understood that, ecological pioneers that they might be, they were nonetheless engaged in a salvage operation to document the original plant geography of the sand hills before it was irretrievably lost." How serious was the human encroachment of 1892, the noticeable impact that required urgency in the actions of young botanists? Compared with now, the threat seems small-but correctly perceived when time remained for a comprehensive solution.

Today, individuals fortunate to drive through remote grasslands in parts of central and western North America may experience scenes such as those encountered by Pound and Smith. However, even on foot, one cannot travel for even the better part of a day without witnessing extensive, often invasive, human impact. Remnants of the prairie ecosystem are frequently all that one can find, particularly along the eastern edge of the prairie-forest border. In a favorite photographic series of an eastern tallgrass prairie remnant in Illinois, the golden arches of a well-known restaurant chain appear in all angles but one—the ultimate prairie remnant. Clearly, such patches are inadequate repositories for protecting both the functional and the aesthetic attributes of an important North American ecosystem.

That North American native grassland is a seriously threatened and poorly understood ecosystem is a major theme of this book. North American grasslands can no longer be taken for granted. Their worth should not be measured primarily in the number of cattle that can be grazed or in the crop-growing potential of the rich prairie soils that underlie much of the region.

Admittedly, some parts of what was only recently an extensive, unfragmented ecosystem have been so thoroughly altered that the best we can hope for is to preserve remnant traces. Native North American prairie, once tilled and converted to farming operations, is irreversibly altered (even extinguished). Equally important, pervasive fragmentation has broken a vast, continuous expanse into mere habitat islands, destroying critical large-scale links in the process. These small remnants no longer periodically host vast numbers of bison and other wide-ranging grazers such as elk and pronghorn.

Under normal situations, natural disturbance leads to local-scale extinction, then followed by reinvasion by seeds or colonizing individuals of species outside the disturbed area. Now, it is often the case that the "outside" is cropland or some other greatly disturbed system so that local extinction is no longer followed by natural replenishment. Since unplowed prairie units are now routinely interspersed among other types of land use, especially agricultural, many regenerating forces have been seriously curtailed. Examples include (1) small disturbances and patches in close proximity that harbored fugitive species, (2) extensive movement by large grazers in a landscape that fostered ready travel, which now is very difficult, and (3) fire, which often promoted natural regeneration of grassland but now is controlled to the point of extinction in many areas, severely disrupting many past processes.

Conservation biologists are rapidly recognizing that fragmentation is a major threat to most remaining natural ecosystems (Soule 1987), and North American grasslands are no exception. Collins and Glenn (Chapter 7) examine the importance of natural disturbance and spatially explicit processes as well as the consequences of fragmentation to the successful functioning of native grasslands in greater detail.

Native grasslands in this country are arguably a historical legacy as important as Independence Hall for preserving key elements of America's history. Without exposure to sufficiently large expanses of grassland, how can we expect to appropriately interpret the history, art, and literature arising from this region? Biologically, North American grasslands as an ecosystem are as important in their own right to the functioning of the hemisphere as the neotropical forests that are readily recognized as threatened. Our present hope is that remaining grasslands can be preserved, the wornout tracts even restored ("rehabilitated," to borrow Seastedt's apt term) whenever possible. Considered use of our grassland heritage must include the scientific, educational, and aesthetic values of the land, often subordinating single-minded economic objectives in the process. Hence, we wrote this book.

The interested, educated citizen will have a much greater impact on prairie preservation and rehabilitation than will a small band of academic scholars. Here, we introduce what is known of processes responsible for maintaining present North American grasslands as understood today. Our intent is to reinforce emerging interests in grasslands as well as provide additional background for ongoing conservation and preservation efforts of native prairies. As interest and expertise increase among the citizenry, more detailed prairie-repair manuals will be required for hands-on action in managing and restoring native grassland. Hopefully, this need will be soon. Prairieminded citizens are our best hope, in the best spirit of Roscoe Pound and his colleagues. Pound, by the way, became a rare interdisciplinary scholar in botany, sociology, and law, ultimately serving as dean of the Harvard law faculty as a theorist of jurisprudence. He retained a lifelong interest in grasslands, providing an admirable role model for citizens developing interest in native grasslands (Wigdor 1974; Hill 1989, in press).

HOW CAN ONE DELINEATE NORTH AMERICAN GRASSLANDS?

What are grasslands? How variable are North American grasslands? Are there obvious boundaries that delineate different grassland types in response to clearly identifiable environmental features? Given the large extent of grasslands on the North American continent, answers to each of these questions help us identify seeming discontinuities, such as (1) the total amount of plant material that grows each year, (2) the types of plant species that predominate (warm versus cool-season, tall versus short grass) and (3) the actual mixes of species (or groups of species) involved. Often, readily identifiable climatic and soil features associated with perceived breaks in vegetation type aid our efforts to classify prairie. A good understanding of most important patterns defining North American grasslands now exists. General descriptions of North American prairie, largely based on results of a large-scale grassland ecosystem project sponsored by the U.S. International Biological Program (IBP) in the 1970s include Risser et al. (1981), Innis (1978), and French (1979). Some additional recent general references on North American grasslands that we recommend for background include Weaver (1954, 1968), Costello (1969), Risser (1985, 1988), Capinera (1986), Reichman (1987), Detling (1988), Huenneke and Mooney (1989), and McNaughton (1991).

Variously called grassland, prairie, and rangeland, the historically grass-dominated regions in North America account for approximately 50% of the land surface area (400 million hectares) (Sims et al. 1978). While land-use practices in the last century greatly altered the landscape, vegetation in this region was historically composed of grasses and forbs with some woody shrubs; trees were not a major feature! Regional climate, often coupled with fire and sometimes soils, directly controls the limits of grasslands and even the transitions from one grassland type to another. Typically, we find grasslands in areas that receive insufficient rainfall to support fully developed forest, but enough rainfall to often support a closed perennial herbaceous layer with little bare soil visible (Coupland 1979). In other cases, sufficient precipitation exists so that woody plants routinely encroach and then take over a grassland tract unless periodic fires kill the invaders. Conversely, arid shortgrass systems seldom exhibit closed canopies, although they may display maximal productivity for the local conditions. Use of the term “prairie” emphasizes a special feature, grasslands maintained by naturally occurring forces representing years of interplay among countervailing pressures. Compare this with the term “grassland,” which includes any grass-covered tract, from native prairie to recent plantings with non-native species. How important are these differences? At the very least, comparative study can provide important insights into grassland community functioning.

The unique environmental demands on grassland species resulted in the evolution of adaptations to persist in environments subjected to grazing, burning, frequent large temperature extremes, and the climatic and soil conditions associated with short- and long-term drought (Risser 1985). As a consequence, sufficient background for prairie enthusiasts to develop an adequate preservation plan will

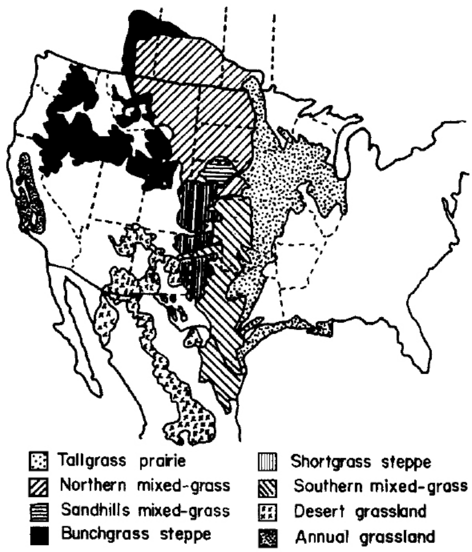

Figure 1.1. Major grassland types in North America. See text for explanation. (Modified from Risser et al. [1981], with permission of Hutchinson Ross)

include an understanding and appreciation for (1) individual adaptations, many of them physiological, that prairie plants and animals exhibit in response to the prairie environment; (2) the physical environment that defines local and regional climates; (3) the factors that permit populations to persist at a locality over time or to colonize new areas and begin new populations; (4) the importance of interactions among species for determining patterns of coexistence and ultimately the factors that constrain the number of species that can coexist in an area; (5) the constraints on energy flow and nutrient cycling, especially regarding soil characteristics and development and the regional or landscape interactions; and (6) biogeographic features, such as the origin and maintenance of species pools available to fill grassland communities with species, and dispersal responses to newly emerging spatial configurations brought about by system fragmentation into small, discrete units. We believe that to successfully preserve or restore native grasslands as a functioning, enduring ecosystem, one must appreciate the links between the dynamic ecological and evolutionary processes, including chance events, and unique natural histories of the component species.

While it is unlikely that absolutely discrete and ideal grassland types exist, an acceptable division of grassland types in North America is depicted in Figure 1.1. A significant east-west climatic gradient exists such that grasslands along the eastern edge of this region receive much more rain (40-60 inches) than those in the intermountain region or those just east of the Rockies (10-15 inches). Important northsouth gradients also affect species composition and seasonal variation in function, largely driven by differences in temperature, season length, and maximum day length. For example, there is a striking latitudinal gradient in the proportion of cool—versus warm—season plants at a site that highlights the importance of such a feature. Biogeographic patterns provide significant insight into key organizational processes in grasslands. Bragg (Chapter 4) describes these patterns and processes in detail.

For our purposes, we distinguish seven grassland types. While local variations of the following grassland categories are important, often representing important examples of shifts in ongoing ecological processes, we are striving for a broad overview at this point. In the Great Plains region, the *tallgrass prairie*, also called the *true prairie*, exists along the eastern, high-rainfall prairie-forest boundary and is dominated by tallgrass species typically 1-2 meters high (especially big bluestem, Indiangrass, and switchgrass). *Shortgrass steppe* (shortgrass prairie) dominates the western boundary of this region, a grassland type characteristic of low rainfall and dominated by shortgrass (less than .25 meter tall), including blue grama and buffalo grass. We recognize two grassland types located between the tallgrass and shortgrass regions: *mixed-grass prairie* and *sandhills prairie*. Mixed-grass prairie contains species from both tallgrass (confined to the moistest places) and shortgrass steppe, but is generally dominated by midgrass species (at about 1 meter height), such as needle-grasses, little bluestem, and wheatgrasses. Sandhills grassland is located primarily in Nebraska and Colorado (edging into adjacent states) and represents large-scale edaphic anomalies based on widespread sand-dune systems composing the soil substrate. While sandhills prairie often has been overlooked as a separate grassland type, we believe that the organizing principles of these grasslands are sufficiently different from the others, largely resulting from the sandy, nutrient-poor, unstable soil. Species characteristic of mixed-grasslands dominate sandhills prairie, but it also includes dominant sand specialists such as prairie sandreed (Weaver 1965).

Several important North American grasslands are not found in the Great Plains region. Desert grasslands are dominated by grama grasses and typically include woody dominants such as creosote bush and mesquite. *Annual grasslands* characteristics of the Central Valley of California consist largely of introduced annual bromegrass and wild oats. Finally, *bunchgrass steppe* dominates the arid intermountain regions of the Northwest, and is characterized by bluebunch wheatgrass and sagebrush.

Water availability, in association with temperature, clearly defines many key features of what we call grassland in its many guises. Precipitation ranges from about 100-200 millimeters to 1000 millimeters of rainfall in North American grasslands. Grassland regions with greater water availability support increased total plant biomass and species mixes vary (Bragg, Chapter 4). The gradient tends to run east—west, so eastern tallgrass prairie produces considerably more plant material per annum than does the shortgrass prairie in the west. Because of species-specific attributes such as maximal potential height, water-use efficiency, ability to tolerate extreme temperatures, and past biogeographic influences, the actual taxa among grassland types vary considerably. In most grasslands, however, the forbs contribute most to species diversity, including often striking floral arrays, while grasses provide most of the biomass.

In the Great Plains region, about 75% of the rainfall falls from April to September; rainfall from October to March is more important in the mountain, northwestern bunchgrass or California annual grasslands (Sims et al. 1978). In semiarid areas of the shortgrass region, precipitation events of less than 10 millimeters accounted for 41 % of the growing-season rainfall and 83% of the rainfall events (Sala and Lauenroth 1982). Water-use experiments performed in the field, for example, documented that blue grama sod responded to 5-millimeter precipitation events following drought conditions, responses that lasted several days. As a baseline, Lauenroth (1979) calculated that 60 millimeters of water is needed annually in a shortgrass prairie to just sustain the plant without growth—the threshold of growth. These figures are minimal estimates of water needed to support growth, levels that typically result in desert if they are sustained. Except for the interplay between such incredible ability to use small amounts of water and the favorable distribution of rainfall throughout the growing season, we would typically observe desert landscapes in the western Great Plains.

HOW RESILIENT ARE NATIVE GRASSLANDS?

Prairie is often distinguished from mere grasslands by a sense that the species associations are well suited for one another and better able to withstand disruption than other combinations of species. Early views provide an extreme comparison to illustrate this point. Grasslands ecologists such as J. E. Weaver, for example, argued that the natural stability and tough perseverance of prairie was central to its understanding. Grassland-dominated communities were so perfectly constructed, he argued, that after thousands of years of evolution, weeds could not penetrate, even when the land was settled and grazed (Tobey 1981). Current beliefs emphasize a more dynamic view, incorporating significantly more flux in the species assemblage in response to routine disturbances (Collins and Glenn, Chapter 7). Disturbance is now seen as part of a native prairie, and so required for appropriate maintenance of features we identify with prairie.

Likelihood of Invasion by Exotic Species

Grassland communities may successfully resist change in species composition in the face of external challenges from invaders. In other cases, often for unknown reasons, these communities may bend or even collapse when confronted with pervasive invasion or disturbance. The likelihood that prairie species will remain unaffected and coherent in response to severe perturbation and return to previous states is a measure of the resilience of the system (Pimm 1991).

Understanding the situations that lead to such invasions is central to present conservation and restoration efforts. How susceptible are native prairies or restored grasslands to disruption by external and/or atypical events? How long will a current grassland community retain its species composition, and what changes can be regarded as normal? If grasslands routinely vary on either short or long time scales, how seriously should we take invasion by non-native, weedy plants into a heavily grazed pasture? Will temperature changes predicted to accompany global climate change seriously impact the remaining native prairies in North America? If natural mechanisms can control invading species (e.g., Hartnett and Keeler, Chapter 5; Joern, Chapter 6; Collins and Glenn, Chapter 7), how well do present range management policies fit into natural processes (Wallace and Dyer, Chapter 9; Bock and Bock, Chapter 10)? A wealth of past evidence indicates that we must take related issues such as these seriously, even though we do not presently understand exactly how each species or ecosystem will respond.

Ongoing, documented invasion of grasslands by exotic plants is ubiquitous throughout North American grasslands (Mack 1986, 1989; Johnson and Mayeux 1992). In general, such invasions are localized and mostly nuisances, seldom altering the character of the ecosystem. This is not always the case, with the exceptions providing worrisome examples.

If you had taken a horseback ride through central California in the mid-nineteenth century, perennial bunchgrasses would have predominated, with flowering heads sometimes brushing against your reins. By the 1880s, "improved farmland" covered up to 75% of the area previously supporting native grassland (Huenneke 1989), and the remaining bunchgrass grassland persisted under siege. Exotic annual grasses from the Mediterranean region, probably introduced in the early part of the century, took over the region such that the character of the whole grassland changed drastically. While the exotic annual grasses were present in California for decades, the actual conversion from perennial bunchgrass prairie to introduced annual grassland seemingly occurred abruptly, over the course of 10 to 15 years in the late nineteenth century (Heady 1977; Jackson 1985). These events occurred approximately 100 years ago. We still do not understand what happened and why, except that the final result was a completely altered grassland (Huenneke and Mooney 1989).

The message is quite clear. In most cases, under low to moderate pressure, grasslands are remarkably resilient. Under concentrated attack, however, the original character of a grassland is lost, perhaps forever. Brown and Heske (1990) describe a revealing experiment at the arid grassland-desert transition zone in eastern Arizona. Experimental disruption of present-day interactions among several species of seedeating rodents resulted in the decline in abundance of native species and the successful takeover by an exotic grass from South Africa. For the California and intermountain grasslands, a variety of poorly understood activities contributed to the shift in grassland from bunchgrass to annual grassland, possibly including

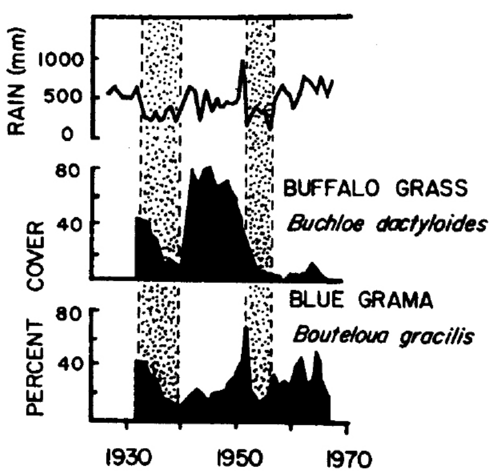

Figure 1.2. Change in biomass of two dominant shortgrass species in relation to precipitation. Percent cover of blue grama and buffalo grass in a shortgrass prairie community near Hays, Kansas, was followed for 40 years. As seen in the rainfall record, two droughts are evident (stippled): 1932-1939 and 1952-1957. The two species were equally abundant in 1932. (Modified from Tomanek and Hulett [1970] and Davis [1986], with permission of the Ecological Society of America)

drought, significant fragmentation of the region, increased grazing pressure from cattle, grasshopper outbreaks, and chance events (Mack 1986; Huenneke and Mooney 1989). In this case, the native grassland ecosystem seemingly bent and then broke under the weight of a rapidly changing environment. Is this situation typical, providing the key to understanding grassland resilience and persistence? For western and central Great Plains grasslands, the question remains unanswered.

Natural Variability in the Composition of Native Grassland

Present evidence indicates that most North American biotas, including grasslands, have experienced a history of flux rather than maintained a stable, strongly conserved community composition (Wells 1970a, 1970b; Tomanek and Hulett 1970; Davis 1986; Graham 1986; Huntley and Webb 1988; Johnson and Mayeux 1992; Collins and Glenn, Chapter 7). Data to assess long-term shifts are sketchy, based on relatively few studies using relatively short-term time sequences or spottily distributed and erratic fossil and pollen remains (Wells 1970a, 1970b; McAndrews 1988; Webb 1988). However, clear evidence of radical shifts in plant and animal distributions emerges.

Various lines of evidence document that North American grasslands exhibited significant past variation at several time scales. Over a short term (ca. 100 years or less), clear shifts in grassland composition have been repeatedly documented, often in association with changed precipitation (Weaver and Albertson 1943, 1944; Albertson et al. 1957; Tomanek and Hulett 1970), but also in response to variable fire (Daubenmire 1968; Collins and Wallace 1990; Bragg, Chapter 4) or grazing regimes (Coppock et al. 1983; Detling 1988; Wallace and Dyer, Chapter 9). As an example, Figure 1.2 illustrates largely out-of-phase responses by two dominant shortgrass species to periods of high versus low rainfall in Kansas. Variable climatic conditions can greatly shift plant species dominance over approximately a 10-year period (Albertson et al. 1957; Albertson and Tomanek 1965), especially when extreme, such as severe droughts, largely a result of different water-use capabilities of different plant species (Kemp and Williams 1980; Sala et al. 1981; Monson et al. 1983). The Great Drought of the 1930s, for example, resulted in significant vegetational changes in North American grasslands (Albertson and Weaver 1942, 1946; Weaver and Albertson 1943). Because of such responses, we obtain an inadequate picture of grassland structure and function without examining the full scope of natural conditions in what might be called ecological time. Ecological time marks the events of an already assembled set of species without accounting for significant evolutionary or biogeographic responses to longer term environmental shifts. Equally important, these responses point out that even small changes to influential driving variables in grasslands can have impact, often reversible. However, as some of the examples indicate, we do not know when small changes become irreversible.

The ecological and floristic history of North American native grasslands has also greatly fluctuated in response to long-term climatic changes, especially those associated with glacial advances and retreats (Bryson et al. 1970; Wells 1970a, 1970b; Huntley and Webb 1988), changes that can be measured over the course of several thousands of years rather than tens or hundreds of years. Reconstructions of ancient vegetation over larger areas can be inferred from the pollen record. Associated with periods of glacial ice advance and retreat, characteristic grassland species separated and then recongealed into species mixes typical of present-day grassland (Figure 1.3) (Gleason 1922; Axelrod 1985; Brown and Gersmehl 1985), but the individual species dispersed in an independent fashion.

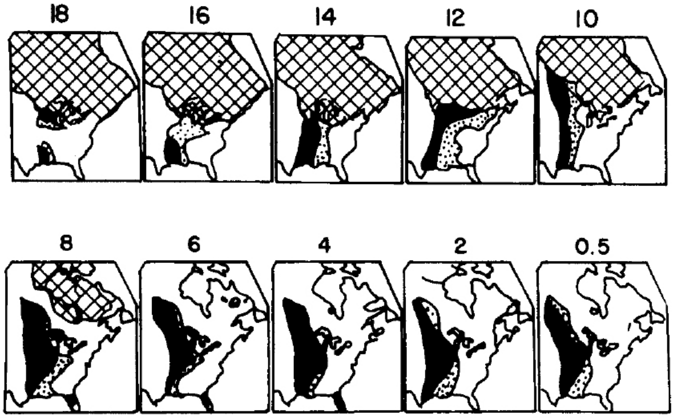

Figure 1.3. Generalized vegetation maps based on pollen analyses from sites throughout the region for prairie forb species to depict changes in the floristic history of the region for the past 18,000 years. Forb species included in the analysis include the sum of *Ambrosia*, *Artemisia*, other Compositae, Chenopodiaceae, and Amaranthaceae pollen. Stippled regions represent areas with 5% forb pollen in samples, and the black areas represent samples with 10% forb pollen. The cross-hatched areas indicate the location of the Laurentide ice sheet. Numbers above each map panel indicate the number of thousands of years before present. (Modified from Webb [1988], with permission of Kluwer Academic)

In addition to dramatic changes in the vegetation of the present grasslands regions, fossil evidence from many sites indicates that most animals responded in a similar manner, including insects (Ross 1970), fish (Cross 1970), birds (Mengel 1970), and mammals (Hibbard 1970; Hoffman and Jones 1970). Several critical features typify these historical features of prairie structure. Distribution (range) limits of plant and animal species moved around, tracking climatic shifts. Range limits expanded and contracted, often over fairly large distances, before reassembling into our present grassland ecosystems. But different species did not move in a coordinated fashion (Huntley and Webb 1988). The community did not remain intact and shift as a single total-species unit. Instead, individual species appear to have dispersed in independent, species-specific ways. Since glacial advances and retreats occurred repeatedly, among other sources of significant climatic variation, it appears unlikely that the same grassland communities existed after each reshuffling.

The presence of species with a restricted, localized distribution often provides important information regarding the isolation of the biota in either time or space. Such plant or animal species are termed endemic to the region in recognition of their local evolutionary and biogeographic history. The presence of many endemics provides evidence for a long, stable biogeographic history. There are few grassland endemic plant (Wells 1970a) or insect species (Ross 1970) in North American plains grasslands; species found in present-day North American grasslands communities and ecosystems can typically be found in other North American biotas. Such data suggest that North American grasslands are a newly assembled group of species, each with antecedents in other geographic regions. It appears that insufficient time and opportunity for speciation events forming species unique to that region existed.

From our perspective, an important message of such results is that North American grasslands, in their present state, are not monolithic species assemblies that have existed for millennia. The evidence does not support a generalization that prairie is an eternal, slowly evolved and necessarily finely tuned entity, an example of Clements's "super-organism" (Clements 1916, 1920). Rather, as entities, many present associations are comparatively young, following periods of significant independent shuffling, Certainly, sufficient time has passed since the last reassembly (probably less than 10,000 years in many cases) to try many natural experiments, time to shake out species recombinations that did not work well in one sense or another. These species assemblies that survived the "shakeouts" are the grassland ecosystems that we see today.

The Question of Planted Prairies

In many areas where prairies were plowed up, people have planted the native species together again. One concept that is particularly appropriate for immediate investigation concerns re-created ecosystems. When does a planted grassland become a prairie? What features are required for it to function so like an unplowed prairie that the differences are negligible? What activities can humans perform to speed up the convergence of planted prairie structure and function to native prairie structure and function?

A traditional line of thinking has been that humans can never restore a plowed ecosystem, and yet we believe that ecological succession will do the job, given 1000 years or so. Is that really the case? Several old planted prairies exist; some sites plowed in the 1930s are very similar to native prairies already; some are still clearly disturbed. Some areas of some prairie states have so thoroughly destroyed their native grasslands that if people want to experience walking in a prairie, one will have to be planted. Thus methods for restoration of the experience of prairies are needed, and then the relation of those prairies to "real" prairies considered. If there is hope of restoring ecosystems, then we can consider expanding native grasslands so they are once again abundant throughout their original range: an urban greenbelt in the central United States might rather be prairie than forest. If planted prairies will not be real prairies for 1000 years, we *must* expand our preservation efforts to protect the virgin remnants that remain.

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