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Productivity of Loessal Grasslands in the Kluane Lake Region, Yukon Territory, and the Beringian "Production Paradox"

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ABSTRACT. The Beringian "Production Paradox" is posed by abundant evidence that large ungulates populated unglaciated portions of northwestern North America and adjacent northeast Asia during the late Pleistocene, while botanical data from the same period suggest a poorly productive tundra environment. It is not clear how the large animals sustained themselves, but portions of Beringia, locally in receipt of loess, may have harbored sufficient forage-producing plants to nourish these animals. Loessal soils in the region today are warm and dry in summer, and are often used as rangelands. The loessal hypothesis was examined on grasslands in the Kluane Lake area, southwest Yukon Territory, at sites which have recently received loess blown from the Slims River delta. The biomass and species diversity of grasslands around the lake increase with the quantity of silt in the soil. Likewise, soil fertility indices, including total nitrogen, available nitrogen (NH_4), and total carbon, increase with silt content, particularly at sites where the soil surface has been stable for some time, and a "humified" loess (Ahk) horizon has developed. These results support the hypothesis that sites in receipt of loess may have played a significant role in the vegetative productivity of the Beringian ecosystem.

Key words: Beringia, production paradox, cryosols, loess, Kluane Lake, Yukon Territory

RÉSUMÉ. Le paradoxe de production Béringien signale que de nombreux indices témoignent de la présence de larges ongulés dans des régions non-glaciées du nord-ouest de l'Amérique du Nord et du nord-est de l'Asie adjacente durant le Pléistocène supérieur, alors que des données botaniques datant de la même époque suggèrent l'existence d'une toundra peu productive. Comment d'aussi larges animaux ont pu subvenir à leurs besoins n'est pas absolument clair mais certaines portions de la Béringie recevant des apports en loess ont pu récéler suffisamment de plantes fourragères pour les nourrir. Aujourd'hui, les sols loessiques de la région sont chauds et secs durant l'été et sont souvent utilisés comme pâturages. L'hypothèse loessique est examinée pour les prairies des environs du lac Kluane, en particulier dans les sites où des loess provenant du delta de la rivière Slims se sont récemment accumulés. La biomasse et la diversité des espèces dans les prairies avoisinant le lac accroissent avec la quantité de silt contenue dans le sol. De même, les indices de fertilité du sol, incluant l'azote total, l'azote libre (NH_4) et le carbone total accroissent avec le contenu en silt, particulièrement dans les sites où la surface est demeurée stable durant un certain temps et où un horizon loessique humifié (Ahk) s'est developpé. Ces résultats confirment l'hypothèse que les sites ayant eu des apports en loess ont pu jouer un rôle significatif dans la productivité végétale de l'écosystème Béringien.

Mots clés: Béringie, paradoxe de production, cryosols, loess, Lac Kluane, Territoire du Yukon

Реферат: Берингийский "Парадокс Продуктивности" заключается в многочисленных свидетельствах существования большой популяции копытных животных на неледниковых участках северо-запада Северной Америки и смежной части северо-восточной Азии в течении позднего плейстоцена и существования одновременно в зтих же местах, по палеоботаническим данным, малопродуктивной тундры. Непонятно, как существовали такие крупные животные, хотя участки берингии локально имеют лессы, которые могли произвести достаточное количество растительного корма для зтих животных. В настоящее время лессовые почвы в регионе летом становятся теплыми и сухими и часто используются для выращивания растений. Лессовая гипотеза была проверена на пастбищах юго-западной части территории Юкон вблизи озера Клуани, над которыми в последние годы развеивали лёссы из дельти Р. Слимс. Биомасса и разнообфазие растительных видов иа пастбищах вокруг озера увеличивались с повышением количества лессового материала в почве. Также с увеличением содержания лессового материала повышались индексы плодородия почвы, включая общее нитратов, утлерода, а также активного нитрата (NH_4), особенно в местах, где поверхность почвы стабильна и где развит лессовый горизонт (Ahk). Зти результаты поддерживают гипотезу о том, что лессовые образования могли играть значительную роль в увеличении растительной продуктивности берингийской зкосистемы. (Перевод Б. Берри)

Ключевые слова: Берингия, Парадокс Продуктивности, Криопочвы, Лёсс, Озеро Клуани, Территория Юкон.

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INTRODUCTION

There is substantial evidence that unglaciated portions of Beringia, i.e., Yukon, Alaska, and northeast Russia, supported a fauna containing large, herbivorous mammals during the late Wisconsinan glacial maximum, regionally termed the Duvanny Yar Interval (Harington, 1978; Hopkins et al., 1982). Many of the species that comprised the fauna are now extinct, but their bones are regularly found by miners working in the perennially frozen surficial deposits of the region, and, occasionally, intact carcasses are recovered (e.g., Guthrie, 1990; Harington et al., 1994). The number and diversity of such fossils suggest that the region supported a well-populated ecosystem. The Beringian "production paradox" stems from pollen studies that interpret late glacial vegetation in the region as being insufficient to support a significant density of grazing animals (e.g., Cwynar and Ritchie, 1980). Intuitively, we assume that late Pleistocene, full glacial conditions might have been less conducive to primary production than the present climate.

The paradox has been debated comprehensively (Hopkins et al., 1982), but remains unresolved. Ritchie and Cwynar (1982) postulate a Beringian landscape of discontinuous herbaceous tundra on uplands and local sedge-grass meadows in lowlands—a landscape unlikely to have supported large ungulate populations. On the other hand, Guthrie (1982) proposes the existence of richly productive arctic-steppe grasslands, supporting herds of ungulates. Schweger et al. (1982:434) suggest that the paradox is:

> a question of how the sparsely vegetated Beringian landscape of Duvanny Yar time could have supported clusters of large-bodied herbivores that, no matter how scattered, still required local richly productive forage areas spaced closely enough to allow energy gained during feeding periods to be balanced, over the course of a year, by the energy lost while moving from one feeding area to the next.

Schweger (1992:41) identifies soils developed on eolian silt (loess) deposits as potential "hot spots" of primary production in the proglacial landscape, and proposes the hypothesis that "the deposition of loess under full glacial conditions was a key factor in maintaining ... the Beringian ecosystem." This paper reports an inductive examination of Schweger's loessal hypothesis—an empirical investigation of the relationship between active loess deposition and productivity of contemporary *Artemisia–Festuca* grasslands in the Kluane Lake region, southwest Yukon Territory.

LOESSAL HYPOTHESIS

Schweger's (1992) consideration of Beringian soils contrasted Orthic and Gleysolic Turbic Cryosols, currently widespread in tundra regions of Alaska and Yukon, with Brunisolic, Orthic, or Regosolic Static Cryosols, which, he suggested, were common during Duvanny Yar time.

Orthic and Gleysolic Turbic Cryosols are generally imperfectly to poorly drained, and support a relatively thick organic surface layer of acidic peat. As a result, the soils have a shallow, cryoturbated active layer, usually 40 to 75 cm thick, and support a vegetation of ericaceous species, mosses, and *Eriophorum* spp.

In contrast, the Static Cryosols are thought to have formed by fundamentally different processes under cold, arid conditions in late Pleistocene Beringia. Schweger et al. (1982) described these productive Beringian soils as nutrient-rich, more deeply thawed, and of higher pH than the present Turbic Cryosols. The Static Cryosols may have been well-drained and vegetated by deeply rooted tundra and steppe species rather than by peat mosses (Schweger, 1992).

Schweger (1992) suggested that a key difference between the development of the Beringian soils and that of present-day Cryosols may have been loess deposition on the ground surface. He used three modern contexts to support his hypothesis.

First, he proposed that the ecological consequences of road dust in northern Alaska (Walker and Everett, 1987) simulate the effects of loess deposition upon the surrounding taiga. Schweger (1992) inferred that changes in plant community composition such as the elimination of ericaceous species and *Sphagnum* moss, increases in soil pH, deepening of the active layer, and rapid snowmelt, which have all been noted following deposition of road dust (Walker and Everett, 1987), are possible analogues of the ecological changes during a pedologic transition from Turbic to Static Cryosol.

Second, Schweger (1992) considered the biochemical effect of loess deposition upon the receiving soil. He reviewed analyses of Antarctic glacial ice by Zeller et al. (1988), which indicate that the ice acts as a sink for atmospheric nitrate and ammonia. He proposed that these nutrients may be attached to suspended particles in glacial meltwater and, upon subsequent redeposition of those particles as loess, enhance the fertility of soils at considerable distances from the ice margin.

Third, Schweger (1992) examined relations documented during a survey of grazing potential in southwest Yukon Territory, where Johansen et al. (1989) had noted high forage production and greatest carrying capacity in grassland communities dominated by *Artemisia* and *Festuca*. These communities, however, were found exclusively at sites close to a source of windblown loess, e.g., the Donjek River, implying a positive association between loess deposition and forage productivity.

Recently, Hoefle et al. (1994) discovered paleosols dating from 17 000 B.P. on the Seward Peninsula, Alaska. These soils were buried by tephra, incorporated in permafrost, and have remained frozen ever since. The paleosols developed in loess, with all horizons containing fine roots. On the basis of cryotexture, active layer depths of 40–70 cm have been interpreted for the paleosols, in comparison with 30–40 cm in modern soils nearby, bearing out Schweger et al.'s (1982) postulation regarding Beringian active-layer depths. Hoefle et al. (1994) suggest that the palaeosol profiles are characteristic of persistent surface aggradation by loess deposition.

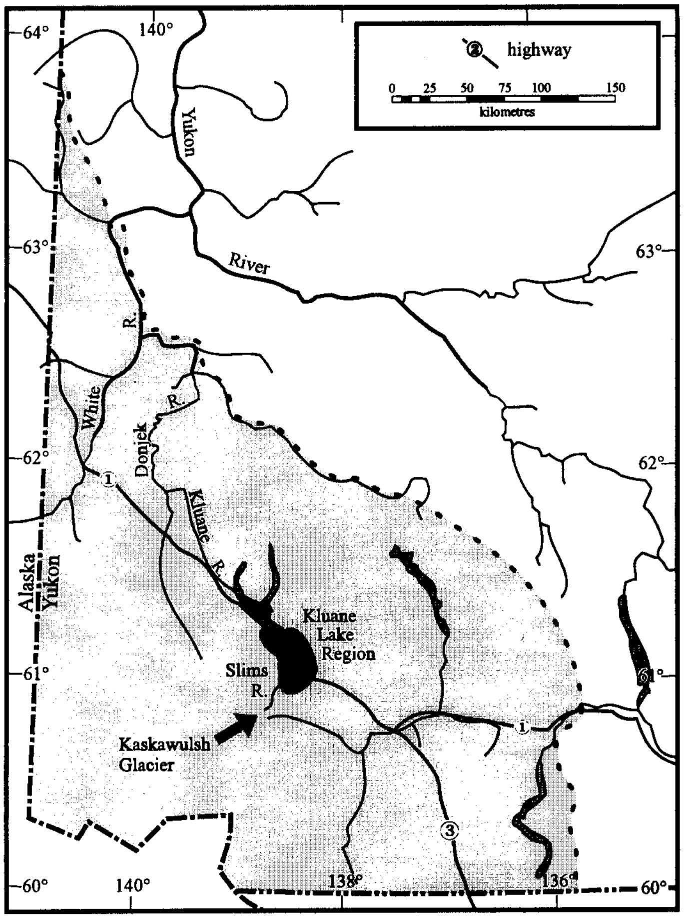

FIG. 1. The Greater Kluane Region, southwest Yukon Territory, indicating, in dark shading, the position of the study area near Kluane Lake (after Johansen et al., 1989).

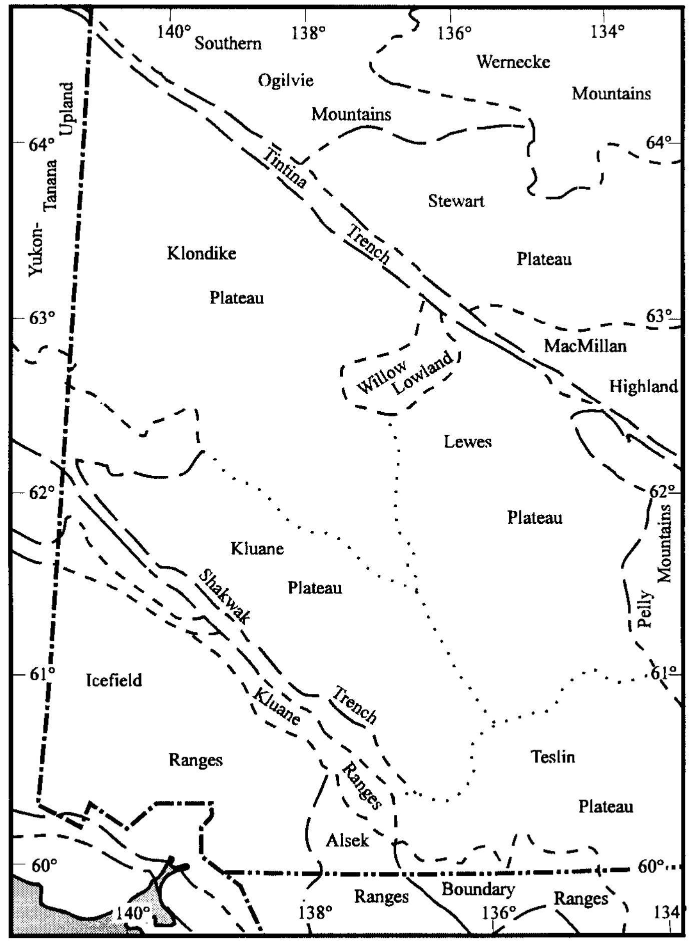

FIG. 2. Physiographic regions of southwest Yukon Territory and adjacent Alaska (after Matthews, 1986).

Working in the same area, Goetcheus et al. (1994) have examined vegetation covered by the tephra. Tufted graminoids and short woody plants characterize the specimens identified, suggesting the region could have supported small mammals at least.

The field investigation reported in this paper was conducted near the site of Johansen et al.'s (1989) survey, and aimed to discern further information regarding the relation between loess deposition and forage productivity. The environment in the study area, on the southern shores of Kluane Lake, has notable similarities with that postulated for Duvanny Yar "hot spots."

KLUANE LAKE AREA

The study area for this research is a small portion of the Greater Kluane Region (Fig. 1), at the southern end of Kluane Lake.

Physiography

The St. Elias Mountains form a prominent topographic barrier between the northeast Pacific Ocean and northwest North America. The Icefield Ranges form the core of these mountains (Fig. 2), supporting the most extensive ice fields in continental North America. Kluane Lake lies in the Shakwak Trench, at the foot of the Kluane Ranges, the easternmost extent of the St. Elias Mountains (Fig. 2). The Shakwak Trench provides a sharp boundary between the St. Elias Mountains and the Yukon plateaus to the northeast (Matthews, 1986).

Climate

There is a marked contrast between the climates on the southwest and northeast flanks of the St. Elias Mountains. Table 1 presents monthly mean air temperature and precipitation data from Juneau and Kluane Lake to illustrate these differences. The mountains not only provide a rain shadow on their lee slopes, but also effectively block the penetration of many maritime air masses into the Yukon, maintaining cool, anticyclonic conditions there in winter. The result is a semiarid, continental climate near Kluane Lake, with cold winters and warm, albeit short, summers.

The aridity of the Kluane Lake region may be analogous to that of Duvanny Yar Beringia, which was caused not only by a rain shadow to the lee of the Cordilleran Ice Sheet, but also by the contraction of the Bering and Chukchi Seas. An

TABLE 1. Mean air temperature and mean total precipitation data for Juneau, Alaska, and Kluane Lake, Yukon Territory.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year
Mean air temperature (˚C)													
Juneau[1]	-5.4	-2.2	0.0	4.0	8.2	11.7	13.2	12.6	9.6	5.4	0.3	-3.0	4.5
Kluane Lake[2]	-20.5	-15.4	-10.9	-1.8	5.4	10.3	12.6	11.2	6.3	-1.6	-9.7	-18.5	-2.7
Mean total precipitation (mm)													
Juneau[1]	94.2	91.2	80.0	71.6	88.1	73.9	106.7	129.5	159.8	188.7	128.3	109.0	1321.3
Kluane Lake[2]	7.2	5.9	5.2	7.9	22.1	32.3	47.0	34.1	17.2	16.3	17.7	11.0	233.9

[1] Data from Arctic Environmental Information and Data Center (1986).

[2] Data from Environment Canada (1982).

important similarity between the environments is the low snowfall (55 mm snow water equivalent at Kluane Lake, Environment Canada, 1982), which gives easy access to forage plants in winter. Today, the Slims River valley serves as an effective funnel for southwesterly katabatic winds off Kaskawulsh Glacier (Hoefs et al., 1978). These winds are responsible for continuing loess transport within the region, and for high evapotranspiration rates at the south end of Kluane Lake. Hoefs et al. (1978) suggest that such high evapotranspiration contributes to the predominance of grassland vegetation in the study area.

Glaciation

The Icefield Ranges host an extensive network of glaciers and ice fields. The Kaskawulsh Glacier is of particular importance to the study area, because one of its proglacial streams, the Slims River, forms a broad delta at Kluane Lake, 23 km downstream from the glacier.

During the late Pleistocene, locally the Kluane glaciation (Denton and Stuiver, 1967; Rampton, 1981), ice extended northwards from the mountains over Shakwak Trench onto the Kluane Plateau (e.g., Tarnocai et al., 1985, Fig. 30.1; see Fig. 2). As the ice retreated, extensive sheets of outwash and other drift materials were deposited. Winds entrained much of the silt-sized fraction of the drift, which accumulated as Kluane loess on the surrounding landscape (Denton and Stuiver, 1966).

Contraction of glacial limits during the early Holocene reduced loess deposition in the Kluane Lake area (Denton and Stuiver, 1966). The Slims paleosol then developed in much Kluane loess (Fig. 3; Denton and Stuiver, 1967). However, expansion of glaciers during Neoglaciation, with the Kaskawulsh Glacier advancing to near its present limit, led to reactivation of the Slims valley train and renewed loess deposition downwind from the Slims River delta. Neoglacial loess today forms a horizon up to 25 cm thick on the surface of grasslands near Kluane Lake (Fig. 3). Towards the base of the Neoglacial loess, a layer of White River tephra (1147 cal years B.P.; Clague et al., 1995) is often found.

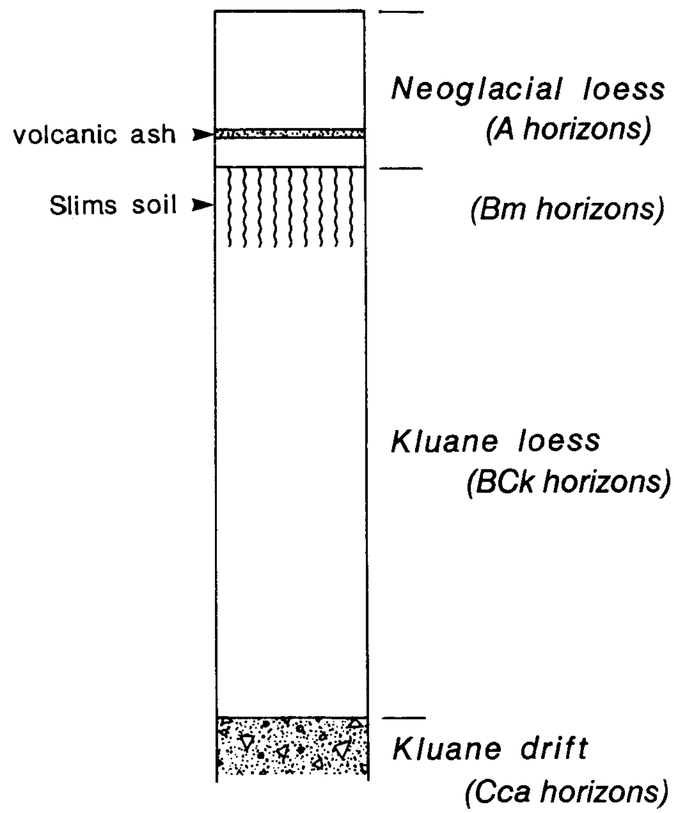

FIG. 3. Schematic soil profile for the Kluane region, Yukon Territory, at a site with Neoglacial loess deposition. The volcanic ash (White River tephra) was deposited between A.D. 694 and A.D. 936, most likely in A.D. 803, 1147 cal years B.P. (Clague et al., 1995).

Active Loess Deposition

The Slims River delta is 7 km^2, and comprises fine sand and silt. Vegetation is sparse, and is confined primarily to sediments near the valley walls. The lack of vegetation cover, low annual precipitation, and fine texture of the sediments make this material susceptible to eolian transport. Small undulations and scour pits, attributed to wind erosion, are regularly observed on its surface (Nickling, 1978). The Slims River valley experiences frequent dust storms (Fig. 4), especially from June to August, generated by katabatic winds flowing down the valley and out onto the lake (Muller, 1967). During this period, the river is at its low stage, exposing a large area of silt and fine sand deposited during the spring freshet, which usually occurs near the beginning of June (see data for neighbouring streams in Environment Canada, 1991).

FIG. 4. Dust storm emanating from the Slims River delta over the south end of Kluane Lake, June 1993.

The silt-sized particles comprise the Neoglacial loess found at the surface of grasslands around Kluane Lake.

Loessal Soils

The loessal soils in the Kluane Lake area are typical of grassland environments elsewhere in northwest Canada and Alaska, being classified as Melanic and Eutric Brunisols (Cannon and Nielsen, 1984; Expert Committee on Soil Survey, 1987). These soils have high pH, high calcium carbonate, and an A horizon rich in organic matter (Johansen et al., 1989). Beneath the A horizon formed in Neoglacial loess, there is usually a Bm horizon, the Slims paleosol, developed in the Kluane loess (Fig. 3). At the base of the profile is glacial drift (IICca horizon). Melanic and Eutric Brunisols differ from Static Cryosols only in terms of temperature: the soil morphology may be identical. The loessal soils are therefore very closely related to the Static Cryosols considered by Schweger (1992).

Péwé (1968) and others have interpreted the extensive silt deposits found in unglaciated areas of Alaska as products of eolian reworking of proglacial outwash (e.g., Tuck, 1940; Hopkins, 1963). These loesses form some prime agricultural land, for instance in the Matanuska Valley, near Palmer, Alaska (Trainer, 1961).

Vegetation

The loessal grasslands comprise part of a boreal (montane) biogeoclimatic zone, ranging in the Greater Kluane Region from valley-bottom elevations to an altitude of about 1160 m (Hoefs et al., 1978). The vegetation on mesic sites in the boreal zone is a white spruce forest, while various grassland associations occupy drier aspects. Johansen et al. (1989) concluded that an *Artemisia-Festuca* community found in association with both open poplar stands and aspen forest is the most productive rangeland in the region (see Table 2), but is confined to soils which receive loess from outwash plains such as the Slims River delta. Areas not receiving loess are dominated by plant communities with less forage production.

TABLE 2. *Artemisia-Festuca* communities in the Kluane Lake Region (after Johansen et al., 1989).

	Grassland Phase	Aspen Phase
Tree	–	*Populus tremuloides*
Shrubs	*Arctostaphylos uva-ursi*	*Salix bebbiana* *Shepheria canadensis*
Forbs	–	*Anemone patens* *Artemisia frigida* *Epilobium angustifolium*
Graminoids	*Festuca saximontana* *Carex obtusata* *Bromus Pumpellianus*	*Agropyron trachycaulum* *Poa glauca*
Forage production	370 kg/ha (37 g/m^2)	450 kg/ha (45 g/m^2)

The vegetation of the rangelands in the Kluane Lake region resembles that of Duvanny Yar hot spots to the extent that the Beringian environment comprised an open landscape that probably supported a range of plant communities, whose variety was likely controlled by aspect, slope, elevation, moisture and drainage. There is no suggestion that the white spruce forests of the Kluane Lake area had a counterpart in Beringia.

DATA COLLECTION AND ANALYSIS

The objective of the field work in June and July 1993 was to gather data on primary production and soil conditions along a gradient of active Neoglacial loess deposition. The premise governing site selection was that active loess deposition declined with distance from the Slims River, and, in order to fulfill this condition, the areal extent of the field survey was limited to the southern shoreline of Kluane Lake (Fig. 5).

Field Work

Fifteen localities were chosen around the lake, and two sites at each locality were surveyed in detail. To minimize the influence of site-specific factors on data variability, all sites had a south-facing aspect, a slope of <30°, an *Artemisia-Festuca* grassland community, and dimensions of at least 10 m by 10 m. The grasslands are currently used by grazing animals, so sites with evidence of recent grazing, particularly horse droppings, were avoided. Sites within Kluane National Park are not grazed by horses, but access by mountain sheep is not controlled. The sites chosen were close to either the Alaska Highway or a little-used bush road on the eastern shore of the lake (Fig. 5). Some highway dust may have been deposited from these sources, but likely very little in comparison with that deposited from storms like the one illustrated in Figure 4.

At each plot, a soil profile description was completed using standard field description documents (Expert Committee on Soil Survey, 1987). The soil pit was dug into drift, at least 20 cm below Kluane loess. Observations were made on the depth, texture, colour, boundaries, effervescence of

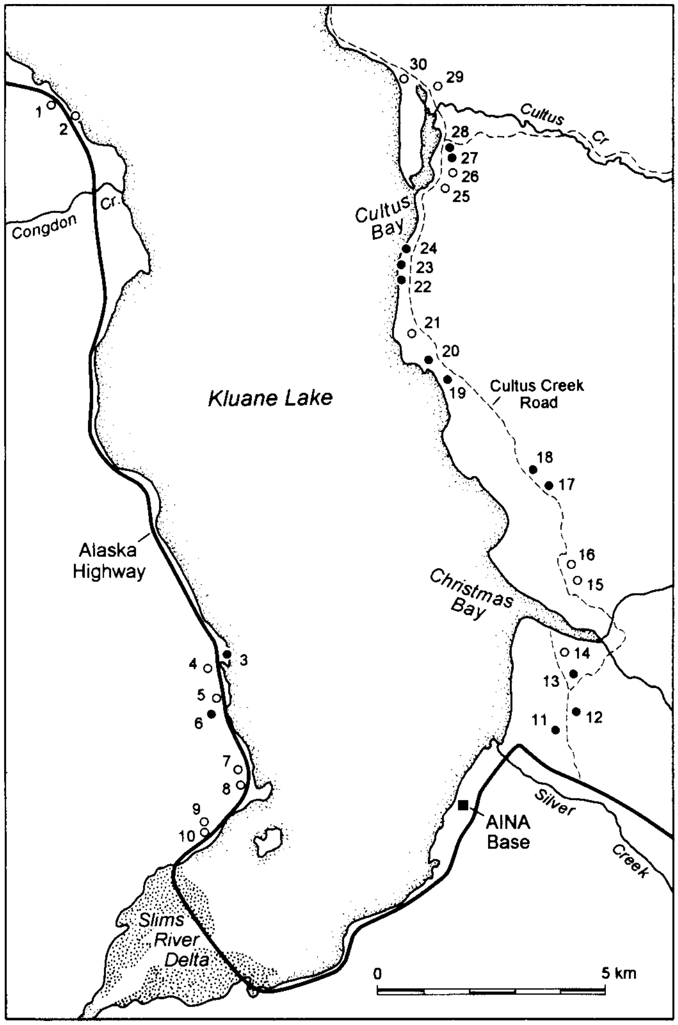

FIG. 5. Location of sample sites, southern end of Kluane Lake, Yukon Territory. Sites with a surficial ACk horizon, indicating active accumulation of loess, are indicated by open circles. At the other sites, the surficial horizon is a humified Neoglacial loess (Ahk), which has been stable for some time.

hydrochloric acid, and abundance and size of roots in each horizon. Samples were collected from the centre of each horizon and bagged for laboratory analysis. Summary results are presented in Table 3.

A 10 × 10 m macroplot with 10 randomly selected 0.5 × 0.5 m microplots was used to record the cover of forbs and graminoids. The identity and percentage cover of the plants in each microplot were recorded. Two quadrats, each one metre square, were then randomly chosen within the macroplot, and all the forbs and graminoids within those quadrats were clipped at the base of the stem and collected to determine the forage productivity.

Laboratory Procedures

Soil particle-size analyses were completed for all samples collected in the field, using sieves and the pipette method for the fine fraction (Sheldrick, 1984). Dispersion of particles was by ultrasonic means, after removal of organic matter with hydrogen peroxide. The organic matter content of the samples was determined by loss on ignition, in this case, heating to 350˚C for eight hours. Soil pH was measured in 0.01 M calcium chloride, following Sheldrick (1984). The total carbon and total nitrogen contents of all samples from A and Bm horizons (Neoglacial loess and Slims paleosol) were determined using a LECO instrument. Total phosphorous and available nitrogen (both ammonium and nitrate) were determined for all samples from A horizons; phosphorus was determined by the Bray method, and ammonium and nitrate by 2N potassium chloride extraction (Sheldrick, 1984).

The plant species in the microplots were identified from Porsild and Cody (1980), Trelawny (1988), and Pratt (1991). All species identified during the fieldwork are listed in the Appendix. The clipped vegetation collected from each quadrat was air-dried and weighed. The mean mass of the two samples was recorded as the vegetative biomass (g/m^2) of each plot.

Statistical Analysis

The degree of association between the various variables measured in the field and laboratory was measured using Spearman rank-correlation coefficients (r_s). The Spearman's coefficient was chosen over the more common Pearson product-moment correlation coefficient, because the data collected were not parametric. Spearman's coefficient uses ordinal values, which are appropriate for initial examination of generalized relations such as the Loessal Hypothesis. Statistical testing is possible with r_s, and in this paper we examine the probability that an observed correlation between two sample variables represents an extant correlation between the populations from which they have been sampled (Ebdon, 1985). The relations are considered statistically significant if they passed a one-tailed test at the 95% level.

The purpose of the analysis was to determine the extent to which forage productivity in the *Artemisia-Festuca* grasslands is associated with (1) the addition of loess to the grassland environments and (2) the properties of the loess/soil in the grasslands.

NATURE AND PRODUCTIVITY OF NEOGLACIAL LOESS

The Loessal Hypothesis applied to the Kluane grasslands proposes that deposition of Neoglacial loess is a key aspect of regional soil productivity. The field and laboratory data are relevant to three aspects of the hypothesis: (1) the nature and origin of Neoglacial loess, (2) the vegetative productivity of grasslands developed on loessal sites, and (3) the nutrient status of soil horizons formed in Neoglacial loess.

Nature and Origin of Neoglacial Loess

Summary textural classifications for the various soil horizons are presented in Table 3. Two types of A horizon were identified in the field: an "active" loess (ACk); and a

TABLE 3. Soil properties summarized from 30 sample plots.

Horizon	Name	Texture	Mineral fraction Sand (%)	Silt (%)	Clay (%)	Organic matter (%)	C (%)	N (%)	NH_4 (ppm)	NO_3 (ppm)	P (ppm)	Thickness (cm)	pH	Colour (Munsell)	Root abundance	Root size	Effervescence of HCl	n
A	Neoglacial Loess		43	55	2	6.2	3.45	0.21	2.33	0.98	5.58							
ACk	"Active" loess	SiL	36	63	1	5.5	2.86	0.17	1.96	1.99	6.60	8.0	7.28	10YR3,2	few	fine/very fine	Mod.	16
Ahk	"Humified" loess	SL	50	47	3	7.0	3.81	0.23	2.87	0.42	5.42	6.5	7.34	10YR2,1	plentiful	fine/very fine	Mod.	29
Bm	Slims Paleosol	SiL	41	54	5	4.5	1.77	0.13				8.0	7.44	7.5YR3,2	few	fine/very fine	None/weak	28
BCk	Kluane Loess	SiL	40	54	6	4.5						9.5	7.64	10YR3,3	few	very fine/fine	Mod.	25
IICca	Kluane Drift	SL	63	33	4	3.8						–	7.76	5Y4,2	few	very fine	Mod./strong	29

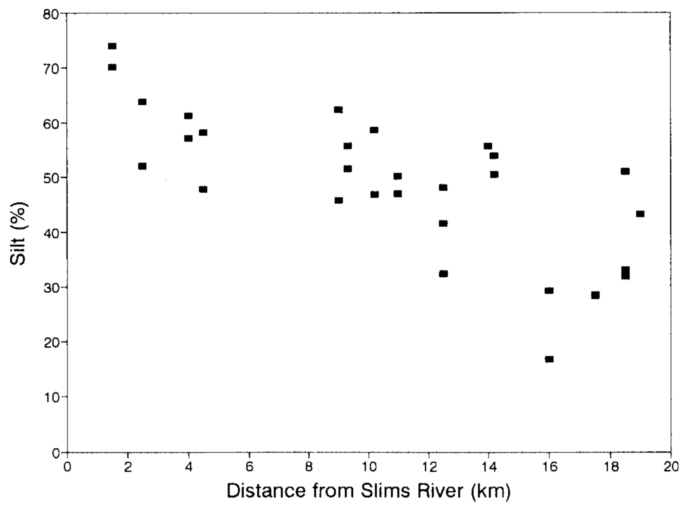

FIG. 6. Scattergram of percentage silt in Neoglacial loess (A horizon) and distance from the Slims River delta for Kluane Lake study sites.

TABLE 4. Spearman's rank-correlation coefficients (r_s) for variation in soil grain size in Neoglacial Loess (A horizon) with distance from the Slims River delta.

Grain size	Initial data	Without sand
sand	**0.64**[1]	0.00
total silt	**-0.73**	-0.30
coarse silt	**-0.67**	0.12
medium silt	**-0.67**	-0.10
fine silt	-0.30	-0.13
clay	-0.20	0.30

[1] Correlation significant at 95% level in **bold**; r_s critical is 0.306. Note: Textural classifications:

2 mm >	sand	> 47 µm
47 µm >	coarse silt	> 20 µm
20 µm >	medium silt	> 05 µm
5 µm >	fine silt	> 02 µm
2 µm >	clay	

"humified" loess (Ahk). The "active" loess was so designated because it was lighter in colour and appeared to contain less organic matter than the Ahk. Subsequently, laboratory analyses indicated that both horizons contained appreciable organic matter, but the field designations were retained; for although we assumed that the entire study area was receiving loess, a surficial ACk horizon recorded at 16 plots (see Fig. 5) implies a recent net accumulation of loess at these sites. A surficial Ahk horizon at 14 sites represents sufficient stability over time for significant accumulation of organic matter, but not enough for carbonates there to be leached from the surface of the soil. An Ahk horizon lay beneath 15 of the 16 ACk horizons. At one site (#25), the ACk was too thin to sample without risking contamination from adjacent layers, and so data from only 15 ACk horizons are analysed. Table 3 indicates that the ACk and Ahk horizons differ in both texture and nutrient status. The ACk has the highest proportion of silt and lowest of sand of all the horizons, while the Ahk has the highest carbon concentration, due to its greater proportion of organic matter. Calcium carbonate partly accounts for the high total carbon in the upper horizons.

The texture of ACk and both B horizons is silt loam, with 36–41% sand and 50–63% silt. The Ahk horizons are sandy loam. Proglacially derived loess deposits generally have less sand in their composition (Smalley, 1966), suggesting that this sand is probably derived locally from the shore of the lake, rather than from the Slims River delta. The average texture of all A horizons, representing the Neoglacial loess, is similar to that of the BCk horizon, the Kluane loess.

A scattergram of the silt-sized fraction of the A horizon and distance of the collection sites from the Slims River delta is presented in Figure 6. The r_s for these variables is -0.73, indicating that the proportion of silt in the profile declines with distance from the delta, as might be expected. The proportion of sand in the horizon increases with distance from the delta (Table 4), suggesting further that sand from local sources may become an increasingly important soil constituent as the availability of silt declines.

If the sand portion is removed from the data to enable examination of changes in the fine fraction (Table 4), then, again, the total silt fraction declines with distance from the Slims River, although r_s is not significant at the 95% confidence level. The proportions of the silt fractions do not change in any statistically significant manner with distance from the Slims River either. Since clay particles are not well represented in the A horizons (Table 3), any changes in the fine fraction with distance from the Slims River are likely physically insignificant.

There is no consistent variation in A horizon depth with any of the factors measured, including distance from the Slims River delta, likely because of varying local contributions to the sand-sized fraction. The scope of the study did not extend to measurement of the rate of loess deposition, but rather considered sites where loess accumulation was either active, as represented by an ACk horizon, or had occurred recently (Ahk).

Vegetative Productivity of Neoglacial Loess

Both biomass and species diversity were measured to determine the forage productivity of the grassland sites. Experimental studies suggest that increases in community diversity are generally associated with higher rates of primary production (e.g., Kareiva, 1994). Figure 7 presents a scattergram of the relation between biomass and species diversity at the Kluane Lake sites. There is a statistically significant correlation between these variables at all sites (r_s = 0.61), and at sites both with (r_s = 0.56) and without (r_s = 0.48) distinguishable ACk horizons.

The biomass recorded at sites with ACk horizons was less than at sites where an Ahk horizon formed the surface. At the sites with surficial ACk, the mean and median biomasses recorded were 21 and 12 g/m^2, while at the sites with surficial Ahk, the respective values are 28 and 22 g/m^2. However, the species diversity at the sites was similar, with both means and medians of nearly 12 species recorded at each group of sites. The range of biomasses recorded was large and skewed, with values between 4.5 and 62 g/m^2, while the range of recorded species diversities was smaller, with standard deviations at sites both with and without ACk horizons of about 4 species. A Mann-Whitney U test for statistical differences between samples indicates that the biomass at sites with a surficial Ahk horizon is greater than at sites with an ACk horizon, with 95% confidence (Ebdon, 1985).

As noted earlier, Johansen et al. (1989) showed that grassland communities in the Kluane area, close to a source of loess, were more productive than neighbouring forests. In central Yukon, however, soils with a late-Wisconsinan loess cap do not support a vegetation community distinct from others in the region (Tarnocai et al., 1985). Although loessal soils may be initially more productive than their neighbours, with time, leaching of base elements may destroy their advantage.

Nutrient Status of Neoglacial Loess Horizons

Correlations between percentage of organic matter, total carbon, total nitrogen, and nitrogen available as ammonium (NH_4) in the A horizons were all positive and statistically significant (Table 5). However, all of these variables were inversely related to the nitrate (NO_3) concentration in the soil. Inverse relations calculated between the concentrations of NH_4 and NO_3 in the soil (r_s = -0.40 for all A horizons, -0.48 for ACk horizons) are to be expected, since nitrate is produced by bacterial conversion of ammonium. However, ratios of NH_4:NO_3 (1:0.5 overall) derived for the A horizons from data in Table 3 are unusual for grassland soils (more commonly 1:5), suggesting either that nitrification is inhibited in these soils, or that nitrate is rapidly taken up by the grassland communities. Detailed investigation of nitrogen dynamics in these soils is beyond the scope of this paper, but the legumes recorded at the study sites, *Astralagus*, *Hedysarum*, and *Oxytropis* spp., were predominantly found at sites with surficial Ahk.

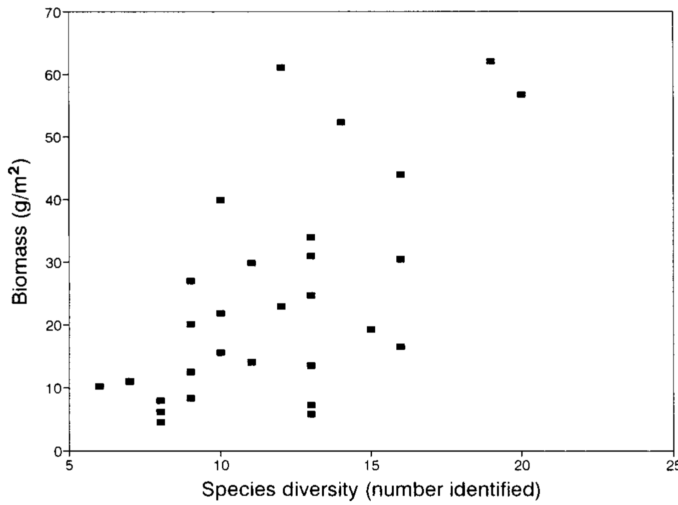

FIG. 7. Scattergram of species diversity and biomass recorded at loessal grassland sites near Kluane Lake.

TABLE 5. Correlation matrix for r_s summarizing relations between indices of soil nutrient status and site productivity for the average of data from all A horizons at all sites.

	Species diversity	C (%)	N (%)	Organic matter (%)	NH_4 (ppm)	Available N (NH_4+NO_3) (ppm)	P (ppm)
Biomass	**0.61**[1]	0.30	0.22	0.29	**0.31**	-0.06	0.12
Species diversity	–	0.19	0.12	0.23	**0.31**	0.07	0.14
Total C		–	**0.86**	**0.91**	**0.57**	0.27	**-0.35**
Total N			–	**0.85**	**0.58**	**0.42**	-0.28
Organic matter				–	**0.67**	0.26	-0.26
NH_4					–	**0.48**	0.07
Available N (NH_4+NO_3)						–	-0.25

[1] Correlation significant at 95% level in **bold**; r_s critical at 95% significance: ± 0.306

The soil phosphorous content was recorded as significantly negatively associated with total carbon, while all other phosphorus relations were weak and statistically insignificant.

Soil pH increases with depth (Table 3), indicating the leaching of carbonate from upper horizons and subsequent redeposition, with sufficient accumulation in the basal horizon for the ca designation (IICca). The prevention of acidification by delivery of carbonate in loess helps to maintain a soil environment suitable for rapid decomposition and cycling of nutrients in the soil organic matter.

Few statistically significant relations were recorded between biomass or species diversity at the sites and the indices of soil nutrient status (Table 5). Biomass and species diversity are significantly associated with the ammonium content of the A horizons, but not with either the total or total available nitrogen. For sites where an ACk formed the surface, no statistically significant relation was obtained between any soil fertility index and either biomass or species diversity, but at sites where an Ahk horizon was at the surface, a significant relation was recorded between species diversity and available nitrogen ($r_s = 0.47$). The higher overall productivity of sites with surficial Ahk, as compared to surficial ACk, may be due to the elevated nutrient status (C, N, and NH_4) of the Ahk horizon.

TEXTURE AND PRODUCTIVITY OF LOESSAL SITES

Examination of the Loessal Hypothesis requires discussion of the relations between soil texture and the fertility and forage production of the study sites. The data comprise three sets of plots: the group of 30 sites as a whole, and two subgroups, divided on the basis of the presence or absence of an ACk horizon. One subgroup had a surficial ACk overlying an Ahk horizon at all sites; in the other subgroup, the Ahk formed the surficial horizon. Data are presented from sites with either a surficial ACk horizon (15 sites), or a surficial Ahk horizon (14 sites), or as the average of all A horizons present (30 sites).

Soil Texture and Forage Productivity

Table 6 reports statistically significant positive correlations between the proportion of silt in the ACk horizon and biomass at the sites, and, in reflection, an inverse relation between the sand proportion and biomass. No relations are apparent between variation in soil texture and biomass at either sites with a surficial Ahk or at the group of sites taken as a whole. Empirical relations between variation in soil texture and species diversity are undefined for the ACk horizons and for the whole population, but are evident at sites where an Ahk horizon forms the soil surface. As noted above, biomass above an Ahk surface is greater than above an ACk, and these results suggest that the silt component of the ACk is associated with the productivity of sites actively receiving loess. At sites where the loess contains more humus, the silt content does not affect productivity, but rather is associated with the complexity of the grassland community. This may reflect the response of vegetation to more mature soil conditions, or to the length of time it has been free from the stress of loess accumulation.

Soil Texture and Nutrient Status

Correlations between particle sizes and nutrient status indices of the Ahk, ACk, and average of all A horizons are also presented in Table 6. There are negative associations between the proportion of sand in the A horizon and all nutrient indices except phosphorus: the statistical inference is that the phosphorous present at the grassland sites is largely derived from the sand fraction. But since the sand fraction is negatively associated with both productivity indices, availability of phosphorus is not a controlling factor in these grasslands (Table 5). There are few statistically significant relations between particle-size composition and the nutrient indices for the ACk horizons.

TABLE 6. Correlation coefficients (r_s) summarizing relations between soil composition of A horizons and productivity and nutrient status indices.

	Biomass (g/m²)	Species diversity	C (%)	N (%)	Organic matter (%)	NH_4 (ppm)	Available N (NH_4+NO_3) (ppm)	P (ppm)
ACk horizon, at 15 sites								
Sand (%)	**-0.46**[1]	-0.10	-0.36	-0.17	-0.16	0.26	-0.15	**0.62**
Total silt (%)	**0.49**	0.12	0.39	0.20	0.18	-0.23	0.12	**-0.61**
Coarse silt (%)	**0.51**	0.19	**0.51**	0.26	0.33	-0.09	-0.01	**-0.58**
Ahk horizon, at 14 sites without ACk								
Sand (%)	-0.25	**-0.51**	-0.45	**-0.48**	**-0.63**	**-0.51**	**-0.48**	0.17
Total silt (%)	0.26	**0.54**	**0.46**	**0.51**	**0.53**	**0.50**	**0.47**	-0.15
Coarse silt (%)	0.26	**0.47**	**0.74**	**0.70**	**0.54**	**0.64**	**0.50**	-0.17
"Average" A horizon, at 30 sites								
Sand (%)	-0.08	-0.03	**-0.38**	**-0.34**	-0.30	-0.07	**-0.35**	**0.48**
Total silt (%)	0.24	0.24	0.27	0.21	0.22	0.07	-0.28	**-0.48**
Coarse silt (%)	0.17	0.12	**0.48**	**0.41**	0.39	0.17	-0.26	**-0.47**

[1] Correlation significant at 95% level in **bold**; r_s critical at 95% for: 30 pairs, 0.306; 15 pairs, 0.441; 14 pairs, 0.456.

In contrast, many nutrient indices of the surficial Ahk horizons show positive and statistically significant association with silt composition, particularly the coarse silt in these horizons. The relations of carbon, nitrogen, and organic matter with particle-size distribution follow from plant growth in these substrates over time. The relations between silt content and ammonium follow from decomposition of the organic matter, which is present in greater quantities as silt increases in the samples.

The plots with surficial ACk horizons represent sites where loess is currently accumulating on the soil surface. At these sites, the proportion of silt in the mineral fraction has a significant positive association with plot productivity (Table 6). Sites with a surficial Ahk horizon are not currently accumulating loess, but have previously received Neoglacial loess. At these sites the positive relation between organic matter content and proportion of silt in the mineral fraction indicates an association between loess receipt and productivity. In summary, the results in Table 6 indicate that the silt fraction of the A horizon is positively correlated with nutrient status and biomass in the grasslands of the Kluane Lake area.

DATA FROM THE EAST SIDE OF KLUANE LAKE

A final set of data considers the relations obtained at the twenty sites located on the east side of Kluane Lake (Fig. 5). These sites are considered because they form a transect with increasing distance from the Slims River delta, and because the extent of grasslands on this side of the lake is greater than alongside the Alaska Highway, where the dominant vegetation is forest. Twenty sites were sampled on the east side of the lake, including site 25 (Fig. 5). The data therefore comprise results from 20 sets of A horizons, divided into two groups, with seven (of eight) sites with surficial ACk, and a dozen sites with surficial Ahk.

TABLE 7. Correlation coefficients (r_s) summarizing relations between silt composition and soil productivity indices for sites on the east side of Kluane Lake.

	Biomass (g/m²)	Species diversity	C (%)	N (%)	Organic matter (%)	NH_4 (ppm)	Available N (NH_4+NO_3) (ppm)	P (ppm)
ACk horizon, at 7 sites								
Sand (%)	-0.61	0.12	-0.46	-0.54	-0.50	0.00	-0.04	-0.14
Total silt (%)	0.61	-0.09	0.46	0.56	0.50	0.00	0.06	0.14
Coarse silt (%)	0.50	-0.23	0.64	0.69	0.64	0.14	0.03	0.29
Ahk horizon, at 12 sites without ACk								
Sand (%)	-0.38	-0.40	-0.48	**-0.59**[1]	-0.48	**-0.56**	-0.02	-0.02
Total silt (%)	0.38	0.43	0.49	**0.63**	**0.52**	**0.56**	0.09	0.09
Coarse silt (%)	0.41	0.40	**0.76**	**0.79**	**0.73**	**0.62**	0.03	0.03
"Average" A horizon, at 20 sites								
Sand (%)	-0.24	-0.18	**-0.43**	**-0.37**	**-0.52**	**-0.38**	-0.28	-0.17
Total silt (%)	**0.43**	0.36	0.34	0.26	0.34	0.30	0.25	0.05
Coarse silt (%)	0.25	0.15	**0.58**	**0.50**	**0.55**	**0.43**	0.26	0.15

[1] Correlation significant at 95% level in **bold**; r_s critical at 95% for: 20 pairs, 0.377; 12 pairs, 0.506; 7 pairs, 0.714.

Table 7 presents statistically significant positive correlations of grassland nutrient status (carbon, nitrogen, ammonium, and organic matter content) and productivity with the silt-size fraction of the A horizon, at sites with surficial Ahk. The results show that these indices of soil nutrient status, and both vegetation indices, are most strongly associated with the coarse silt fraction. The values of r_s presented in Table 7 are higher than those in Tables 5 and 6, because the conditions on this side of the lake are distinct from the more uniform forest on the west side: hence, a confounding source of variation is eliminated.

Table 8 indicates that there are significant decreases in both nutrient status and biomass with distance from the Slims River delta, the source of the loess. A remarkable relation (r_s = -0.87) is recorded between the distance from the Slims River delta and biomass at sites with an ACk horizon, supporting the hypothesis that soil productivity is linked to the total quantity of Neoglacial loess input, for the silt content of the ACk also declines with distance from the Slims River delta (r_s = -0.60). The relation between silt content and biomass (r_s = 0.61, Table 7), though not statistically significant, bears this out.

CONCLUSIONS

Schweger's (1992) hypothesis proposes that deposition of loess was key to maintaining "hot spots" of forage-producing plants in Duvanny Yar Beringia, upon which the Beringian fauna fed. The following conclusions summarize quantitative evidence supporting that hypothesis, derived from a study of soils, nutrient levels, and forage production in loessal grasslands of the Kluane Lake region.

(1) The statistically significant decrease in total silt with increasing distance from the Slims River delta supports the assertion that the silty soils in the region are derived from Slims River loess.

(2) Statistically significant positive correlations between the proportion of silt in the A horizon and the biomass of the associated grassland, especially at sites with active loess horizons (ACk), support the assertion that loess deposition increases the productivity of the sites.

(3) At sites where the surface has been stable long enough for some pedogenesis (Ahk horizon), total carbon, total nitrogen, and ammonium concentration in the soil increase in direct association with the silt fraction, and those sites are more productive than the ones where loess deposition is presently active.

TABLE 8. Correlation coefficients (r_s) for relations between nutrient and productivity indices and distance from the Slims delta for sites on the east side of Kluane Lake.

	Biomass diversity (g/m²)	Species	C (%)	N (%)	Organic matter (%)	NH_4 (ppm)	Available N (NH_4+NO_3) (ppm)	P (ppm)
ACk	**-0.87**[1]	-0.22	-0.31	0.07	-0.19	0.51	0.66	-0.15
Ahk	0.23	-0.26	**-0.61**	**-0.40**	**-0.73**	-0.41	-0.45	-0.01
A	-0.18	-0.12	**-0.46**	-0.27	**-0.54**	-0.18	-0.13	-0.04

[1] Correlation significant at 95% level in **bold**; r_s critical at 95% for: 20 pairs, 0.377; 12 pairs, 0.506; 7 pairs, 0.714.

Johansen et al. (1989) noted that the receipt of loess in the entire Kluane Lake region makes it significantly more productive than surrounding regions. The data presented in this paper support the notion that productivity of grassland ecosystems, like those in the Kluane Lake area, increases with deposition of loess. By analogy, loess-fed soils may have supported forage-producing hot spots, contributing to the sustenance of a complex trophic structure of ungulates in Duvanny Yar Beringia.

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APPENDIX
FORMAL NOMENCLATURE OF PLANTS IDENTIFIED AT GRASSLAND PLOTS

Sub-shrubs:	
Arctostaphylos uva-ursi (L.) Spreng.	Kinnikinnick
Potentilla fructicosa L.	Shrubby Cinquefoil
Rosa acicularis Lindl. s.lat.	Prickly rose
Shepheria canadensis (L.) Nutt.	Soapberry
Herbs:	
Anemone multifida Poir. s.lat.	Cut-leaf anemone
Anemone narcissiflora L. ssp. *alaskana* Hult.	Narcissus-flowered anemone
Anemone parviflora Michx.	Windflower
Antennaria rosea (Eat.) Greene	Pink everlasting
Arabis Holboelli Hornem. var. *retrofracta* (Grah.) Rydb.	Holboell's rockcress
Arnica alpina (L) Olin ssp. *angustifolia* (J.Vahl) Maguire	Alpine arnica
Artemisia frigida Willd.	Prairie sagewort
Aster L. spp.	Aster species
Astragalus L. spp.	Milk-Vetch species
Castilleja Mutis spp.	Indian paintbrush
Carex spp.	Sedge
Epilobium angustifolium L., s.lat.	Fireweed
Erigeron L. spp.	Fleabane
Galium boreale L.	Bedstraw
Geocaulon lividum (Richars.) Fern.	Northern Comandra
Hedysarum Mackenzii Richards.	Liquorice-Root
Linum Lewisii Pursh	Wild Blue Flax
Oxytropis varians (Rydb.) K.Schum.	Northern Oxytrope
Oxytropis splendens Dougl.	Showy Locoweed
Penstemon Gormanii Greene	Yukon Beardtongue
Pulsatilla Ludoviciana (Nutt.) Heller	Prairie Crocus
Saxifraga L. spp.	Saxifrage
Solidago canadensis L. var. *salebrosa* (Piper) Jones	Goldenrod
Vicia americana Muhl.	Vetch
Graminoids:	
Agropyron trachycaulum	Wheat grass
Agropyron sibiricum (L.) P.B.	Wheat grass
Agropyron violaceum (Hornem.) Lange ssp. *violaceum*	Wheat grass
Bromus ciliatus L.	Brome-grass
Bromus Pumpellianus Scribn. var. *Pumpellianus*	Brome-grass
Calamagrostis canadensis (Michx.) Beau var. *canadensis*	Reed-Bentgrass
Calamagrostis purpurascens R. Br.	Reed-Bentgrass
Festuca ovina L. ssp. *alaskana* Holmen	Fescue

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