EVOLUTION IN STEPPE WITH FEW LARGE, HOOVED MAMMALS

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Communities are organized through both the proximate and evolutionary constraints that shape the structure of populations and the interaction among species. Proximate constraints can be manipulated experimentally to assess the relative influence of a component species on the overall structure of a community, as in analyses of keystone (Paine 1969) or dominant species. These analyses are instructive in detecting how current selection pressures influence populations. Responses of species to current interspecific interactions, however, are not made in an evolutionary vacuum, but rather reflect the history of prior selection pressures that have molded the species' traits. Overall structure of some communities in turn may be influenced to a large extent by a few traits evolving in the most abundant species in response to continuous strong selection pressure. Assessment of the effect of these particular traits or suites of traits on community organization is difficult on an experimental basis as it necessitates removal of traits within species rather than species themselves (e.g., Windle and Franz 1979).

Grasses with their basal intercalary meristems are cited commonly as having evolved with large herbivorous mammals (Osborn 1910; Love 1959; Barnard and Frankel 1964). Yet temperate grasslands and specifically steppes differ greatly in the extent of habitation by large mammals throughout the Neogene and hence the plants in these grasslands differ in the extent to which they have traits adapted to large mammalian grazers. In this paper we consider the structure of steppes on either side of the Rocky Mountains in an attempt to understand how differences in the history of acquisition of mammal-selected traits by plants and interactions with mammalian grazers can influence overall grassland structure.

GRASSLANDS AND NATIVE LARGE HERBIVORES IN WESTERN NORTH AMERICA

The steppes dominated by perennial hemicryptophytic grasses east and west of the Rocky Mountains are referred to as the *Bouteloua gracilis* (dominated mainly by rhizomatous/stoloniferous species) and *Agropyron spicatum* (dominated by caespitose grasses) Provinces, respectively, by Daubenmire (1978b) (nomenclature throughout follows Hitchcock et al. 1969). The Tertiary antecedents of each Province formed with mountain uplift to the west, thereby diminishing the

influence of maritime air from the Pacific Ocean. With increasing aridity temperate mesophytic forest was supplanted east of the Rockies in early Tertiary, and in early Pliocene the area between the Cascade/Sierra Nevada Range in the Rocky Mountains also became dry (Axelrod 1948; Smiley 1963). The Cascade/Sierra Nevada Range, however, is not high enough to eliminate all maritime influence, so the moderating effect of the Prevailing Westerlies on climate persists in the Intermountain West (i.e., between the Rocky Mountains and Cascade/Sierra Nevada Ranges). As a result the physical environments of the two steppe provinces differ most notably in the distribution of annual precipitation which centers in early summer (the so-called June bulge) east of the Rockies rather than an autumn-winter precipitation pattern west of these mountains (Visher 1954).

There is virtually no Neogene fossil record of the grasses that arrived in the regions on either side of the Rockies. Consequently, interpretations of the time of emergence of grassland vegetation are largely inferred here as elsewhere from the mammalian faunal record (e.g., horse, camel; Webb 1977). *Agropyron, Poa,* and *Festuca* probably arrived in the Intermountain West from the north (Daubenmire 1975), but as Wolfe (1969) points out this does not necessarily indicate boreal origin, but perhaps only transit through northern North America from Eurasia.

Events in the Quaternary enhanced the differences between the biota of the two regions, especially in regard to the presence of large herbivorous mammals. Successive waves of *Bison* immigration coupled with extensive rapid evolution of *Bison* in North America resulted in quite different distributions for these large herbivorous mammals. East of the Rockies much of the ice-free midcontinent was occupied continuously by one or more taxa of *Bison. Bison* occurred throughout central and western North America during the time of Wisconsin glaciation (Guthrie 1970; Wilson 1978). After Wisconsin glaciation *Bison bison* proliferated in the *Bouteloua* Province and may have exceeded 40 million animals by the time of European contact (England and DeVos 1969). In contrast it seems unlikely that large herds of bison resided in the open steppe west of the Rockies (Durrant 1970; Gustafson 1972; Grayson 1977, in press). The few prehistoric records of bison on the Columbia Plateau of Washington and Oregon indicate a regional decline to virtual extinction since 2500 B.P. (Schroedl 1973).

Historical records substantiate the rarity of these animals throughout much of the *Agropyron* Province. For example, there are no confirmed reports of bison sightings by Europeans in the steppe of eastern Washington, although animals were seen repeatedly in the Upper Snake River Plain until mid-nineteenth century (Schroedl 1973; Butler 1978). At the southern limits of the province in northern Nevada and Utah, bison were equally rare or missing altogether according to the records of early naturalists (Steward 1938; Roe 1951). Reasons for the low numbers of bison west of the Rockies are diffuse, but the lack of accessibility of these grasslands is not in itself a convincing explanation of low numbers. Haines (1967) cites at least four avenues for probable bison immigration westward across the northern Rockies.

The phenology of the dominant plants in the intermountain grasslands, however, may have been an important constraint on bison numbers. Calving in bison occurs in late April through early June (Roe 1951; Shult 1972; R. A. Karges,

personal communication), as in other ungulates in the northern United States (e.g., Skinner 1922; Golley 1954; Peterson 1955). If milk production in bison is also similar to other ungulates, then maximum milk production probably occurs about 3 wk later (Robbins et al. 1981). This pattern is well suited to the staggered phenology of the C_3 and C_4 grass mixture in the *Bouteloua* Province, where different grasses are available to bison throughout the summer and the remainder of the year (Peden et al. 1974; Peden 1976). This pattern does not mesh easily with the growth cycle of the dominant C_3 grasses west of the Rockies, which aestivate during much of summer (table 1).

Perhaps small herds persisted in the steppe west of the Rockies only by withdrawing to sites of permanent water during the summer. Nevertheless, bison herds in recent time certainly did not reach the numbers seen in the Great Plains in the early nineteenth century. Elk and deer also occurred in these treeless communities (Rickard et al. 1977), but probably with similar restrictions.

Distribution of close ecological associates of large mammals in North America indicates further that the steppe communities west of the Rockies long have lacked herds of large herbivores. No native species of *Onthophagus*, a nearly worldwide genus of dung beetles occurs in the *Agropyron* Province. In contrast 34 species occur east of the Rockies (Howden 1966). With the shift in prominence from bison to cattle in the *Bouteloua* Province, native dung beetles persisted by using cattle dung (Hayes 1927). But in the *Agropyron* Province the dung deposited by large resident herds of alien bovids could not be rapidly assimilated by the native decomposers. As a result the alien *Onthophagus nuchicornis*, introduced into British Columbia, has been evaluated as a possible remedy to the problem (Macqueen and Beirne 1975). These events parallel closely the consequences of cattle introduction into arid Australia, which also lacked large ungulates in grasslands (Bornemissza 1960; Hughes 1975); the largest native mammalian grazers are red and Eastern grey kangaroos (Frith and Calaby 1969).

INTRODUCTION OF CATTLE

Cattle introduction provided much more than simply a demonstration of the deficiency of dung scavengers in the one province versus the other. In the *Bouteloua* Province one bovid essentially replaced another as cattle occupied the habitat in the grassland once occupied by exterminated bison. Bison and cattle are both predominantly graminoid feeders (Peden et al. 1974). Either in semiferal range herds or when pastured, cattle frequently congregate. Local site disturbance by cattle through pasturing is analogous to the reportedly severe grazing and "wallowing" seen in bison herds (Roe 1951; England and DeVos 1969). Particularly in terms of succession, only the specific agent and frequency of disturbance rather than the nature of the disturbance changed. Disturbed sites continue to be recolonized by predominately native annual dicots, or by aliens that are soon replaced by native perennials (most of which form a sod; Costello 1944; Weaver 1958; Quinn and Hervey 1970; fig. 1a). The alien *Poa pratensis* locally persists with intense disturbance on subirrigated sites (Branson 1953).

In sharp contrast, caespitose grass-dominated steppe in the Intermountain West

TABLE 1

COMPARISON OF FEATURES BETWEEN DOMINANT PERENNIAL GRASSES IN THE *Agropyron spicatum* VERSUS *Bouteloua gracilis* PROVINCES

Species	Sensitivity to Clipping Grazing	Habit	Photosynthetic Pathway	Flowering/ Vegetative Culm Ratio	Meristem Position
Agropyron spicatum	very sensitive in late spring[a,d,c]	caespitose (rhizomatous)[n]	C_3[r]	high[u]	elevated early[f]
Festuca idahoensis	sensitive to light grazing[k]	caespitose	C_3		
Poa sandbergii	sensitive to light grazing[o]	caespitose	C_3[r]	high[t]	
Poa pratensis (alien)	delayed response, if any[c]	rhizomatous	C_3[r]	low[g]	at ground level, throughout season[g]
Bouteloua gracilis	delayed response, if any[c]	tufted, but forming a sod[b]	C_4[r]	low[g]	at ground level throughout season[g]
Agropyron smithii	less sensitive than A. spicatum[p]	rhizomatous[b]	C_3[r]	low[g]	elevated early[g]
Buchloe dactyloides	delayed response, if any[c]	stoloniferous extensive stolons forming a dense sod[b,s]	C_4[r]	low[g]	at ground level throughout season[g]

PHENOLOGY

Species	Breakage Characteristics	Seedling Root Depth + Number in 60 Days	Resumption of Growth	Anthesis	Plant Dry
A. spicatum	weak culm[f]	10 cm, <2[i]	4/5[i]	6/25[i]	8/15[i]
F. idahoensis	weak culm[h]		3/30[i]	6/5[i]	7/9[i]
P. sandbergii					
P. pratensis					
B. gracilis		60 cm, multiple[m]	4/30[i]	7/7[i]	10/15[i]
A. smithii			4/1[j]	6/15[j]	10/21[j]
B. dactyloides			4/30[i]	6/20–9/15[i]	8/10–8/30[i]

NOTE.—[a] Daubenmire 1940; [b] Harrington 1954; [c] Jameson 1962; [d] Reynolds and Packer 1962; [e] Blaisdell and Pechanec 1949; [f] Hyder and Sneva 1963; [g] Branson 1953; [h] Stoddart et al. 1975; [i] Blaisdell 1958; [j] Dickinson and Dodd 1976; [k] Pond 1960; [l] Harris 1967; [m] Weaver 1930; [n] Daubenmire 1960; [o] Rickard, Uresk and Cline 1975; [p] Branson 1956; [q] Caldwell et al. 1981; [r] Gould 1975; [s] Waller and Lewis 1979; [t] unpublished data at Pullman, WA. (Agropyron/Poa h.t.).

reacted in a profoundly different manner to a comparable level of domestic cattle herbivory. Instead of succession continuing to be characterized by native species recolonizing disturbed sites, Eurasian weeds soon arrived and dominated both seral and climax sites. By the turn of the century considerable alteration of the *Agropyron* Province had already occurred as the alien *Bromus* spp. (particularly *B. tectorum*) and *Elymus caput-medusae (Taeniatherum asperum)* quickly became new range dominants in < 40 yr (Daubenmire 1970; Young et al. 1972; Mack 1981; fig. 1*d*). Mack (1981) discussed the role of livestock in the rapid spread of these grasses. For steppe at the moist end of the precipitation gradient (annual precipitation > 450 mm), the rhizomatous *P. pratensis* became similarly ubiquitous. One cultural result of the basic difference in the physiognomy of these two vegetation provinces is that neither the phrase "sod-busting" (in reference to plowing previously nonarable land) nor building a "sod-house" (from the stacked blocks of cut sod), so prevalent in the jargon of midcontinent settlers, appears in the terminology of pioneers in the *Agropyron* Province.

Repeatedly the correlation has been drawn between the lack of large herbivorous mammals in the late Quaternary of the Intermountain West and the region's striking susceptibility to domestic ungulates (cattle, sheep, and horses; Larson 1940; Tisdale 1961; Daubenmire 1970; Dyer 1979). Missing, however, has been comprehensive documentation of those features of these treeless ecosystems which would support clear cause:effect relationships. We believe the evidence resolves about two main interrelated themes: (1) the morphological, ecological, and some physiological characteristics of the native caespitose grasses inhabiting the *Agropyron* Province which in turn created a physiognomy influencing (2) the character and prominence of the cryptogam layer in these steppes.

NATIVE GRASSES OF THE INTERMOUNTAIN WEST

Comparison of perennial grasses in relation to their varying susceptibility to the activities of large herbivorous mammals has traditionally revolved about the plant growth form, whether caespitose or rhizomatous (with either rhizomes or stolons), in relation to grazing. As a morphologic group caespitose grasses (such as those which dominate the *Agropyron* Province) are more susceptible to ungulate activity and may be altered to a prostrate growth form with repeated grazing (Hickey 1961). Other morphologic features identified with susceptibility to ungulates include: (1) early seasonal resumption of apical meristem growth and the meristems' elevation above the soil surface (Branson 1953; Heady 1975); (2) inability to produce axillary buds with removal of the apical meristem (Jewiss 1972); (3) the high ratio of flowering to vegetative culms per genet (Branson 1953); (4) tiller breakage well below the point grasped by ungulate mouthparts (Heady 1975).

Some bunch grasses possess most or all of these features. The differentiation of tillering mode, whether extra- or intravaginal may have been in itself a seminal event in the evolution of grasses in response to ungulate interaction. Caespitose grasses with intravaginal tillering place the emerging culm in a more exposed position to herbivory than the horizontally emerging extravaginal tillers of

rhizomatous grasses. Such culm elevation can affect species growth and repro-
duction. For example, the grazing vertebrate causes plants to be perpetuated in a
vegetative state, by continuously removing floral buds (Harper 1977). For
rhizomatous species only the potential for sexual reproduction is lost as one or
few immortal individuals or genets are maintained by the cropping action. For
caespitose grasses with their dependence on seed production for maintenance on
the site, the consequences are much more serious.

While features relating to grazing susceptibility per se have been identified for
grasses in western North America (Baker 1978) and elsewhere, we doubt that
proper emphasis in the *Agropyron* Province has been given to the ancillary effects
of large herbivorous mammals. Ant-colonies, badger-mounds, and vole trails are
all common in these communities and initiate small but regularly occurring coloni-
zation sites, but collectively these agents of disturbance are not as likely to favor
the rhizomatous forms as is the trampling activity of hooved mammals. Trampling
damage in a rhizomatous grass mat creates at least the opportunity for recovery as
the grass regenerates from severed rhizomes and each segment of the disarticu-
lated turf may survive individually.

Consequences from trampling death are aggravated in the *Agropyron* Province
by the life history of the dominant grasses. *Agropyron spicatum,* for example,
does not flower and fill seed with yearly regularity (Daubenmire 1978*a*). Further-
more, most apparently viable seed of the dominant perennial grasses either fail to
germinate or the seedlings die soon after emergence from frost-heaving, and/or
root desiccation (Harris 1967). Comparison between dominant grasses on either
side of the Rockies reveals further significant differences for grasses subjected to
continuous interaction with herbivorous mammals (table 1). Clipping only simu-
lates part of the grazing action, yet genets of *A. spicatum,* for example, may die if
clipped during late spring (Daubenmire 1940; Blaisdell and Pechanec 1949). In
addition *A. spicatum* develops neither a deep nor multibranched rooting system
within 2 mo of germination, thereby increasing the potential for "pull-up" even
with light grazing. The length of the growing season in grasses in the *Bouteloua*
Province is similar in effect to the deterministic pattern in grasslands in East
Africa (McNaughton 1979*b*).

Recovery from disturbance even before introduction of Eurasian weeds must
have been problematical. Seral grasses included *Festuca microstachys, F.
octoflora,* and the caespitose forms of *A. spicatum* (Daubenmire 1960) and
Bromus carinatus (fig. 1*c*). The colonizing ability of these species is largely
unknown, and remains in doubt because of their virtual replacement by Eurasian
winter annuals (Mack 1981). The ecosystem changed with introduction of live-
stock, causing further change as the flora contained few rhizomatous perennial
grasses.

RHIZOMATOUS GRASSES IN THE INTERMOUNTAIN WEST

The steppes of the Intermountain West have only a few, locally distributed
rhizomatous grasses. These include the rhizomatous form of *Agropyron spicatum,*
and *Poa ampla* (considered as the often rhizomatous form of *Poa juncifolia,*

Hitchcock et al. 1969). Rhizome production in *A. spicatum* has been attributed to the light-limiting conditions of the meadow steppe (annual precipitation > 450 mm) rather than to any greater prior ungulate activity in the steppe/forest ecotone (Daubenmire 1960). Lack of prior adaptation to ungulates is substantiated by the demise of both the caespitose and rhizomatous forms of wheatgrass with grazing (Daubenmire 1970). It further illustrates that these native grasses possess an assemblage of features making them susceptible to large herbivorous mammals, rather than one causal feature such as the caespitose habit alone.

Habitat modification of meadow steppe by ungulates, however, favored grasses, principally the alien *Poa pratensis*. This rhizomatous "sod-forming" perennial now occupies many sites including those never plowed but apparently grazed only lightly. Collectively, the numerous *P. pratensis* biotypes and cultivars constitute an ideal extratropical grass for association with ungulates. Features which have been attributed to impart resistance to trampling and grazing in *P. pratensis* include: (1) a conduplicate stem and leaf; (2) bud height at ground level throughout the growing season; (3) short leaves and generally low stature; (4) tolerance of puddling (i.e., being covered by mud); (5) underground rhizomes (Bates 1935); (6) low flowering to vegetative culm ratio (Branson 1953); and (7) high shoot density (Shildrick 1974). Trampling resistance in other rhizomatous grasses correlates with extensive sclerenchyma and a high percentage of lignified cells in leaves (Shearman and Beard 1975).

Rhizomatous wheatgrasses (*A. trichophorum, A. riparium,* and *A. dasystachyum*) occur in the arid steppe (Hafenrichter et al. 1968) but were not abundant even in presettlement time (Sandberg and Leiberg n.d.) Instead of any perennial grasses alien winter annuals such as *Bromus tectorum* are now dominant. This plant's disseminule type, seedling establishment requirements, seed bank residence time, rapid rate of growth, and resiliency to grazing all allow association with grazers, particularly under conditions with little moisture (< 450 mm precipitation annually; Hulbert 1955). Initial occupation of disturbed sites by such autogamous bromes is common in Eurasia with succession to hemicryptophytic grasses, but in the arid steppe of western North America succession ends with brome entry.

Comparison of the rhizomatous grasses of the arid Intermountain West with those of Eurasia provide abundant intriguing questions, but as of yet few answers. Why did the native sod-forming grasses (e.g., *A. riparium, A. dasystachyum*) not increase with the introduction of cattle? Which features of *A. cristatum* (now a widespread introduction from Eurasia) versus *A. spicatum* owe their retention to prior selection by large herbivorous mammals? Why is the sere to perennial grasses not seen in these stands even though the major components (the winter annuals and some perennials) have been introduced from Eurasian steppe?

THE CRYPTOGAM LAYER

Dominance by caespitose grasses has implications for other components of the steppe. Caespitose grass-dominated communities may be viewed as scattered grass tussocks with a matrix occupied by all other species in the community,

including cryptogams (mosses, lichens, and liverworts). In contrast, rhizomatous grasses may form a mat in which the dense tillers and rhizomes place restrictions on the abundance of ground-dwelling cryptogams. This view is supported by the consistent differences in the prominence of a cryptogam cover between these two physiognomically distinct provinces.

In the *Bouteloua* Province cryptogams are rarely more than minor species on either a biomass or coverage basis. *Selaginella densa* can be prominent with disturbance (Van Dyne and Vogel 1967). Much more commonly, terricolous lichens (Moir and Trlica 1976; Hanson and Dahl 1957; Boutton et al. 1980) and mosses (Shantz 1906) occupy a very small fraction of the soil surface (excluding epiphytes and saxicolous forms), even in communities which lack a substantial grass mat (Hanson and Dahl 1957).

In the most arid communities of the *Agropyron* Province, cryptogams cover all undisturbed soil surfaces not occupied by vascular plants (Daubenmire 1970); such cryptogam cover may exceed 50% on a unit area basis (Poulton 1955). This terricolous layer is comprised of acrocarpous mosses, including *Bryum argentatum lanatum, Tortula brevipes,* and *T. ruralis,* and mainly crustose lichens, including *Parmelia esasperata, Lecanora hageni,* and *Physcia grisea* (Daubenmire 1970). Even in the dense *Festuca/Symphoricarpos* association where a combination of rhizomatous *A. spicatum* and a high LAI (leaf area index) of perennial forbs may restrict light, the soil surface is also covered by lichens and pleurococcus mosses (Daubenmire 1970). The light regime in this steppe is comparable to rhizomatous swards and implies that interactions among plants alone do not explain the virtual absence of cryptogams in communities east of the Rockies.

In communities elsewhere in which cryptogam cover is extensive these slow-growing organisms respond adversely to regular grazing by large animals (Pegau 1970; Oksanen 1978). Maintenance of cryptogams in boreal and arctic regions is apparently dependent on comparably low continuous ungulate activity by migratory herds, the prominence of large fruticose species (Inglis 1975) versus small crustose lichens, resistance of lichens when moist (Pegau 1970), and more rapid growth rates of fruticose versus crustose forms (Beschel 1961; Scotter 1963).

Presence of large ungulates even at low density in the *Agropyron* Province results in rapid, permanent loss of cryptogams through trampling (Poulton 1955; Daubenmire 1970). In turn the broken cryptogam crust is a major source of microsites for alien grass establishment. Prior to domestic livestock introduction common ungulates were small (e.g., pronghorn antelope versus cow/bison, 70 vs. 500 kg) and/or present in low numbers; their localized trampling damage could be tolerated even by communities ill-equipped to cope with such disturbance. It appears that herbivorous mammals are incompatible with maintenance of steppe where cryptogams (particularly crustose lichens) occupy a significant fraction of the soil surface.

THE ROLE OF THE PREVAILING WESTERLIES

Events leading to organization of the caespitose grass-dominated *Agropyron* Province and its ultimate decimation in the nineteenth century were probably set into motion by the inland reduction of the Prevailing Westerlies' influence with

rise of the Cascade Range in the Pliocene. The resultant climate, while basically arid, is still influenced by the annual shift in latitude of the Westerlies; the bulk of precipitation occurring in winter, with little rain falling as the air currents move north in summer (Day and Sternes 1970). Consequently selection was for species which could tolerate seasonal drought coinciding with summer. Low July minimum temperatures (Teeri and Stowe 1976) may contribute to the shift in the amount of total daily carbon gain that C_3 grasses display relative to C_4 species in progressively northern habitats (Ehleringer 1978). Under such a regime *Agropyron, Poa,* and *Festuca* residing to the North immigrated into the newly formed intermountain trough (Daubenmire 1975). From the standpoint of microclimate control, the caespitose habit may be similar to the growth form of arctic cushion plants, as the appressed morphology of cushion plants imparts considerable resistance to sensible and latent heat flux (Addison 1977). In the scheme envisioned here, the caespitose form, persistent in the boreal regions as an adaptation to energy conservation, preadapted these genera for the newly arid (yet winter cold) conditions. In the emerging steppe climate plant resistance to heat transfer including the aggregate canopy resistance of the caespitose habit, also serves to retard water vapor transfer. Resistance to heat transfer may continue to be important as the erect clums retain an insulating blanket of snow in winter (Courtin 1968). Furthermore, a caespitose habit increases soil heat flux (Addison 1977), speeding spring thaw (Chapin et al. 1979) resulting in resumption of the growing season earlier in late winter than would otherwise be possible. Such phenology is an advantage in a climate where vegetative growth must be largely completed by midsummer.

With the matrix surrounding the vascular plants otherwise unoccupied, the cryptogam layer formed with any species which could tolerate the same general macroclimatic conditions. We suspect that the caespitose grasses and community matrix of cryptogams persisted through the Quaternary as a result of insufficient large-hooved congregating mammals to override basically macroclimate-driven selection for this grass form. This general community pattern was probably preserved even with spatial displacement during repeated Pleistocene glaciations.

This community pattern was altered swiftly and permanently with introduction of domestic livestock. Represented as a Forrester-type schematic the present steppe in the *Agropyron* Province can be seen to have a missing loop in the sere back to perennial grasses (fig. 1*d*). With herbivorous mammal disturbance as the "driver" in the system, the bromes (or *P. pratensis* in the meadow steppe) have become an absorbing state. If conspicuous heritable change in community composition can occur via different grazing regimes in as little time as 4 mo (Brougham and Harris 1967) or a few years (McNaughton 1979*a*), there can be little doubt as to how a lack of such selective pressure over 10^3 yr could cause substantial change in the whole community and the growth habits of the component species (Elton 1966; Harper 1977).

OTHER TEMPERATE GRASSLANDS

The community consequences of the introduction of large herbivorous mammals observed in western North America are not unique. For example, the
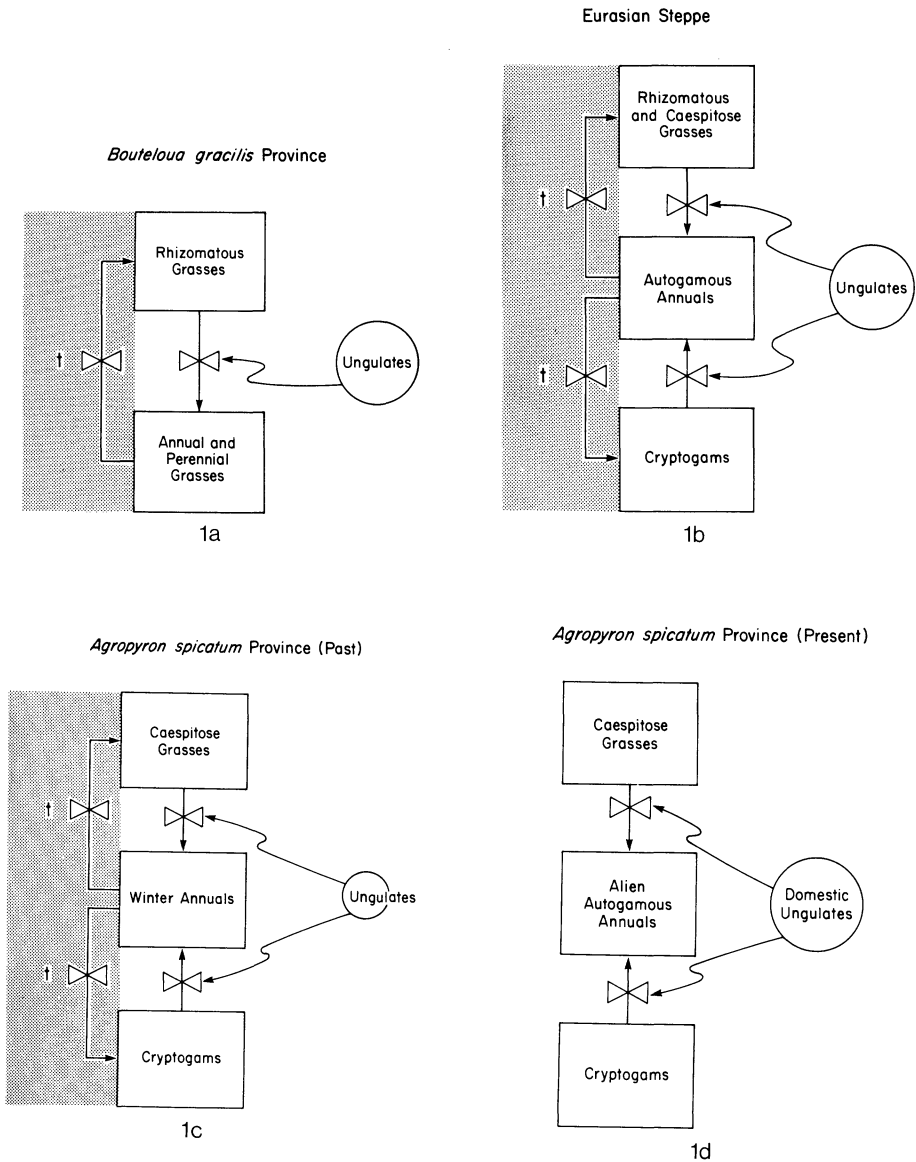
FIG. 1.—Suggested organization of the four generalized ecosystems discussed here repre-
sented by Forrester-type schematics. In the *Bouteloua gracilis* Province in North America
succession after ungulate disturbance is short term (fig. 1*a*). In much of the Eurasian steppe
winter annuals colonize disturbed sites, but are succeeded by perennial hemicryptophytic
grasses (fig. 1*b*). In the late Quaternary history of steppe in the Intermountain West (*Agropy-
ron* Province) succession (fig. 1*c*) was permanently altered with introduction of domestic
livestock in the nineteenth century. Today (fig. 1*d*) Eurasian winter annuals permanently
dominate sites with large mammal disturbance, leading to the replacement of the original
components of the ecosystem.

tussock grasslands of New Zealand have experienced extensive replacement with alien rhizomatous grasses since the mid-nineteenth century (Godley 1975). Throughout the world those tussock grasslands lacking prior association with large herbivorous mammals have consistently been altered once subjected to cattle and sheep (Moore 1959; Godley 1975; Baker 1978). In contrast, no rhizomatous grass-dominated communities in temperate regions display human-induced change to the same degree, as all rhizomatous grasslands probably evolved with ungulates. These complementary lines of evidence suggest that the extent of coevolution between congregating mammals and plants in an extratropical grassland may be predicted to some extent from the habit of the area's dominant grasses.

Steppe in an increasingly arid broad belt from the Ukraine through Kazakstan to Central Asia provides an intriguing exception to any general statement on grass life form as a result of ungulate association. Most of the dominant grasses throughout this huge region are caespitose (Sochava 1979) or "laxly caespitose" (Tutin et al. 1980). These species include: *Koeleria gracilis, Agropyron cristatum, Festuca pseudovina,* and *F. sulcata* (Demorenko 1975; Nikolaevskii and Nikolaevskaya 1972; Zvereva and Eremenko 1975). The cryptogam layer may be prominent, particularly in the arid steppe (Lavrenko and Sochava 1956; Bourlière 1964).

Long-term association with congregating ungulates (e.g., *Saiga tartarica,* Vereshchagin 1959; *Camelus dromedarius,* Bourlière 1964; and *Gazella Gazella* and *Equus hemionus*) is a certainty here and for much of arid Central Asia (Roberts 1977; Sochava 1979; fig. 1b). Did these animals fail either through lack of individual size or numbers to provide selection pressure similar to *Bison*? Hunting man long ago eliminated the opportunity to view these animals in an undisturbed state (Vereshchagin 1959, 1967). Nevertheless the Asiatic horse has been observed in herds > 100 animals (Walker 1968) and Roberts (1977) cites historic accounts of *Antilope cervicarpa* herds with 8,000–10,000 individuals. While several of these species are comparable in size to pronghorns, this fauna included into modern time adult aurochs and asses, which weigh > 200 kg (Walker 1968). How then are the caespitose grass and cryptogam components of these communities maintained? In clipping defoliation experiments the Eurasian caespitose grass *Agropyron desertorum* displays more flexible resource allocation, more new tillers coupled with curtailed root growth as compared to *Agropyron spicatum* (Caldwell et al. 1981). These results suggest that Eurasian caespitose grasses may have traits adapted to mammalian grazers, but we know very little about the nature of these selection forces.

CONCLUSIONS

Seen in as broad an evolutionary context as our information permits, conclusions at several levels may be drawn. Features in grasses as sought by turf-breeders such as rigidity, elasticity, texture, and verdue (*sensu* Turgeon 1980) may have their origin in the prior animal association examined here. The native range of ancestral stocks for highly tolerant varieties of turf seems to provide a clue to

the nature of past animal associates. This prior evolution with large herbivorous mammals has meant that most pasture grasses are also rhizomatous. Of 40 principal pasture grasses cultivated worldwide (Hartley and Williams 1956) only 13 are caespitose or tufted species (including among temperate species, *Agropyron cristatum, Arrhenatherum elatius, Festuca ovina, Dactylis glomerata*). The high proportion of Eurasian species in the list may reflect some bias because of their origin in areas of long-term human habitation, but nevertheless these species arose (such as in the north-central Mediterranean Region) with large herbivorous mammals. While we have not been concerned here with applied aspects of grasslands, we see some explanation in this evolutionary context for the chronic problems that arise when grassland management schemes are implemented without awareness of a flora's history.

Temperate grasslands display features both in species composition and structure that cannot be explained simply by insufficient moisture for trees in the region. As comparing the *Agropyron* and *Bouteloua* Provinces indicates, a grass need not, per se, be rhizomatous to be a dominant in an extratropical grassland. The most common evolutionary pathway down which grasses evolving with ungulates travelled appears to be the evolution of extravaginal tillering and the rhizomatous habit plus an assemblage of associated features. The caespitose habit could be preserved with a lack of such sustained selection pressure. Much of the rest of grassland structure was dictated once one of these two pathways was followed.

SUMMARY

The morphology of rhizomatous and caespitose grasses reflects the two extremes to which perennial grasses have evolved at least in partial response to continuous high versus low selection pressure by large congregating mammals. In North America steppe of the *Bouteloua* Province east of the Rockies is dominated by a mix of mainly rhizomatous C_3 and C_4 grasses which have long been associated with large herds of *Bison* and more recently with cattle. Introduction of cattle into these grasslands had much less effect on community structure than did livestock introduction into steppe of the *Agropyron* Province west of the Rockies which lacked large herds of mammals throughout the Holocene (and perhaps earlier). The underlying cause of native ungulate sparseness may have been related to the moisture cycle of the Prevailing Westerlies, which may have largely excluded C_4 species, thereby severely controlling *Bison* numbers. In these communities both the dominant C_3 caespitose grasses and the prominent cryptogam layer were soon destroyed by domestic ungulates and replaced largely by alien winter annuals. The relative changes in these two Provinces over the past 200 yr illustrate the importance in plants of herbivore-adapted traits in generating the overall physiognomy of some steppes and the resiliency of those grasslands to the introduction of novel selection pressure.

ACKNOWLEDGMENTS

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