Philip J. Burton, Kenneth R. Robertson,
Louis R. Iverson, Paul G. Risser

4. Use of Resource Partitioning and Disturbance Regimes in the Design and Management of Restored Prairies

ABSTRACT

The natural processes responsible for the origin and maintenance of native grasslands must be understood in order to restore North American prairies effectively. Grasslands historically have predominated where the climate ranged from semiarid to mesic but with periodic droughts, and where fires repeatedly removed dead aboveground biomass and retarded encroachment of woody invaders. As in most North American ecosystems, however, the particular assemblage of species naturally found at a site is frequently of recent origin and is not necessarily a stable combination.

The establishment and persistence of many mature prairie species may depend on specific soil moisture conditions that facilitate their localized competitive superiority. Both successional and climax prairie species may depend on some sort of general or local disturbances to free space for seedling establishment. Frequent disturbance in the form of fire, grazing or mowing is needed to remove standing dead plants and accumulated litter but this can cause varying effects on community composition. Established perennials are difficult to displace. Poor establishment from seed and constant invasion by exotic C_3 grasses, forbs and woody plants are the most common problems in prairie

restoration efforts. Successful restoration methods emphasize the use of local genotypes, transplanting to enhance floristic diversity, and the use of manual weeding and fire to control exotic species.

Niche quantification may provide a means to match species more accurately to prevailing site conditions and to each other, in order to completely utilize the "resource space" so that invasion by exotics becomes less likely. The use of native C_3 grasses may also reduce invasion by such exotic cool season species as *Poa pratensis* and *Bromus inermis*. Native annuals may likewise form a more acceptable cover crop than exotic weeds or cereals. Ecosystem reconstruction provides many opportunities for testing fundamental theories of community ecology, which, in turn, could further enhance future restoration efforts.

INTRODUCTION

This chapter addresses problems associated with the restoration of a high level of species diversity in a comparatively mesic climate. We discuss the grasslands of the Central Plains of North America, with emphasis on the tallgrass prairie. Grasslands are supposedly restricted to semiarid zones (Holdridge 1947), but they achieve their richest development in terms of productivity and diversity of species in areas that receive 750 to 1000 mm of annual precipitation (Oosting 1956). Prairie plants must cope with intense biotic pressure from competition and grazing as well as the abiotic stresses of periodic drought, extreme temperatures and fire.

Natural grasslands once occupied one-quarter of the Earth's land area and 3.5 to 4.0 million km^2 (19.2%) of continental North America (Lemon 1970, Stevenson 1972, Risser et al. 1981, Singh et al. 1983). Generally characterized by level or gently rolling terrain, deep soils, low-to-moderate rainfall, and a moderately long growing season, North American grasslands have been largely converted to agriculture. The extent of destruction has often been proportional to native productivity and diversity: much shortgrass prairie remains in native pasture, while mixed-grass prairie is now predominated by wheat fields, and tallgrass prairie has been almost totally replaced by maize and soybean row crops. Klopatek et al. (1979) estimate that 92% of the original Bouteloua-Buchloe (shortgrass) grasslands, 36% of the Agropyron-Stipa (mixed-grass) grasslands, and only 15% of the Andropogon-Panicum-Sorghastrum (tallgrass) prairies of the United States remain.

The productivity of these prairies and their soils has been responsible for their demise, and hence the impetus for their restoration. Other aspects of their ecology, namely the maintenance of their diversity and their adaptation to aboveground stress (drought, grazing and fire) can provide us with some useful guidelines for the most effective design and management of restored prairies.

The Concept of Restoration--Ecosystem restoration is a powerful concept in land management and in the testing of ecological theory (Aber and Jordan 1986). It is a central policy of many national park services around the world and of conservation organizations such as The Nature Conservancy (Jenkins 1973). The idea of restoring wildlands in addition to preserving them was a direct consequence of the nearly total destruction of tallgrass prairies by the 1930s. Local representatives of this ecosystem had become so scarce (especially northeast of the Missouri River and east of the Mississippi River) that reconstruction of the system de novo was virtually essential if prairie biota and processes were to be studied. The University of Wisconsin pioneered these efforts with the dedicated work of H. C. Greene and J. T. Curtis in establishing a diverse prairie landscape at the University of Wisconsin Arboretum beginning in 1936. Although similar efforts were initiated simultaneously elsewhere (e.g., the Trelease Grassland at the University of Illinois [Kendeigh unpublished]), the Wisconsin work is widely recognized as having laid the foundations of prairie restoration science. Such projects continue to be undertaken by universities as well as by state agencies, county and municipal park districts, and by conservation-minded landscapers and private landowners.

Despite the guidelines of the Surface Mining Reclamation and Control Act of 1977, efforts to restore natural vegetation in the United States are more prevalent in the tallgrass prairie region than in more arid grassland and desert regions, again because intact tallgrass prairie is so rare. Examples of restoration methods in this chapter, therefore, are drawn only from the tallgrass region; however, the principles should be generally applicable.

Objectives of Restoration--The ultimate objective of restoration is to create a stable ecosystem that is compositionally and functionally similar to that which existed prior to human disturbance. This ideal goal can never be completely attained (due to the dynamics of biogeography, local extirpations, difficulties in reestablishing native invertebrates, microflora and large carnivores, and the importance of innumerable chance events during community development), but it remains a reasonable and worthwhile objective. Whether restoration is economically feasible or whether it represents an appropriate use for a designated parcel of land are questions not addressed in this discussion. Nevertheless, the ultimate land use envisioned (e.g., preservation of genetic diversity, education, recreation, soil and water conservation, wildlife habitat) and the role of that parcel of land in the regional landscape (Risser et al. 1984) must be carefully considered. Restoration efforts can be time consuming, expensive, and subject to uncertainties, so the decision to undertake them should be weighed carefully. Prairie reconstruction should not be considered an alternative to the preservation or ecological enhancement of existing prairie remnants, since these latter efforts are more cost-effective and more likely to succeed.

Case studies and practical guidelines for prairie restoration (e.g., proceedings of the biennial Midwest or North American Prairie Conferences, and Reclamation and Management Notes) indicate that success depends as much on personal dedication and perseverance as on the application of scientific principles. The commitment to undertake years of manual seeding, transplanting, and weeding is laudatory but represents tremendous inputs of time and energy. As a consequence, successful prairie restoration projects tend to be few, small, and often private. Forty years of restoration efforts have developed many practical and effective "rules of thumb" but have not necessarily been guided by controlled experimentation and the systematic application of ecological theory. This chapter, therefore, attempts to bridge mainstream ecological research and mainstream restoration practice. Case studies of successful restoration efforts are provided and experimental methods for undertaking ecologically stable restoration are proposed. The theme we wish to emphasize is that a thorough understanding of the processes controlling the composition and maintenance of natural grasslands could result in more effective restoration efforts than can the simple mimicry of the floristics of prairie remnants. The more imaginative restoration efforts which result can, in turn, bring data to bear on many questions of community ecology theory.

WHAT MAKES A PRAIRIE?

Factors responsible for the origin and maintenance of North American grasslands have been debated for over a century. Ecosystems are a function not only of their abiotic environment and the properties of the species present but also of their history. Before attempting to reconstruct a prairie community, it is necessary to understand the factors responsible for the natural distribution, composition, and dynamics of native grasslands.

Phytogeography and Paleohistory--The major grasslands of North America (Fig. 1) are typically found in regions where patterns of summer precipitation and/or soils result in droughty conditions. Grasslands occur throughout a wide range of climatic zones and geological substrates. They exhibit local differences in topography and drainage as well as significant floristic differences. To infer a single explanation for the origin and natural maintenance of the physiognomic category we call "grassland" would be misleading. Principles of prairie restoration, therefore, are likely to be regionally specific.

The great continuous grasslands of the Central Plains stretch 1600 km from east to west and 3000 km from north to south (Fig. 1). They are typically divided into shortgrass, mixed-grass, and tallgrass zones, which follow a gradient of decreasing aridity from west to east in the rain shadow of the Rocky Mountains (Allen 1967, Sprague 1974). The dominant grass genera vary from

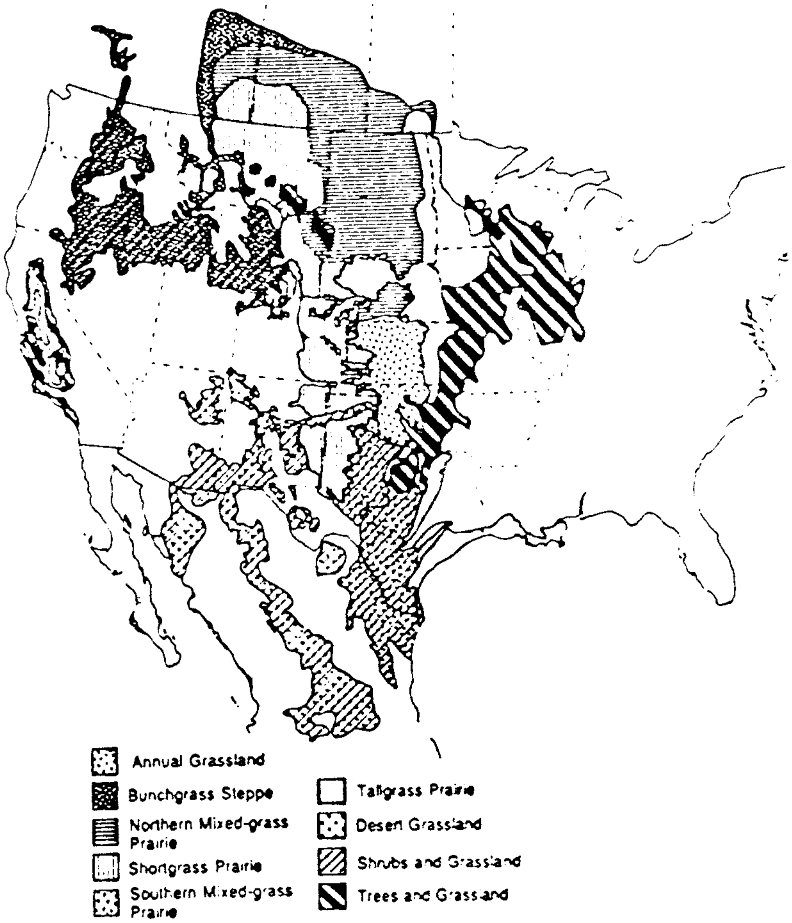

Fig 1. Major grassland types of North America. Modified from Risser et al. 1981.

Bouteloua and *Buchloe* in the west, through *Agropyron* and *Stipa* to *Andropogon*, *Sorghastrum*, and *Sporobolus* in the east. Some climatic, floristic and ecological trends are summarized in Table 1.

Secondary uplift of the Rocky Mountains 30 million years ago created an elevational barrier responsible for a massive rain shadow in their eastward lee (Singh et al. 1983). The development of grasses and grasslands then

Table 1. Salient features of American prairies.

Attribute	Shortgrass	Mixed-grass	Tallgrass
Küchler (1964) Veg. Types	64,65	66,67,68,69,70	74,75,76,77,78,81,82
Presettlement Area,* km2	507,970	510,316	745,680
Remaining Area,* km2	332,910	264,070	198,710
Remaining Area,* %	63.6	51.7	26,6
Annual Precipitation,** cm	25-50	40-75	50-100
Potential Evapotranspiration** (P.E.T.), cm/year	89-195	71-160	62-139
Precipitation to P.E.T. Ratio** (during growing season)	0.3-0.5	0.4-0.7	0.6-1.0
Species Richness,*** spp./approx. 50 m2	13-28	37-44	31-57
Canopy Height, cm	15-60	40-120	80-180
Fire Periodicity,+ years	5-10	2-7	1-3
Dominant Grasses:++	*Aristida purpurea* *Bouteloua gracilis* *Buchloe dactyloides* *Hilaria* spp.	*Agropyron* spp. *Aristida longiseta* *Bouteloua curtipendula* *Koeleria cristata* *Schizachyrium scoparium* *Stipa* spp.	*Andropogon gerardi* *Elymus canadensis* *Panicum virgatum* *S. scoparium* *Sorghastrum nutans* *Spartina pectinata* *Sporobolus heterol* *Stipa spartea*
Dominant Forbs:++	Artemisia frigida Opuntia spp. Phlox hoodii Yucca spp.	*Chrysopsis villosa* *Gutierrezia sarothrae* *Haplopappus spinulosus* *Psoralea* spp. *Ratibida columnifera* *Solidago missouriensis*	*Amorpha canescens* *Echinacea pallida* *Eryngium yuccifol* *Liatris punctata* *Phlox pilosus* *Ratibida pinnata* *Silphium* spp. *Solidago rigida*

Principal Sources:
* Klopatek et al. 1979
** United States Geological Survey 1970
*** Vestal 1949
+ Sauer 1950, Wright and Bailey 1982
++ Weaver 1954, Weaver and Albertson 1956, Gould and Shaw 1983

progressed until their distribution approximated current patterns one to five million years ago (Dix 1964, Stebbins 1981). Pleistocene glaciation subsequently caused massive shifts in the climatic and vegetational zones of the continent (Davis 1976). Repeated advances and retreats of glacial ice and colder climate resulted in countless extirpations and expansions of local populations. Not until the relatively recent hypsithermal (warm and dry) interval of 8300 to 1000 years ago did the grasslands fully reestablish their range in the tallgrass prairie region (Wright 1968).

Although we have scanty evidence of the composition of pre-glaciation grasslands, post-glacial grasslands are clearly composed of a flora with diverse and comparatively recent biogeographic affinities (Stebbins 1981). Many of the common shortgrass genera (*Bouteloua*, *Buchloe*, *Aristida*) are of Mexican and Central American origin and have C_4 photosynthetic pathways (Teeri and Stowe 1976, Risser 1985); on the other hand, common mixed-grass dominants such as *Koeleria*, *Agropyron*, *Elymus*, *Poa*, and *Carex* are of northern origin (Clements 1936, Stebbins 1981). Curtis (1959) likewise interprets the species of dry sites within the tallgrass region as derived from the southwestern deserts, while the lowland species have affinities with Alleghenian meadow and southeastern woodland or marshland species. Wells (1970) notes that some eastern coastal lands from Long Island to Florida are floristically similar to tallgrass prairies in the Midwest, being dominated by the same or related species of *Andropogon*, *Schizachyrium*, *Sorghastrum*, *Panicum*, and *Spartina*, all of southeastern woodland origin. All three components (southwestern, northern, southeastern) of the Great Plains flora appear to have had their origins in woodland habitats and achieve their greatest diversity there. Yet only in the Great Plains do they achieve physiognomic dominance, along with a marked lack of speciation (Wells 1970). Floristic diversity within a given prairie locality can, however, be rather high (e.g., over 100 native species in prairie remnants of less than two ha), an important consideration in prairie restoration and management.

Theories of Grassland Maintenance--There are two primary theories that attempt to explain why prairies persist, differing in the importance they ascribe to climate and to disturbance, namely fire. Holdridge (1947) defines a "steppe climate" to exist where the mean annual temperatures fall between 6° and 12°C, where average total precipitation ranges from 250 to 500 mm/yr, and where the ratio of evaporation to precipitation ranges from 1.0 to 2.0. Clements and Shelford (1939) also emphasize the close relationship of grassland distribution to climatic moisture conditions. Borchert (1950) noted the remarkable fit of the central North

American grasslands to the "wedge" of westerly air in the rain-shadow of the Rocky Mountains. This region narrows from west to east as moist Arctic air masses influence the Northeast and moist tropical air from the Gulf of Mexico affects the Southeast. The same general boundaries also match critical isopleths of winter precipitation, July rainfall and temperature patterns in drought years (Borchert 1950). The relationship between climate and prairie boundaries was demonstrated by the drought of the 1930s. Thousands of hardwood trees bordering the prairie region died while shortgrass and mixed-grass prairies extended their eastern boundaries by hundreds of kilometers (Weaver and Albertson 1956). Prairie restorations, therefore, are best restricted to drought-prone sites which had once been native grassland.

Climate alone, however, cannot explain the persistence of grasslands because dozens of planted tree species grow well in the "grassland climate." Treelessness in presettlement times was clearly maintained by wildfires (Wright and Bailey 1982). Early European travelers remarked on the extent and frequency of prairie fires, often set by Indians in the fall to drive game, or by lightning strikes (see quotations in Sauer 1950, Curtis 1959). Most juvenile trees and shrubs are killed or repressed by fire, but grasses and many forbs (non-graminoid herbs) recover because their perennating organs are protected beneath the soil. In many ways, this hemicryptophytic growth form (Raunkiaer 1934) represents a general adaptation of grasses to aerial disturbance, effective in coping with fire, drought, and grazing, all of which exerted sharp selective pressure throughout evolutionary history (Stebbins 1981, Anderson 1982). The boundary between grasslands and forests (principally trembling aspen [Populus tremuloides], oak [Quercus spp.] or pine [Pinus spp.]) fluctuates as fires alternately destroy trees and wet periods allow tree seedlings to establish (Gleason 1913). The role of fire seems indisputable, as the suppression of wildfires since European settlement, accompanied by no detectable climatic cooling or moistening in the last 100 years, has resulted in the rapid natural forestation of oak savanna understories in Wisconsin (Curtis 1959), the coalescence of trembling aspen groves in Saskatchewan (Looman 1979), and numerous examples of woody encroachment in present-day prairies.

Prairie fires occur in the spring and fall or during droughts, when accumulated grass litter and standing dead material are more abundant than green foliage. Spring or fall fires retard the growth of such cool-season species with C_3 metabolism as Kentucky bluegrass (*Poa pratensis*; Curtis and Partch 1948, Engle and Bultsma 1984), smooth brome (*Bromus inermis*), and many annual weeds. Native warm-season (C_4 metabolism) prairie species are usually dormant at this time and therefore are relatively unharmed. Fire is thus the most powerful tool for excluding (predominantly C_3) exotic and woody invading plant species in remnant and restored prairies, while it promotes the growth of C_4 and native fire-adapted C_3 species (Steuter 1987). Because fire removes shade and ground litter, it stimulates the productivity, vigor, and diversity of native prairie species by allowing the soil and hence the plant roots to warm up more rapidly in the spring. Significant growth is thus initiated when moisture is still plentiful (Rice and Parenti 1978). These positive effects of fire are not universal in grasslands and can instead be negative when the vegetation is already stressed, as is frequently the case in the more drought-prone region west of the 100th meridian (Dix 1960). Surprisingly, the effects of nutrient release from the burning of plant material appear to be negligible (Kucera and Ehrenreich 1962, Risser et al. 1981, Wright and Bailey 1982, Hulbert 1984). Grasslands are "fed from the bottom up," with much nutrient cycling achieved through the death and decomposition of fine roots, thereby producing chernozemic soils rich in organic matter and highly desirable for agriculture.

In summary, neither a droughty climate nor fire alone explains the distribution and maintenance of prairies of the Great Plains: fire in a forest climate retards forest development and may result in scrub; fire in a prairie climate usually helps to maintain and even to enlarge the prairie (Transeau 1935). Although climate can be a critical consideration in choosing appropriate locales and species for prairie restoration, fire is the most powerful tool for the maintenance and enhancement of remnant, degraded and reconstructed grasslands.

Distinctive Properties and Processes--Grassland ecosystems exhibit a number of characteristics that are often direct or indirect consequences of adaptation by grasses and prairie forbs to the overriding influences of period drought and fire. Unlike forest ecosystems, grasslands tend to have more biomass below the soil surface than above it. Rooting depths of 2 to 5 m are not uncommon in prairie plants with heights less than 0.4 to 2.0 m (Weaver 1954), presumably an evolutionary response to frequent moisture deficits in the surface soil horizons. The crowns of most prairie plants are also at or below the soil surface and are thereby protected from drought, fire, grazing, and severe cold. Unlike the stress-adapted plants of deserts and tundra, however, prairie grasses have the potential for high productivity even under rather adverse conditions.

Because of the sharply seasonal climate, this tremendous aboveground standing crop dies back each fall. Decomposition rates are reduced during the subfreezing or cold-wet winters and droughty summers of the tallgrass region, so about 20 months are required for 50% of the annual litter production to disappear (Kucera et al. 1967). Because aboveground productivity is typically more than 20% greater than the rate of decomposition, litter accumulates (Golley and Golley 1972). Future growth, therefore, will be depressed unless the shading and mechanical barriers associated with this "excess" biomass are removed by grazing or by fire. While grazing and fire appear to be equivalent in their removal of standing dead and litter, the selectivity of grazers and the greater soil disturbance accompanying their activity can result in quite different consequences to prairie community composition (Collins 1987).

Grasslands are also unusual among terrestrial ecosystems in the relative magnitude of grazing and detrital energy pathways. Insects and rodents often consume more foliage than do large ruminant grazers, and the amount of foliage that falls to the ground and is subsequently decomposed by bacteria and fungi can be even greater (McNaughton et al. 1982). Like fire, moderate grazing stimulates the diversity and productivity of grasslands through mechanisms that are not yet completely understood. Trampling by hoofed animals accelerates the breakdown of litter and exposes mineral soil for colonization by ruderal species, today often exotic weeds. Redistribution and concentration of nutrients, particularly nitrogen, in the form of urine and feces also has a stimulatory and heterogenizing effect on vegetation (McNaughton et al. 1982, Yonker and Schimel 1986). Despite the importance of microbial components of the ecosystem, we know little about such basic aspects of microbial biology as substrate specificity and responses of metabolic activity and population growth to changes in environmental conditions. These additional trophic levels have traditionally remained unaddressed in prairie restoration efforts.

GRASSLAND COMMUNITY ORGANIZATION

All autotrophic terrestrial plants use the same basic resources: sunlight, carbon dioxide, soil water, and mineral nutrients suspended in soil water. Since they compete for much the same resources, how are hundreds of plant species able to coexist in the prairie ecosystem, how is diversity maintained, and how can we promote diversity and persistence in reconstructed ecosystems?

<u>Competition and Niche Differentiation</u>--Community diversity and organization can be explained as the products of equilibrial or nonequilibrial processes (Connell 1978). Theories of equilibrium assume that plants sort themselves out according to their inherent attributes or niches and that each species survives and prospers at sites where it is adapted to the local abiotic environment and where it is competitively superior to other species in the acquisition of one or more resources. This sorting process may occur through coevolutionary adaptation (the differential survival and reproduction of interspecifically compatible genotypes; Turkington and Aarssen 1984) or simply by differential mortality among species at each microsite. Because plants must rely on the same basic resources, they partition them by having different optima of resource acquisition in space, time, or abundance. Some grass species, for example, avoid competition during the dry summer by extracting water from different depths; other species (cool-season grasses) grow mostly in the spring and fall (Bazzaz and Parrish 1982). Mycorrhizal fungi, symbiotic nitrogen-fixing bacteria, insect pollinators, and insect or vertebrate seed dispersers are essential resources for some plant groups but not for others,

thereby representing further potential for interspecific divergence in resource needs.

Bazzaz and Parrish (1982) propose that coexistence in grasslands occurs (1) by niche separation on the beta-scale, i.e., among habitats within a landscape or region; (2) by alpha-niche differentiation involving coevolution or pre-adaptation to reduce competition for resources among plants sharing the same location or "neighborhood"; and (3) by regeneration characteristics that enable species to become established on disturbed sites. The niche of a species can be envisioned as a multidimensional hypervolume composed of axes that represent all factors important to survival and reproduction (Hutchinson 1957). Species tend to differ in their optimal and tolerable responses to these factors and hence have different niches. The degree of niche overlap between two or more species defines the degree to which they are competing for the same resources or are likely to be interacting in the same place and time. Competition for limited resources, however, is not the only negative interaction between plants. The unknown importance of allelopathic influences in community organization should not be overlooked (Rice 1983).

Beta-niche differentiation in grasslands is governed principally by available soil moisture. The increasing rainfall and decreasing evapotranspiration encountered from the Rocky Mountains eastward to the Mississippi River can be thought of as one large but complex resource gradient. Shortgrass, mixed-grass, and tallgrass communities have developed in response to differences in moisture availability, although some elements of the flora can be found across the gradient. The same effect can be found in a topographic gradient (a catena covering hilltop, slope, and draw) on a more localized scale within the tallgrass region; again distinctive "dry," "mesic," or "wet" communities result (Weaver and Albertson 1956). Many practical guides to prairie restoration (e.g., Schramm 1978, Rock 1981, McClain 1986) use three to five basic moisture-level categories (e.g., wet, wet-mesic, mesic, dry-mesic, and dry) as the primary criteria for matching plant species with site conditions.

Other inter-habitat gradients exist as well, notably temperature and soil factors. Despite some remarkable floristic similarities over as much as 1000 km, north-south differences related to temperature tolerances are clearly found (Gould and Shaw 1983). Differences in soil texture, fertility, and salinity also promote distinctive vegetation within grasslands (Looman 1980). Many of these factors, however, may also be important because of their impact on plant moisture relations: temperature affects stomatal behavior and hence water loss; soil texture determines the amount of water retainable in the soil column; and salinity lowers the water potential of soils (Redmann and Reekie 1982, Risser 1985).

Competition within communities is also reduced by means of niche differentiation in time. Northern, predominantly C_3, grasses may grow and reproduce during the cool, wet spring and fall. Southern, predominantly C_4, grasses are more tolerant of high temperatures and low moisture, and hence grow mostly in midsummer (Teeri and Stowe 1976). Species requiring high nutrient levels may accomplish most of their growth at times of the year when flushes of nitrate are released by soil microorganisms (Russell 1973), but the generality of this phenomenon remains to be demonstrated.

Staggered timing of various growth and reproduction processes is a common method of alpha-niche differentiation. In addition to the differences in growth phenology mentioned above, the range of flowering times varies widely. Species such as Anemone patens and Erythronium mesochoreum grow and reproduce before most grasses have even turned green. Competition for generalist pollinators within a community is reduced when the flowering times are staggered through the season or when flowers open and close at different times of the day or in response to weather-mediated cues (Parrish and Bazzaz 1979). Good reproductive success in a particular plant species may depend on including a number of plant species with flowering times that complement each other, in order to attract and maintain a sufficient population of appropriate pollinators (Parrish and Bazzaz 1979). Selecting plants to ensure a range of flowering times (typically 25% spring, 50% summer, 25% fall) and colors is common in prairie restorations planned for residential landscaping (Diekelmann and Schuster 1982). In this case, species selections made for aesthetic reasons also follow ecological principles of avoiding competition for pollinators.

Other forms of alpha-niche differentiation involve the physical stratification of resource-acquisition organs. Although forests may have tens of meters of aboveground structure within which to "carve out" specialized niches based on shade tolerance and stature, grasslands typically have less than one meter of foliage depth. Grasslands experience wide variation in light penetration and fairly high light intensity at 10 or 20 cm above ground level for much of the year (Old 1969). Canopy stratification nevertheless exists and the range of maximum plant heights in the prairie flora is wide. Many species occupy understory positions and can be expected to have intermediate levels of shade tolerance.

Diversity in growth form is also found belowground. Extensive excavations made by Sperry (1935), Weaver (1954), and others demonstrate that species vary greatly in rooting depth, density, and branching and in the overall distribution of primary rootlets in the profile. The dense fibrous sod of most grasses rarely extends to depths much greater than their maximum canopy height, but many prairie forbs have single taproots that may extend four or five m below the surface (Table 6.5 in Risser et al. 1981). Presumably, plants that have active roots at different locations in the soil profile will not compete so intensely with each other for soil resources. Rootlet density, root turnover rates, and root activity measurements suggest that deep roots function principally in securing water during times of drought.

Differences in the timing of root growth can also be important in avoiding competition (Harris 1967, 1977, Parrish and Bazzaz 1976). It remains to be tested whether a community purposely constructed of species with minimal root overlap is more productive, or more stable, than a random assemblage or a naturally occurring mixture of species.

Disturbance and Random Factors--In contrast to the importance ascribed to competition and niche differentiation in equilibrial theories, nonequilibrial theories place more importance on the randomness of interactions among species (Hubbell 1979) and on disturbance at many different scales (Pickett and White 1985). According to this theory, the persistence of a species in a community depends on its ability either to resist displacement by disturbance (Risser unpublished) or to take advantage of space vacated by disturbance. Once established, plants are considered very difficult to displace, and "squatter's rights" of site occupancy often prevail over competitive ability. Site occupancy and competitive ability are both probably operative to some extent, and both attributes can be useful to prairie restoration. Many plant seedlings tend to "sort themselves out" so that different species attain dominance at sites with different substrate conditions. Nevertheless, established perennial species (whether native or exotic) are also very difficult to displace.

Nonequilibrial processes may operate at several levels to maintain community diversity. Some infrequent prairie species persist by high rates of dispersal in space or time (via a seed bank) to disturbances as small as the mounds created by burrowing mammals and ants or even the mineral soil exposed by hoofprints or bird scratchings. An entire guild of ruderal plant species depends on local disturbance in this manner (Platt 1975, Platt and Weiss 1977, Havercamp and Whitney 1983). These species are typically prolific and disperse widely or have dormancy mechanisms that allow them to take advantage of periodic openings in the canopy. Unfortunately, most native prairie ruderals have been replaced by Eurasian taxa that are particularly widespread as agricultural and roadside weeds.

The dominant prairie species have an impressive set of adaptations to moderate levels of disturbance in the form of drought, fire, and grazing. These adaptations (Table 2) generally allow prairie plants to respond favorably to water shortages, to temperature extremes, and to the removal of shoot material, often through the same "hide-below-ground" mechanism. These adaptations can be used to advantage by those seeking to include the most appropriate native species and to exclude non-native components from artificial prairie communities. Even when the dominant plants are very persistent and resilient, weed species showing rapid growth from seeds will prevail if fresh mineral soil is exposed. Site cultivation prior to planting prairie species is risky unless full weed control can be achieved through repeated shallow disking or by chemical means. Natural disturbances caused by moderate levels of animal activity, however, serve to maintain floristic diversity. Controlling the mode and scale of disturbance, therefore,

Table 2. Physiological-morphological adaptive strategies of grassland plants. From Risser 1985.

Drought
Mechanisms, such as closing of stomata, leaf curling, pubescence, and paraheliotropism, reduce water loss.
More belowground labile carbohydrates are stored under adequate moisture, thus reducing vulnerability of energy storage compounds
Dark respiration decreases under drought stress conditions, thereby preserving substrate.
Gas exchange processes are maintained under water potentials of -2.0 to -4.0 MPa.
Water use efficiency is increased with C_4 pathway, generally favored in drier climates.
Earlier seasonal growth, when moisture is adequate, is characterized by major investment in structural carbohydrates.
Dormancy avoids adverse season
Germination is delayed over more than one year.
Seed has ability to germinate under relatively dry soil conditions.
Primary root grows rapidly and adventitious roots develop rapidly.
Root strength withstands shrink-swell characteristics of clay soils.
Temperature
Photosynthetic optima are related to carbon fixation pathway and coincident with prevailing temperature regime.
Plant acclimatizes to photosynthetic temperature optimum.
Root respiration temperature optima are correlated with optimum temperatures for photosynthesis
Nutrients
Rapid nutrient uptake occurs during season when nutrients are available and soil moisture is adequate.
Plant internally stores and recycles nutrients.
Nutrient uptake and consequent increase in forage quality occurs during season when plant is most tolerant to grazing.
Legumes harbor nitrogen-fixation mechanism, and while associated vegetation acquires some nitrogen from legumes, these other herbaceous plants are more efficient than legumes at scavenging soil nitrogen.
Ammonia lost from the soil surface is absorbed by the plant canopy.
Mineral loss of nutrients occurs via leaching from grass leaves.

Grazing
Plants offer various antiherbivore devices: toxic compounds, low palatability, course seed stalks, and short growth cycle.
Intercalary meristems permit continuous regrowth, and buds may be near soil surface and thereby protected from grazing.
Increase in total herbage production and rate of photosynthesis occur with light to moderate grazing, and reduction of inefficient photosynthetic tissue coincides with grazing pressure.
Plant increases allocation of assimilates to young leaves and regrowing tillers, a process that increases photosynthetic capacity, but may account for reduced root growth
Reduced water supply may increase energy translocation to roots and crowns, but grazing increases energy translocation to young leaves.
Burning
Meristematic tissue is protected from burning.
Plants have rapid regrowth potential, especially in response to elevated soil surface temperatures.
Seed production increases following burning.

is important in maintaining the diversity and integrity of the prairie community and in managing prairie remnants and restorations.

Community Dynamics and Succession--The factors of disturbance, microhabitat heterogeneity, climatic fluctuation, and the regenerative attributes of plant species may be so dynamic and pervasive that compositional equilibrium with the physical environment rarely arises (Pickett and White 1985). An apparently uniform landscape of waving grasses randomly punctuated with the color of wildflowers may be either a highly organized and locally adapted association (as implied by the equilibrial theories) or a dynamic, haphazard jumble of establishing, growing, reproducing, and dying plants. The persistence strategies listed in Table 2 may result in a shifting exchange of propagules and species among patches as all (even climax) species capitalize on their ability to occupy ground. These different modes of community organization probably all operate simultaneously as well, with different equilibrial and nonequilibrial processes predominating under different circumstances. Little research has been done on the relative importance of competition and disturbance in grassland communities, though see Platt (1975), Platt and Weiss (1977) and Collins (1987). The general consensus is that undisturbed prairies are "closed communities" because of the usually dense sod and canopy structure. Although some native prairie species are known to be aggressive increasers when introduced to unvegetated sites, this expansion typically stops after the canopy closes, when sod forms, and when plants attain their mature stature. An established perennial can rarely be replaced without disturbance, a fortunate circumstance that allows us to plan a community and expect it to maintain itself after it is established.

Succession nevertheless occurs in grasslands, and even "mature" prairie is not a static entity. Ecologists and restorationists do not fully understand the successional trends, cycles, and preferences of many prairie species. Although prairies do not exhibit the pronounced changes in growth form and stature typical of forest succession, disturbances usually induce colonization by a suite of species that is eventually replaced over many years as the "climax" community recovers. This concept of community development through domination by successive suites of species is a central paradigm in ecology (McIntosh 1980). In recovering from intensive disturbances such as cultivation or surface mining, most ecosystems, including prairies, go through a loosely predictable sequence of domination by fast-growing annuals, followed by smaller, short-lived perennials, and finally by a self-maintaining ("climax") stand of large-stature, long-lived perennials. Weedy annuals and short-lived perennials currently find refuge in the agricultural fields and roadsides that cover the continent, but at one time they were restricted to gopher mounds, ant hills, buffalo wallows, and dry creek beds (Weaver and Fitzpatrick 1934, Roe 1951, Koford 1958, Curtis 1959, Platt 1975). Following severe drought, overgrazing or (to a lesser extent) fire, these species increase in abundance and hence are termed "increasers" by rangeland managers, for whom they are indicative of poor range conditions (Heady 1975). The differential survival and reinvasion of plant species on the Great Plains during and after the great drought of the 1930s clearly involved species replacement and recovery from disturbance (Weaver et al. 1935, Weaver and Albertson 1943). Fire alone rarely initiates the replacement of species in prairies because the dominant vegetation is well adapted to fire. Under severe environmental conditions such as drought in the semiarid shortgrass steppe region, however, fire can induce the invasion of annual weeds (Clarke et al. 1943, Curtis and Partch 1948, Dix 1960). Because the agricultural cultivation of grasslands typically entails complete destruction of the native vegetation, the recovery of abandoned fields is a slow process often limited by inadequate or negligible seed availability (Costello 1944, Rice et al. 1960, Fitch and Kettle 1980). Depending on the degree of soil degradation, the accumulation of organic matter and buildup of nitrogen (often with the aid of soil cyanobacteria) may facilitate successional development (Rice et al. 1960).

Studies in recent years have complicated this simple theory of succession: (1) the successional series often represent differences in dominance, not necessarily in presence, because the climax species may be present from the start but may take longer to establish; (2) although dramatic changes occur in old-field succession, the native prairie flora evolved in response to such disturbances as fire, drought, and grazing, events that do not induce such distinctive replacement sequences; (3) species replacement, when it occurs, may be the result of microsite modification (resource depletion, microclimate amelioration, shade and organic matter buildup) or may simply be the result of differential competitive ability or longevity; and (4) a dynamic mosaic of large and small disturbances in various stages of recovery is found even in climax communities. True succession, in terms of the replacement of species, may be more important in prairies on the scale of hoof prints and animal burrows than at the level of the landscape.

Some aspects of successional theory may be useful in prairie restoration; at the same time, restoration may also help to resolve a number of theoretical questions regarding succession. For example, colonizing annuals can either inhibit or facilitate the establishment of perennial species and a climax plant community (Iverson and Wali 1982). There is some debate over whether weed control during the first year or two of community reconstruction is worth the effort since the native prairie species (with their superior competitive ability and greater persistence) should eventually prevail. We know that annual cover crops such as wheat and oats can reduce the presence of weeds without persisting in a forage community (Smith 1962), and their use in prairie reconstruction is widespread but sparsely documented. Some authors (e.g., Rock 1981, Burton et al. 1988) suggest using native annuals (e.g., _Ambrosia artemisiifolia_, _Cassia fasciculata_, _Helianthus annuus_) to provide this original cover crop, but these annuals must be vigorous enough to compete successfully with agricultural weeds. Practicing restorationists, however, are reluctant to introduce aggressive or otherwise noxious annual species because these plants may reseed and persist or spread. If we think of successional time as a niche axis, the absence of colonizing annuals in a seed mixture represents an empty niche, an open invitation to unwanted invaders. To fill that niche with native species would, therefore, be best. Another approach is to mow colonizing annuals during the first year of restoration, thereby hastening successional replacement by the planted perennials (Iverson and Wali 1987). Simple experiments are needed to test the long-term compositional effects of diligent manual weeding, of no weed control, of weed control by mowing, of the use of a cereal cover crop such as oats, and of the use of a cover crop of native annuals.

In general, the best guideline to maintaining the stability and quality of a restored prairie after initial seedling establishment is to employ the forces responsible for natural grassland maintenance. This means proper siting to encourage droughtiness (use original prairie land, or south-facing slopes, hill crests, or sandy areas elsewhere), no use of irrigation or fertilizer, and repeated use of controlled fire and perhaps grazing (or its substitute, mowing). If the appropriate species are present, they should persist and thrive under these conditions.

RESTORATION CASE STUDIES FROM ILLINOIS

Numerous approaches to prairie restoration have been tried over the last 40 years. Most have been local "learn-as-you-go" programs, with little published information and no widely accepted practices on which to base plans. Many of these independent efforts have developed effective techniques that are now widely accepted. We discuss several successful prairie reconstructions in Illinois to illustrate three major approaches: (1) large-scale, labor-intensive; (2) large-scale, mechanical; and (3) small-scale. These three case studies represent current practices in prairie restoration, demonstrating methods that vary in their effectiveness and in their underlying ecological assumptions. All restoration efforts are experimental by virtue of their trial-and-error nature, though the "experiments" may not be designed to test any general ecological theories. These and other examples could readily lend themselves to the explicit testing of a number of interesting hypotheses.

Large-scale Labor-intensive Approaches: The Morton Arboretum Prairie--The Morton Arboretum Prairie (now about seven ha in size) near Lisle, Illinois, was planted from 1963 to 1973. It was closely modelled after the Curtis and Greene Prairies established earlier at the University of Wisconsin Arboretum, near Madison, Wisconsin (Greene and Curtis 1953). Whereas parts of the Wisconsin prairie were established by direct seeding of prairie species into a bluegrass turf, all of the plantings at the Morton Arboretum were made into bare soil, primarily with seedlings started in a greenhouse (Schulenberg 1970). This effort has been characterized by a horticultural approach and has relied on dedicated volunteers for seed collection, propagation, transplanting, and weeding. About 6000 m^2 were added to the prairie in this manner every year for ten years (Armstrong 1986).

Seeds were collected from prairie remnants within about 50 km of Chicago, and these areas also served as models for species composition and proportions. Seeds of all species (grasses as well as forbs) were stratified and propagated in greenhouse flats in early winter. Site preparation involved shallow disking three or four times to promote the germination of weeds which were then killed by the next disking. The soil was disturbed as little as possible so that deeply buried weed seeds would not be exposed. Plants were typically outplanted in May. Seedlings were planted on a grid, one plant per ft^2, in a ratio of three grasses to two forbs. Efforts at irregular planting, though more naturalistic, made manual weeding difficult. Weeding was necessary three times in the first year and once in the following spring. Subsequent control of exotics has been principally by annual spring fires. Persistent individuals or small patches of weeds continue to be removed manually or by using a broad-spectrum herbicide such as "Roundup," usually in conjunction with the transplanting of prairie plants into the same areas. Mechanical seeding was attempted, but results were patchy and the larger area was difficult to maintain.

A large corps of volunteers has helped with the prairie since 1979, manually removing weeds, cutting brush, and transplanting greenhouse seedlings of rare species. This approach, with its careful placement of individual plants, a high proportion of forbs, and intensive weeding, has produced an exceptionally diverse and aesthetically pleasing prairie with the appearance of a "wildflower meadow" (Armstrong 1986). The Morton Arboretum Prairie illustrates the value of using local genotypes, spacing seedlings widely so that competition among prairie species does not result in a loss of valuable plant material, and controlling competition from annuals. The key to the management and enhancement of this prairie has been the control of exotics through hand weeding and fire. Succession is not assumed to occur, with exotic weeds being manually replaced by native perennials instead. Tests of density-dependent mortality and weed invasion could be easily incorporated into this approach, as could tests of the stability or invasion-resistance of specific species mixtures.

Large-scale Mechanical Approaches: The Knox College Field Station--The Knox College Biological Field Station Prairie (located 32 km east of Galesburg, Illinois) was started in 1955, but most of it has been established since 1970 using drill seeding (Schramm 1970, 1978). Some of the grass seed was originally obtained commercially from suppliers in Nebraska, but most grass and forb seed has since been collected from local prairie remnants. Seed was stratified by mixing it with vermiculite and storing it at 2^{o}C in plastic garbage cans. Following plowing, the site was shallowly disked and harrowed for a year (or at least at two-to-three-week intervals during the spring) for weed control. Grasses and forbs were sown in separate passes or from different seeder boxes, using a Nesbit seed drill. A mixture of *Andropogon*, *Schizachyrium*, *Sorghastrum*, and *Panicum* was seeded at 50.4 kg/ha using three passes; forbs were seeded at 22.4 kg/. Rates in each instance refer to the seed/vermiculite mix. This mixture makes comparison difficult, but other authors (e.g., McClain 1986) recommend seeding rates for grasses of 16.8-22.4 kg/ha for total pure live seed.

Schramm (1978) summarizes a number of strategies to overcome the weed problem that inevitably arises after the prairie seed is in the ground. The first is to use late planting (in Illinois, the first two weeks of June) to allow mechanical control of the first crop of spring weeds. After seeding, mowing weeds to 30 cm whenever they reach 60 to 100 cm prevents most of them from going to seed during the first year or two. The annual use of fire (starting 10 or 11 months after seeding, if possible) every March or April also helps to control weeds. Finally, Schramm stresses that patience is simply required if native prairie species are to overtake weeds; their perenniality, deep rooting, and general tolerance to stress allows them to establish and eventually to dominate.

Hand-planting at the Knox College Prairie is reserved for forb enrichment of the grass matrix and for species highly sensitive to competition. These species are planted into hand-weeded areas as hardened seedlings. Prairie reconstruction by planting successive small areas every year is recommended in order to avoid committing an entire site in a single year that may experience disastrous weather. Small areas also allow manageable weed control in the early stages and permit the testing of alternative methods. Tests of native cover crops, manual or chemical weed control, weed mowing, regular burning and no weed management could be readily incorporated into this framework, as could tests of the stability of different species mixtures.

A program similar to that used at Knox College and based on mechanical matrix planting followed by manual enrichment with forbs is also recommended by McClain (1986). With emphasis on restoring an expansive prairie landscape, the approach places greater faith in succession and the competitiveness of native prairie species, but often (in practice) at the expense of high native diversity.

Small-scale Approaches: Home Landscaping--The most rapidly growing type of prairie restoration is residential and commercial landscaping (e.g., Smith and Smith 1980, Smyser 1982, Diekelmann and Schuster 1982, Diekelmann et al. 1986). While gardeners have long propagated native wildflowers in discrete beds, the reconstruction of entire plant communities under the concept of naturalistic landscaping has become popular only in the last few years. A landscaper or homeowner often tries to recreate the appearance of one or more ecosystems--an open meadow, an alpine rock garden, a woodland stream or understory--relying on a combination of exotic cultivars and native plants. This approach, however, has now developed to the point where the purist desires a landscape composed completely of species once native to the site, and that form of landscaping essentially represents ecosystem restoration on a small scale.

This mode of restoration benefits from a history of landscape design that includes an analysis of local geology, topography, hydrology, soils, climate, and presettlement vegetation, a degree of site analysis that may be lacking in other restoration efforts. Both a "functional analysis" of the anticipated long-term uses of the planting and a "visual analysis" of its imagery can be quite involved. The layout of grasses and forbs can be designed to generate patches of different color combinations at different times of the year, and the selection of plants of varying heights allows the creation of backdrops and depth (Diekelmann et al. 1986). Choosing plants with diverse flowering phenologies may also result in a range of growing periods that maximizes resource use during the year. Such variety inevitably facilitates resource partitioning and high local diversity. The generally smaller scale of a residential prairie makes weed control more practical, although regular burning may be difficult. Because complete weed control is feasible, resource supplementation (irrigation, fertilization) is also permissible, thereby promoting rapid establishment and "community development" with no dependence on succession. A reasonably attractive "prairie" can be established in as little as three years.

Armstrong (1985) recently described her experiences in establishing a prairie at her suburban home in Naperville, Illinois. Based on a desire to create a home that is part of the natural environment, her passive solar house integrates insulative architecture and prairie-savanna landscaping. In addition to carefully planted beds of tall grasses and forbs using the Morton Arboretum method, Armstrong has established a buffalo grass (Buchloe dactyloides) lawn, desirable for its short stature, low moisture requirements, and resistance to trampling (Evander 1986, Knoop 1986). Small swards of this native American grass could represent a nice experimental system for testing the balance of resource levels (water, fertilizer) and initial spacing (plant density) that best maintains the population, perhaps with and without weeding or mowing, under the rich local site conditions.

Armstrong (1985, 1986) advises that watering promotes rapid establishment and flowering of prairie plants, that spring planting (following weed control) is preferable to fall planting, and that natural landscaping--like field-scale restoration efforts--is best undertaken in small parcels. The tasks of seed collection and propagation can be enjoyable in themselves, but weeding is a perpetual chore. Diplomatic explanation or even court battles may be required in dealing with neighborhood objections or municipal weed ordinances that do not distinguish between untended weeds and natural landscaping.

Similarities Among the Three Approaches--The three case studies we have reviewed all share in the application of a number of ecological principles. Some restorationists place more importance than others on the use of locally collected genotypes, but all recognize the importance of carefully selecting species to match the prevailing site conditions. Prairie species clearly exhibit a variety of moisture preferences, rooting depths, canopy structures, temperature optima, and flowering times; these traits should fit the constraints of the site. Further, species should complement each other to minimize competitive interactions. Nearby prairie remnants are frequently a good model for prairie restoration, but other combinations of species are also aesthetically pleasing and apparently just as stable. Promoting high species richness or diversity is a universal goal but has usually been dependent on manual introduction of transplants. The establishment and maintenance of a reconstructed prairie community depend on control of competition by weeds and on using an appropriate disturbance regime such as fire. If a lot of time and seed are available, the processes of natural succession can be allowed to govern prairie establishment and enrichment; human intervention (by weeding, transplanting, even irrigating) can accelerate these processes. All restorations could readily include replicated trials to test different species mixtures or management regimes.

USING PRAIRIE RESTORATION TO TEST HYPOTHESES OF COMMUNITY ORGANIZATION

Restoration techniques like those described above, in combination with the classic surveys and experiments of such researchers as F. E. Clements, J. E. Weaver, F. W. Albertson, and the International Biological Programme Grassland Biome group, have told us as much about the ecological properties of prairies as we know about any other natural system. Yet prairie restoration efforts are time consuming, frustrating, and prone to failure because of the difficulty in controlling weeds and woody plants while promoting a diverse, self-maintaining association of native species. Given these difficulties, prairie reconstruction should never be considered an alternative to the preservation or ecological enhancement (through selective species removal and addition) of even the most degraded prairie remnants.

Why is the reassembly of this biological community so difficult? Historical changes in a number of ecological factors are clearly important. The current climate is slightly cooler and moister than that of the hypsithermal interval (8300 to 1000 years ago) when the present-day prairie established itself following glacial retreat (Dorf 1960). Such agents of disturbance as wildfires and herds of free-roaming bison are no longer a part of the landscape, although they can be reintroduced on a limited scale. Finally, European settlement has created landscapes dominated by crop monocultures, exposed mineral soil, and a biogeographic explosion of exotic colonizers that thrive in disturbed areas.

Given these de facto changes in the environment, what can be done to enhance the success of restoration efforts? We believe that restoration science would benefit by incorporating ideas from the more academic or theoretical aspects of plant ecology. Restoration science should borrow basic information and approaches from such ecological subdisciplines as autecology (the study of species site relationships and requirements), community organization theory (especially the quantification of interspecific competition and compatibility), and stability theory (with its emphasis on disturbance regimes). There is a general need for an enhanced scientific approach to supplement what has often been an empirical, trial-and-error approach that has focused simply on learning how to grow different plant species. Now that successful propagation techniques have been identified for most prairie species, efforts should be shifted to replicated field trials that test the compatibility and persistence of various combinations of species. In general, restoration efforts would benefit most from a more conscientious application of the scientific method in the many experimental trials now being carried out. All innovations should be replicated (ideally across several soil types, landform types, and even climate regimes) and compared with controls through repeated quantitative monitoring. Results should be assessed statistically and reported in the literature. In turn, theoretical ecology would benefit from such empirical tests of its hypotheses and predictions.

Prairie restoration, therefore, offers a useful mechanism for investigating many issues of theoretical community ecology, especially since we have more than 40 years of accumulated information on more than 200 candidate species. In addition, demand is growing for the reintroduction of these species and the restoration of naturalistic prairie landscapes for a variety of scientific, educational, aesthetic, and historical reasons.

Niche Quantification and Resource Partitioning--To illustrate how ecological theory can be applied to prairie restoration, we recently described how niche quantification and site-matching techniques might be used to select plant species that would improve the long-term stability of reconstructed prairie communities (Burton et al. 1988). First, variability in soil moisture (generally the factor governing grassland organization) is described by means of a frequency distribution (histogram) of soil moisture measurements made over time or over space during periods of partial drought. Smoothing this distribution to form a curve, we describe the polygon (the area under the curve) so formed as defining the available "environmental space" (the ES curve in Fig. 2). It approximates the range and frequency of conditions to which plants at this location will be exposed, thereby indicating the range and abundance of resource levels (i.e., soil moisture states) available for exploitation. We then use the results of direct gradient analysis surveys (e.g., Nelson and Anderson 1983) or experimental growth studies to describe the performance of all candidate plant species across the full range of resource levels (soil moisture conditions). These gradient response curves describe the fundamental niche (if based on the experimental performance of species grown in monoculture) or the realized niche (if based on observed performance within the natural vegetation) of each species (sensu Hutchinson 1957). Response curves are standardized so that each species has an optimum performance of 100%; this procedure allows us to compare curve location and shape independent of the magnitude of a given response. The standardized gradient response curves are then overlaid on the environmental space curve, as shown for six graminoid species in Fig. 2.

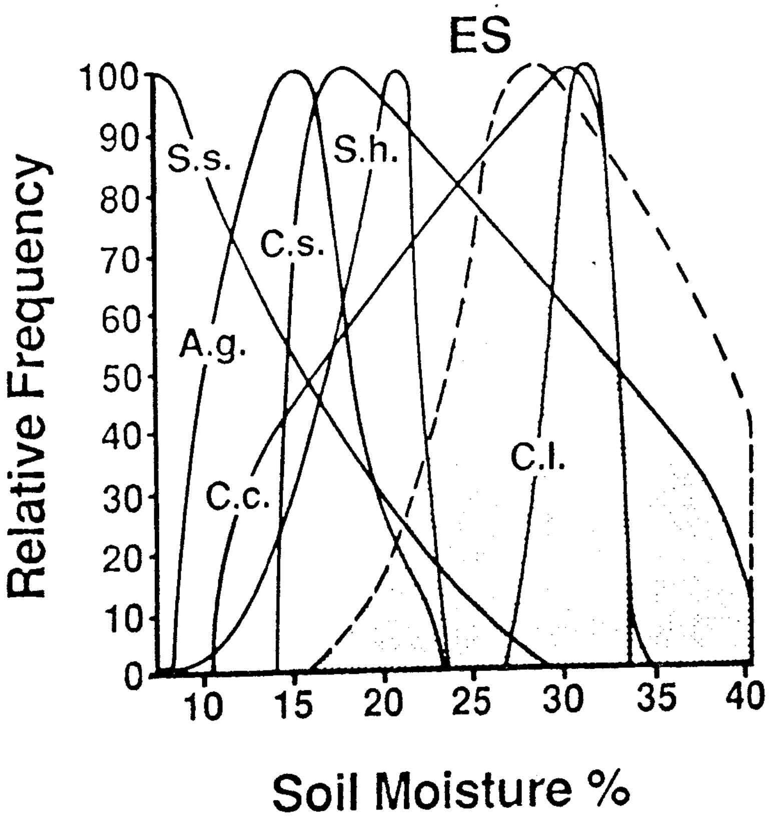

Fig. 2. Overlay of standardized moisture response curves for six graminoid species and a moisture-defined environmental space (ES) for a particular locale. Species abbreviations are as follows: S.s. - *Schizachyrium scoparium*; A.g. - *Andropogon gerardii*; C.c. - *Calamagrostis canadensis*; C.s. - *Carex stricta*; S.h. - *Sporobolus heterolepis*; and C.l. - *Carex lacustris*. Species curves are modified from Nelson and Anderson 1983. The shaded area represents the maximum occupancy (83.15%) of the environmental space possible for this set of species. From Burton et al. 1988.

We now try to fill the environmental space as fully as possible with desired species, on the assumption that the absence of an adapted species at a critical location in space or time (e.g., very wet site conditions) would leave the community open to invasion by exotics that can take advantage of this "vacant niche" with its unexploited resources. The total percentage occupancy of the environmental space (measured by the area under the curves) achieved by selected combinations of six graminoid species is presented in Table 3. The overlap values reported in Table 3 are simple computations of the area of overlap among the standardized curves of specified species, expressed as a percentage of the total

Table 3. Occupancy of environmental space (ES) and interspecific overlap values calculated for selected combinations of species. From Burton et al. 1988.

No. of Spp.	Mixture	Species Composition	Occupancy of ES (%)	Species Overlap (% of ES)	Occupancy Minus Overlap
1	A	Ss, Schizachyrium scoparium	10.64	-	10.64
	B	Ag, Andropogon gerardii	5.44	-	5.44
	C	Cs, Carex stricta	69.92	-	69.92
	D	Sh, Sporobolus heterolepis	9.00	-	9.00
	E	Cc, Calamagrostis canadensis	67.11	-	67.11
	F	Cl, Carex lacustris	28.51	-	28.51
2	G	Ss,Sh	9.36	7.45	1.91
	H	Ag,Cs	69.92	5.44	64.48
	I	Ag,Cl	33.17	0	33.17
	J	Cs,Cc	83.15	53.89	29.26
	K	Sh,Cl	37.51	0	37.51
3	L	Ss,Sh,Cl	14.87	7.81	7.06
	M	Ag,Cs,Cc	83.15	59.33	23.82
	N	Cs,Cc,Cl	83.15	102.97	-19.82
4	O	Ss,Ag,Cs,Sh	69.92	37.25	32.67
	P	Ss,Ag,Sh,Cl	38.79	21.05	17.74
	Q	Ss,Cs,Cc,Cl	83.15	154.70	-71.55
	R	Cs,Sh,Cc,Cl	83.15	153.06	-69.91
5	S	Ss,Ag,Cs,Cc,Cl	83.15	160.14	-76.99
	T	Ss,Ag,Cs,Sh,Cl	76.92	79.94	-3.02
	U	Ss,Cs,Sh,Cc,Cl	83.15	163.70	-80.55
	V	Ag,Cs,Sh,Cc,Cl	83.15	158.50	-75.35
6	W	Ss,Ag,Cs,Sh,Cc,Cl	83.15	169.14	-85.99

area under the environmental space curve. Any of the many mathematical indices designed to measure niche overlap (Giller 1984) could be chosen to measure both environmental space occupancy and interspecific overlap, but we use a simple geometric method here to foster an intuitive interpretation of "overlap area." These calculations allow us to select the best single and multi-species matches to the site. While the average amount of utilized environmental space increases with the number of species, note that maximum occupancy can also be attained with only two species (_Carex stricta_ and _Calamagrostis canadensis_). Additional species add to the degree of interspecific overlap but not to the overall occupancy of the environmental space. It is worth noting that many wet-mesic prairies in northern Illinois, Iowa and Wisconsin are, in fact, dominated by these same two species (Nelson and Anderson 1983).

A number of theoretical and practical questions regarding the determinants of competitive pressure and community stability can now be raised. Four hypotheses for compositional stability clearly make mutually exclusive predictions that could be tested by establishing and monitoring the compositional stability of the species mixtures listed in Table 3.

(1) If total occupancy of environmental space (first column in Table 3) is a reliable indicator of stability, then mixture G (9.36% occupancy) should rapidly become more weedy than mixture J, also consisting of two species but with 83.15% occupancy.

(2) If diffuse competition or diversity _per se_ is important, then mixture W (six species) should be more stable than mixture J (two species), though each has 83.15% occupancy.

(3) If minimization of overlap among species (second column in Table 3) is important, then mixture M (59.33% overlap within the environmental space) should be more stable than mixture N, another three-species mixture with 102.97% overlap; both mixtures have 83.15% occupancy.

(4) If the difference between occupancy of environmental space and overlap of species (third column in Table 3) is most important, then mixture I (+33.17% net difference) should behave much like mixture O (+32.67% net difference), though they have different occupancy and niche overlap values.

This approach can be used with other resource axes as well. Separation of species along a moisture gradient or a moisture-derived environmental space can represent beta-niche or alpha-niche differentiation in terms of the ability of species to withstand various extremes of soil moisture over space or during a season. Other alpha-niche axes worth exploring include the vertical and horizontal deployment of leaves and roots, light intensity (shade tolerance), and the phenology of growth and flowering. Once again, the guiding principle is to occupy the environmental space fully and to minimize deleterious interactions among desired species. The unproven nature of these suggestions means that the efficacy of filling the environmental space and minimizing niche overlap needs to be tested for each niche axis. It is not difficult, however, to imagine highly practical benefits from incorporating this element of design into the prairie restoration process. For example, the persistence of exotic cool-season grasses such as Poa pratensis in restored prairies suggests that there is an "empty" niche in terms of growth form and position on the phenological axis. We suggest testing the use of high densities of fast-growing, native, rhizomatous cool-season graminoid species (e.g., Hierochloe odorata and some Carex spp.) in the original prairie planting in order to more fully occupy the phenological space and thereby retard the invasion of Poa.

The Need for Greater Latitude in Experimentation--Purists may argue that we cannot experiment with species composition in bona fide restoration efforts because our objective should always be to emulate the pre-existing natural vegetation or some nearby remnant of it. This concern seems unnecessarily restrictive if we consider the great fluidity of species distributions in the Great Plains region. The relatively short history of our modern prairies, their diverse floristic origins, and the low rates of endemism (Wells 1970, Stebbins 1981, Axelrod 1985) all suggest that we could allow greater latitude in the assembly of stable communities than is exhibited by remnant prairies today, themselves often isolated and no longer controlled by natural pressures. Pollen cores retrieved from the sediments of lakes and bogs reveal that forest communities were dismantled and reassembled with little fidelity to the community types we recognize today (Davis 1976, 1981, Delcourt and Delcourt 1987); the same process can be inferred for grasslands.

Some species are naturally restricted to very specific habitats and associations, while other widespread species, such as *Schizachyrium scoparium*, can be a component of most prairie communities. Benninghoff (1968) has suggested that a history of repeated disturbance has resulted in dominance by broad-niched species capable of coping with great physical stresses through intraspecific variability and plasticity. This theory would explain the remarkable similarity in species composition sometimes found in rather different grassland habitats (Weaver 1954). These observations suggest that common prairie species should be successful in most restoration efforts, but they do not mean that less common species should only be planted with their (present-day) natural associates.

The species assemblages that we understand to typify virgin prairie do not represent an ancient, immutable "super-organism" perfectly synchronized to its environment. Rather, these associations are a few of the countless potential "snapshots" portraying the endless ebb and flow of more or less independently assorting species responding to climate and disturbance (Gleason 1926, 1939). For over 20 million years, species have been mixed and stirred by recurring periods of hot and cold and wet and dry conditions (Risser et al. 1981). Particular species or species groups were alternately favored or repressed by changes in climate, topography, and competitive neighborhood. This interpretation of the dynamic nature of grassland composition and the independent assortment of species is supported by direct observations during and after droughts (Weaver and Albertson 1956, Coupland 1958). Yet floristic dynamism has often been overlooked in the planning of ecosystem restoration efforts because we tend to revere remnants of undisturbed vegetation as perfectly structured ecosystems that define our ideal objectives in restoration. We must guard against the romantic notion that an unplowed patch of vegetation represents an *optimal* combination of species, genotypes, and interactions for a particular site. Rather, it more probably represents one of any number of stochastic but *tolerable* combinations.

With some coordination, it would not be difficult to incorporate experiments (such as those proposed above) into the prairie restoration plans of various agencies or institutions. Since restoration is best attempted on small parcels of land, each plot could quite easily and usefully be a replicate for testing one of the many hypotheses posed regarding the role of annual colonizers, the degree to which and rate at which species sort themselves out according to local site differences, the relationships between diversity and stability, the existence of vacant phenological niches, the equivalence of mowing, grazing and fire, and so forth. These experimental plots, on which long-term observations are generally desired, can be part of the desired restored landscape while also providing data which, in turn, could enhance future prairie restoration efforts and our understanding of the principles of community ecology.

In our efforts to conserve genetic diversity, to preserve the prairie landscape, and to learn more about how communities function, we should more often take the initiative to establish and monitor artificial arrays of species and artificial disturbance regimes. While the inquisitive dismantling of ecosystems (reductionism) has proven useful in the past, we may now learn even more by attempting to reassemble these complex systems.

ACKNOWLEDGMENTS

We appreciate the critical comments and discussion offered by E. B. Allen, R. C. Anderson, P. K. Armstrong, F. A. Bazzaz, T. A. Day, A. S. Hodgins, W. E. McLain, R. C. Moran, J. A. D. Parrish, P. Schramm, M. K. Solecki and three anonymous reviewers. Support for the principal author was provided by the Illinois Department of Transportation.

LITERATURE CITED

Aber, J. D., and W. R. Jordan, III. 1986. Restoration ecology (Abstract). Page 73. Program of the Fourth International Congress of Ecology, August 10-16, 1986, Syracuse, New York, USA.

Allen, D. L. 1967. The life of prairies and plains. McGraw-Hill, New York, New York, USA.

Anderson, R. C. 1982. An evolutionary model summarizing the roles of fire, climate, and grazing animals in the origin and maintenance of grasslands: an end paper. Pages 297-308 in J. R. Estes, R. J. Tyrl, and J. N. Brunken, editors. Grasses and Grasslands: Systematics and Ecology. University of Oklahoma Press, Norman, Oklahoma, USA.

Armstrong, P. K. 1985. Life at Prairie Sun: weeds, water bans, and worried neighbors. Morton Arboretum Quarterly 21:17-30.

______. 1986. Lectures presented at the Grand Prairie Friends Prairie Plant Propagation Workshop. April 12, 1986, Penfield, Illinois, USA.

Axelrod, D. I. 1985. Rise of the grassland biome, central North America. Botanical Review 51:163-201.

Bazzaz, F. A., and J. A. D. Parrish. 1982. Organization of grassland communities. Pages 233-254 in J. R. Estes, R. J. Tyrl, and J. N. Brunken, editors. Grasses and Grasslands: Systematics and Ecology. University of Oklahoma Press, Norman, Oklahoma, USA.

Benninghoff, W. S. 1968. Biological consequences of Quaternary glaciations in the Illinois region. Pages 70-77 in R. E. Bergstrom, editor. The Quaternary of Illinois. University of Illinois College of Agriculture Special Publication No. 14, Urbana, Illinois, USA.

Borchert, J. R. 1950. The climate of the central North American grassland. Annals of the Association of American Geographers 40:1-39.

Burton, P. J., K. R. Robertson, L. R. Iverson, and P. G. Risser. 1988. Suggested applications of ecological theory to prairie restoration. Paper 01.16 in A. Davis and G. Stanford, editors. The Prairie: Roots of Our Culture; Foundation of Our Economy. Proceedings of the Tenth North American Prairie Conference, June 22-26, 1986, Denton, Texas. The Native Prairie Association of Texas, Dallas, Texas, USA.

Clarke, S. E., E. W. Tisdale, and N. A. Skoglund. 1943. The effects of climate and grazing practices on short-grass vegetation in southern Alberta and southwestern Saskatchewan. Canadian Department of Agriculture, Publication No. 147, Ottawa, Ontario, Canada.

Clements, F. E. 1936. Origin of the desert climax and climate. Pages 87-140 in T. H. Goodspell, editor. Essays in Geobotany in Honor of William Albert Setchell. University of California Press, Berkeley, California, USA.

Clements, F. E., and V. E. Shelford. 1939. Bioecology. John Wiley & Sons, New York, New York, USA.

Collins, S. L. 1987. Interaction of disturbances in tallgrass prairie: a field experiment. Ecology 68:1243-1250.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199:1302-1310.

Costello, D. F. 1944. Natural revegetation of abandoned plowed land in the mixed prairie association of northeastern Colorado. Ecology 25:312-326.

Coupland, R. T. 1958. The effects of fluctuations in weather upon the grasslands of the Great Plains. Botanical Review 24:273-317.

Curtis, J. T. 1959. The vegetation of Wisconsin. University of Wisconsin Press, Madison, Wisconsin, USA.

Curtis, J. T., and M. L. Partch. 1948. Effect of fire on the competition between blue grass and certain prairie plants. The American Midland Naturalist 39:437-443.

Davis, M. B. 1976. Pleistocene biogeography of temperate deciduous forests. Geoscience and Man 13:13-26.

_____. 1981. Quaternary history and the stability of forest communities. Pages 132-153 in D. C. West, H. H. Shugart, and D. B. Botkin, editors. Forest Succession: Concepts and Application. Springer-Verlag, New York, New York, USA.

Delcourt, P. A., and H. R. Delcourt. 1987. Long-term Forest Dynamics of the Temperate Zone: a Case Study of Late-Quaternary Forests in Eastern North America. Springer-Verlag, New York, New York, USA.

Diekelmann, J., J. Harrington, and E. A. Howell. 1986. An approach to residential landscaping with prairie. Pages 242-248 in G. K. Clambey and R. H. Pemble, editors. The Prairie-Past, Present and Future: Proceedings of the Ninth North American Prairie Conference, 29 July-1 August 1984. Tri-College University, Moorhead, Minnesota, USA.

Diekelmann, J., and R. Schuster. 1982. Natural landscaping: designing with native plant communities. McGraw-Hill, New York, New York, USA.

Dix, R. L. 1960. The effects of burning on the mulch structure and species composition of grasslands in western North Dakota. Ecology 41:49-55.

_____. 1964. A history of biotic and climatic changes within the North American grassland. Pages 71-89 in D. J. Crisp, editor. Grazing in Terrestrial and Marine Environments. Blackwell Scientific Publications, Oxford, England.

Dorf, E. 1960. Climatic changes of the past and present. American Scientist 48:341-364.

Engle, D. M., and P. M. Bultsma. 1984. Burning northern mixed prairie during a drought. Journal of Range Management 37:398-401.

Evander, J. 1986. Buffalograss as a low-maintenance lawn turf. Tenth North American Prairie Conference Abstracts, June 22-26, 1986, Denton, Texas. The Native Prairie Association of Texas, Dallas, Texas, USA.

Fitch, H. S., and W. D. Kettle. 1980. Ecological succession in vegetation and small mammal population on a natural area of northeastern Kansas. Pages 117-121 in C. L. Kucera, editor. Proceedings of the Seventh North American Prairie Conference, August 4-6, 1980. Southwest Missouri State University, Springfield, Missouri, USA.

Giller, P. S. 1984. Community structure and the niche. Chapman and Hall, London, England.

Gleason, H. A. 1913. The relation of forest distribution and prairie fires in the Middle West. Torreya 13:173-181.

_____. 1922. The vegetational history of the Middle West. Annals of the Association of American Geographers 12:39-85.

_____. 1926. The individualistic concept of the plant association. Bulletin of the Torrey Botanical Club 53:7-26.

_____. 1939. The individualistic concept of the plant association. The American Midland Naturalist 21:92-110.

Golley, P. M., and F. B. Golley, editors. 1972. Papers from a symposium on tropical ecology with an emphasis on organic productivity. Institute of Ecology, University of Georgia, Athens, Georgia, USA.

Gould, F. W., and R. B. Shaw. 1983. Grass systematics. Second edition. Texas A&M University Press, College Station, Texas, USA.

Greene, H. C., and J. T. Curtis. 1953. The re-establishment of an artificial prairie in the University of Wisconsin Arboretum. Wild Flower 29:77-88.

Harris, G. A. 1967. Some competitive relationships between Agropyron spicatum and Bromus tectorum. Ecological Monographs 37:89-111.

______. 1977. Root phenology as a factor of competition among grass seedlings. Journal of Range Management 30: 172-177.

Havercamp, J., and G. G. Whitney. 1983. The life history characteristics of three ecologically distinct groups of forbs associated with the tallgrass prairie. American Midland Naturalist 109:107-119.

Heady, H. F. 1975. Rangeland management. McGraw-Hill, New York, New York, USA.

Holdridge, L. R. 1947. Determination of world plant formations from simple climatic data. Science 105:367-368.

Hubbell, S. P. 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. Science 203:1299-1309.

Hulbert, L. C. 1984. Causes of fire effects in tallgrass prairie (Abstract). Bulletin of the Ecological Society of America 65:180.

Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology 22:415-427.

Iverson, L. R., and M. K. Wali. 1982. The reclamation of coal mined lands: the role of Kochia scoparia and other pioneers in early succession. Reclamation and Revegetation Research 1:123-160.

Iverson, L. R., and M. K. Wali. 1987. Mowing of annual colonizers to enhance revegetation after surface mining in North Dakota. Reclamation and Revegetation Research 6:157-161.

Jenkins, R. 1973. Ecosystem restoration. Pages 23-27 in L. C. Hulbert, editor. Third Midwest Prairie Conference Proceedings. Kansas State University, Manhattan, Kansas, USA.

King, J. E. 1981a. Late Quaternary vegetational history of Illinois. Ecological Monographs 51:43-62.

_____. 1981b. The prairies of Illinois. The Living Museum 43:42-45.

Klopatek, J. M., R. J. Olson, C. J. Emerson, and J. L. Joness. 1979. Land-use conflicts with natural vegetation in the United States. Environmental Conservation 6:191-199.

Knoop W. E. 1986. Buffalograss for home lawns. Tenth North American Prairie Conference Abstracts, June 22-26, 1986, Denton, Texas. The Native Prairie Association of Texas, Dallas, Texas, USA.

Koford, C. B. 1958. Prairie dogs, whitefaces, and blue grama. Wildlife Monographs 3:1-78.

Kucera, C. L., R. C. Dahlman, and M. R. Koelling. 1967. Total net productivity and turnover on an energy basis for tallgrass prairie. Ecology 48:536-541.

Kucera, C. L., and J. H. Ehrenreich. 1962. Some effects of annual burning on central Missouri prairie. Ecology 43:334-336.

Küchler, A. W. 1964. Potential natural vegetation of the conterminous United States. American Geographical Society, New York, New York, USA.

Lemon, P. C. 1970. Prairie ecosystem boundaries in North America. Pages 13-18 in P. Schramm, editor. Proceedings of a Symposium on Prairie and Prairie Restoration. Knox College, Galesburg, Illinois, USA.

Looman, J. 1979. The vegetation of the Canadian Prairie Provinces. 1. An overview. Phytocoenologia 5:347-366.

_____. 1980. The vegetation of the Canadian Prairie Provinces. II. The grasslands, Part 1. Phytocoenologia 8:153-190.

McClain, W. E. 1986. Illinois prairie: past and future: restoration guide. Illinois Department of Conservation, Springfield, Illinois, USA.

McIntosh, R. P. 1980. The relationship between succession and the recovery process in ecosystems. Pages 11-62 in J. Cairns, Jr., editor. The Recovery Process in Damaged Systems. Ann Arbor Science Publishers, Ann Arbor, Michigan, USA.

McNaughton, S. J., M. B. Coughenour, and L. L. Wallace. 1982. Interactive processes in grassland ecosystems. Pages 167-193 in J. R. Estes, R. J. Tyrl, and J. N. Brunken, editor. Grasses and Grasslands: Systematics and Ecology. University of Oklahoma Press, Norman, Oklahoma, USA.

Nelson, D. C., and R. C. Anderson. 1983. Factors related to the distribution of prairie plants along a moisture gradient. The American Midland Naturalist 109:367-375.

Old, S. M. 1969. Microclimate, fire, and plant production in an Illinois prairie. Ecological Monographs 39:355-384.

Oosting, H. J. 1956. The study of plant communities. Second edition. W. H. Freeman and Co., San Francisco, California, USA.

Parrish, J. A. D., and F. A. Bazzaz. 1976. Underground niche separation in successional plants. Ecology 57:1281-1288.

Parish, J. A. D., and F. A. Bazzaz. 1979. Difference in pollination niche relationships in early and late successional plant communities. Ecology 60:597-610.

Pickett, S. T. A., and P. S. White, editors. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, New York, New York, USA.

Platt, W. J. 1975. The colonization and formation of equilibrium plant species associations on badger disturbances in a tallgrass prairie. Ecological Monographs 45:285-305.

Platt, W. J., and I. M. Weis. 1977. Resource partitioning and competition within a guild of fugitive prairie plants. American Naturalist 111:479-513.

Raunkiaer, C. 1934. The life forms of plants and statistical plant geography. Clarendon, Oxford, England.

Redmann, R. E., and E. G. Reekie. 1982. Carbon balance in grasses. Pages 195-231 in J. R. Estes, R. J. Tyrl, and J. N. Brunken, editors. Grasses and Grasslands: Systematics and Ecology. University of Oklahoma Press, Norman, Oklahoma, USA.

Rice, E. L. 1984. Allelopathy. Second edition. Academic Press, New York, New York, USA.

Rice, E. L., and R. L. Parenti. 1978. Causes of decreases in productivity in undisturbed tall grass prairie. American Journal of Botany 65:1091-1097.

Rice, E. L., W. T. Penfound, and L. M. Rohrbaugh. 1960. Seed dispersal and mineral nutrition in succession in abandoned fields in central Oklahoma. Ecology 41:224-228.

Risser, P. G. 1985. Grasslands. Pages 232-256 in B. F. Chabot and H. A. Mooney, editors. Physiological Ecology of North American Plant Communities. Chapman and Hall, Ltd., London, England.

Risser, P. G., E. C. Birney, H. D. Blocker, S. W. May, W. J. Parton, and J. A. Wiens. 1981. The True Prairie Ecosystem. Hutchinson Ross Publishing Co., Stroudsburg, Pennsylvania, USA.

Risser, P. G., J. R. Karr, and R. T. T. Forman. 1984. Landscape ecology: directions and approaches. Illinois Natural History Survey Special Publication No. 2, Champaign, Illinois, USA.

Rock, H. 1981. Prairie propagation handbook. Sixth edition. Milwaukee County Department of Parks, Recreation and Culture, Wehr Nature Center, Whitnall Park, Hales Corners, Wisconsin, USA.

Roe, F. G. 1951. The North American buffalo: a critical study of the species in its wild state. University of Toronto Press, Toronto, Ontario, Canada.

Russell, E. W. 1973. Soil conditions and plant growth. Tenth edition. Longham, London, England.

Sauer, C. O. 1950. Grassland climax, fire, and man. Journal of Range Management 3:16-21.

Schramm, P. 1970. A practical restoration method for tall grass prairie. Pages 63-65 in P. Schramm, editor. Proceedings of a Symposium on Prairie and Prairie Restoration. Knox College, Galesburg, Illinois, USA.

_____. 1978. The "do's" and "don'ts" of prairie restoration. Pages 139-150 in D. C. Glenn-Lewin and R. Q. Landers, Jr., editors. Proceedings of the Fifth Midwest Prairie Conference, August 22-24, 1976. Iowa State University, Ames, Iowa, USA.

Schulenberg, R. 1970. Summary of Morton Arboretum prairie restoration work, 1963-1968. Pages 45-46 in P. Schramm, editor. Proceedings of a Symposium on Prairie and Prairie Restoration. Knox College, Galesburg, Illinois, USA.

Singh, J. S., W. K. Lauenroth, and D. G. Milchunas. 1983. Geography of grassland ecosystems. Progress in Physical Geography 7:46-80.

Smith, D. 1975. Forage management in the north. Third edition. Kendall/Hunt Publishing Company, Dubuque, Iowa, USA.

Smith, J. R., and B. S. Smith. 1980. The prairie garden: seventy native plants you can grow in town or country. University of Wisconsin Press, Madison, Wisconsin, USA.

Smyser, C. A. 1982. Nature's design: a practical guide to natural landscaping. Rodale Press, Emmaus, Pennsylvania, USA.

Sperry, T. M. 1935. Root systems in Illinois prairie. Ecology 16:178-202.

Sprague, H. B., editor. 1974. Grasslands of the United States: their economic and ecologic importance. Iowa State University Press, Ames, Iowa, USA.

Stebbins, G. L. 1981. Coevolution of grasses and herbivores. Annals of the Missouri Botanical Garden 68:75-86.

Steiger, T. L. 1930. Structure of prairie vegetation. Ecology 11:170-217.

Steuter, A. A. 1987. C_3/C_4 production shift on seasonal burns--northern mixed prairie. Journal of Range Management 40:27-31.

Stevenson, A. J., directing editor. 1972. Webster's new geographical dictionary. G. & C. Merriam Co., Springfield, Massachusetts, USA.

Teeri, J. A., and L. G. Stowe. 1976. Climatic patterns and the distribution of C_4 grasses in North America. Oecologia 23:1-12.

Transeau, E. N. 1935. The prairie peninsula. Ecology 16: 423-437.

Turkington, R., and L. W. Aarsen. 1984. Local-scale differentation as a result of competitive interactions. Pages 107-127 in R. Dirzo and J. Sarukhan, editors. Perspectives on Plant Population Ecology. Sinauer Associates, Sunderland, Massachusetts, USA.

United States Geological Survey. 1970. The national atlas of the United States of America. U.S. Department of the Interior, Washington, D.C., USA.

Vestal, A. G. 1949. Minimum areas for different vegetations, their determinations from species-area curves. Illinois Biological Monographs 20(3):1-129.

Weaver, J. E. 1954. North American prairie. Johnsen Publishing Co., Lincoln, Nebraska, USA.

Weaver, J. E., and F. W. Albertson. 1943. Resurvey of grasses, forbs, and underground plant parts at the end of the great drought. Ecological Monographs 13:63-117.

Weaver, J. E., and F. W. Albertson. 1956. Grasslands of the Great Plains. Johnsen Publishing Co., Lincoln, Nebraska, USA.

Weaver, J. E., and T. J. Fitzpatrick. 1934. The prairie. Ecological Monographs 4:109-295.

Weaver, J. E., L. A. Stoddart, and W. Noll. 1935. Response of the prairie to the great drought of 1934. Ecology 16:612-629.

Wells, P. V. 1970. Historical factors controlling vegetation patterns and floristic distributions in the Central Plains region of North America. Pages 211-221 in W. Dort, Jr. and J. K. Jones, Jr., editors. Pleistocene and Recent Environments of the Central Great Plains. Department of Geology, University of Kansas, Special Publication 3, Lawrence, Kansas, USA.

Wright, H. A., and A. W. Bailey. 1982. Fire ecology: United States and southern Canada. John Wiley and Sons, New York, New York, USA.

Wright, H. E., Jr. 1968. History of the prairie peninsula. Pages 78-88 in R. E. Bergstrom, editor. The Quaternary of Illinois. University of Illinois, College of Agriculture Special Publication No. 14, Urbana, Illinois, U.S.A.

Yonker, C., and D. S. Schimel. 1986. Geomorphology and grassland biogeochemistry (Abstract). Page 361. Program of the Fourth International Congress of Ecology, August 10-16, 1986, Syracuse, New York, USA.

Burton, P.J., Robertson, K.R., Iverson, L.R., Risser, P.G., 1988. Use of resource partitioning and disturbance regimes in the design and management of restored prairies. In: Allen, E.B. (Ed.), The Reconstruction of Disturbed Arid Lands: An Ecological Approach. Westview Press, Inc., Boulder, CO, pp. 46-88.

REPRINTED FROM:

The Reconstruction of Disturbed Arid Lands

An Ecological Approach

Edited by Edith B. Allen

AAAS Selected Symposium **109**