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# PALEOECOLOGICAL IMPLICATIONS OF PLANT/ANIMAL GRAZING RELATIONS ON THE MAMMOTH STEPPE OF EASTERN BERINGIA

Andre Antinori

*This paper reassesses the areal extent of Mammoth Steppe in Eastern Beringia and discusses some of the ways in which grazing and topography entered into the maintenance of the Mammoth Steppe. Large, generalist grazing mammals, by their grazing style, helped maintain the Mammoth Steppe by removing old-growth and by stimulating grass plants to reproduce vegetatively. These grazers also promoted uniformity in growth-form and uniformity in plant biomass (phytomass) above and below the ground surface. During the late Pleistocene these large, generalist grazers were eliminated from interior Alaska by PaleoIndian hunters and their predatory animal companions. The loss of these large, generalist grazers precipitated a change in the structure of the Mammoth Steppe grassland and this eventually led to the replacement of steppe grassland by herb tundra.*

## Broadcast

burning by humans and naturally-occurring fire are two reasons classically given for the formation and maintenance of grasslands. Grazing is another. This paper explores grazing in a human habitat. Habitat, nature and natural resource are categories that are defined by people rather than objects defined by their own intrinsic qualities. Without human definition habitats are no more than systems among systems within a universe of systems. Mammoth Steppe was human habitat in Siberia before the human occupation of eastern Beringia (Powers 1973). It remained human habitat until its disappearance from the Beringian landscape. If Mammoth Steppe

were not human habitat there would be little reason for geographers or anthropologists to study it.

This paper is an attempt to describe the full-glacial vegetation of interior Alaska/Yukon and to explain the role of grazing and topography in the maintenance of Mammoth Steppe. The understanding of grazing relationships not only benefits anthropologists and geographers who focus their attention on humans in grassland settings but is also of value to the archaeologist who deals with hunting and pastoral peoples before and after the advent of livestock raising. Hopefully this paper will put human action in perspective by casting people as a proximate rather than the ultimate cause of environmental change and provide

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another way of looking at human impact on grassland ecosystems.

## **PaleoIndians in Beringia**

Humans may have entered North America as early as 50,000 years before the present (yrs BP) as part of the Siberian faunal assemblage that crossed the Bering Land Bridge (Fig. 1) during that time (Kurten and Anderson 1980; Turner 1984). However this date is purely speculative. Actual dated material from Bluefish Caves in the Yukon place humans in eastern Beringia around 24,800 yrs BP well within the time-frame dealt with by this paper. At Bluefish Caves Morlan concluded:

Human presence is inferred from a variety of flaked stone tools, including burins, microblades, and a microcore, several kinds of bone tools, numerous butchering marks on bones, bone breakage patterns, and selective representation of anatomical parts (Morlan 1987:38)

The human artifacts were found in association with thousands of well-preserved bones of local ice-age mammals. Prior to this time humans in eastern Beringia may have chosen to use tools of expedience such as splintered animal bones. Tools of this type would have left little or no artifactual record.

## **Paleoenvironmental Interpretation**

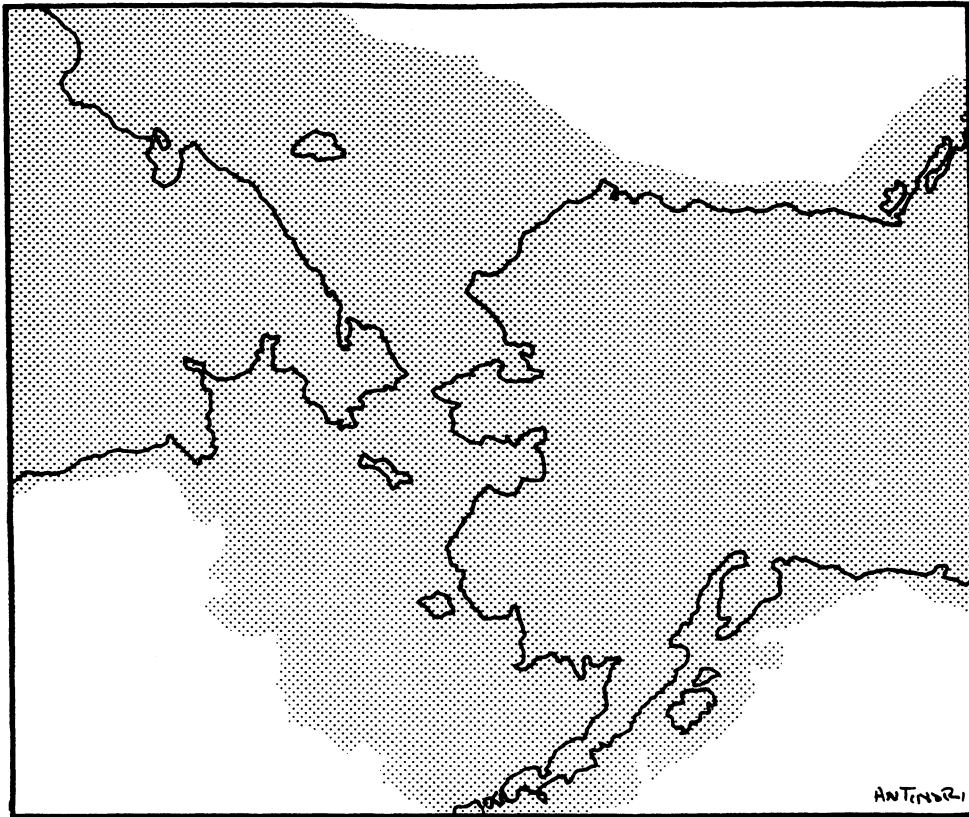
By its very nature fossil pollen data is usually biased toward woody species, exotic pollen influx and local taxa that either produce an overabundance of pollen or are locally abundant at the depositional site. As a result of this bias a

diversity of opinions have arisen about the nature of the Beringian landscape during the last full-glaciation (about 35,000 to 16,000 yrs BP).

Consequently many of the scenarios, theories and models used to describe and explain the past vegetation of Beringia are highly speculative and do not necessarily represent observable, demonstrable facts nor even accepted opinions.

## **Vegetation in Beringia**

Two major vegetation types (herb tundra and grassland steppe) probably existed in interior Alaska during the period of the last glaciation. Boreal forest tree species were confined to isolated refugia to the southwest (Hopkins 1972) and east (Anderson 1985, 1988). The general look of the summer landscape was green and treeless with shrubby willows in situations favorable to their growth. A number of smaller environments were found within the two major vegetation types such as the sand dunes and shallow fresh-water marshes, ponds and bogs of the exposed Chukchi Sea shelf (Elias et al. 1992). Familiar Alaskan boreal forest tree species of today (spruce and fir) did not re-invade interior Alaska and the Yukon until sometime during the most recent deglaciation (13,000 to 11,500 yrs BP) (Ritchie 1984).



**Figure 1. The Bering Land Bridge showing western (Asiatic) and eastern (American) Beringia**

## **Herb Tundra**

During the last full-glacial, the vegetation of northwestern Canada has been reconstructed by Ritchie and Cwynar as sparse, discontinuous herb tundra in uplands and continuous grass-sedge marshes with local willow thickets in lowlands (Cwynar and Ritchie 1980; Cwynar 1982; Ritchie 1984). The climate was cold and dry analogous to the modern-day mid-arctic climate of the northern portions of Banks and Victoria Islands (July mean 2-6 degrees C) (Ritchie 1984). At approximately the same

time eastern Hokkaido (today's northern island of Japan) and the exposed northwestern Pacific shelf was a refugium for boreal forest and tundra/tundra parkland species. The climate there was cold and wet (Heusser and Morley 1985).

From 16,000 to 12,000 yrs BP herb tundra gave way to willow tundra and scattered dwarf birch. This vegetation type dominated upland sites until about 11,500 yrs BP. The modern analog climate for this vegetation are the southern portions of Banks and Victoria Islands where the July mean is 10-13 degrees C (Ritchie 1984). Dwarf birch, a

familiar tundra shrub, spread across northcentral and northwestern Alaska during this period. However it was not common in the region until 12,000 yrs BP or later (Anderson 1988).

Herb tundra (Fig. 2) occurred throughout eastern Beringia below the mountain glaciers of the Brooks Range, Alaska Range and Richardson Mountains and between these mountain ranges and the grasslands of the Mammoth Steppe. According to Barnosky and associates this vegetation was a drier tundra in northeastern Alaska and northwestern Canada and a wetter (more mesic) tundra in northwestern Alaska (Barnosky et al. 1987). The fossil pollen sites used to map this vegetation type are scattered throughout interior Alaska and the Yukon (Barnosky et al. 1987).

The predominant taxa of the herb tundra zone were various species of sedge, grass, sage (*Artemisia*) and willow (*Salix*). The genus and species of individual grasses and sedges cannot be resolved by fossil pollen analysis. The presence of sage in this vegetation belt may be alternatively interpreted as dry, rocky upland habitats, river banks, meadowy terraces or even areas of disturbance (Cwynar 1982; Anderson 1988; Paus 1988). "In neither the upland nor lowland setting, however," says Anderson, "is *Artemisia*, by itself, indicative of widespread steppe or grassland" (Anderson 1988:271).

Cwynar and Ritchie's reconstruction is supported by data from a number of authors who worked in interior Alaska south of the Brooks Range. These authors are summarized in Anderson (1985). Building on their

findings and her own field work, Anderson later concluded that the vegetation of her fossil pollen sites was "perhaps more similar" to mid-arctic tundra than to arctic meadows (Anderson 1988:270). Both of these interpretations are probably correct and her characterization of the herb zone as "a complex mosaic of tundra types with no latitudinal or longitudinal pattern" seems reasonable (Anderson 1985:271).

### Smaller Environments

In the central Brooks Range, Brubaker and associates found that both sparse, discontinuous herb tundra and meadow plant communities existed simultaneously. She proposed "...that both vegetation types existed under the same regional climate, depending on local soil-drainage conditions" (Brubaker et al. 1983:206), thus lending support to the mosaic-crafters of Alaskan and Yukonan paleoecology such as Young (1982).

The role of soil (edaphic) and microclimatic factors of the environment to the success or failure of plants is well known to geographers and ecologists. Climatic regimes vary over several levels of spatial resolution and soil varies in both structure and texture within relatively small areas. Hinds found that microclimatic factors produced a potential for variation in seedling establishment in cheatgrass (Hinds 1975).

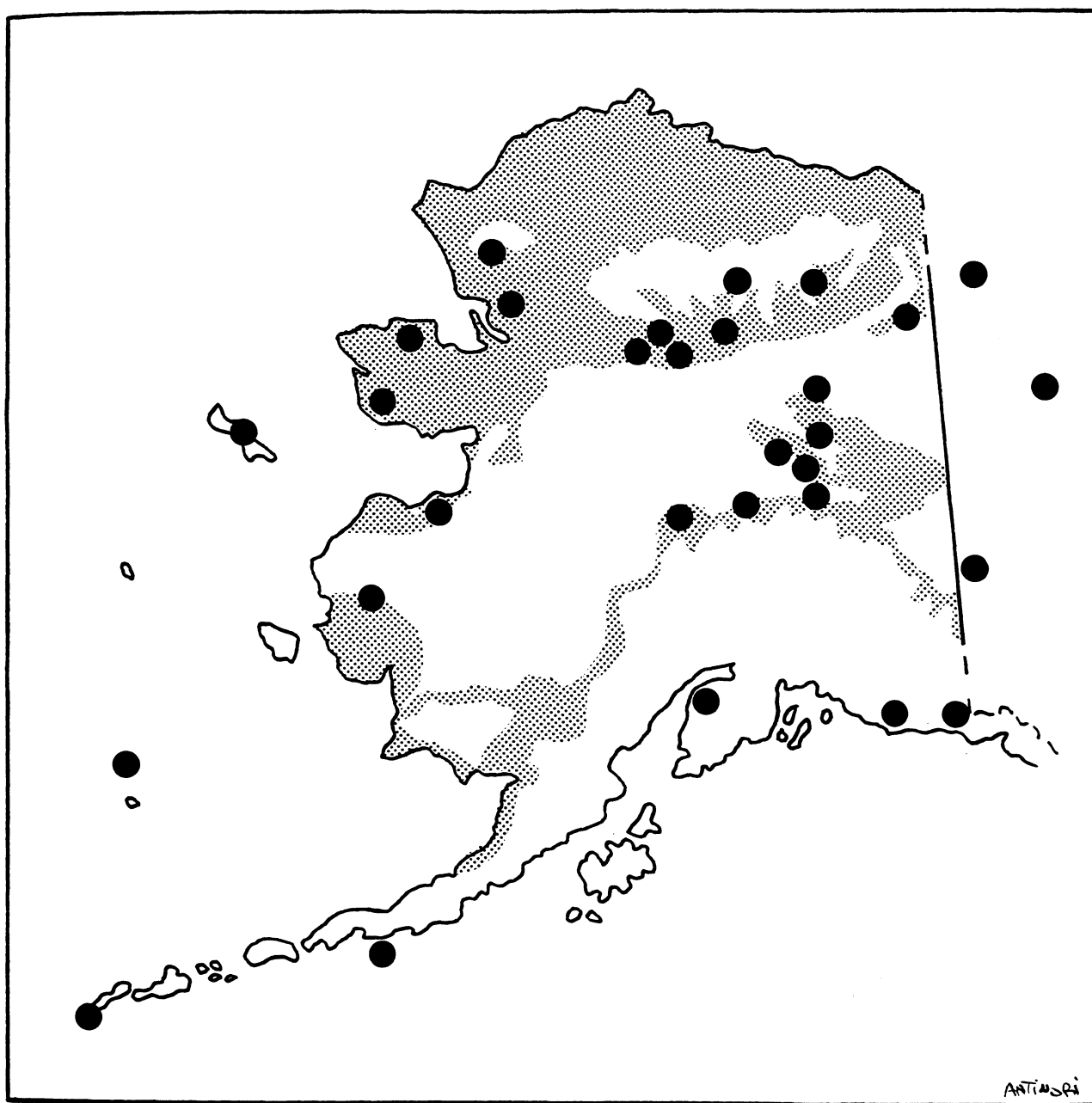


Figure 2. Herb Tundra vegetation in Alaska during the last full-glacial period, noting fossil pollen sites.

Zedler and Zedler found that differences in soil texture influence germination success and that soil texture may interact with smaller-scale features of a place to produce small-scale variations in climate and runoff patterns (Zedler and Zedler 1969). Mott and McComb working in western Australia found soil texture and microtopography produced variations in nutrient levels of the soil (Mott and McComb 1974). Schimel and associates found that the soil of low places (swales) are frequently higher in organic matter and mineral nutrients than are the soils of uplands (catenas) (Schimel et al. 1985). Guthrie claims that localized factors such as these (especially aridity) are the key to understanding the Mammoth Steppe (Guthrie 1990).

### **Mammoth Steppe**

Based on the occurrence of numerous large, grazing mammals (especially bison, horse, mammoth) and their predators (especially wolf, lion, bear) in late Pleistocene sediments near Fairbanks, Alaska, Guthrie proposed the existence of a steppe/grassland that has come to be known by the name Mammoth Steppe (Guthrie 1982). To Guthrie "the high percentage of grazers in the fossil community suggests that interior Alaska was a grassland environment during the late Pleistocene" (Guthrie 1968:353).

Mammoth Steppe is frequently seen as an alternative to the paleoecological interpretation of Cwynar and Ritchie (1980). It is, however, probably more realistically viewed as simply another vegetation type of the last glacial maximum. As early as the late

19th century European and Russian paleontologists recognized that the late Pleistocene climate and vegetation was different than at present and more times than not invoked the idea or the ideal of *steppe* as a landscape that supported a diversity of large mammals.

### **Steppes and Mammoth Steppe**

Present-day grasslands can be categorized into climatic, successional, and agricultural types. Climatic grasslands occur where the water-balance is below the threshold for tree growth (Daubenmire 1978). Successional grasslands are maintained or moved through various levels of succession by physical or biological factors of the environment. An agricultural grassland is planted and maintained by humans for a particular cultural purpose such as livestock grazing or outdoor recreation. Apparently Mammoth Steppe was a combination of climatic and successional. It was developed under a climate regime that was both regionally variable and different from any modern-day high latitude climate because of a change in land/sea/ice relationships brought about by the lowering of sea level and resultant exposure of a large part of the Bering continental shelf (Hopkins 1972, 1982; CLIMAP project members 1981; Ritchie 1984; Heusser and Morley 1985).

Based on several lines of evidence Guthrie reconstructed the winter weather of this region as cold, windy and dry which kept the region relatively snow-free and provided the potential for year-around grazing (Guthrie 1984; Guthrie and Stoker 1990). After establishment

Mammoth Steppe was probably maintained at some given level of succession by heavy grazing by large, herbivorous mammals.

Mammoth Steppe grassland (Fig. 3) occurred throughout interior Alaska in areas that were not occupied by tundra or riverine associations. At present this vegetation type is replaced by boreal forest and it is presently restricted to refugia as was boreal forest during the last full-glacial epoch. Today the remains of Mammoth Steppe can be found on south-facing slopes, bluffs, and in isolated enclaves throughout American and Asiatic Beringia (Yurtsev 1982; Edwards and Armbruster 1989; Walker et al. 1991).

Guthrie sees Mammoth Steppe as a diverse complex of herbaceous and woody steppe plants organized into a mosaic of vegetation associations which in turn supported a great diversity of grazing mammals and their predators (Guthrie 1984). It forms a complex of steppe habitats very similar to those found today in Wyoming and Montana where associations of cold- and warm-season grasses, evergreen and deciduous shrubs/semishrubs are punctuated by wooded bluffs and water-courses.

### **Grazing Relations: Adaptations to Grazing**

Grasses have one or more adaptations to each of the limiting factors of environment. Several of these adaptations enhance survival under semiarid conditions and promote tolerance to grazing pressure.

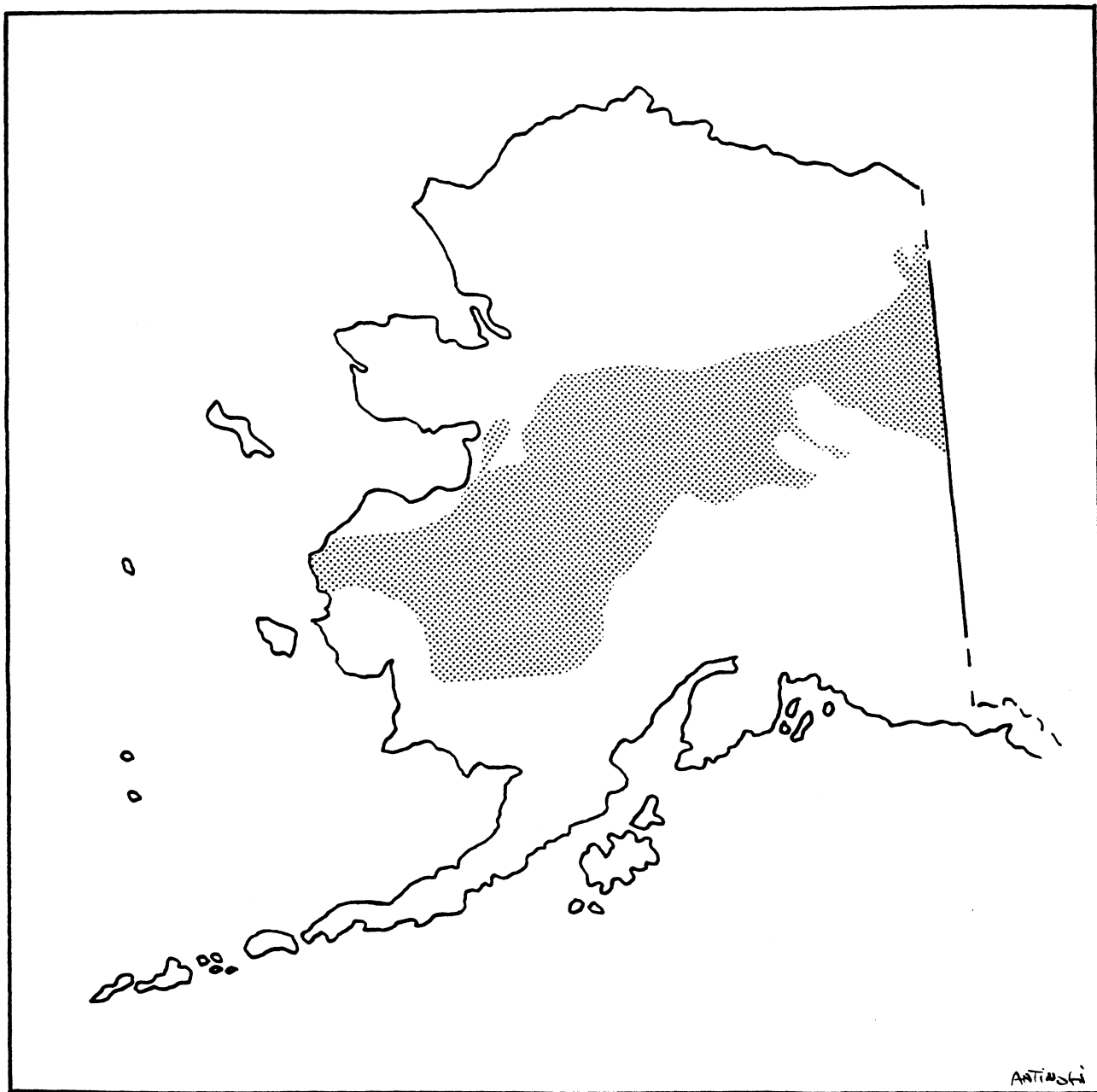
Coughenour discussed how basal meristems, rapid growth, deciduous shoots, relatively small stature, high shoot density, and below-ground nutrient reserves allow grasses to evade, escape and endure dry conditions and tolerate grazing (Coughenour 1985). Meristematic cells are the source of all postembryonic plant growth including vegetative reproduction.

Milchunas and associates suggest that these structures are due to the fact that both water stress and stress from grazing periodically result in the same thing: loss of organs (Milchunas et al. 1988). Tolerance to one necessarily includes tolerance to the other. Both drought and herbivory provide selective pressure to minimize the impact of organ loss. Because of these factors plants can respond to grazing in ways that increase rather than decrease their competitive success.

### **High Intensity / Low Frequency Grazing**

In the Serengeti of East Africa grazing, by large, generalist grazers such as wildebeest, is beneficial to grasslands. Wildebeest heavily graze a specific unit of ground for a short period of time and then move to the next unit. This grazing style is called high intensity / low frequency grazing. The term low frequency is relative. Units may be regrazed more frequently than expected or other species may use the same unit soon after another. However, on a year to year basis, grazing remains low frequency.





**Figure 3. Mammoth Steppe vegetation in Alaska during the last full-glacial period.**

High intensity / low frequency grazing keeps grass plants palatable and nutritious by removing old-growth and stimulates grass plants to produce new stems by tillering and spread vegetatively by stolons and rhizomes (McNaughton 1976, 1983). Tillering refers to the movement of grass shoots above and below the ground surface. Stolons are usually above ground, rhizomes are always below ground. Both are capable of reproduction by budding.

High intensity / low frequency grazing not only increases the net primary productivity of the grassland and facilitates grazing for other grazing species such as Thompson gazelle but it also increases the competitive advantage of the grazed species over potential invader species (McNaughton 1983).

In the central Great Plains, in the absence of grazing, the warm-season grass, blue grama, grows and dies. The result is a build-up of litter which shades and cools the soil. This leads to the demise of this warm-season grass and provides a window of opportunity for the establishment of cool-season grasses, forbs, and eventually, even shrubs. With active grazing the warm-season grass is maintained.

### **Grazing in a Shortgrass Grassland**

In the Colorado shortgrass grassland communities studied by Milchunas and associates, blue grama (*Bouteloua gracilis*) made up 90% of the basal cover recorded whereas the remaining 10% was divided between

plains prickly pear (*Opuntia polyacantha*) and various other plant species (Milchunas and Lauenroth 1989; Milchunas et al. 1989). Under heavy grazing by cattle, blue grama increased in basal cover on grazed swales. No significant difference between wet and dry years or between ungrazed swales or uplands was found during the study. The density of grass was also greater on grazed sites and grass was most abundant in grazed swales. Shrubs and semishrubs were most abundant on ungrazed sites, in swales and in the dry years. Plains prickly pear was more abundant on uplands and increased during dry years on uplands. It also obtained a slightly greater basal cover under heavy grazing. Litter build-up was evident on ungrazed sites and on swales and on grazed sites during wet years.

### **Ecological Segregation**

The segregation of plant populations with respect to topographic factors was indicated by swale to swale similarity and upland to upland similarity. Population segregation and plant diversity were generally greater on ungrazed sites and plant communities on the grazed sites were very uniform. These conditions suggest that cattle tend to reduce plant diversity of a site when they graze it. Plant species diversity was greatest on ungrazed swales in both wet and dry years. However wet and dry years had little effect on the segregation of plant populations (Milchunas et al. 1989).

## Root Phytomass and Grazing

In addition to the uniform distribution of above-ground plant parts on grazed sites, Milchunas and Lauenroth (1989) found a greater uniformity in the horizontal distribution of below-ground plant parts as well. This extended McNaughton's (1984) concept of grazing lawns (the origin of uniform, lawn-like growth form) to the subsurface dimension. Milchunas and Lauenroth (1989) also discovered that 45-years of heavy grazing of surface plant parts had very little effect on shallow root phytomass. The effect was similar on lightly grazed uplands and heavily grazed swales. Grazing had only a small effect on the vertical distribution of roots and the changes were different for swales and uplands. The largest effect of grazing on root structure was in horizontal distribution of roots. The horizontal distribution of roots on grazed sites was more uniform.

In terms of Grubb's (1977) concept of regeneration niche this means that favorable localities for establishment would be less likely to occur where root density is uniform. This is one reason why the density of invader species and species richness in general is less on grazed sites.

## Conclusion

Of the many features of grasslands none is more striking than their ability to favorably respond to grazing by large, generalist grazers. Grasses provide grazers with relatively high quality feed that can be used for growth and maintenance or that can be readily

converted to the energy required for everyday life. In return grazers help maintain the grassland by removing old-growth and excess leaf production. These benefits increase forage quality and quantity for all the grazers in the system. It is a reciprocal relationship which can not be changed without consequence.

Sometime during the late Pleistocene certain large, generalist grazers were eliminated from eastern Beringia. The loss of these grazers precipitated change in the grassland steppe and eventually led to the encroachment of Mammoth Steppe by herb tundra.

Although widely accepted in both scientific and popular circles the existence of Mammoth Steppe remains somewhat problematic. This paper has presented one mechanism by which Mammoth Steppe could have been maintained under the conditions available in Beringia during the late glacial period. It has also provided a reason for the elimination of Mammoth Steppe from Beringia. Future research must be broad-based and expand its focus beyond archaeological and fossil pollen sites to the habitats that made those sites possible.

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