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Managing Species Diversity in Tallgrass Prairie: Assumptions and Implications

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Abstract: *Conservation and restoration ecology efforts may conserve or restore a particular image of a community, a variety of plausible images, or maximum biological diversity. The choice is a policy decision that should reflect relevant history and sound science. Here I argue that common methods of conserving and restoring tallgrass prairie have a weak scientific rationale, are not consistent with plausible history, and threaten prairie biodiversity. Dormant-season burns and grazer exclusion are human interventions that may promote artificially consistent dominance of large grasses utilizing the C₄ photosynthetic pathway, thereby relegating hundreds of other prairie plants to small populations that are vulnerable to local extinction. I recommend an experimental approach to large remnant conservation and restoration in which varied conditions alter dominance, thereby increasing short-term species richness. I also recommend prescribed burning during the summer, to simulate the timing of lightning fire, and light-to-moderate grazing by different ungulates, to simulate historical grazing history. Both should favor plants that are consistently infrequent or rare in many managed prairies. Varied regimes of burn season, burn interval, and large-mammal grazing should promote greater overall species diversity and should more realistically represent varied conditions under which grassland taxa evolved.*

Manejo de diversidad específica en praderas de "Tallgrass":
Supuestos e implicaciones

Resumen: *Los esfuerzos de conservación y de la ecología de restauración pueden conservar o restaurar una imagen particular de una comunidad, una variedad de imágenes posibles, o la diversidad biológica máxima. La elección es una decisión de manejo que debería reflejar una historia relevante y una ciencia sólida. Yo sostengo que los métodos comunes de conservación y restauración de las praderas de "tallgrass" tienen un fundamento científico débil, no son consistentes con una historia plausible y ponen en peligro la biodiversidad de la pradera. La quema durante la estación latente y la exclusión del pastoreo son intervenciones humanas que podrían promover artificialmente la dominancia consistente de pastos altos utilizando la ruta fotosintética del C₄, y, por consiguiente, relegando cientos de otras plantas de las praderas a pequeñas poblaciones que son vulnerables a la extinción local. Yo recomiendo una aproximación experimental a la conservación y restauración de grandes remanentes en los cuales, diversas condiciones alteran la dominancia y por consiguiente incrementan la riqueza de especies a corto plazo. También recomiendo el tratamiento de quemadas durante el verano para simular el tiempo de ignición y duración del fuego a los efectos de moderar el pastoreo por diferentes ungulados y así simular la historia de pastoreo. Ambos deberían favorecer plantas que son consistentemente poco frecuentes o raras en muchas de las praderas bajo manejo. Regímenes diversificados de estación de quema, intervalos de quema y pastoreos por grandes mamíferos debería promover una mayor diversidad global de especies y representar más realísticamente las condiciones variadas bajo las cuales los taxones de praderas evolucionaron.*

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Introduction

As recently as 300 years ago tallgrass prairies occupied more than 570,000 km² of the central North American continent, extending from Nebraska and Kansas east through the "Prairie Peninsula" to Ohio and western Pennsylvania (Transeau 1935; Risser et al. 1981; Stuckey & Reese 1981; Anderson 1990). Tallgrass developed through the interaction of drying climate, grazing by ungulates, and fire set by lightning or people (Sauer 1950; Wells 1970; Pyne 1982, 1986; Webb 1983; Axelrod 1985; Anderson 1990). At issue in this paper are prescribed burn schedules and grazer exclusion used to conserve and restore prairies. I ask whether they reflect plausible historical forces or a convention that creates a simplified anthropogenic tallgrass community that may ultimately threaten prairie biodiversity.

Human intervention helped create, eliminate, and shape what we know as eastern tallgrass prairie. Native Americans expanded the "Prairie Peninsula" by setting fires that killed woody vegetation and precluded ecological succession to forest. Within the last 200 years, cultural practices converted more than 99% of tallgrass prairies to intensive agriculture, eliminated most antelope and bison herds, added livestock, altered water tables, suppressed natural fire, prescribed dormant-season fire, and dissected prairie remnants with roads, railways, and other cultural barriers to fire and movements of wild or domestic ungulates. Two controlling factors in tallgrass ecology—fire and large-ungulate grazing—were eliminated or placed under direct human control.

Tallgrass prairies must now be managed to be preserved. Government agencies, environmental groups, and individuals protect prairie remnants and restorations from woody succession with prescribed "dormant-season" burns set in autumn, winter, or early spring for convenience (McClain 1986), for aesthetics (Rock 1981), to simulate Native American practices (Hulbert 1973), or to promote large grasses utilizing the C_4 photosynthetic pathway (C_4 grasses) to simulate "presettlement" prairie (Ehrenreich & Aikman 1963). Tallgrass remnants are also often protected from grazing for logistical reasons or to maximize growth and presence of C_4 grasses that are preferentially grazed by livestock (see Weaver 1954, 1968; Penfound 1964; Hazel 1967). Much of what is known of tallgrass prairie is from remnants or restorations burned in the dormant seasons and protected from grazing.

The question is whether several hundred native prairie species are well served by dormant-season fire and grazer exclusion that promote consistent dominance of a few taxa, thereby relegating most species to small populations that over time may be vulnerable to local extinction. In the absence of much experimental evidence, varied management regimens, or a theoretical rationale

for dormant-season fire and grazer exclusion, this question is unanswerable. Analysis of assumptions and implications of current practice and alternatives does suggest how experimental conservation and restoration might provide answers.

The Point of Prairie Conservation and Restoration

A central question in conservation and restoration should be "What is to be conserved or restored?" Should managers maintain or re-create a particular image of presettlement prairie climax determined by soil, hydrology, and climate? Or should their goals include several historically plausible images of grassland communities? Or should their objective be to maximize grassland species diversity for its own sake?

Each approach may result in quite different species abundance distributions if fire season or ungulate grazing constitute "top-down" forces that alter composition in a hierarchical fashion (see Hunter & Price 1992; Power 1992; also Pickett et al. 1989), or even if individual species respond differently to fire season, grazing, or their interactions (Gleason 1926, 1927; Glenn-Lewin 1980). The resulting assemblages could be dominated by a variety of species, depending on the interaction of chance and the conditions imposed.

Conscious goal selection is important because unexamined convention could favor communities that are historically implausible and depauperate. For instance, if dormant-season fires and ungrazed grassland were rare during the 30 million years over which prairie taxa evolved, a convention employing both might promote dominance patterns that consistently relegate many species to low populations and idiosyncratic local extinction (MacArthur 1972). With more realistically varied conditions, many suppressed species might be far more common.

Alternatively, re-establishment of a variety of historically plausible dominance structures could maintain far higher species diversity by favoring currently infrequent and rare species. A further effort to maximize species diversity could impose a variety of conditions that favor the widest variety of species, including such commonly employed practices as dormant-season burns that rarely occur unless humans set them.

I recommend a shift in objectives. The shift should be away from re-creation of presettlement communities shaped by anthropogenic practices and depleted ungulate populations just before and during European colonization. The shift should be toward methods that encourage the varied conditions that favored many prairie taxa over their 30 million year evolution.

Assumptions and Implications

Four largely unexamined premises underlie current tallgrass conservation and restoration practices: (1) "Tallgrass prairie" is a coherent assemblage of plants dominated by late-flowering C_4 grasses and forbs defined by a few indicator species; (2) Fire itself, rather than fire season, is the treatment for maintaining or encouraging tallgrass prairie; (3) Ungrazed prairie is a legitimate goal of tallgrass management; and (4) Maintenance of a C_4 grass climax maximizes species richness.

Premise 1: Tallgrass prairie as a coherent assemblage. Tallgrass prairie is classified by a few dominant C_4 grasses, such as *Andropogon-Panicum-Sorghastrum* "True Prairie" of the eastern Great Plains or the *Quercus-Andropogon* "Forest Type" of the upper Midwest (tallgrass savanna; see Risser et al. 1981). Nonwoody components of tallgrass remnants are dominated by such warm-season C_4 grasses as *Andropogon gerardii*, *Panicum virgatum*, *Sorghastrum nutans*, and *Schizachyrium scoparium* and such warm-season forbs as mints (Lamiaceae: including species of *Monarda*, *Pycnanthemum*) and sunflowers (Asteraceae: including many species of *Aster*, *Helianthus*, *Silphium*, *Solidago*). Weaver (1968:55–57) found that ungrazed tallgrass prairie had a mean cover of late-flowering species in Iowa > 95%; in Nebraska > 85%; and in Kansas > 98%. Anderson and Adams (1981) reported that half of the species in an Oklahoma prairie flowered early, but were rare, while half flowered late and covered 91% of the area. Tallgrass prairie is defined by key dominants of a late-flowering phenological guild of grasses and forbs.

Historical highlights. Tallgrass prairie developed within the last 5000–9000 years during the most recent interglacial period (Axelrod 1985). Fossil pollen and bones indicate that communities of earlier interglacial periods often did not resemble each other or present forests or grasslands (Davis 1976, 1981, 1986; Graham 1986). Earlier Tertiary grasslands were more varied than treeless plains of recent centuries. Enormous ungulate assemblages, perhaps exceeding those of Africa today, suggest a varied and dynamic mix of steppe, savanna, and forest 5–15 million years ago (Kurten 1971; Webb 1983; Anderson 1984; Guthrie 1984). The "true prairie" of today is one of many grassland and savanna permutations likely to have occurred in the recent and distant past.

Species representation. Dominant species are not good predictors of other species in prairie flora. Prairie remnants harbor up to 350 species of vascular plants (Hill & Platt 1975; Risser et al. 1981:56). As Curtis (1959) notes, the preeminence of four common grasses in Wisconsin prairies predicts little about the distribution or abundance of hundreds of other prairie grasses and forbs. Absence of close associations between par-

ticular dominants and particular subdominants suggests loosely defined communities of circumstance or unpredictable species loss to local extinction.

Most ecologists associate prairies with a few late-flowering grasses and forbs, but published species lists give a different picture (Table 1; see Gleason 1963a, 1963b, 1963c; Swink & Wilhelm 1979; Mohlenbrock 1986). In Illinois, tallgrass prairie includes at least 358 species of grasses (41), sedges (22), and forbs (295) identified by authorities as routinely occurring in "prairies" and 317 additional species of grasses (41), sedges (42), and forbs (234) identified by the same authorities as occurring in such nonprairie habitats as meadows, pastures, and fields. These categories are not exclusive because "prairie" plants occur in other habitats and "nonprairie" plants occur in prairies.

Characteristics of the entire flora defy stereotypes in other ways. Most Illinois prairie species are not late-blooming, despite the statistically peculiar late-blooming dominants (Table 1). Here species are early-flowering if flowering is completed before mid-July when lightning fires become common, mid-flowering if flowering spans at least June, July and August, and late-flowering if flowering occurs after mid-July. Of prairie species in Illinois, 133 (37%) flower early, 99 (28%) flower through the middle of the season, and 126 (35%) flower late. If it were not for 16 grasses (4%) and 64 members of the Asteraceae (18%), the overwhelming majority of prairie species would flower in early or mid-season. A random sample of 12 species from each large family eliminates the bias of large numbers, preserving the flowering disposition of each taxon (Table 1, parentheses). Totals for each flowering season of this random sample suggest, if anything, a bias toward early flowering even within large and successful prairie families. The lesson is that current ecological conditions favor late-flowering grasses and sunflowers far out of proportion to their representation in species lists.

Table 1. Comparison of flowering phenologies of families with at least 12 prairie species.*

Family	Early Season	Midseason	Late Season
Asclepiadaceae	5 (5)	7 (7)	0 (0)
Asteraceae	13 (1)	5 (0)	64 (11)
Cyperaceae	14 (9)	7 (2)	1 (1)
Fabaceae	13 (5)	4 (2)	8 (5)
Lamiaceae	5 (3)	12 (8)	5 (1)
Liliaceae	11 (8)	1 (1)	3 (3)
Poaceae	8 (1)	17 (5)	16 (6)
Scrophulariaceae	10 (6)	3 (3)	5 (3)
Total	79 (38)	56 (28)	102 (30)

* In parentheses are random samples of 12 species from each large family shown to eliminate the bias of large numbers and to preserve the flowering disposition of each taxon. Sources of flowering times: Gleason (1963a, 1963b, 1963c); Swink & Wilhelm (1979); Mohlenbrock (1986).

Other taxa are poorly represented in cover analyses and may have declined in representation. Disproportionate numbers of early-flowering plants are in 34 species-poor families (<12 prairie species per family) compared with eight species-rich families (≥ 12 prairie species per family; Tables 1 and 2, $X^2 = 20.11$, $df = 2$, $p = 0.001$). Inspection shows that 28 of the 34 species-poor families hold less than six prairie species. Early species are both rare, as shown by cover analyses, and are in taxa of low and perhaps diminishing diversity in prairies.

The Illinois flora also includes at least 316 species usually identified with fields, meadows, pastures, and other nonprairie grasslands. In the absence of strict prairie endemism, these are likely to be at least occasional colonists of managed or restored prairies. Of these species, 74 (23%) flower early, 134 (42%) flower through the middle of the season, and 109 (34%) flower late, showing that nonprairie grassland species tend to flower

Table 2. Comparison of flowering phenologies of families with less than 12 prairie species.

Family	Early Season	Mid-season	Late Season
Acanthaceae	0	1	0
Apocynaceae	1	2	0
Boraginaceae	5	1	0
Brassicaceae	4	1	0
Burmanniaceae	0	0	1
Caesalpiniaceae	0	0	1
Campanulaceae	0	1	1
Caryophyllaceae	1	1	1
Commelinaceae	2	1	0
Convolvulaceae	1	1	1
Euphorbiaceae	0	4	2
Gentianaceae	0	0	7
Geraniaceae	1	0	0
Iridaceae	7	0	0
Juncaceae	0	2	3
Mimosaceae	0	1	0
Nyctaginaceae	0	1	2
Linaceae	0	2	0
Orchidaceae	2	2	1
Orobanchaceae	0	1	0
Oxalidaceae	1	1	0
Papaveraceae	1	1	0
Plantaginaceae	0	1	0
Polemoniaceae	1	2	0
Polygalaceae	0	2	2
Primulaceae	1	2	0
Ranunculaceae	8	1	0
Rosaceae	5	1	1
Rubiaceae	7	1	0
Santalaceae	0	1	0
Saxifragaceae	3	0	0
Solanaceae	1	3	1
Valerianaceae	2	0	0
Verbenaceae	0	5	0
Total	54	43	24

Sources of flowering times: Gleason (1963a, 1963b, 1963c); Swink & Wilhelm (1979); Mohlenbrock (1986).

later than prairie species ($X^2 = 20.91$, $df = 2$, $p < 0.001$).

Which species would gain from conditions that favored early-season plants? Of the 675 species listed in Illinois grasslands, 207 (31%) flower early. Most (64%) are native prairie species now in low frequencies and cover. Management practices that favor early-season species should favor native prairie species, in addition to some early-season native or alien species from the "non-prairie" grasslands.

Premise 2: Fire as the treatment

Fire often determines whether prairie or forest exists in the central United States (see Curtis 1959; Daubenmire 1968; Hulbert 1969; Old 1969; Wells 1970; Risser et al. 1981). Numerous studies show that fall or spring burns kill woody seedlings or saplings and otherwise promote increased productivity of many prairie forbs and grasses (see Hulbert 1969, 1986, 1988; Old 1969; Hill & Platt 1975; Peterson 1983; Knapp 1984, 1985; Knapp & Scastedt 1986; Collins 1987; Collins & Wallace 1990). Annual spring burns favor late warm-season grasses, while longer intervals favor forbs (Hulbert 1986). The argument that fire slows woody succession and stimulates currently dominant prairie vegetation is beyond serious dispute.

What should be disputed is whether dormant-season or early spring burns have a historical rationale or serve the entire tallgrass biota well. Perhaps because the overriding effect of fire is usually seen to be elimination of woody vegetation and stimulation of large late-season C_4 grasses, fire or fire interval rather than the seasonal timing of fire is the perceived treatment in prescribed burns for management and in experimental prairie ecology. The first critical question is whether the fire season influences prairie floristics. If so, which fire seasons are desirable for the goals management sets?

Effects of fire season. It would be surprising if the seasonal timing of fire did not change the competitive relations of plants. An April fire should destroy early foliage critical for root production of cool-season plants, leaving late-season plants unscathed (Fig. 1). An August fire should burn the largely inactive foliage of early-season species and spare their spring and autumn growth, but it should destroy foliage, maturing reproductive organs, and capacity for root elaboration of warm-season grasses that compete with early-season species (see Tieszen et al. 1980; Barnes et al. 1983). Early-growing species set back by fire in April or May should yield to later-growing species not so disadvantaged, while later-growing species with shoots destroyed by midsummer fire should compete less well against early species that often have already finished growth and reproduction for the year.

Moreover, fire season could have idiosyncratic ef-

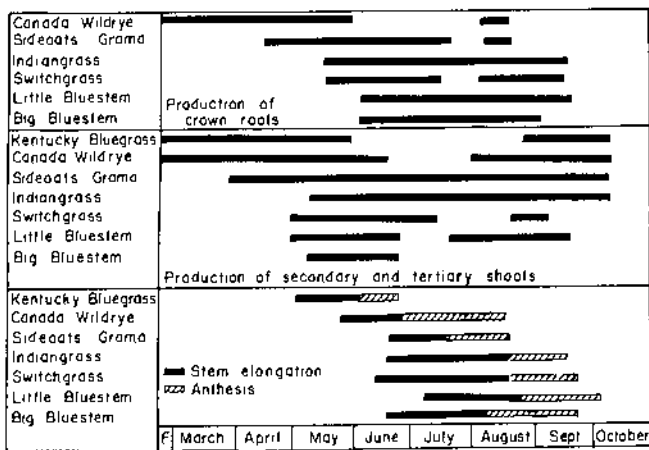


Figure 1. Seasonal development of roots, shoots, and anthesis in seven Tallgrass Prairie species. From Neiland and Curtis (1956); copyright 1956, The Ecological Society of America.

fects. Fire season could affect prairie composition if species respond differently to removal of thatch or to warmed soil, if seeding phenologies or germination requirements differ, or if some recruit from rhizomes better than others after burns in different months. For predictable or idiosyncratic reasons, prairies burned in the growing season should differ markedly from those burned at other times of the year.

Recent studies illustrate several seasonal burn effects on grass and forb communities. Despite substantial site and yearly differences, fire season is known to affect the following:

- (1) Reproductive activity of grasses and forbs. A review by Glenn-Lewin et al. (1990) shows that early spring burns increase flowering in many warm-season species (up to 3700% in *Andropogon gerardii*, 150% in *Panicum virgatum*, and 73% in *Solidago canadensis*) while depressing flowering of early species (to -70% in *Poa pratensis* and -186% in *Dodecatheon meadia*). Henderson et al. (1983) and Lovell et al. (1983) show that the timing of the burn during the spring (March/April versus May) affects grass and forb flowering. Platt et al. (1988) found that summer fires increased flowering activity of late-flowering forbs in southern pine understory.
- (2) Seedling recruitment. Glenn-Lewin et al. (1990) found that seedling recruitment amounted to 0.5 to 0.9 per square meter in established prairie, while June and August burns produced 5-10 monocot and 100-150 dicot seedlings/m².
- (3) Tiller production. Glenn-Lewin et al. (1990; also Svejcar 1990) reported that tiller production increased the year after a June burn in late-flowering

Andropogon gerardii and *Sorghastrum nutans* but was repressed the year after an August burn. Cool-season *Poa pratensis* tiller production was higher a year following an August burn than after a June burn.

- (4) Cover of grasses and forbs. I found (Howe 1994) that early-season species gained after July burns, while late species were favored by March burns (Fig. 2). Early-season species response to summer fire was due to an increase in cool-season *Agropyron repens* (a weedy opportunist) and early-flowering *Rudbeckia hirta*, as well as by less common species. A retreat of late-flowering vegetation after summer fire was due to a precipitous drop of *Panicum virgatum*, as well as less common species. Biondini et al. (1989) demonstrated differences in diversity and composition of prairie forb communities in response to spring, summer, and fall burn and unburned treatments; several late species suffered from summer burns, while two early species (*Galium boreale* and *Lotus purshianus*) were stimulated by summer burns.

Lightning fire. Prior to human occupation of the continent, prairie fires were started by growing-season lightning storms (Komarek 1964, 1966, 1967, 1986; Vogl 1974; Higgins 1984, 1986; also Cope & Chaloner 1985), and dormant-season burns were probably rare. Most lightning storms, and most lightning-caused fires, occur in mid-summer (Komarek 1964; Bragg 1982; Higgins 1984). In the Northern Great Plains less than 1% of naturally occurring lightning fires occur in April, a fa-

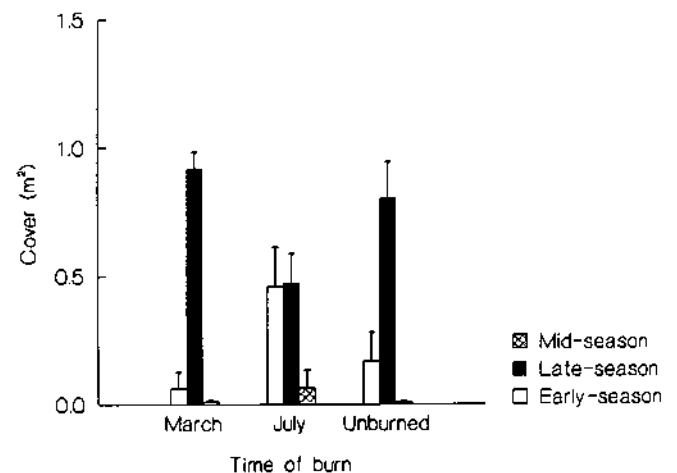


Figure 2. Effects of seasonal burns on cover of early-, middle-, and late-season flowering groups the year following a burn in a prairie restoration in which replicates received the same seeding density. From Howe (1994).

vored month for prescribed burns under modern management practices (Fig. 3). Prairie vegetation burns easily during the summer if litter accumulates for more than a season (Bragg 1982; Ewing & Engle 1988; Howe 1994), and Vogl (1974) notes that "dry lightning" occurs regularly on the Great Plains and that grassland dries so quickly that smoldering fires ignited by lightning can spread within hours after heavy rains. Where fires are unimpeded, lightning strikes can cause immense grassland and savanna fires. The Plum Fire of May 5, 1965 started by lightning (Wolfe 1972; Westover 1976) and burned more than 7300 hectares of Nebraska grassland and forest. Komarek (1966) points out that broad unstable fronts ignite dozens of lightning fires as they traverse the continent, from the southern to the northern plains and across the Midwest. Where extensive grasslands and savannas exist, most wildfires are still caused by summer lightning storms (Komarek 1964; Gipe 1974; Vogl 1974). When fuel was more abundant and fire suppression did not exist, such annual events probably spawned summer fires throughout the Prairie Peninsula.

Fire suppression, habitat fragmentation, and reduction of fuel by heavy livestock grazing and dormant-season burns make lightning fire less and less likely (Vogl 1974). On the Great Plains, active suppression and habitat fragmentation allowed only two of 293 summer lightning fires to exceed several hundred hectares (Higgins 1984). In what are now Iowa, Illinois, Wisconsin, Indiana, and Ohio, almost all (>99%) tallgrass habitat has been converted to inflammable corn, soybeans, forest, and pasture. The remainder is broken by roads or

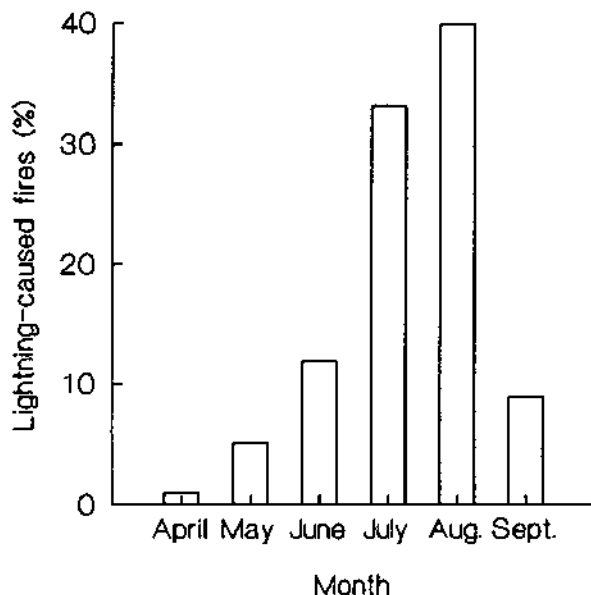


Figure 3. Seasonal distribution of 293 lightning fires in grassland and savanna on the northern Great Plains. Data from Higgins (1984).

is fuel-deficient due to commercial grazing or management by dormant-season burns. These cultural factors leave small targets for dry-lightning strikes and limit the spread and effect of whatever summer fires do start. If prehuman (<15,000 years BP) storm seasonality resembled the present in North America, it appears inescapable that wildfire was summer lightning fire over millions of years of grassland history.

Widespread summer prairie fire affects the historical justification for what should be conserved or restored. Higgins (1984) predicted that a higher percentage of lightning fires during summer than anthropogenic burns during the dormant seasons should favor short over tall species and cool-season over warm-season grasses. Before human intervention, North American grasslands probably often were shorter and in many places included a number of common or even dominant cool-season taxa.

Premise 3: Ungrazed prairie as an objective.

Many large herbivorous mammals evolved on North American steppes and savannas during the 30 million years prior to human settlement (Kurten 1971; Webb 1983). Grazer diversity in the fossil record rises dramatically from 15 to 7 million years ago, when grazers accounted for well over half of 40 large ungulate genera in North America (Fig. 4). Ten million years ago nine genera of grazing horses coexisted with three genera of browsing horses, which soon became extinct. The mix and variety of North American rhinos, horses, camels, mastodons, mammoths, antelope, deer, and bison at least equalled present African faunas, only giving way to a depauperate assemblage of bison, antelope, and deer (including elk) during the last ice age. Mack and Thompson (1982) and Milchunas et al. (1988) note that a preponderance of rhizomatous plant species resistant to grazing on the Great Plains indicates that heavy grazing persisted into recent millennia.

It follows that tallgrass taxa evolved under conditions unlike the immediate past of human occupation of less than 15,000 years—one two-thousandth of the evolutionary period in question—and quite different from the 300 years of European settlement. Tallgrass species apparently evolved under a far greater diversity of habitats than the vast savannas and treeless plains immediately prior to human settlement. Paleobiologists guess that large ungulates coexisted in a mosaic of forest, woodland park, marsh, savanna, grassland, and scrub (Guthrie 1984; Axelrod 1985; Janzen 1986) in densities of 20–30 animals/km² (calculated from Martin 1973). Not surprisingly, grass fossils from the Tertiary are dominated by such armed genera as *Aristida* and *Stipa* (Elias 1942). Monotonous steppe became common within the last 2–5 million years, resulting in losses of ungulate

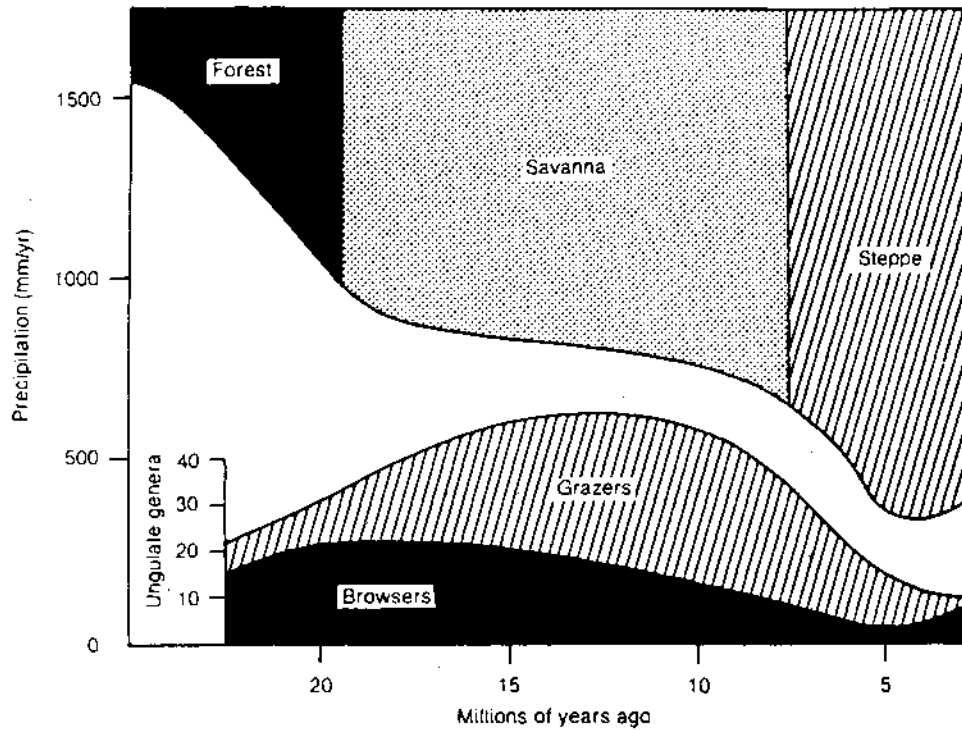


Figure 4. Shift from browsing to grazing ungulate genera in central North America. From Webb (1983).

niches and most of the large mammalian fauna (Webb 1983). Present tallgrass prairie assembled more recently in response to a warming and drying continental climate, declining grazer diversity, and anthropogenic fire.

Finally, experimental evidence suggests how heavily grazed primeval grasslands might have differed from ungrazed tallgrass. Ungrazed tallgrass, like subhumid African savanna, loses plant diversity if tall dominants are permitted to exclude smaller species ("vegetative stagnation" of McNaughton 1993). In the Serengeti grassland, which is comparable in productivity to American tallgrass prairie, wildlife exclosures result in greater dominance and reduced species diversity (McNaughton 1979a: Table 3.2; Belsky 1986a, 1986b). In southwestern Oklahoma, fenced mixed-grass prairies increase in dominance and reduce diversity parallel to the Serengeti experiments (Collins & Barber 1985). Short of intense overgrazing, ungulates increase plant diversity by reducing dominance and altering competitive dynamics.

How do animals change plant species composition? First, animals eat different seeds or foliage, thereby reducing competition for species they do not prefer. This starts with a preference by rodents for larger rather than smaller seeds, which can dramatically alter plant species composition in grasslands and deserts (Batzli & Pitelka 1970; Borchert & Jain 1978; Brown et al. 1986; Brown & Mitchell 1989; Brown & Heske 1990). Larger herbivores then feed preferentially on different plant foliage, often changing dominance and thereby altering the rel-

ative abundance of subdominants (see Fig. 5). Sometimes grazers reduce overall dominance, thereby increasing overall species diversity. Grazing preference varies with idiosyncracies of species and size (Jarman & Sinclair 1979; Van Soest 1982; Howe & Westley 1988; Hofmann 1989). Prairie dogs, bison, and pronghorn all alter the composition of contemporary grasslands by feeding on different species in the same localities (Bonham & Lerwick 1976; Uresk & Bjugstad 1980; Coppock et al. 1983a, 1983b; Collins & Barber 1985; Krueger 1986; Whicker & Detling 1988). Consequently, the relative abundance of mammalian herbivores affects the composition and relative abundance of plant species.

Second, animals may change the structure of the community by disturbing the soil or by eliminating some life forms. Badgers (Platt 1975) and bison (Collins 1987) create patches of open ground through burrows or wallows, creating habitats for plant species that otherwise would be crowded out. At the other extreme, African elephants (probably like pre-Pleistocene and Pleistocene relatives in North America) frequently convert forest to grassland by killing trees (Mulkey et al. 1984). Such activities do more than change dominance structure, they change entire communities.

Finally, historical ungulate assemblages were not confined, adding stochasticity to grassland development that is less evident in ungrazed prairies, small remnants, and fenced pastures. Confined grazers must eat whatever is within the fence, constraining foraging choices

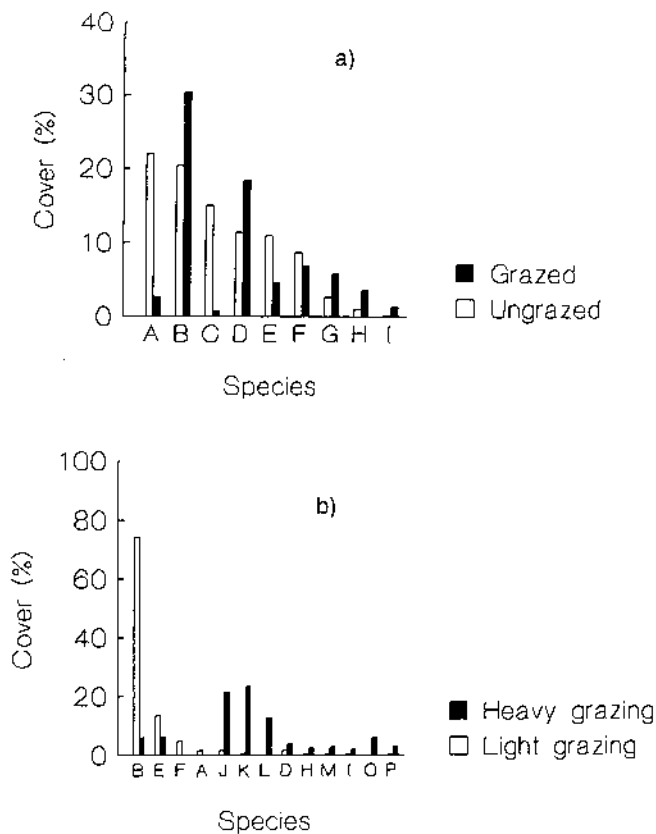


Figure 5. Canopy cover in Oklahoma prairie under different grazing regimes: grazed by cattle or ungrazed (a; data from Penfound 1964) and heavy or light grazing by cattle (b; data from Hazel 1967). Both sites share many species, but rank order differs with treatment: species ranked from ungrazed Penfound data—A = *Panicum virgatum*, B = *Schizachyrium scoparium*, C = *Symphoricarpos orbiculatus*, D = *Bouteloua curtipendula*, E = *Andropogon gerardii*, F = *Sorghastrum nutans*, G = *Leptoloma cognatum*, H = *Panicum Scribnerianum*, I = *Paspalum pubescens*; and species ranked from Hazel data J = *Buchloe dactyloides*, K = *Sporobolus asper*, L = *Andropogon saccharoides*, M = *Bouteloua gracilis*, N = *Chloris verticillata*, O = *Carex spp.*

and seasonal movements (Senft et al. 1987). Unconfined animals seek preferred food wherever it is common, leading to spatial, temporal, and seasonal variability in animal movements due to water availability, climate, predation, and abundance of highly preferred forage (see McNaughton 1976, 1983, 1985; Senft et al. 1987). Dramatic variations in consumption for reasons that are only tangential to short-term foraging optimization increase the role of chance in animal effects on prairie composition.

There is overwhelming reason to expect that ungrazed remnants and restorations develop differently than comparable grazed areas, and ample justification to

expect that variations in the abundances of different seed-eating and folivorous vertebrates affect plant succession. Perhaps the best insights into ancient communities will come from experimental approaches to restoration and conservation that determine how different vertebrates influence plant-species abundance distributions.

Premise 4: Tallgrass prairie as a static image.

The concept of a climax tallgrass community is deeply rooted in historical views of stable, self-replacing communities (see Clements 1916). In modern terms, such a perspective may predict a single equilibrium community under given climatic conditions (see Westoby et al. 1989; Laycock 1991), quite likely represented in restoration and conservation biology as a "Prime Directive" that unconsciously imposes a sentimental monotony on a community that otherwise would take many forms (Brown 1994). There are overwhelming theoretical and empirical reasons to doubt the sufficiency of a static image of tallgrass ecology.

Relative abundances of species offer standards for community comparisons. Ecological communities have truncated log-normal species abundance distributions with a few very common species, many more of intermediate abundance, and a large number of rare species represented by one or a few individuals (Preston 1948, 1962; Magurran 1988). The pattern holds for taxa as different as birds (Preston 1948), soil mites (Hairston 1969), moths at lights (Ricklefs & O'Rourke 1975), and tropical trees (Hubbell & Foster 1983). Cloning makes counts of individual prairie plants difficult, but Curtis (1959) notes that species incidence in prairies invariably shows a few very common species and over 250 species that are infrequent or rare.

Sharply skewed species abundance distributions have well-known implications for maintenance of biodiversity because small populations are prone to idiosyncratic local extermination (Preston 1962; MacArthur & Wilson 1967; MacArthur 1972; Appendix 1). To the degree that the same species consistently occupy most space in a set of replicated communities, all other species are consistently infrequent or rare and consistently subject to local extinction.

For example, the frailty of a static image of tallgrass prairie is evident from the ease with which factors such as grazing and fire season change species abundance distributions.

Grazing by livestock alters species abundance distributions (Fig. 5; also references in Belsky 1986a, 1986b; McNaughton 1993; West 1993). Light grazing depresses but does not eliminate some warm-season dominants of ungrazed prairies, such as *Panicum virgatum* and *Andropogon gerardii*, thereby favoring other warm-season grasses such as *Schizachyrium scoparium* and *Boute-*

Ioua curtipendula, as well as cool-season grasses such as *Panicum Scribnerianum*, that otherwise occur only in trace densities (Penfound 1964). Heavy grazing strongly depresses *S. scoparium* and *A. gerardii* in favor of native species that otherwise would barely exist in these communities (Kelting 1954; Hazel 1967). Short of extreme overgrazing, partial suppression of aggressive dominants would be expected to increase short-term biodiversity.

Fire season also alters species abundance distributions (Fig. 6). In Wisconsin, Howe (1994) found that cover of species in 84 samples of one square meter in three restorations—unburned, burned in March, and burned in July—produced the expected strong dominance of 1–4 species, but the top dominant was different in each treatment (Fig. 6). Rankings of subdominants after summer burns differed sharply from rankings in other treatments. The pre-eminence of C_4 grasses was determined by their high seed densities at planting, so species that responded positively to a midsummer fire were opportunistic early-season weeds or a few native experimentals (such as *Rudbeckia hirta* and less common species). If present, more native early-season plants should fill the space taken by volunteers.

Such results do not suggest a singular coherent community, nor does contemporary ecological theory imply that such a community should exist. Contemporary variations of tallgrass prairies could reflect several stable states (see Laycock 1991), transitional communities on different successional trajectories (see Connell & Slatyer 1977; Connell 1978; Huston 1979; Westoby et al. 1989), or different stages of a successional process reset by fire or grazing (Connell 1978; Huston 1979; Lauenroth 1979). The “natural” state of tallgrass is variability in the composition of species that hierarchically or individually respond to changes in the environment. Neither history, theory, the experience of grazing managers, nor emerging experimental evidence allows much confidence in a management rationale based on a singular, static view of prairie composition.

Conclusion

History, recent experiments, and theory suggest that there is little compelling scientific argument for conservation or re-creation of a monotonous “tallgrass type.” Historical and experimental evidence suggests that tallgrass assemblages should be diverse, different from each other, and dynamic. Short-term manipulation of species abundance distributions and long-term use of historically plausible burn and grazing regimes may conserve or re-create a more species-rich tallgrass assemblage than would encouragement of consistent domination by a few C_4 grasses.

The practical issue is that in ecological communities

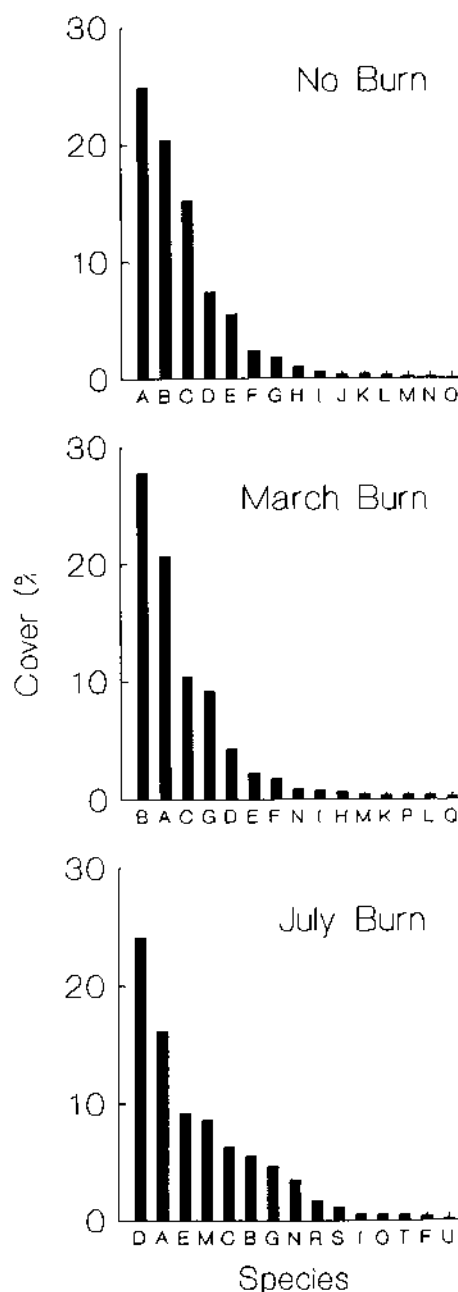


Figure 6. Cover of species one year after fire-season treatments of a prairie restoration in southern Wisconsin. Species ranked with reference to the unburned treatment: A = *Andropogon gerardii*, B = *Panicum virgatum*, C = *Solidago altissima*, D = *Agropyron repens*, E = *Phalaris arundinacea*, F = *Aster similis*, G = *Elymus canadensis*, H = *Solidago gigantea*, I = *Sorghastrum nutans*, J = *Solidago rigida*, K = *Rudbeckia subtomentosa*, L = *Rubus spp.*, M = *Rudbeckia hirta*, N = *Erigeron annua*, O = *Aster ericoides*; add March treatment: P = *Aster pilosus*, Q = *Cirsium arvense*; add summer treatment: R = *Oenothera biennis*, S = *Conyza canadensis*, T = *Achillea millefolium*, U = *Bromus inermis*. See Howe (1994) for further discussion.

some species are always common, while most are always infrequent or rare. A management ethic that favors occupation of a 80–95% of the space by the same 1–4 species—whether C_4 dominant grasses or others—will inexorably doom most species to idiosyncracies of local extinction. Over time, such a practice leaves the fate of a large majority of species to a lottery of chance variations in the environment that may or may not result in local extinction.

To maximize prairie biodiversity, a variety of species abundance distributions should be promoted. The decoupling of particular dominants from associations with particular less common plants precludes a precise prediction of composition under different treatments. A short-term strategy would increase richness by depressing dominance; a mixture of fire intervals, seasonal burns, grazing frequencies, and grazing intensities by different animals should produce the maximum species diversities within and between habitats. A long-term strategy including historically plausible growing-season burns and grazing should favor some species now eclipsed by large C_4 dominants. The point is to avoid uniformity of treatments that artificially simplifies what probably was once a far more varied set of communities than now exists.

This examination of assumptions and implications is preliminary because quantitative tests are rare. However, the extent to which current practice threatens diversity will not be known without experimental analysis of relevant processes. A rethinking of management priorities will be needed if such experiments continue to suggest that prairie biodiversity could be managed out of existence.

Recommendations

Recommendations for small threatened remnants would be premature, but enough is obvious to recommend a shift to experimental management of restorations and portions of large remnants. Useful principles might include:

- (1) Managers may use varied fire and feasible grazing regimes to decrease total dominance (by any species) and promote short-term increases in species richness. The key is variability of treatments, not historical plausibility of treatments (dormant-season burns and grazer exclusion may be useful in some treatments). However, novel dormant-season fire and protection from grazers should not be used to the exclusion of diverse forces that shaped grassland plant evolution.
- (2) Some treatments should encourage increases in abundance of native early-season and other species in a long-term strategy to favor plants cur-

rently suppressed by large C_4 dominants. Here historical plausibility is important: summer burns or light grazing in parts of large remnants harboring relict populations of native plants might consistently favor many rare species by putting aggressive C_4 dominants at a disadvantage. Restorationists should pay the extra expense of including a variety of early-season species in plantings; these now comprise a minor percentage of seed mixes because their seeds are more expensive than those of C_4 grasses and late forbs. Restorations that impose late-season C_4 dominance at planting without including early-flowering species risk opportunistic weeds under summer fire and grazing regimes.

Varied treatments and the experimental use of historically plausible growing-season burns and light to moderate grazing by different ungulates may be the best compromise between the present convention of dormant-season burns and grazer exclusion and management for maximum possible biodiversity. The goal should be to develop scientific rationales for restoration and conservation, rather than rely on unexamined convention.

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