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STEPPE-TUNDRA TRANSITION: A HERBIVORE-DRIVEN BIOME SHIFT AT THE END OF THE PLEISTOCENE

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Abstract.—A simulation model, recent experiments, and the literature provide consistent evidence that megafauna extinctions caused by human hunting could have played as great a role as climate in shifting from a vegetation mosaic with abundant grass-dominated steppe to a mosaic dominated by moss tundra in Beringia at the end of the Pleistocene. General circulation models suggest that the Pleistocene environment of Beringia was colder than at the present with broadly similar wind patterns and precipitation but *wetter* soils. These and other observations suggest that the steppelike vegetation and dry soils of Beringia in the late Pleistocene were not a direct consequence of an arid macroclimate. Trampling and grazing by mammalian grazers in tundra cause a shift in dominance from mosses to grasses. Grasses reduce soil moisture more effectively than mosses through high rates of evapotranspiration. Results of a simulation model based on competition for water and light and plant sensitivity to grazers and nutrient supply predict that either of two vegetation types, grass-dominated steppe or moss-dominated tundra, could exist in Beringia under both current and Pleistocene climates. The model suggests that moss-dominated tundra is favored when grazing is reduced below levels that are in equilibrium with climate and vegetation. Together these results indicate that mammalian grazers have a sufficiently large effect on vegetation and soil moisture that their extinction could have contributed substantially to the shift from predominance of steppe to tundra at the Pleistocene-Holocene boundary. Our hypothesis suggests a mechanism by which the steppe ecosystem could be restored to portions of its former range. We also suggest that mammalian impacts on vegetation are sufficiently large that future vegetation cannot be predicted from climate scenarios without considering the role of mammals.

The structure of natural vegetation correlates closely with current climate, allowing vegetation to be classified according to bioclimatic zones (Holdridge 1947). Similarly, the distribution of individual species or floristic groups is often correlated with specific climatic parameters (Young 1971; Whittaker 1975). These vegetation-climate relationships have been used to explain the current distribution of species (Whittaker 1975) and major biomes (Woodward 1987; Prentice et al. 1992). The present vegetation-climate relationships have been used to deduce past climate based on paleoecological indicators of past vegetation (Davis 1981;

Grichuk et al. 1984; COHMAP 1988) and to predict future vegetation distribution based on general circulation model (GCM) projections of future climate (Pastor and Post 1988). The implicit assumption behind these climatic reconstructions is that climate is the major factor determining the distribution of vegetation. However, animals also strongly influence the species composition, structure, and processes of ecosystems (O'Neill 1976) such as steppe (Vysotskii 1901; Pachosskii 1917; Prozorovskii 1940 [as cited in Kucheruk 1985]; Walter 1979), savanna (McNaughton 1979; Owen-Smith 1987, 1988), and boreal forest (Pastor et al. 1988, 1993; Bryant et al. 1991). Consequently, changes in animal abundance can radically alter the structure and species composition of vegetation, for example, converting grassland to shrubland or forest (Owen-Smith 1987; Schlesinger et al. 1990). Moreover, factors extraneous to climate (e.g., human hunting pressure) can strongly influence animal densities and, therefore, the animal impact on vegetation. Predicting the future structure and distribution of ecosystems (Pastor and Post 1988) may, therefore, require consideration of trophic interactions as well as direct effects of climate on vegetation.

One of the most dramatic vegetation changes of the last 20,000 yr was the conversion of a vegetation mosaic dominated by a semiarid, grass steppe with a well-developed grazing megafauna to a mosaic dominated by wet moss tundra (including forest tundra with scattered trees) without a large grazing fauna. In this article, we refer to this unproductive tundra and forest tundra as tundra. This change occurred at the end of the Pleistocene 10,000–12,000 yr before the present (B.P.). In addition, boreal forest expanded northward at the end of the Pleistocene into areas that had been predominantly steppe, presumably in response to climatic warming. In the remainder of this article, we emphasize those areas of Beringia (eastern Russia, western Alaska, and the intervening continental shelf) presently occupied by tundra, even though these patterns also extended south and west into areas presently occupied by forest.

The vegetation changes at the end of the Pleistocene have generally been ascribed to climatic change (see, e.g., Hopkins et al. 1982; Grichuk 1984). More recently, Owen-Smith (1987, 1988) proposed the *keystone-herbivore hypothesis* to explain the widespread vegetation change that occurred globally at the end of the Pleistocene. This hypothesis, based primarily on temperate and tropical evidence, suggests that large grazing mammals are "keystone" species that maintain an open vegetation that undergoes succession to woodland or shrubland when grazers are removed. In this article, we apply the keystone-herbivore hypothesis to vegetation of the Far North of Russia and western Alaska. Based on evidence from the literature, recent experiments, and a simulation model that we developed, we suggest that the Pleistocene grazing megafauna played a major role in maintaining steppe conditions during the Pleistocene and that its disappearance, which coincided with increased human hunting, contributed strongly to the transition from steppe to tundra at the end of the Pleistocene.

HYPOTHESES FOR THE STEPPE-TUNDRA TRANSITION

The *Pleistocene overkill hypothesis* suggests that increased human hunting pressure caused or contributed to megafaunal extinction at the end of the Pleisto-

cene (Hopkins 1967; Jelinek 1967; Martin and Klein 1984). Early humans may
have coexisted with steppe megafauna in the mid-Pleistocene, using sharpened
bones and antlers as their hunting weapons. However, 10,000–15,000 yr B.P.
Beringia became occupied by an anatomically modern people who hunted with
stone microblades (stone chips) inserted into wooden or bone shafts (West 1981;
Guthrie 1990) and who fed extensively on the steppe megafauna (Haynes 1982).
In much of Beringia, the spread of this modern microblade hunting technology is
correlated in time with the extinction of the steppe megafauna and with vegetation
change from steppe to tundra. Wrangel Island to the north of Siberia was isolated
from human hunting (Lister 1993). Here, mammoths survived until 3,700 yr B.P.,
that is, well into the Holocene (Vartanyan et al. 1993), a time that coincided with
human arrival on Wrangel Island (Lister 1993). This suggests that survival of
Pleistocene grazing mammals into the Holocene was possible in the absence of
human hunting.

The *climatic hypothesis* for megafaunal extinction assumes that an arid, conti-
nental climate prevailed in Beringia during the Pleistocene, causing low summer
precipitation and dry soils (Velichko 1973; Yurtsev 1974; Giterman 1976; Hopkins
et al. 1982; Grichuk 1984; Sher 1988; Vereshchagin 1988). Well-drained soils and
warm summers promoted a productive steppe vegetation that supported popula-
tions of large grazers (mammoths, bison, and horses) (Hopkins et al. 1982;
Guthrie 1990). Dry soils facilitated animal movement. According to the climatic
hypothesis, the climate became wetter during the Holocene: rainfall increased, a
moss-lichen cover developed, the amount and productivity of the herbaceous
vegetation decreased, and snow depth increased. Together these factors caused
the extinction of the steppe megafauna (Tomirdiaro 1978; Yurtsev 1982; Shilo et
al. 1983; Guthrie 1990).

The major evidence for the climatic hypothesis comes from Pleistocene pollen
and macrofossils of grasses, *Artemisia,* and other steppe taxa that today are most
abundant in the arid regions of central Asia (Yurtsev 1974, 1982; Grichuk et al.
1984; reviewed in Guthrie 1990). Today, steppelike vegetation occurs in the tun-
dra zone primarily as isolated islands on arid, south-facing bluffs (Yurtsev 1982;
Murray et al. 1983; Edwards and Armbruster 1989; Walker et al. 1991), which
leads to the assumption that the warm, dry *micro*climate that characterizes this
habitat today may also have characterized the Pleistocene *macro*climate. Mega-
fauna fossils are common in deposits with steppe vegetation but generally absent
from Holocene deposits (Guthrie and Matthews 1971; Guthrie 1982, 1984*b*, 1990),
although the precise timing and rate of these changes is debated (Mead and
Meltzer 1984). Thus, there is a general correlation among the presence of dry
soils, steppe vegetation, and megafauna.

There are several sources of uncertainty in reconstructing the Pleistocene
steppe landscape (Colinvaux 1964; Ritchie and Cwynar 1982; Anderson 1985;
Barnosky et al. 1987; Edwards and Armbruster 1989; Guthrie 1990). First, many
of the taxa that differentiate steppe (grasses and *Artemisia*) from tundra (sedge)
pollen assemblages cannot be identified to species and today contain taxa that
can be found on both wet and dry soils. Second, it is difficult to reconstruct
landscape-level vegetation patterns from pollen cores taken largely from lakes
(Schweger 1982; Barnosky et al. 1987; Edwards and Armbruster 1989). Finally,

controversy over pollen influx rates raises questions as to whether the steppe vegetation was unproductive (Ritchie and Cwynar 1982; Colinvaux and West 1984) or highly productive (Guthrie 1990). Based on the bulk of the evidence, it seems likely that the Pleistocene steppe vegetation of Beringia was productive and occurred on dry soils (Guthrie 1990). This vegetation mosaic was probably variable geographically and topographically, but steppe grassland was probably a widespread community type (Barnosky et al. 1987; Edwards and Armbruster 1989).

The keystone-herbivore hypothesis draws heavily on both the overkill and the climatic hypotheses and links them by assuming strong interactions between animal grazing and ecosystem processes. As with the climatic hypothesis, the keystone-herbivore hypothesis assumes that a productive steppe vegetation was necessary to support megaherbivores. It extends the Pleistocene overkill hypothesis by suggesting that grazing by megaherbivores was essential to the maintenance of a productive grass-steppe vegetation, which produced dry soils through high rates of evapotranspiration. This is illustrated as a conceptual model (fig. 1) that shows strong interactions among climate, animal grazing, and ecosystem processes in which the extinction of the megafauna could cause a transition from predominance of steppe to predominance of moss-dominated tundra (i.e., tip the balance in favor of tundra). Because the vegetation data and paleoindicators of soil moisture are consistent with both the climatic and the keystone-herbivore hypotheses, we cannot use vegetation-based climate reconstructions to differentiate between these hypotheses. Instead, we address two questions: Was the climatic change at the end of the Pleistocene sufficient to cause a transition from steppe to tundra? Are there plausible mechanisms by which the loss of megafauna could cause a shift from steppe to tundra?

EVIDENCE AGAINST AN EXCLUSIVELY CLIMATIC EXPLANATION FOR STEPPE

Changes in Aridity of Climate

The major difficulty in reconstructing the causes of past steppe vegetation and its change to tundra is the paucity of *direct* evidence for the nature of the Pleistocene climate in Beringia. Here we present indirect evidence from a variety of sources suggesting that the Beringian climate was cold but not necessarily more arid during the Pleistocene than today. Large ice sheets occupied Canada, Greenland, and northern Europe during the Pleistocene 20,000 yr B.P., but northern Russia, Alaska, and the Beringian continental shelf separating these two areas were unglaciated, except for localized mountain glaciers (Hopkins 1967; Nekrasov et al. 1973; CLIMAP 1981; Serebryanny 1984). Oxygen-isotopic composition of fossil foraminifera indicate that sea-surface temperatures in the north Pacific south of Beringia were $2°-8°C$ colder during the Pleistocene than at present (CLIMAP 1981; Rind 1987). Together these data indicate a colder climate in Beringia than exists today. Consequently, sea ice extended $10°$ latitude farther south than at present (CLIMAP 1981; Kutzbach and Guetter 1986).

The geographical pattern of the Pleistocene climate 20,000 yr B.P. has been

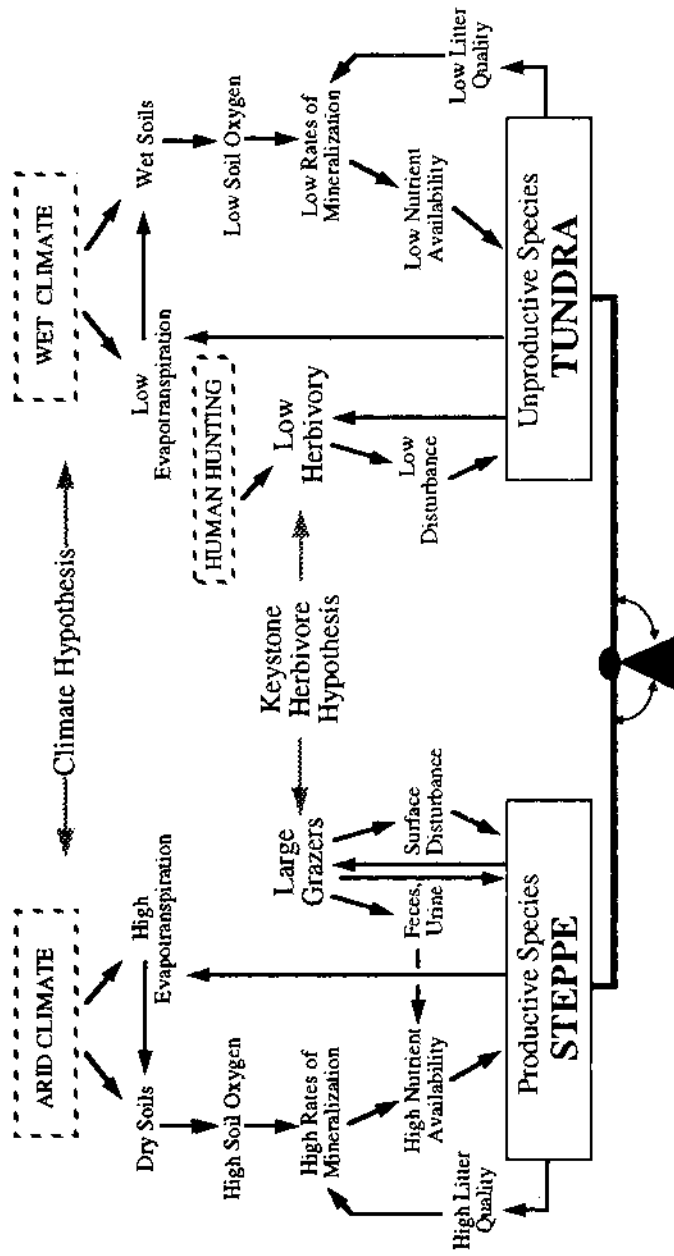Fig. 1.—Interactions among climatic, vegetation, and soil processes leading to either tundra or steppe. The balance between tundra and steppe can be shifted by changes in either of two independent variables (shown in dashed boxes): climate (climatic hypothesis) or human hunting, which alters the abundance of large grazers (keystone-herbivore hypothesis). This figure follows the scheme presented in Schlesinger et al. (1990).

simulated using GCMs that incorporate data on the Pleistocene distribution of land, ocean, glaciers, sea ice, sea-surface temperatures, and albedo (Kutzbach and Wright 1985; Manabe and Broccoli 1985; Kutzbach and Guetter 1986; Rind 1987). These paleoclimatic reconstructions using three different GCMs suggest that the Pleistocene climate of Beringia was 2°–5°C colder in summer and 10°–20°C colder in winter than at present, the growing season was shorter, and much of the jet stream was deflected southward around the large continental ice sheets in eastern North America and western Eurasia (Kutzbach and Wright 1985; Manabe and Broccoli 1985; Kutzbach and Guetter 1986; Rind 1987). However, these GCM simulations suggest that precipitation and surface and jet-stream wind patterns *in Beringia* were broadly similar to present patterns, although in the past (as today) there was probably substantial geographical variation in climate within Beringia. For example, there may have been more southerly winds directly west of the Laurentide ice sheet (Kutzbach and Wright 1985) but more northerly or continental winds elsewhere in Beringia. Because of similar precipitation and colder summers between the Pleistocene and present climate, these models predict *higher* soil moisture in Beringia (Rind 1987) or geographically variable soil moisture (dry soils immediately east of the European ice sheet and similar or higher soil moisture elsewhere in Beringia) (Manabe and Broccoli 1985). These GCM simulations conflict with assumptions that a warm, arid summer macroclimate throughout Beringia was responsible for the widespread distribution of steppe vegetation and dry soils (Grichuk 1984; Velichko 1984; Guthrie 1990).

Mountain glaciers of northeast Asia and Alaska were more extensive in the late Pleistocene than at present (although less extensive than during earlier glaciations) (Pewe et al. 1965; Hamilton 1982; Hopkins 1982; Serebryanny 1984). Mass balance of mountain glaciers is governed primarily by snow inputs and summer melting. Given that sea-surface and air temperatures were lower during the Pleistocene than at present and that sea ice extended farther south, the extensive mountain glaciers of Beringia during the Pleistocene were more likely due to cold summers than to wetter winters (Lebedeva and Khodakhov 1984; Rind 1987; Zimov and Chuprynin 1991), which suggests that the Pleistocene did not have a warm summer climate.

Despite cold summers and low climatic potential for evapotranspiration, Pleistocene soils were drier than at present. Extensive Pleistocene dunes of sand and silt throughout Beringia (Hopkins 1982; Tomirdiaro 1982) suggest either that the climate of the Pleistocene was too cold to support productive vegetation (Ritchie and Cwynar 1982; Colinvaux and West 1984) or that the soils were extremely dry (Hopkins 1982; Tomirdiaro 1982; reviewed in Guthrie 1990). Alternatively, dunes may have been produced during relatively short time periods and may not reflect the average Pleistocene climate. Carbonate and salt accretion in these deposits also indicate high actual evapotranspiration rates from these soils (Tomirdiaro 1982; Walker and Everett 1991). The vegetation data also suggest drier soils but are not conclusive evidence of a dry macroclimate. Many of the Pleistocene grasses were mesophyllous (Yurtsev 1981, 1982), and some steppe species (e.g., *Artemisia arctica*) may be indicators of disturbance and dry soils rather than of dry macroclimate (Webber 1978).

The radiative index of aridity (I_a, the ratio of net energy input to energy re-

TABLE 1

AVERAGE PRECIPITATION (NOVEMBER–MARCH, APRIL–OCTOBER, AND TOTAL), NET TOTAL SOLAR RADIATION, AND INDEX OF ARIDITY (SEE TEXT) IN 16 WEATHER STATIONS OF NORTHEAST ASIA

| LOCATION | LATITUDE, LONGITUDE | PRECIPITATION (mm) | | | NET RADIATION (kcal cm^{-2} yr^{-1}) | INDEX OF ARIDITY |
		Nov.–March	April–Oct.	Total		
Kotelnyi	75°N,140°E	40	101	141	11.1	1.5
Priobrocheniya	74°N,110°E	28	144	172	15.8	1.7
Wrangel Island	72°N,180°E	65	117	182	23.8	2.4
Chetyrekhstolbovoi	71°N,160°E	46	101	147	20.5	2.6
Mostakh Island	71°N,129°E	55	177	232	14.7	1.2
Ayan	70°N,168°E	52	137	189	24.7	2.5
Olenek	68°N,112°E	47	219	266	21.3	1.5
Verkhoyansk	68°N,133°E	27	120	147	23.8	3.0
Cape Schmidt	68°N,180°E	81	173	254	26.3	1.9
Srednekolymsk	67°N,153°E	57	131	188	26.3	2.6
Uelen	67°N,173°W	125	261	386	19.1	.9
Srednekan	64°N,153°E	149	268	417	23.4	1.0
Markova	64°N,171°E	107	230	337	27.1	1.3
Oimiakon	63°N,142°E	32	143	175	31.0	3.3
Yakutsk	62°N,129°E	36	166	202	29.3	2.7
Aldan	58°N,126°E	89	457	546	26.4	.9

NOTE.—Data are averages for the entire record (up to 1980) of each station ($n > 20$ yr) from regional volumes of the *Climatic Atlas of the Soviet Union* (Zimov and Chuprynin 1991).

quired to evaporate annual precipitation) provides an objective index of aridity (Budyko 1984):

$$I_a = \text{PET/PPT} ,$$

where PET = potential evapotranspiration, and PPT = precipitation (see app. A for definitions and units). A value of three indicates there is enough radiation input to evaporate three times the annual precipitation. Values of I_a in northeast Asia (an area currently dominated by wet tundra) range from about one to three among 16 meteorological stations (table 1), values that are similar to areas in central Asia that support steppe (I_a = 1–2) or semidesert (I_a = 2–3) vegetation (Budyko 1984).

Variations in macroclimate across Beringia (Manabe and Broccoli 1985; Kutzbach and Guetter 1986; Rind 1987) and in microclimate with slope, aspect, and elevation (Barnosky et al. 1987; Edwards and Armbruster 1989) were probably greater than the magnitude of change in these parameters between the Pleistocene and today (Manabe and Broccoli 1985; Kutzbach and Guetter 1986; Rind 1987). Thus, we might expect a greater abundance of steppe in the present vegetation mosaic, if macroclimate were the only factor responsible for the vegetation shift across the entire area of Beringia.

Effects of Aridity on Vegetation

A major dilemma for the climatic hypothesis is to explain how the late Pleistocene vegetation could have been sufficiently productive to support the large size

and rapid growth rates of the Pleistocene megafauna (Guthrie 1984a, 1990; Owen-Smith 1987). Because it is unlikely that the colder temperatures of the Pleistocene would have promoted productivity, it has been suggested that dry summers prevented waterlogging of soils and contributed to a high productivity of the Pleistocene steppe (Hopkins et al. 1982; Guthrie 1990). However, the distribution of current tundra ecosystems indicates a negative correlation between aridity and productivity (Yurtsev 1982). As discussed below, it is more likely that the species composition of steppe was more nutritious to megafaunal grazers than is that of tundra.

Direct Climatic Effects on Fauna

The climatic hypothesis suggests that climatic change at the end of the Pleistocene could have contributed directly to megafauna extinction through increases in snow depth (reducing access to winter food) and soil moisture (reducing summer mobility) (Guthrie 1990). However, today's snow cover is <30 cm in the central plains of Yakutia and in the basins of the Yana and Indigirka Rivers in northern Yakutia (Gavrilova 1973). At 61 of 83 Yakutian meteorological stations, winter precipitation is <50 mm (also see table 1) (Zimov and Chuprynin 1991). Areas that support natural or introduced bison populations, such as the Great Slave Lake of Canada or the Delta Junction area of Alaska, currently have greater snow depth than northern Yakutia. Yakutian horses, a hardy northern breed, obtain sufficient food to sustain themselves during the winter from beneath a 50- to 60-cm snowpack (Tikhonov 1987). Moreover, these horses graze in wet riparian meadows in summer in preference to communities with drier soils (S. A. Zimov, personal observation), which suggests that summer soil moisture does not greatly restrict habitat use.

In summary, the Pleistocene climate was probably colder than at present, but changes in aridity are uncertain. If the climate had been more arid in the past, it would probably have reduced rather than increased the productivity of the vegetation. Thus, there is not strong evidence that a change in macroclimate alone caused a change in relative abundance from productive grassland steppe to less productive tundra.

POTENTIAL MECHANISMS FOR THE STEPPE-TUNDRA TRANSITION

We suggest that the keystone-herbivore hypothesis (Owen-Smith 1987) is a useful alternative to the climatic hypothesis because it provides a mechanism to explain high productivity and dry soils of the Pleistocene steppe without assuming a more favorable climate for plant growth. The climatic hypothesis assumes that an arid Pleistocene climate produced dry soils that were necessary for steppe vegetation and, therefore, steppe megafauna (fig. 1) (Guthrie 1990). The keystone-herbivore hypothesis argues that the presence of animal-induced steppe vegetation could have produced drier, more fertile soils than occur in tundra.

Vegetation Effects on Soil Moisture

Vegetation strongly influences soil moisture because most water evaporating from vegetated surfaces derives from transpiration (Jarvis and McNaughton

1986). Transpiration rate correlates with photosynthesis at the leaf level because stomatal conductance is adjusted to match the biochemical potential for photosynthesis (Farquhar and Sharkey 1982; Field et al. 1992) and at the canopy level because both processes correlate with leaf-area development (Collatz et al. 1991; Field et al. 1992). Consequently, transpiration is proportional to photosynthetic carbon gain (Chapin 1993) and net productivity (about 400–500 g water/g production) (Larcher 1980; Field et al. 1992). If primary productivity during the late Pleistocene grass-dominated steppe was higher than that of the moss-dominated tundra of the Holocene, the Pleistocene soils could have been drier because of the greater evapotranspiration rather than because of drier climate (fig. 1).

High plant productivity reduces soil moisture. When agricultural lands remain fallow in arid climates, soil moisture increases. Removal of forest trees reduces regional evapotranspiration and increases runoff (Bormann and Likens 1979). Computer simulations linked to GCM models predict that a conversion of tropical forest to grassland would reduce evapotranspiration, thereby increasing soil moisture (Shukla et al. 1990). Addition of nutrients to tussock-tundra vegetation in Alaska increased productivity and reduced soil moisture (Chapin et al. 1995). The presence of large grazers increased the productivity of steppe vegetation and reduced soil moisture (Kucheruk 1985).

To determine whether differences among tundra vegetation types could cause large effects on evapotranspiration and soil moisture, we measured evapotranspiration from different species and associated soils in weighing lysimeters at the Northeast Scientific Station in the Kolyma lowlands during a 6-wk experiment. When soils were maintained at field capacity, vascular plants characteristic of steppe (i.e., grasses, sedges, and *Artemesia*) transpired more water (174 ± 18 mm) than nonvascular plants characteristic of tundra (69 ± 13 mm) (table 2). When plants received only natural rainfall, mosses evaporated less water (42 ± 3 mm) than bare ground (55 mm) because mosses lack a root system and have limited access to soil water. By contrast, steppe species evapotranspired 99 ± 12 mm of water (all the available water in the soil profile) and subsequently wilted. These experiments demonstrate that steppe vegetation transpires more water and produces drier soils than moss-dominated tundra vegetation.

Vegetation Effects on Soil Fertility

To explain differences in productivity between steppe and tundra, without invoking a change in climate, we must understand the role of mosses and grasses in plant-soil feedbacks. Mosses reduce rates of decomposition and nitrogen mineralization (Coulson and Butterfield 1978; Johnson and Damman 1991; Van Cleve et al. 1991) because of their low nitrogen concentration and high concentrations of recalcitrant lignin-like polymers (Chapin et al. 1986), low thermal conductance that reduces soil temperature, and low rates of evapotranspiration, which promote the development of waterlogged soils. The resulting low nutrient availability limits the productivity of vascular plants (Chapin and Shaver 1985). By contrast, moss growth is limited more strongly by water than by nutrients (Skre and Oechel 1979, 1981), so the moist, nutrient-deficient soil environment promotes moss growth. Eventually, as the mosses grow, thaw depth decreases to the point that

TABLE 2

RATES OF EVAPOTRANSPIRATION FROM PLANTS PLUS ASSOCIATED SOILS PLACED IN 21-CM-DEEP WEIGHING
LYSIMETERS IN THE KOLYMA LOWLANDS DURING 1989

| | MAXIMUM EVAPOTRANSPIRATION RATE (mm d^{-1}) | | AVERAGE RATE OF EVAPOTRANSPIRATION (mm d^{-1}) | |
SURFACE TYPE	Field Capacity	Natural Precipitation	Field Capacity	Natural Precipitation
Free water	6.7	. . .	3.5	. . .
Soil:				
Steppe loam	6.4	1.3	3.3	1.0
Sand	3.6	. . .	1.5	. . .
Tundra plants:				
Lichen (*Cladonia*)	3.3	1.5	1.6	.9
Moss	6.1	1.0	2.8	1.0
Steppe species:				
Agropyron	16.2	4.3	6.7	2.5
Eriophorum	9.6	5.6	5.3	3.0
Equisetum	8.8	3.1	4.0	1.6
Artemesia	14.7	3.6	6.1	2.3
Probability of difference between nonvascular and meadow/steppe species*	.03	.01	.03	.02

NOTE.—Each lysimeter contained bare soil, open water, or complete plant cover. Samples were collected from an area of loess soil typical of the region. Water was added to bring each soil to field capacity. Lysimeters were weighed twice daily, and water was added weekly to maintain constant weight. Measurements were made with lysimeters maintained either at field capacity ($n = 2$) or with natural precipitation ($n = 1$). We present both the maximum observed rate and the average rate during July 1989. Average environmental conditions during the experiment were as follows: air temperature (25°C), wind speed (4 m s^{-1}), relative humidity (45%), daily direct irradiance (21 h d^{-1}), and precipitation (7.4 mm wk^{-1}).

* Probability value from *t*-test, treating each species as a separate sample.

only the moss layer itself thaws (Kriuchkov 1973; Chernov 1978; Van Cleve et al. 1983), and grasses, which require access to thawed mineral soil, are excluded from these communities. Because of these feedbacks (fig. 1), moss ecosystems develop readily in the Far North. For example, in northwestern Siberia, 60%–70% of the forested area disappeared during historical time because of moss development and associated waterlogging of soils (Kriuchkov 1973), and Alaskan forests succeed to moss-dominated muskegs and spruce forests in the absence of fire (Van Cleve et al. 1991). Moss-dominated ecosystems are avoided by mammalian herbivores (Wolff 1980) because the low tissue-nutrient and high secondary-metabolite concentrations in the vegetation cause low digestibility and low palatability to animals (Bryant and Kuropat 1980; Pastor et al. 1988).

In more fertile grass-dominated meadows, an alternative set of feedbacks promotes productivity and grazing (fig. 1) (Chapin 1991). Growth of grasses in the current tundra environment is stimulated by nutrient inputs from fertilizers (McKendrick et al. 1978; Shaver and Chapin 1986), animal carcasses, and feces (Batzli et al. 1980; McKendrick et al. 1980) or intensive disturbance by humans (Chapin and Shaver 1981; Zimov 1990) or animals (Batzli and Sobaski 1980).

Mowing stimulates the aboveground production of steppe grasslands fivefold (Kucheruk 1985) and of sedge tundra threefold (Peshkova and Andreiashchkina 1983), which indicates that grazing stimulates aboveground productivity in these ecosystems. This grass-dominated vegetation has higher tissue-nutrient concentrations than mosses or dwarf shrubs, is more digestible, and attracts grazers (White and Trudell 1980). Both the high litter quality and the rapid turnover of nutrients by grazers stimulate decomposition, mineralization, and nutrient turnover (Batzli et al. 1980; Chapin 1991) and reduce soil moisture (Chapin and Shaver 1985). The dense vascular litterfall shades out or physically smothers mosses, which leads to a decline in their abundance (Chapin et al. 1995). In high-fertility sites many grasses are covered with snow while green and, therefore, maintain their high forage quality throughout the winter (Tishkov 1985), which leads to intense overwinter microtine grazing (Batzli et al. 1980; Chapin and Shaver 1981). These feedbacks, which maintain grasslands, are also well documented in temperate and tropical climates (McNaughton 1979; Huntly 1991), but they occur only in isolated locations of intensive lemming grazing in the Far North, because there are no large grazing mammals that feed mainly on grasses.

Possible Triggers for Vegetation Change

Given that both moss-dominated tundra and grass-dominated steppe ecosystems can create their own self-sustaining soil moisture and nutrient regimes (fig. 1), what could have triggered a change in the relative abundance of steppe and tundra at the Pleistocene-Holocene boundary? Four factors were potentially important: climatic warming, the cessation of loess deposition, increases in atmospheric CO_2, and the loss of large mammalian grazers.

Arctic grasses and mosses both photosynthesize and grow effectively at low temperature (Oechel and Sveinbjörnsson 1978; Tieszen 1978) and exhibit broad latitudinal distributions, so it seems unlikely that warming would directly cause a shift from grass to moss dominance at the end of the Pleistocene.

The substantial Pleistocene loess deposition in the Beringian lowlands ceased at the beginning of the Holocene (Tomirdiaro 1982). When the average deposition rate is greater than 1 mm yr^{-1}, grasses have a competitive advantage as colonizers (Zimov and Chuprynin 1991). Sediments provide a rich mineral source for grasses and eliminate slowly growing mosses, lichens, and evergreen shrubs (Walker and Everett 1987, 1991; Zimov and Chuprynin 1991).

In the low-CO_2 Pleistocene climate (Webb and Bartlein 1992), stomates must have remained open longer and transpired more water to absorb a given amount of CO_2 compared to the Holocene (Larcher 1980; Field et al. 1992). Thus, even assuming no change in climate, a low-CO_2 Pleistocene environment must have caused greater competition for water, lower soil moisture, and a more xerophytic vegetation than in current tundra. Most of this change in atmospheric CO_2 occurred before 12,000–15,000 yr B.P. (Webb and Bartlein 1992) and thus preceded the transition from steppe to tundra.

The loss of large mammalian grazers at the Pleistocene-Holocene boundary (see above) could have contributed to the transition from steppe to tundra. Ungrazed,

unfertilized meadows are unstable in the absence of herbivores or continued disturbance (Chernov 1978). When dry, uneaten litter accumulates, nutrients are sequestered in undecomposed organic matter, and nutrient turnover declines (Batzli 1977). Dry grass litter is highly reflective, reducing radiation gain, and is an effective heat insulator, minimizing heat input to soil during the short summer season, cooling the underlying soil, reducing the depth of soil thaw, and promoting the growth of mosses and evergreen shrubs (Batzli 1977). Conversely, herbivores can cause a conversion from tundra to grass-dominated meadow. Despite its effectiveness in excluding other vegetation, moss cover is fragile when trampled or grubbed by animals (Chernov 1980). Areas of Russian tundra covered by deep snow, such as ravines, support lemming populations, which both destroy the mosses and fertilize the soil. During population outbreaks, lemmings expand into areas between ravines and eliminate mosses by grubbing (Chernov 1978), which contributes to the maintenance of meadows, which are 8- to 10-fold more productive than moss associations (Chernov et al. 1983). The high productivity of meadows is associated with an 8–10-fold increase in biomass of soil invertebrates and with rapid nutrient cycling (Chernov 1978; Chernov et al. 1983). Similarly, in Alaskan lowland polygonal tundra, troughs between ice-wedge polygons have deeper snow, larger lemming populations, and more rapid nutrient cycling than adjacent microhabitats (Batzli et al. 1980). Similarly, reindeer grazing causes the expansion of graminoids and reduced cover of mosses and shrubs (Thing 1984). Snow geese also stimulate productivity and nutrient cycling in coastal salt marshes of northern Canada and Alaska (Cargill and Jefferies 1984). On a larger scale, where fire or human disturbance destroys the moss turf, meadow vegetation develops and becomes a focus for activity of mammalian herbivores (Fox 1978; Wolff 1980; Bryant and Chapin 1986).

In the following section, we present results of a simulation model to test whether the impact of mammalian grazers on vegetation is sufficiently strong that the loss of the grazing megafauna could cause a transition from steppe to tundra in Beringia (fig. 1). The model was originally developed (Zimov and Chuprynin 1991) to predict the global distribution of vegetation based on patterns of annual radiation input and precipitation, competition among functional groups of plants for climatically determined resources (radiation and water), and grazing by large mammals. In this article, we apply the model to the interaction between grazing and climate in Beringia.

<div align="center">A MODEL SIMULATION OF MEGAFAUNAL IMPACTS IN THE FAR NORTH</div>

Overview of Model

The model has three functional groups: "trees" (woody plants, including shrubs), "grasses" (herbaceous vascular plants), and "mosses" (nonvascular plants, including lichens). Each functional group has a characteristic maximum growth rate that is diminished when supplies of light, water, or nutrients are suboptimal. This growth rate, which determines a group's resource "demand," is further modified by competition coefficients that are determined by the priority

of access of each group to a limiting resource (i.e., radiation or water). For example, mosses compete with trees and grass for water but not for light (because of their shorter stature); trees and grass compete with one another for light in the Far North where trees (i.e., shrubs) are short, but elsewhere trees are better competitors for light than are grasses and mosses. Comparable rules of competition for water are governed by rooting depth. The model is outlined briefly in appendix B and described in detail elsewhere (Zimov and Chuprynin 1991).

Nutrient supply, which is linked less directly to climate, is assumed to affect competition through differential effects on growth (i.e., response of grasses > trees > mosses) (Chapin and Shaver 1989) rather than being the resource for which plants compete. Nutrient supply can be varied in the model to simulate the increased soil fertility associated with Pleistocene loess deposition.

Mammalian grazers affect vegetation through consumption and destruction of biomass. We assume that grazers have no long-term detrimental effect on grass biomass in a steady-state ecosystem controlled by climate and predators because predators prevent overgrazing on the long timescales (centuries) simulated by the model, and grassland production in tundra compensates effectively for grazing through a variety of ecosystem feedbacks (Peshkova and Andreiashchkina 1983; Cargill and Jefferies 1984; Kucheruk 1985). Predictions of the model were qualitatively similar when this assumption was relaxed to allow grass response to grazing to range from moderately detrimental to moderately stimulatory (app. B)—that is, the range of grazing response observed in natural ecosystems.

Climatic data (radiation input and precipitation) were estimated for each terrestrial 5° grid point of longitude and latitude (Budyko 1984). The model, which includes grazing as a natural process, was solved for the equilibrium biomass (B) of each functional group ($dB/dt = 0$) at each 5° grid point, assuming each of four values of nutrient availability, to estimate patterns of functional-group composition. At the two intermediate soil fertility levels, the simulated distribution of functional groups closely matched observed vegetation patterns both within Beringia and globally (fig. 2), providing model validation. From these data we determined the combinations of Beringian climatic conditions that could be occupied by each functional group on infertile and fertile soils.

The model was then run to equilibrium with an annual time step to simulate patterns in productivity of each functional group on fertile and infertile soils under a representative Pleistocene Beringian scenario of cool climate, loess deposition, and presence of large grazers. We then ran four simulations of possible changes from Pleistocene to Holocene conditions (table 3): the complex of conditions that changed at the end of the Pleistocene (climatic warming, elimination of grazers, and elimination of loess deposition); climatic warming; elimination of loess deposition; elimination of large grazers. We did not include CO_2 effects in the model. Each of these simulations was run under two conditions of soil fertility (to represent topographic and geologic variation in nutrient supply) and two initial densities of colonizing species (i.e., mosses and trees) until biomass came to equilibrium with the new conditions. A 10-fold variation in initial colonizer density altered the rate of vegetation change but not the equilibrium species composition, so we present results from only the higher colonizer density (table 3). The climatic

FIG. 2.—Maps of vegetation simulated by the model at the climates of each 5° terrestrial grid point at low soil fertility ($s = 1.0$; *upper panel*) and high soil fertility ($s = 1.3$; *lower panel*). At each grid point the most abundant functional group is shown at the left, and other coexisting functional groups are shown at the right. Trees are indicated by vertical lines, grasses by dots, mosses by horizontal lines, and lack of vegetation by a zero. At some grid points (e.g., Beringia) there were two stable vegetation types, and these are shown one on top of the other.

TABLE 3

CHANGES IN MODEL PARAMETERS TO SIMULATE POSSIBLE CHANGES FROM PLEISTOCENE
TO HOLOCENE CONDITIONS

Model Assumptions	Potential Evapotranspiration (mm yr^{-1})	Herbivore Impact on Moss Biomass	Soil Fertility
Pleistocene conditions	350	.5	1.3,1.6
Holocene conditions:			
Elimination of large grazers	350	.2	1.3,1.6
Elimination of loess deposition	350	.5	1.0,1.3
Climatic warming	400	.5	1.3,1.6
Climatic warming, elimination of grazers, and elimination of loess deposition	400	.2	1.0,1.3

NOTE.—Initial Pleistocene vegetation had a greater biomass of grasses (B_g = 0.25) than of trees and mosses ($B_t = B_m = 0.1$). Identical equilibrium vegetation composition occurred with a low density of initial colonizers ($B_t = B_m = 0.01$). Parameters are defined in appendix A.

warming scenario we present is the range from Pleistocene to present in incoming net radiation (potential evapotranspiration [PET] increased from 300 to 500 mm yr^{-1}). To test the generality of these results, we reran the climate warming scenario with PET = 600 mm yr^{-1} (the maximum net radiation currently reported anywhere in Beringia) and found that this extreme climatic warming differed only slightly from the "realistic" scenario. We do not present data from this maximal climatic warming.

Model Results

When the model was run for all terrestrial climates, it gave a realistic geographical distribution of each functional group (fig. 2), which gave us confidence that the model reasonably captures the general climatic controls over vegetation distribution, assuming a natural grazing regime. When the equilibrium biomass of major functional groups was calculated in Beringia under Pleistocene conditions, grasses were abundant under the entire range of climatic conditions, mosses were abundant in dry climates, and trees were restricted to the warmest, wettest climates, regardless of soil fertility (fig. 3). This pattern is consistent with the Pleistocene pollen record and with the maintenance of these grasslands by climate, grazers, or loess deposition. When grazers were removed in the model, mosses expanded dramatically, grasses declined (especially at low fertility), and trees increased slightly. By contrast, a change in the climate from Pleistocene to Holocene conditions resulted in a large increase in trees under moist conditions, a change in the moisture dependence of mosses, and modest changes in grasses. The loss of loess deposition under infertile conditions reduced grass growth and enhanced tree growth but had no major effect on mosses. Under fertile conditions, the loss of loess deposition had no major effect on species composition. The change from Pleistocene to present conditions in all three parameters (grazers, climate, and loess) caused a complete replacement of grasses by mosses and trees at low fertility and coexistence of all three types at higher soil fertility,
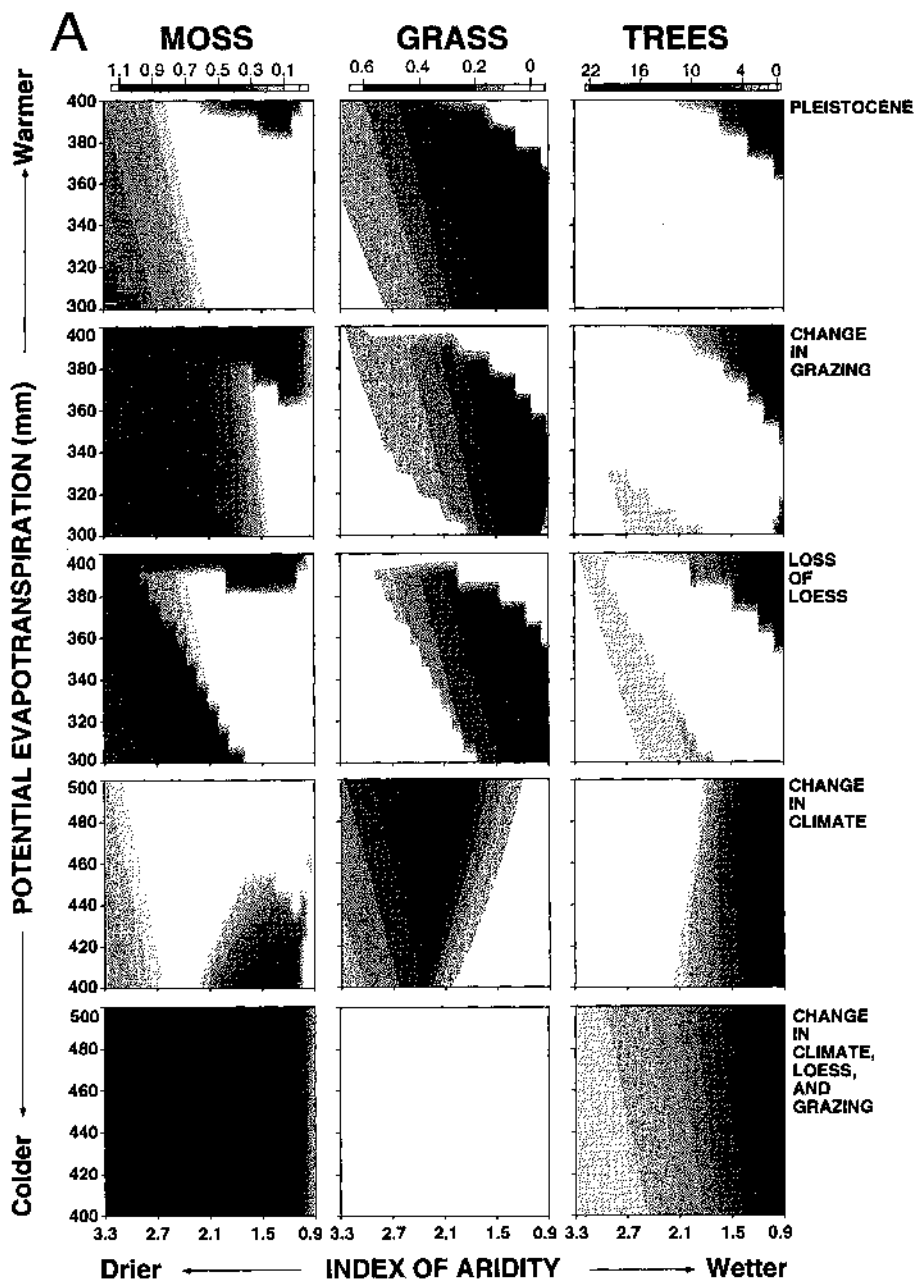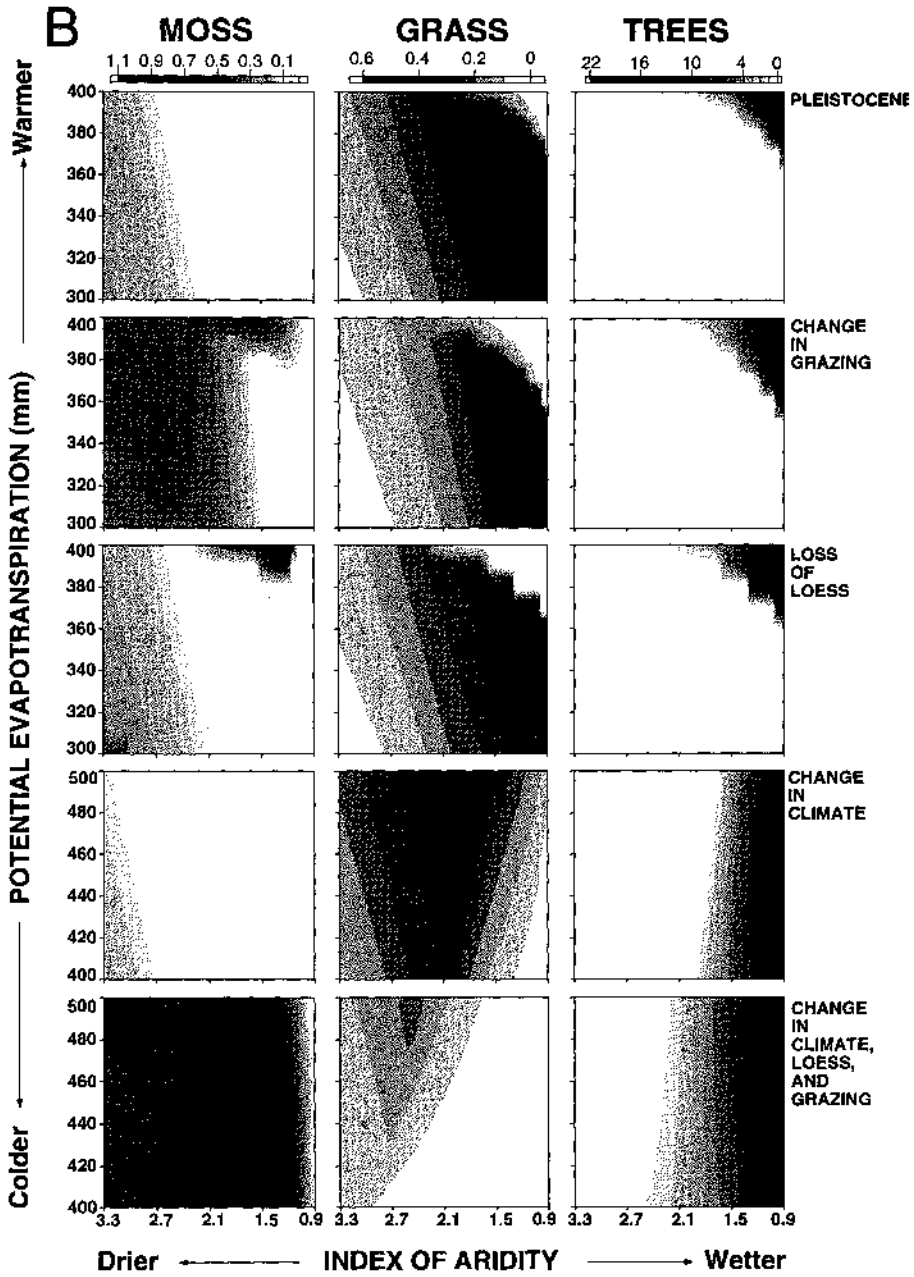
FIG. 3.—Predicted equilibrium biomass of major functional groups under the range of Pleistocene conditions of potential evapotranspiration and index of aridity in Beringia and under four possible scenarios of change from Pleistocene to Holocene conditions: loss of grazers, elimination of loess deposition, climatic warming, and combined change in all conditions including climatic warming, loss of loess deposition, and loss of large mammalian grazers. Each of these biome-change scenarios began with Pleistocene conditions (>99% grass) and was tested at low densities of colonizers ($B_m = B_t = 0.01$), moderate density of colonizers ($B_m = B_t = 0.1$), and low fertility (s = initial fertility = 1.0; A) and high fertility (s = initial fertility = 1.3; B). Equilibrium biomass was independent of initial colonizer density. See appendices A and B for the definition and explanation of terms and table 3 for parameter values.

B

MOSS   GRASS   TREES

MOSS: 1.1 0.9 0.7 0.5 0.3 0.1

GRASS: 0.6 0.4 0.2 0

TREES: 22 16 10 4 0

PLEISTOCENE

CHANGE IN GRAZING

LOSS OF LOESS

CHANGE IN CLIMATE

CHANGE IN CLIMATE, LOESS, AND GRAZING

Warmer

Colder

POTENTIAL EVAPOTRANSPIRATION (mm)

Drier ← INDEX OF ARIDITY → Wetter

patterns similar to those observed presently in northern Beringia. These results suggest that change in several factors, especially grazers and climate, could cause a biome shift from dominance by grasses to dominance by mosses and shrubs and that neither climate change nor loss of grazers was sufficient as a single factor in causing observed vegetation change from Pleistocene to Holocene vegetation.

In summary, the model suggests that many factors contributed to vegetation change at the Pleistocene-Holocene boundary but that climate warming was particularly important to the invasion of woody plants and that the loss of grazers had the greatest effect on the balance between mosses and grasses. These results are consistent with paleorecords showing a switch to forest where climate permits a woody growth form to reach large size. However, it suggests that loss of grazers was critical to the switch from grass to moss dominance in areas presently occupied by tundra. Thus, the modeling supports our contention that extinction of the Pleistocene megafauna by human hunting in areas presently occupied by tundra could have caused a shift in the vegetation mosaic from predominance of grass-dominated steppe to predominance of moss-dominated tundra, even in the absence of a large climatic change. The model also suggests that other factors, particularly changes in climate and loess, contributed to this change and enhanced growth of woody plants.

RECONSTRUCTION OF THE MAMMOTH-STEPPE ECOSYSTEM

A large-scale reintroduction of mammalian grazers to tundra would be the best experimental validation of our simulation model. Musk oxen have been successfully reintroduced into northern Siberia and northern Alaska (Klein 1988), and bison have been brought into the mountains of central Alaska (Guthrie 1990). These reintroductions demonstrate that large mammalian grazers can withstand current climatic conditions and successfully exploit tundra vegetation, when human hunting is controlled. Moreover, mammoths persisted in northern Beringia until 3,700 yr B.P., when protected from human hunting (Vartanyan et al. 1993).

The reestablishment of grassland-grazing ecosystems is globally important because grasslands have been more strongly impacted by anthropogenic change throughout the world than any other ecosystem type, both by conversion to agriculture and by overhunting of native fauna. The Russian Far North is perhaps the only large area where the reconstruction of grassland-grazing ecosystems might be attempted (Zimov and Chuprinin 1989; Zimov 1990). Here, fragments of the steppe vegetation occur on dry, south-facing slopes (Yurtsev 1982; Murray et al. 1983), and meadows of sedges and grasses occur along rivers and thermokarst depressions (alases). These species provide the genetic basis of Beringian steppe vegetation and might expand into other environments, if competition from mosses and other typical tundra species were controlled by mammalian grazers. To test this hypothesis, we initiated an experiment to generate a population of wild Yakutian horses in the lowland tundra of Kolyma, 100 km inland from the Arctic Ocean. In 1988, 25 yearling foals were transplanted 500 km from the south. They successfully acclimatized and are reproducing without supplemental food or water (Zimov and Chuprynin 1991). The only assistance given the herd was

protection from poachers. In areas in which the activity of this herd is concentrated, grasses increased in abundance, while mosses declined (S. A. Zimov, F. S. Chapin III, and J. F. Reynolds, personal observation), consistent with our hypothesis that grazing mammals can generate grass-dominated vegetation. Caribou and reindeer, which were also important components of the Pleistocene megafauna, are still important herbivores in the north but eat shrubs and lichens more than grasses. The maintenance of an effective grazing regime could be improved by adding other grazers typical of the Pleistocene steppe (e.g., bison, musk oxen). Predators, such as the tiger, were also essential components of the Pleistocene ecosystem (Vereshchagin 1988). The Amur tiger occurs in the Russian Far East and formerly extended into cold regions of central Yakutia. This tiger is presently an endangered species because of a lack of suitable prey. Large cats have been important components of all grazing ecosystems. If introduced to the north, the tiger could serve the dual purpose of providing a viable habitat for tigers and controlling grazer density in Beringia.

Steppe reconstruction has important implications for current ecological and social problems. Northern moss and forest communities are sensitive to human disturbance (Kriuchkov 1973), and northern Siberia is currently a region of widespread human disturbance (Zimov 1990). Because grasses and other steppe species are less sensitive to disturbances such as human activity (Chapin and Shaver 1981), it may be easier to convert some highly disturbed tundra areas to steppe than to restore the original tundra. If steppe reconstruction were successful, the grazing mammals could provide a sustainable food source for northern peoples and a model for reconstruction of grazing ecosystems throughout the world.

CONCLUSION

We will never know the relative importance of the multiple causes of the transition from steppe to tundra at the end of the Pleistocene. The keystone-herbivore hypothesis discussed here, however, provides a plausible explanation for the high productivity of forage species that must have been necessary to support megafauna in a Pleistocene climate that was colder than at present. Our analysis indicates that northern grazers have sufficiently large impacts on vegetation and ecosystem processes that their role must be considered in any effort to predict the pattern and productivity of past or future vegetation.

Under what circumstances are mammalian herbivores likely to cause large biome shifts? In forested regions, mammals preferentially browse early successional species, which speeds succession and increases the abundance of late-successional forests in the landscape (deToit et al. 1991; Pastor et al. 1993). However, it is primarily at ecotones between biomes, where climate is suitable for more than one ecosystem type, that mammals will have their greatest impact. Here overgrazing can shift the balance between tundra and steppe (this article) or between grassland, shrubland, and desert (Schlesinger et al. 1990), which could cause changes that could not be predicted on the basis of vegetation response to climate.

APPENDIX A

TABLE A1

DEFINITION OF SYMBOLS AND UNITS USED IN THE MODEL

Symbol	Description	Value(s) Used in Simulations
AET	Climatic maximum potential evaporation rate (mm yr^{-1})	Computed
a	Growth rate (yr^{-1})	Computed
a^0	Maximum growth rate under optimal resources (yr^{-1})	$a_g^0 = 8, a_m^0 = .4,$ $a_t^0 = .2$
a'	Resource-determined growth rate (yr^{-1})	Computed
B	Plant biomass (kg m^{-2})	Computed
b	Scalar governing nutrient supply to plants	Computed (0–1)
c	Rate of biomass loss to grazing and trampling by herbivores (yr^{-1})	$c_g = 0, c_m = 1,$ $c_t = .1 \cdot c_m$
d	Natural mortality rate (yr^{-1})	$d_m + r_m = .25,$ $d_g + r_g = 1.5,$ $d_t + r_t = .06$
e	Fraction of AET due to transpiration (0–1)	.8
F	Rate of resource consumption by the plant community (mm yr^{-1})	Computed
GPP	Gross primary productivity (kg m^{-2} yr^{-1})	Computed
g	Subscript indicating values for grasses	
I_a	Index of aridity (PET/PPT)	Computed
K_{ij}	Competition coefficient describing effect of species i on species j (0–1)	Computed
L	Latent heat of evaporation (kcal m^{-3})	.59
m	Subscript indicating values for mosses	
n	Coefficient governing plant nutrient requirement (dimensionless)	$n_g = 1, n_m = .01,$ $n_t = .33$
PET	Potential evapotranspiration (mm yr^{-1})	Computed
PET*	Maximum potential evapotranspiration (mm yr^{-1})	850
PPT	Precipitation (mm yr^{-1})	Varies, typical values = 140–600
R	Radiation input (kcal cm^{-2} yr^{-1})	Varies, typical values = 175–250
r	Respiration rate (yr^{-1})	See d
s	Coefficient governing effect of soil fertility on nutrient supply (dimensionless)	.7–1.6
T	Transpiration rate (mm yr^{-1})	Computed
t	Subscript indicating values for trees	
u	Maximum potential gross productivity corresponding to complete consumption of the limiting resource	Computed
V	Rate of supply of limiting resource (mm yr^{-1})	Computed
w	Coefficient governing climatic influence on nutrient supply	Computed
Ω	Constant relating productivity to transpiration (mm m^2 kg^{-1})	250

APPENDIX B

BRIEF DESCRIPTION OF THE MODEL

The model addresses vegetation change over long timescales (decades to centuries) and, therefore, excludes seasonal and demographic processes. In this version, we also ignore abiotic disturbance and insect herbivory. The model is run with an annual time step under constant conditions to determine steady-state values of biomass ($dB/dt = 0$). Whereas the original model was programmed in FORTRAN (Zimov and Chuprynin 1991), to examine model structure and confirm its behavior, we reprogrammed the model in Stella (*Stella II User's Guide* 1990) and C++ based on the description given below and elsewhere (Zimov and Chuprynin 1991) and obtained similar results. All symbols and units are defined in appendix A.

UNIFORM VEGETATION MODEL

First, we describe the general structure of the model in terms of a homogeneous plant community. Change in biomass is given by

$$\frac{dB}{dt} = (a - r - d - c) \cdot B,$$ (B1)

where B is the community biomass per unit area, a is the growth rate, r is the respiration rate, d is the mortality rate, and c is the rate of biomass loss to grazing and trampling by herbivores. The value of a is a function of a^r, a resource-determined growth rate, and the balance between the supply of the limiting resource (V) and rate of consumption (F) by the community, that is,

$$a = a^r \cdot \frac{(V - F)}{V}.$$ (B2)

In this version of the model, we consider two climate-related resources to be potentially limiting—water and nutrients.

Influence of Water Availability

The relationship of water availability to community productivity is incorporated into the model via its effects on V and F using two general relationships. First, across various ecosystems, gross primary productivity (GPP) is approximately proportional to transpiration (T) (Rosenzweig 1968; Leith 1975). Thus, the rate of consumption of water (F), which is equal to T, is given by

$$F = \Omega \cdot \text{GPP} = \Omega \cdot a \cdot B,$$ (B3)

where Ω is a proportionality constant (250 mm m^2 kg^{-1}) (Leith 1975). The second generalization is that the supply of water for transpiration (V) tends to be limited across ecosystem types either by precipitation (PPT) in arid and semiarid climates or by the evaporative climate (i.e., potential evapotranspiration, PET) in subhumid and humid climates. We use Budyko's (1984) simple approach to quantify the trade-off between PPT and PET in controlling actual evapotranspiration (AET) and ultimately V (AET minus evaporation). This approach is based on the fact that over a sufficient period of time (e.g., week, month), PET is highly correlated with solar radiation (R) across many communities (Campbell 1977; Jensen et al. 1990), such that a reasonable approximation is

$$\text{PET} = \frac{R}{L},$$ (B4)

where L is the latent heat of vaporization. The crossover point on the climatic continuum between PPT and PET control of AET is then determined by the ratio of PET to PPT, which Budyko (1984) refers to as the index of aridity (I_a):

$$I_a = \frac{PET}{PPT} = \frac{R/L}{PPT}.$$ (B5)

The climate-controlled AET for the community is thus determined as

$$AET = \begin{cases} PET & \text{for } I_a < 1 \\ PPT & \text{for } I_a \geq 1 . \end{cases}$$ (B6)

The value of AET, whether from PET or PPT, however, represents the supply of water for both transpiration and evaporation. Therefore, we define e as the fraction of AET due to transpiration, so that

$$V = e \cdot AET .$$ (B7)

Although e depends primarily on plant cover, the type of community, and, to a lesser extent, the degree of stomatal control of water loss (Jarvis and McNaughton 1986; Jensen et al. 1990), we use a constant value of 0.8 for the simulations presented here.

Influence of Nutrients

Nitrogen and other nutrients generally affect mechanisms by which long-term water and radiation balances govern productivity (Gutierrez and Whitford 1987; Chapin et al. 1988; Vitousek and Howarth 1991). Hence, climatic effects of nutrient supply on productivity are included via their effects on the growth rate, a, which from equations (B2)–(B3) can be written as

$$a = \frac{a^r \cdot V}{a^r \cdot \Omega \cdot B + V},$$ (B8a)

where

$$a^r = a^\circ \cdot b ,$$ (B8b)

$$b = 1 - \exp\left\{\frac{-s \cdot w}{n}\right\},$$ (B8c)

and

$$w = \frac{\sqrt{PET \cdot PPT} \cdot [2 \cdot PET^* - PET] \cdot e^{-(1/I_a)}}{0.43 \cdot [PET^*]^2}.$$ (B8d)

In this equation, a° is the maximum growth rate given optimal resources, b is a scalar (0–1) governing nutrient supply to plants, s is a soil fertility parameter that varies with soil type (sandy soils < loams) and increases under conditions of loess deposition, w describes the climatic influence on nutrient supply, n is a parameter that determines a plant's demand for nutrients (0, low requirement, to 1, high requirement), and PET^* is set to 850 (evaporation equivalent of solar radiation observed at a net radiation of 30 kcal cm^{-2} yr^{-1}—the net radiation giving maximum production; neither light nor water limited) (table 1). Also, w is an empirical function that assumes nutrient supply is maximal at intermediate values of PET and I_a, with nutrient supply being reduced at low and high PET due to temperature effects, at high I_a due to drought, and at low I_a due to leaching losses. Detailed justification for equation (B8d) is given elsewhere (Zimov and Chuprynin 1991).

MODEL FOR COMPETING FUNCTIONAL GROUPS

Competitive Interactions

We now divide vegetation into three functional groups: grasses (herbaceous vascular plants), mosses (including lichens), and trees (including shrubs), indicated by subscripts g, m, and t, respectively. These functional groups compete for the general resource V.

The rate of resource consumption by each functional group is determined by its consumption rate (F_j, where $j = g, m, t$) and that of its k competitors. Thus, following equations (B2)–(B3),

$$a_j = a_j^o \cdot \frac{V - F_j - F_{kj}}{V}, \tag{B9}$$

where $F_j = \Omega \cdot a_j \cdot B_j$, and $F_{kj} = \Sigma K_{ji} \cdot \Omega \cdot a_i \cdot B_i$ ($i = g, m, t$ and $i \neq j$). For example, the value of $V - F_{kj}$, in the case with $j = g$, is the resource supply available to grasses, and K_{ij} is the competition coefficient describing the effect of mosses and trees ($i = m, t$) on resource capture by grasses ($0 \leq K_{ij} \leq 1$). If canopy or roots of any group i are in the same layer as, or higher than, those of group j, it is a competitor ($K_{ij} > 0$), while, if they are lower, then $K_{ij} = 0$, and this functional group is not a competitor. If, on the average, the canopy is lower but its volume overlaps with that of the higher functional group, then group i is a partial competitor. We specify K_{ij} values as functions of canopy/root position and the radiative index of aridity (I_a).

Functional-Group Parameters

All model parameters were estimated from measurements, experiments, or the literature, except for nutrient supply (s) (eq. [B8c]), a scaling parameter that was adjusted until the model gave a reasonable balance of moss and grass. This was determined by running the model at all 5° terrestrial grid points for each of four values of s (0.7–1.6). A value of $s = 1.3$ gave an excellent match of the global distribution of functional groups with observed vegetation (fig. 2), and a value of $s = 1.0$ slightly underestimated the abundance of grass (Zimov and Chuprynin 1991). We use these values of s to represent high- and low-fertility soils in simulations for Beringia. No other tuning of the model was necessary. Parameters a^o, r, d, and e differ among these three functional groups, but we assume that these parameters are not altered by climate within a group (i.e., for any climate we use the same parameter values for a given group). Since we consider general functional groups rather than particular species, we assume that for each climate there are species of moss, grass, and trees for which this climate is close to optimal. If the actual values of these parameters vary with climatic zone, this variation is probably similar for mosses, grasses, and trees and, therefore, would not alter our predictions for the outcome of competition. For example, we assume that growth rate (a) for northern mosses, grasses, and trees is the same as in the south. In the north, however, the total resource supply (V) is less, so that production (GPP) is less than in the south. We assume that $a_m^o = 0.4$, $a_g^o = 8.0$, $a_t^o = 0.2$—that is, that the maximum relative growth rate (RGR) of grasses is greater than that of mosses, which is greater than that of trees (Grime and Hunt 1975; Furness and Grime 1982). The loss of biomass of mosses, grasses, and trees through death and respiration is $d_m + r_m = 0.25$, $d_g + r_g = 1.5$, and $d_t + r_t = 0.06$ yr^{-1}, respectively; that is, growth-form differences in senescence and respiration parallel those in relative growth rate (Langer 1966; Chapin 1980). We assume that, in the absence of competitors, grasses, trees, and mosses may grow in any climate if the nutrient supply is adequate. We tested the model with two initial densities of colonizing species ($B_m = B_t = 0.01, 0.1$) relative to the density of grass ($B_g = 0.25$).

The competition coefficients were estimated as follows. Under arid conditions in Beringia, mosses (including lichens) have ready access to limited precipitation and tolerate dry conditions more effectively than do grasses and trees. Mosses, therefore, displace grasses and trees in extremely dry climates: As I_a goes from zero to infinity, K_{mg} and K_{mt} go from zero to one. This pattern is particularly evident in northern regions (Alexandrova 1980; Wielgolaski et al. 1981). However, grasses and trees are superior competitors to mosses for light, because mosses are beneath the vascular plant canopy. Therefore, as I_a goes from zero to infinity, K_{gm} and K_{tm} go from one to zero. In order to make this a smooth function of I_a (vs. an abrupt threshold) that can be readily incorporated into the analytical solution of the model, we used the empirical function, $p = (1 - \exp[-1.23 \cdot I_a])^2$, which produces a smooth transition between zero and one. At high I_a (arid climates)

$p = 1$, and at low I_a (wet climates) $p = 0$. The justification for this function is discussed elsewhere (Zimov and Chuprynin 1991). Therefore, $K_{gm} = K_{tm} = 1 - p$ and $K_{mg} = K_{mt} = p$.

In tundra, where PET < 300 mm, competition between trees and grasses is always reciprocal ($K_{tg} = K_{gt} = 1$) because trees (actually shrubs) and grasses are similar in height. In the boreal-tundra transition (300 < PET < 400), the relationship between trees and grasses depends on both moisture and energy. In warm, wet climates trees always compete with grasses, whereas grasses are generally not competitors with trees, because light is the limiting factor in wet climates (i.e., $K_{tg} = 1$, $K_{gt} = 0$). As radiation declines (PET goes from 400 to 300 mm) or as the climate becomes drier (I_a goes from zero to one), grasses have a progressively greater effect on trees (including shrubs). Taking these conditions into account,

$$K_{gt} = \begin{cases} 1, & \text{if } p + K^* \geq 1 \\ p + K^*, & \text{if } p + K^* < 1, \end{cases} \tag{B10}$$

where

$$K^* = \begin{cases} 1, & \text{if PET} \leq 300 \\ (400 - \text{PET})/100, & \text{if } 300 < \text{PET} < 400 \\ 0, & \text{if PET} \geq 400. \end{cases}$$

Although groups do not explicitly compete for nutrients, nutrients influence the outcome of competition because each species has a different nutrient requirement (n), a factor that influences its maximum growth rate (a°) (Ingestad and Ågren 1991). We assume that the grass requirement for nutrients is $n_g = 1$, that trees have a lower nutrient requirement because of their slower biomass turnover ($n_t = 1/3$) (Berendse et al. 1987; Chapin 1993), and that moss growth is not nutrient limited ($n_m = 0.01$) (Skre and Oechel 1979).

Effects of Grazers

We assume that the rate of biomass loss to mammalian grazers is proportional to grazer biomass, which, in turn, is proportional to biomass of their food, which consists, by definition, mainly of grass (B_g). Thus, consumption/destruction of biomass for grasses, mosses, and trees are (from eq. [B1]) $c_g \cdot B_g$, $c_m \cdot B_g$, and $c_t \cdot B_g$, respectively, where c_i is the sensitivity of each species to a given grazer biomass. We assume that over long time periods (decades to centuries) predators keep herbivore density at a level optimal for grass growth so that overgrazing does not occur. Since moderate grazing promotes growth of grasses in tundra (Peshkova and Andreiashchkina 1983; Kucheruk 1985), the negative impact of grazers on grasses is compensated by a positive one, so that $c_g = 0$; that is, grazers have no long-term direct effect on grass biomass. The net result is that in an ecosystem in which there is no hunting and grazers are in equilibrium with their food supply, grazers have an intermediate effect on mosses ($c_m = 0.5$), which decline ($c_m = 0.2$) when large grazers are absent (i.e., when only small grazers like lemmings are present). Lastly, we assume that trees are an order of magnitude less sensitive to the presence of grazers than are mosses ($c_t = 0.1 \cdot c_m$).

We did an extensive analysis of the sensitivity of our model results to our assumption that grazers have no long-term direct effect on grass biomass. For each set of conditions illustrated in figure 3, c_g was varied from $-0.1 \leq c_g \leq 0.1$, in increments of 0.05, and compared to final biomass when $c_g = 0$. The maximum biomass difference was less than 10% and did not change any of the patterns we observed when $c_g = 0$.

The Community Model

Combining the above equations, we can include the effects of competition and grazing on changes in biomass of each functional group:

$$\frac{dB_g}{dt} = (a_g - r_g - d_g - c_g \cdot B_g) \cdot B_g, \quad B_g \geq 0, \tag{B11a}$$

$$\frac{dB_m}{dt} = (a_m - r_m - d_m - c_m \cdot B_g) \cdot B_m, B_m \geq 0,$$ (B11b)

and

$$\frac{dB_t}{dt} = (a_t - r_t - d_t - c_t \cdot B_g) \cdot B_t, B_t \geq 0,$$ (B11c)

where

$$a_m = a_m^0 \cdot (u - a_m \cdot B_m - k_{gm} \cdot a_g \cdot B_g - k_{tm} \cdot a_t \cdot B_t)/u,$$

$$a_g = a_g^0 \cdot (u - a_g \cdot B_g - k_{mg} \cdot a_m \cdot B_m - k_{tg} \cdot a_t \cdot B_t)/u,$$

$$a_t = a_t^0 \cdot (u - a_t \cdot B_t - k_{mt} \cdot a_m \cdot B_m - k_{gt} \cdot a_g \cdot B_g)/u,$$

and $u = V/\Omega$, which is the maximum potential gross productivity corresponding to complete consumption of the limiting resource.

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