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A Study of Loessal Grasslands in the Kluane Lake region,
southwest Yukon Territory, in reference to the Beringian
Production Paradox

by

NICOLA LAXTON, B.A. (Hons)

A thesis submitted to
the Faculty of Graduate Studies and Research
in partial fulfillment of
the requirements for the degree of
Master of Arts
Department of Geography

Carleton University

Ottawa, Ontario

21st September 1994

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SOUTHWEST YUKON TERRITORY, IN REFERENCE TO THE BERINGIAN
PRODUCTION PARADOX"

submitted by Nicola Frances Laxton, B.A Honours,
in partial fulfillment of the requirements for
the degree of Master of Arts.

A handwritten signature in dark ink, appearing to read 'C. Laxton', is written over a horizontal line.

THESIS SUPERVISOR

A handwritten signature in dark ink, appearing to read 'M. Smith', is written over a horizontal line.

CHAIR, DEPARTMENT OF GEOGRAPHY

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21st September 1994

ABSTRACT

The Beringian production paradox refers to the late Pleistocene epoch, when ecosystems in northwest North America supported large ungulates under conditions seemingly less conducive to primary production than those of today. The "loessal hypothesis" proposes that the deposition of loess, derived from glaciofluvial outwash, elevated the productivity of soils in selected areas of Beringia, to sustain substantial mammal populations.

This thesis investigates a region similar to periglacial Beringia. The loessal hypothesis is tested on grassland soils and vegetation in the Kluane Lake area, Yukon Territory. The silt in the soils is loess emanating from the Slims River delta. The biomass and species diversity of the grasslands increase with the quantity of loess in the soil. Likewise, soil nitrogen, carbon and organic-matter content increase with soil loess content. The results support the hypothesis that sites actively receiving loess may have played a significant role in the Beringian ecosystem.

ACKNOWLEDGEMENTS

This thesis could not have been written without the invaluable guidance and supervision of Chris Burn. I gratefully acknowledge his support and enthusiasm throughout the writing of this thesis and moreover throughout the duration of my time in Canada. I am indebted to Scott Smith for his expert field advice, identification of the study area, and for his comments on the manuscript. Thanks are also due to Ken Torrance, Carleton University, for his assistance in the laboratory, and to Scott Armbruster and various other workers at the Kluane Lake Research Station for their help in identifying plant species in the field.

I would like to thank Claire Wilson, for her "outstanding" field assistance, her cheerful attitude and her ability to make the best of any situation; Andy Williams and the Kluane Lake Research Station, for their logistical support in the field; and C.R. Burn's N.S.E.R.C. grant which funded this research. I am also grateful to Tiffani Fraser and Debbie Williams, for their companionship in the field and the classroom; to Bethany Maggs and Jason Verburg, for their help with laboratory analysis; and to the Johnson family for their hospitality and contribution to the completion of this thesis.

Finally, very many thank are extended to my friends, especially Karen and Rach, and my family, for their prayerful support and their encouragement throughout.

TABLE OF CONTENTS

	PAGE
Acceptance Sheet	ii
Abstract	iii
Acknowledgments	iv
Table of Contents	v
List of Tables	ix
List of Figures	xi
 CHAPTER 1: INTRODUCTION	 1
 CHAPTER 2: THE FULL GLACIAL ECOSYSTEM OF BERINGIA	 11
2.1 Geological Approach:	11
Sparse herb-tundra hypothesis	
2.2 Ecological Approach:	20
Mammoth-steppe hypothesis	
2.3 Literary Evolution of the Production Paradox	23
2.4 Paleoecology of Beringia: A Synthesis	34
2.5 Beringian Ecosystem Model	36
2.5.1 Climate and Microclimate	
of the Duvanny Yar Interval	37
2.5.2 Interactions between Mammoth fauna	38
2.5.3 Edaphic factors: "loessal hypothesis"	39

CHAPTER 3: LOESSAL HYPOTHESIS	41
3.1 Loessal Hypothesis: Background review	45
3.2 Kluane Lake Region: A "modified analogue"	47
CHAPTER 4: STUDY AREA	52
4.1 Physiographic and Geologic Setting	52
4.2 Regional Climate	55
4.3 Glaciation	58
4.3.1 Kaskawulsh Glacier and Kluane Lake	58
4.3.2 Glacial Chronology and Stratigraphy	61
4.4 Active Loess deposition	69
4.5 Local climatic conditions	72
4.6 Vegetation	75
4.7 Soil	78
CHAPTER 5: DATA COLLECTION	79
5.1 Sample plot location	79
5.2 Field procedures	82
5.2.1 Soil	82
5.2.2 Vegetation	84
5.3 Laboratory procedures	85
5.3.1 Soil	85
5.3.2 Vegetation	86

5.4 Statistical procedures	86
CHAPTER 6: RESULTS AND DISCUSSION	89
6.1 Loessal Hypothesis: Premises	89
6.1.1 Neoglacial loess	90
6.1.2 Nutrient status of Neoglacial loess	100
6.1.3 Vegetative productivity of grasslands	100
6.2 Loessal Hypothesis: Results	104
6.2.1 Correlation of soil texture and nutrient status	106
6.2.2 Correlation of soil texture and productivity	106
6.2.3 Summaries of soil texture, nutrient status and productivity correlations	109
6.2.4 Correlation of distance from the Slims River delta and nutrient status	111
6.2.5 Correlations of distance from the Slims River delta and productivity	114
6.2.6 Summaries of distance from the Slims River delta, nutrient status and productivity correlations	114
6.2.7 Correlations of nutrient status and productivity	116
6.2.8 Data from the east side of Kluane Lake	116

CHAPTER 7: CONCLUSIONS	124
7.1 Paleoenvironmental reconstruction	124
7.2 Contemporary rangeland management	126
7.3 Opportunities for further research	126
REFERENCES	129
APPENDIX: List of observed vegetation species	138

LIST OF TABLES

TABLE	DESCRIPTION	PAGE
2.1	Chronological distribution of Alaskan Pleistocene Bison, Horse and Mammoth	32
4.1	Climatic statistics from selected stations in Yukon and Alaska	57
4.2	<i>Artemisia-Festuca</i> Community in Kluane Lake Region	77
6.1	Summary properties of soil horizons averaged over study area	92
6.2	Initial and recalculated correlation coefficients of variation in soil texture with distance from the Slims River delta	97
6.3	Correlations between percentage nutrient content of Neoglacial loess horizons	101
6.4	Correlation coefficients between nutrient status and soil texture	107
6.5	Correlation coefficients between productivity and soil texture	108
6.6	Correlation coefficients between distance from the Slims River delta and nutrient status	113
6.7	Correlation coefficients between distance from the Slims River delta and productivity	115
6.8	Correlation coefficients between nutrient status and productivity	117

6.9	East side of Kluane Lake: Correlation coefficients between soil texture and nutrient status	119
6.10	East side of Kluane Lake: Correlation coefficients between distance from the Slims River delta and nutrient status	120
6.11	East side of Kluane Lake: Correlation coefficients between nutrient status and productivity	122

LIST OF FIGURES

FIGURE	DESCRIPTION	PAGE
1.1	A comparison between time stratigraphic nomenclature proposed for Beringia	2
1.2.	Location map of Beringia	4
1.3	Diagram of the Beringian ecosystem model	7
2.1	Sketch map of locations of Lateral Pond and Hanging Lake	14
2.2	Summary pollen influx diagram for Lateral Pond	16
2.3	Influx values of the main pollen types at Hanging Lake	18
2.4	Spatial extent of Beringia and the Mammoth Steppe	22
2.5	Kaiyak Lake herbaceous pollen influx	29
3.1	Hypothetical soil profile contrasting Beringian soil edaphic conditions	43
3.2	Location of Greater Kluane Region and Kluane Lake Region, southwest Yukon Territory	49
4.1	Physiographic Regions of southwest Yukon Territory	53
4.2	Drainage routes near Kluane Lake	60
4.3	Glacial limits, in southern Yukon Territory	62
4.4	Late Pleistocene glacial chronology of northeastern St. Elias Mountains	63

4.5	Typical loess profile in Slims River valley	67
4.6	Photograph of typical loess profile in Kluane Lake region	68
4.7	Photograph of Slims River delta	70
4.8	Photograph of dust storm in Slims River valley	71
4.9	Loess deflation and deposition in Kluane Lake region	73
5.1	Map showing location of sample sites around Kluane Lake	80
5.2	Photograph illustrating a typical glacial site in the Kluane Lake region	81
6.1	Photograph of soil profile in Kluane Lake region depicting ACK and Ahk horizons	94
6.2	Spatial distribution of sites "WITH ACK" and "WITHOUT ACK" horizons around Kluane Lake	95
6.3	Neoglacial loess (A): Scatterplot of percentage silt and distance from the Slims	98
6.4	Neoglacial loess (A): Scatterplot of productivity variables	103
6.5	Model of Kluane Lake natural ecosystem	105
6.6	Humified loess (Ahk): Scatterplot of carbon and distance from the Slims River delta	112
6.7	East side of Kluane Lake: Scatterplot of biomass and distance from the Slims River delta	121

CHAPTER 1: INTRODUCTION

Paleoecology is a multidisciplinary field of geographical enquiry, involving the study and understanding of relations between past organisms and their environment. Quaternary paleoecology deals specifically with the changing environments of the last two million years and in practice manifests itself in the "reconstruction of past ecosystems" (Birks and Birks 1980, p.1).

This thesis considers a contemporary periglacial ecosystem, in southwest Yukon Territory, as a "modified analogue" of the ecosystem in unglaciated northwest North America and adjacent Siberia during the Wisconsinan glacial period. The purpose of the thesis is to contribute towards understanding the "production paradox" whereby larger, more diverse mammal populations are thought to have existed in an environment seemingly less conducive to primary production than at present.

Temporal and spatial considerations are essential to environmental reconstruction. The time period relevant to the thesis is the last full glacial period of the Pleistocene, from 45,000 to 11,000 years B.P. (Figure 1.1). This period has been named the "Duvanny Yar" (Hopkins 1982) after a time-stratigraphic section on the lower Kolyma River, eastern Siberia. Spatially, the thesis deals with those portions of Canada, Alaska and central Siberia that

Figure 1.1 A comparison between time stratigraphic nomenclature proposed for unglaciated regions (Hopkins 1982) and the chronology and nomenclature of the glacial sequence in the Yukon Cordillera (Vincent and Klassen 1989).

General chronostratigraphy					Unglaciated Berinda (Hopkins 1982)	Yukon Cordilleran icesheets (O.L. Hughes)	
Time	Period	Epoch	Stage				
10	Q U A T E R N A R Y	HOLOCENE					
20		P L E I S T O C E N E	L A T E	W I S C O	LATE	Duvanny Yar Interval	McConnell Glaciation = Macauley Glaciation
30					MIDDLE	Boutellier Non-glacial Interval > 37 ka	Boutellier Non-glacial Interval > 37 ka
60					EARLY		
80				SANGAMONIAN			
130		MIDDLE	ILLINOIAN		Happy Interval	Reid Glaciation = Mirror Creek Glaciation	
320						Pre-Reid interglacial	
730		EARLY	PRE-ILLINOIAN				Klaiza Glaciation and Nansen Glaciation

were not covered by ice during the Quaternary (Figure 1.2). This ice-free region is known as Beringia and is renowned for its periglacial environment which provided refugia for flora and fauna during the Pleistocene glacial periods.

The "production paradox" is a concept regarded by many authors as central to studies of the unglaciated Arctic during the late Pleistocene. The paradox has come to the forefront of Beringian research in the last two decades, and deals with the fact that in Beringia:

vertebrate fossils indicate that from 45,000 to 11,000 years B.P. (the Duvanny Yar period) an environment considerably more diverse and productive than the present existed, whereas the botanical record, where it is not silent, supports a far more conservative appraisal of the region's ability to sustain any but the sparsest forms of plant and animal life (Hopkins et al. 1982, p.xi).

This incongruous reconstruction of depauperate vegetation cover and comparatively abundant mammal life stems from the application of two contrasting intellectual approaches to the composition of Beringia's late Pleistocene environment.

The first approach is geological. It has, as its major aim, the reconstruction of past environments in time and space from available palaeontological, lithological and geochemical data (Colinvaux 1983). The approach is largely historical and empirical and considers the botanic (strictly fossil pollen) record for the presence or absence of taxa.

The second approach is ecological. This approach places emphasis not only on reconstructing and describing past

Figure 1.2. Location map of Beringia (Hopkins 1982, Fig. 1).

populations, communities and environments, but also on the quantitative dynamics, responses and interactions of populations and communities over extended time periods (Birks 1985). It permits scientists to reconstruct the landscape in accordance with assumptions regarding the climate and food requirements of the large, gregarious herbivores once present in Beringia.

These contrasting scientific methods have presented a disparity of evidence which currently forms the essence of a debate that has puzzled Beringian researchers for several decades. The debate centres upon the paradoxical former abundance and diversity of large ungulates in a region which presently supports very few large mammals. The paradox is heightened by

the apparent presence of this larger, more diverse ungulate fauna at a time when the colder world climate (might have supported) ... ecosystems less productive than those of the present time (Hopkins et al. 1982, p.425).

Explanations of the "production paradox" have led to dramatically different environmental reconstructions. On one side Ritchie and Cwynar (1982) postulate a Beringian Pleistocene landscape of discontinuous herbaceous tundra on upland sites and of local sedge-grass meadows on lowland sites - a landscape that seemingly could hardly have supported large ungulate populations.

At the other extreme Guthrie (1982,1985,1990) proposes a late Pleistocene arctic steppe whose richly productive

grasslands supported herds of ungulates similar to the game populations in the grassland vegetation of the present African Serengeti Plain (Hopkins et al. 1982).

The controversies surrounding the "production paradox" are expanded upon in chapter 2, however as a literary argument, the paradox remains unanswered. Hopkins et al. (1982) suggest that the "production paradox"

resolves itself into 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 (p.434).

These authors conclude, therefore, that the environment of the Duvanny Yar interval must have contained well-dispersed productivity "hot spots". In light of this statement they propose that the crux of Beringian ecosystem reconstruction must be "an understanding of these patches of significant productivity" (p.434). Hopkins et al. (1982) outline a means of achieving this understanding. They suggest that the study of edaphic factors, climatic and microclimatic factors, and interactions and feedback effects of ungulate fauna will facilitate the interpretation of these postulated "hot spots". The dynamic relationship between these variables is illustrated in a simplified ecosystem model (Figure 1.3) which was developed and applied to Beringia for the last glacial interval by Schweger (1992)

Figure 1.3 Diagram of the seven components and their interactions which make up the Beringian ecosystem model (Schweger 1992, Fig. 1).

Beringian Ecosystem Model (28-13 ka B.P.)

The literature documents progress in the climatic and vegetative fields of enquiry. Evidence of investigations into the edaphic factors, however, is negligible in comparison. This is unfortunate as recognised by Schweger's (1992) statement which advocates that

extra attention be given to the edaphic component of the ecosystem since it is through the soil that we see the integration of so many physical, chemical, biological and climatic factors and it is with the soil that one must first approach the issue of productivity (p.40).

Various researchers have commented upon the nature of late Pleistocene soils. Hopkins et al. (1982), for example, suggest that a persistent observation amongst Beringian scientists is the "direct evidence of dry, firm, easily excavated soils ..." (p.435). In addition, researchers propose that to have supported the Beringian ecosystem, full glacial soils would necessarily have been nutrient-rich (Schweger 1992). High nutrient status is often attributed to the accumulation of loess in the Duvanny Yar environment (e.g., Guthrie 1982; Velichko et al. 1984).

Loessial sediments originate from glacial outwash deposited beyond the glacial terminus. The sediments are picked up by the wind and deposited some distance from their source. They comprise fine-grained, permeable, wind-sorted and wind-deposited aeolian material (Clark 1985). Their deflation, transport and subsequent deposition is most efficient in environments characterised by wind and aridity, conditions which are thought to have prevailed throughout

the Duvanny Yar interval in Beringia (Hopkins 1982).

The link between loess and fertility, and the active formation of loess deposits during the late Pleistocene, led Schweger (1992) to propose the "loessal hypothesis". The hypothesis states that

the deposition of loess under full glacial conditions was a key factor in maintaining the highly productive ... soils and, ultimately, the Beringian ecosystem (p.41).

Schweger (1992) used qualitative means to test the hypothesis. The current thesis employs a quantitative research design. Its central objective is to investigate the extent to which active loess deposition influences the productivity of contemporary *Artemisia*-grasslands in the Kluane Lake region of southwest Yukon Territory.

The descriptive approach to paleoecology proposes the use of "the present to model the past by extending observations about processes within present ecosystems backwards in time" (Birks and Birks 1980, p.3). Because the grassland ecosystems of the Kluane Lake region are considered to be a modified analogue of the grasslands in late Pleistocene Beringia (e.g., Geist 1978; Young 1982), the current thesis employs the descriptive paleoecological approach to investigate the concept of Duvanny Yar productivity "hot spots", posited by Hopkins et al. (1982).

Data collection for the thesis involved soil and vegetation sampling from thirty grassland sites around the southern perimeter of Kluane Lake, followed by laboratory

analyses of field samples. Statistical analysis elucidated quantitative data which support the argument that loess deposition was a key factor in maintaining the relatively high productivity of the Duvanny Yar "hot spots". In addition, the data has a contemporary significance to the Yukon Territorial Government in contributing to understanding and management of rangeland ecosystems in southwest Yukon Territory.

The following chapters expand upon the "production paradox" and the nature of the Duvanny Yar ecosystem (chapter 2); outline the background to Schweger's "loessal hypothesis" and explain the criteria behind the Kluane Lake region as a "modified analogue" of the Beringian ecosystem (chapters 3 and 4); describe the system of data collection employed in both the study area and the laboratory (chapter 5); analyse and discuss the significance of the results obtained in the context of the "loessal hypothesis" (chapter 6); and finally depict the limitations of the current work and propose avenues for its continued research (chapter 7).

CHAPTER 2: THE FULL-GLACIAL BERINGIAN ECOSYSTEM

Two intellectual perspectives, geological and ecological, prevail in the literature concerning the reconstruction of the Beringian ecosystem. This chapter discusses the conflicting evidence revealed by each approach and provides summaries of the palynological and palaeontological interpretations of the Beringian full-glacial environment. The chapter outlines the literary evolution of the debate surrounding the "production paradox" and focuses upon those studies which synthesise the apparently contradictory environmental data. It concludes with a review of the theoretical development of the "loessal hypothesis" in the context of the Beringian ecosystem model (Schweger 1992).

2.1 Geological Approach: Sparse herb-tundra hypothesis

The geological approach to paleoecology uses evidence from fossils to reconstruct past environments (Colinvaux 1983). Pollen analysis (palynology) is the principal Quaternary reconstruction technique. Pollen grains do not decay in nonoxidizing situations (Frenzel 1973) and usually constitute the most abundant fossil preserved in Quaternary sediments (Birks and Birks 1980).

Vegetation is a feature of major importance in a

landscape. It is responsive to fluctuations in environmental factors and largely determines the abundance of animals that an ecosystem can support. Reconstruction of past vegetation contributes to a spatial and temporal awareness of former regional conditions. In the Beringian context, Schweger (1982) is convinced that the first trophic level is the only reasonable starting point for environmental reconstruction. He believes that a satisfactory reconstruction of the full-glacial Beringian environment cannot be achieved or modeled until the vegetative characteristics of the ecosystem have been established.

For ice-age Beringia the process of environmental reconstruction began over one hundred years ago (Hibbert 1982). Eric Hulten first stated ecological Beringian issues in a modern way in the 1930s (Colinvaux and West 1984). He described the land presently covered by the Bering and Chukchi seas as a sub-continent, not as a bridge. He saw Beringia less as a "station for organisms hurrying from one continent to the other" (Colinvaux and West 1984, p.10), and more as a centre of dispersal and a "homeland" for Beringian fauna.

Hulten (1937) apparently used biogeographical data to interpret the full-glacial landscape of Beringia as characterised by tundra species (Colinvaux and West 1984) and initial Beringian pollen studies undertaken in the 1960s strongly endorsed his data. The publication of the first

Beringian pollen diagram in 1963 showed that pollen influx in glacial periods was lower than at present, implying the prevalence of a sparse herb-tundra or polar desert across the Bering Land Bridge (Colinvaux 1980).

In the 1980s, two late Pleistocene pollen records were published which supported the "sparse herb-tundra" or "polar desert" hypothesis. The records came from sites in the mountains of northern Yukon Territory: Lateral Pond (Ritchie 1982) and Hanging Lake (Cwynar 1982) - see Figure 2.1. These sites are deemed representative of easternmost Beringia due to their contrasting environmental locations. Lateral Pond is located 620 m above sea level close to the western flanks of the southern extremity of the Richardson Mountains. Its mountainous terrain and mixture of calcareous and non-calcareous sedimentary bedrock types support a rich variety of tundra and forest plant communities. Hanging Lake is on a ridge of shale and sandstone near the Barn Mountains north of the treeline in an area of tundra. Four main community types prevail - tussock tundra, sedge meadows, heath meadows and fell-field discontinuous dwarf shrub tundra. Both sites lie just outside the western limit of Wisconsinan glaciation and are 275 km apart (Cwynar and Ritchie 1980).

A third pollen profile referred to in the context of Duvanny Yar environmental reconstruction comes from St. Paul Island, one of the Pribilof Islands in the Bering Sea (Colinvaux 1980). The flora of the Pribilof Islands numbers

Figure 2.1 Sketch map of north Yukon and adjacent Northwest Territories depicting the location of Lateral Pond and Hanging Lake (Ritchie 1982, Fig. 1).

The heavy discontinuous line indicates the western limit of the maximum Laurentide ice sheets. The dotted line indicates the western limit of the final extension of Laurentide ice.

only about 190 species of vascular plants and the vegetation is predominantly herb-tundra.

Cwynar, Ritchie and Colinvaux put forward certain propositions regarding these pollen cores. First, they deduce from the low pollen influx values that the vegetation was scant at the height of the full-glacial interval. They believe the influx data to be so low that it is comparable only to present-day High Arctic barren tundra or polar desert. Second, they contend that the glacial taxa of these pollen records are restricted to tundra species found in present day northern environments and third, they believe that pollen data infers such harsh glacial environmental conditions that the ecosystems could not possibly have supported the diverse "mammal fauna" proposed by the palaeontologists.

These three palynological arguments will be considered in turn, beginning with the low pollen influx claims. The herbaceous pollen taxa from the base of the Lateral Pond core (Figure 2.2) present influx values as low as 50 - 500 grains/cm²/year (Ritchie 1982). These values infer a relatively sparsely vegetated full-glacial Beringian environment with a cold and harsh climate. The Lateral Pond core, however, extends back to only 16,000 yr B.P. and consequently the lack of full-glacial-aged data implies a relatively subjective interpretation of the late-Pleistocene Beringian landscape by Ritchie (1982).

Figure 2.2 Summary pollen influx diagram for Lateral Pond
(Ritchie 1984, Fig. 23).

The Hanging Lake core (Cwynar 1982), on the other hand, has sufficient radiocarbon control to allow acceptable calculation of pollen influx rates back to 30,000 B.P. (Figure 2.3). The core elucidates an even lower pollen influx (5 - 50 grains/cm²/year) than Lateral Pond and is down to as much as one third of that calculated for Holocene herb-tundra. Cwynar (1982) concludes, from this core, that during the glacial period the area was meagrely vegetated in comparison to present day tundra, and that its vegetation cover was probably more like that of modern arctic plant communities: essentially polar desert.

The combination of the Lateral Pond and the Hanging Lake pollen influx data sets led Cwynar and Ritchie (1980) to describe the regional late-glacial Beringian environment as "a sparse, discontinuous vegetation of herbaceous tundra on upland sites and local sedge-grass meadows on lowlands" (p.1377).

The second palynological proposition is based on studies of Duvanny Yar pollen spectra which show glacial taxa as confined to tundra species found in present day northern environments. The Lateral Pond core, for example, displays late Pleistocene plant communities which distinctly resemble the tundra vegetation of today's ridges and summits (Ritchie 1982; 1984). Species include *Aconitum*, *Astragalus*, *Dryas*, *Hedysarum* *Oxytropis*, *Phlox*, *Polemonium*, *Polygonum viviparum* and species of *Saxifraga*. At Hanging Lake the

Figure 2.3 Influx values of the main pollen types at the Hanging Lake site, plotted against radiocarbon age (Ritchie 1984, Fig. 21).

Duvanny Yar section of the pollen core is dominated by open-ground taxa such as *Dryas*, *Saussurea*, *Phlox*, *Polemonium*, *Bupleurum triradiatum*, *Lesquerella arctica*, *Androsace*, *Saxifraga tricuspidata*-type and *Thalictrum*.

Other scattered cores from Alaska and from Siberia (e.g., Edwards and Brubaker 1985, 1986; Anderson 1988; Anderson et al. 1988) support the concept of a spatially consistent Beringian tundra landscape during the last glacial period. The environmental reconstruction from the Imuruk Lake core on the Seward Peninsula in Alaska exemplifies this in its portrayal of the Beringian vegetation as "reduced to the most frigid form of arctic tundra, a tussockless grassy expanse, spotted with frost scars and loess deposits and devoid of all trees and shrubs except willows" (Colinvaux 1964, p.323). As a result palynologists conclude that the glacial vegetation resembled a barren tundra which equates with the current environment of the very far north.

The third and final proposition put forward by palynologists is the inference from pollen data that Duvanny Yar environmental conditions were so harsh that the ecosystems could not possibly have supported the "mammal fauna" proposed by the palaeontologists. Their assertion is reinforced by the apparent lack of dated large mammal fossils from full glacial times (Colinvaux and West 1984). This assertion, however, is opposed by proponents of the

"mammoth steppe hypothesis". This hypothesis and associated evidence is reviewed in the following section. The third palynological proposition is then discussed in light of this evidence in section 2.3.

2.2 Ecological Approach: Mammoth-steppe hypothesis

The ecological approach to paleoecology utilises the fossil mammalian record to reconstruct the nature of the habitats supporting the late Pleistocene Beringian fauna. It concentrates on community ecology, ecomorphological patterns and population dynamics, and it investigates mammalian characteristics such as social behaviour and dietary requirements to postulate the nature of paleoenvironmental conditions.

According to palaeontological reports, the full glacial period of Beringia was characterised by a phenomenal diversity of mammals (Guthrie 1985, 1990). Most Pleistocene vertebrate remains in Yukon Territory and Alaska come from near the base of frozen organic-silt "muck" deposits overlying gold-bearing gravels (Harrington 1978, 1981, 1987; Porter 1988). Mammalian bones from central and eastern Siberia are found buried in "yedoma silt" (Tomirdiaro 1982). The fossil evidence suggests that a mixture of extinct animals such as woolly mammoths, hyenas, sabretoothed cats, camels, horses, rhinoceroses, steppe bison, asses, deer,

lions and sagia antelope inhabited the area (Guthrie 1982). Many animals found in the same region today inhabited the area as well, including caribou, moose and small rodents (Guthrie 1982).

Despite the diversity of species found in the fossil record, there appears to be a dominance of large grazing mammal remains such as mammoth, bison and horse (Guthrie 1990). This group of animals has been termed the "mammoth fauna" and has led palaeontologists to the conclusion that the Beringian landscape during the full-glacial period contained productive grasslands.

This grassland-environment hypothesis is known as the "mammoth steppe" and is characterised by productive grasslands with dry summers, a windy climate and shallow snow cover. Various researchers (e.g., Guthrie 1984, 1990; Vereshchagin and Baryshnikov 1982) propose that this environment was not confined specifically to Pleistocene Beringia but rather extended as far west as Europe (Figure 2.4). Ecological evidence supporting this vast spatial reconstruction of steppic environment emanates primarily from two sources (Guthrie 1990): (1) comparisons of glacial fauna with their nearest modern analogues (e.g., Kubiak 1982; Olivier 1982) and (2) information about anatomical specializations (e.g., Martin 1982; Vereshchagin and Baryshnikov 1982).

Guthrie (1985, 1990) contributes significantly to the

Figure 2.4 Spatial extent of Beringia and the Mammoth Steppe
(after Guthrie 1990, Fig. 9.12).

"mammoth steppe" hypothesis. He focuses upon physiological characteristics of Beringian fossils and mummies, and projects these characteristics into a reconstruction of the full glacial environment. Tooth and stomach content studies show that the fauna were grazing specialists. Their foot morphology indicates adaption to travel across firm substrate, a condition not manifest by the moister soils of contemporary arctic tundra. Large mammalian body size suggests that the animals required substantial quantities of productive forage. Vereshchagin and Baryshnikov (1982), for example, claim that "... very large individuals of mammoth would have required 200 to 300 kg of succulent feed daily" (p.268). Finally, the length of leg characteristic of most "mammoth fauna" suggest that the mammals thrived in low snow-cover conditions, since their short legs were adapted to wind-swept and arid land, indicative of grassland environments (Guthrie 1985). Palynologists, however, have taken issue with this ecological data and their arguments are expanded in the context of the "production paradox" (section 2.3).

2.3 Literary Evolution of the Production Paradox

The palynological and palaeontological research frontiers present contrasting environmental reconstructions of the Beringian full-glacial ecosystem. The disparity of

evidence manifests itself in a geological interpretation of late-Pleistocene Beringia as a sparsely vegetated, unproductive region which paradoxically sustained abundant populations of large, gregarious ungulates. The paradox is heightened by the ecological interpretation of a diverse herbivorous fauna at a time when colder world climates would seem to have made for ecosystems less productive than those of the present.

The development of these conflicting environmental reconstructions can be traced through the literature. Colinvaux (1964), for example, was amongst the first to put forward the barren-tundra interpretation of the Beringian landscape. Guthrie (1968), on the other hand, significantly advanced the rich mammalian fauna thesis in a publication addressing various paleoecological issues. Primarily, he investigated the species of large mammal that inhabited Beringia, focusing specifically upon the relative density and interrelations between the animals. In addition he proposed explanations for the existence of this type of fauna during glacial times. Guthrie (1968) concluded, from the high percentage of grazing species in the fossil record, that interior Alaska was a grassland environment during the late Pleistocene.

This grassland hypothesis, however, was challenged by various Beringian palynologists. Cwynar and Ritchie (1980) criticised the grassland interpretation on the basis of low

influx values for the Duvanny Yar period (herb zone) in the Lateral Pond and Hanging Lake pollen cores. To these authors

... the "arctic steppe biome" never existed in Beringia during the late Quaternary ... (and) ... (T)he large and diverse ungulate populations probably were present during Pleistocene interstadials ... rather than during the time of the herb zone, 30,000 to 14,000 years ago (p.12).

Colinvaux (1980) supported Cwynar and Ritchie's (1980) interpretation of an unproductive tundra environment. He believed that the interpretation of the environment as "steppe" or "grassy" was "inadmissible on the pollen evidence" (p.7) and he adamantly concluded that "(T)he vegetation of the Bering land bridge was tundra; different in subtle ways from all modern tundra and with rather more *Artemisia* - but definitely tundra" (p.15).

The "mammoth steppe" hypothesis was again discounted in 1984, by Colinvaux and West. These researchers attributed the concept as having stemmed from a misuse of language, notably the term "steppe" which has a Russian meaning, denoting high arctic vegetation and climatic conditions typical of Beringia during the late Pleistocene. They claimed, however, that North Americans had twisted the Russian usage of the word "steppe" to mean a grassland environment and they state that, contrary to pollen evidence for barren tundra

... the magic word "steppe" opened a Pandora's box of speculations about how bones found scattered in various deposits throughout Alaska and Yukon Territory could be put together to describe a vanished productive (grassland) biome (p.11).

Colinvaux and West (1984) suggested that if the Russian term for "steppe" had been used correctly, in the sense of a bleak "polar desert", then the "... mammoth steppe concept would hardly have been taken seriously. We were misled by language" (p.11).

These palynological critiques of the hypothetically productive Beringian grassland prompted the palaeontologist, Guthrie (1985), to respond. He claimed that the palynologists had "... greatly misread their own data" (p.9) and instead proposed that pollen data in fact actually strongly support the "mammoth steppe" concept.

The palynologists argue three main points (outlined in section 2.1) as evidence refuting the "mammoth steppe" concept. Guthrie (1985) addressed each palynological argument in turn and then contributed new ecological evidence in support of the productive grassland hypothesis.

In response to the low pollen influx values recorded for the full-glacial period (Cwynar and Ritchie 1980; Ritchie and Cwynar 1982; Ritchie 1984), Guthrie (1985) interpreted low influx as a characteristic of the species' pollen producing capabilities rather than as an indicator of sparse regional vegetation. Guthrie (1985) stated that herbs are generally not big pollen producers, particularly in comparison to trees and therefore argued that no meaningful comparison could be made between total pollen influx of Holocene forests and glacial-age herb communities.

Guthrie (1985) also claimed that certain species of grass, though abundant, may not demonstrate high pollen influx values as they shift from sexual reproduction to vegetative reproduction in response to grazing pressure. Evidently scanty pollen data are not necessarily evidence for ancient polar desert or barren tundra environments (Guthrie 1985).

In addition, Guthrie (1985) made the argument that the pollen records used by the palynologists to formulate reconstructions of late Pleistocene Beringia were inadequate. The Hanging Lake core, for example, spans a depth of 3.5 m, yet whilst the Holocene section comprises 3 m of the core, the Duvanny Yar (herb zone) section is confined to the lower 0.5 m of the core. This fact led Guthrie (1985) to propose that during glacial periods, Hanging Lake was in fact not a lake. If this proposition is correct, pollen would therefore have been exposed to erosion during this time, and would not have been preserved within the core.

Guthrie (1985) used similar criteria to discount the validity of the St. Paul Island (Cagalog Lake) core. He maintained that this core is well dated down to about 10 000 years, but further down the core is mainly sand, suggesting that a permanent pond was not established in this area until the beginning of the Holocene. As is the case at Hanging Lake, the earlier condensed portion of aerobically exposed

wind blown sand in the St. Paul core, has virtually no pollen. Although, there are intermittent layers of silt in the sand, the sedimentary rates during this time are unknown and it is therefore not possible to accurately determine influx rates.

Having discredited these two cores, Guthrie (1985) proposed four alternative pollen profiles from Alaskan lakes which he considered more dependable than Hanging Lake and St. Paul Island for the paleoreconstruction of Beringia. Each core was taken from the central part of Beringia and met the sedimentary constraints for pollen influx studies (Guthrie 1985). Squirrel River core (Anderson 1982, 1985) dates beyond 23 000 years B.P.; the base of Kaiyak Lake core dates beyond the limits of radiocarbon range (Anderson 1985); Joe Lake core dates back to 28 000 years B.P. (Anderson 1988); and Imuruk Lake core extends back at least to the late glacial and Holocene (Colinvaux 1964).

The Kaiyak core is illustrated in Figure 2.5. It presents a fairly consistent picture of the paleoenvironment with relatively high herb influx during the peak glacial, as compared to late Holocene segments. Guthrie (1985) noted that grass pollen reaches its peak during the Duvanny Yar, contrary to Ritchie and Cwynar's (1982) conclusions. *Artemisia* also peaks during the full glacial; the same is true for the non-graminoid herbs. Herb pollen is least during the late Holocene, despite the fact that herbaceous

Figure 2.5 Kaiyak Lake herbaceous pollen influx (Guthrie 1990, Fig. 9.3).

vegetation comprises a large part of the flora in those areas today. Guthrie (1985) concluded from this that both today and in the late Holocene, herbs produced relatively little pollen, compared to the full glacial time period.

The most striking deduction made from these cores, however, is that herb pollen influx during full glacial times, as compared to the Holocene, was not reduced as Colinvaux, Ritchie and Cwynar had proposed; but rather that herb pollen production was increased and maintained an annual influx rate of about 400 grains/cm²/year.

In response to the palynologist's second argument that the pollen species of glacial periods do not exactly match the pollen species of present day grasslands, Guthrie (1985) suggested that identical pollen signatures are not necessarily a requisite criterion for meaningful comparison. Indeed, Guthrie noted that on a global scale, full-glacial environmental conditions would have differed significantly from those of the present, and that the diversity of vegetation characteristic of late-Pleistocene grasslands would likely have been markedly different from that of present-day grasslands. Furthermore, Guthrie (1985) claimed that since it is difficult to identify herb pollen to the species level, similarities between southern and northern grasslands could not be completely ruled out.

The third palynological argument against the "mammoth steppe" hypothesis proposes that there is a lack of dated

large mammal fossils from full glacial times. Palynologists argue that most fossil dates cluster in the warmer intervals of the Pleistocene, both before and after the glacial. Guthrie (1985) refuted this argument claiming that it is the result of sampling biases and research design. Bones collected from archaeological sites near Old Crow, for example, have been dated to the pre- and post-late Pleistocene glacial period. This, however, is explained by the fact that during the glacial period, Old Crow was the site of a pro-glacial lake which consequently prevented human and mammal habitation at that time.

Guthrie (1985) proposed that there is ample evidence of fossil remains dating from the height of the full-glacial. Table 2.1 shows bison, horse and mammoth fossils from Alaska dating from the Duvanny Yar interval. The dates are scattered continuously through the full-glacial and oppose the proposition that large mammals were concentrated, or confined to the interglacials (Ritchie and Cwynar 1982; Ritchie 1984; Colinvaux and West 1984).

Guthrie (1985) concluded by pointing out the flawed logic of Colinvaux and West's (1984) statement that scarcity of radiocarbon dates on large mammal bones (of one date per thousand years) implies a scarcity of mammal fauna. Guthrie maintained that this is comparable to saying that the few pollen cores studied from Alaska mean that there are few lakes. He suggested instead that the existing radiocarbon

Table 2.1 Chronological distribution of Alaskan Duvanny Yar
Bison, Horse and Mammoth (after Guthrie 1990).

BISON:

DATE (yrs BP)	CONF.LEV. (yrs)	LAB NO.	LOCALITY
25 090	1070	SI-850	Upper Cleary Creek
24 140	2200	SI-445	Fairbanks Creek
22 540	900	SI-292	Fairbanks area
21 780	310	DIC-1334	Porcupine Cave
21 300	1300	L-601	Fairbanks area
20 445	885	SI-837	Fairbanks Creek
18 000	200	SI-841	Manely Hot Springs

HORSE:

24 070	680	I-9320	Birch Creek
24 070	+380/-410	DIC-3098	Lost Chicken
23 920	620	I-9321	Fairbanks area
23 910	470	I-9318	Ikpikpuk River
23 340	388	DIC-3094	Lillian Creek
22 370	+300/-310	DIC-3093	Lillian Creek
21 050	+320/-340	DIC-1333	Porcupine Cave
20 810	410	I-9274	Ikpikpuk River
19 250	360	I-9371	Ikpikpuk River
18 640	205	DIC-3096	Lost Chicken
18 450	+200/-210	DIC-3091	Cleary

MAMMOTH:

22 850	250	V-48-152	Colorado Creek
21 900	320	GSC-1760	Melville Island
21 050	310	DIC-1333	Porcupine Cave
19 440	290	I-8578	Tununuk

dated bones are in fact a tiny sample of the tens of thousands of mammal bones that have been and still are discovered in Beringia.

The literature has demonstrated very little response to Guthrie's (1985) publication and following these heated debates of the early 1980s, discussion of the "production paradox" has waned. Mostly recently, Guthrie (1990) has again published information concerning the "mammoth steppe", this time describing his own excavations of a 36 000 year old bison mummy from an Alaskan placer mine. His arguments for the "mammoth steppe", however are identical to those of his 1985 article.

A puzzling aspect of these literary debates denotes that even with the increasing elucidation of palynological and palaeontological evidence, no plausible explanation for the existence of the "production paradox" has been put forward. At one point in the 1980s there was an attempt at a compromise (Guthrie 1990). From this the concepts of "tundra-steppe", "steppe-tundra" and "mosaic model" were born. Supporters of these concepts have not argued for a barren tundra nor a productive grassland, but instead have attempted to merge the two camps into a hybrid (Guthrie 1990). They contend that there was neither steppe nor tundra, but a mosaic of the two (Hopkins et al. 1982). The synthesis of this paleoecological evidence is considered more fully in the following section (2.4).

2.4 *Paleoecology of Beringia: A Synthesis*

Hopkins et al. (1982) present the most well known synthesis of the Beringian ecosystem. In June 1979 the Wenner-Gren Foundation for Anthropological Research sponsored a conference in Burg Wartenstein, Austria, to address the contradictory methodology and evidence that prevails within Beringian research. The conference volume embodies the standpoints of various scientists specialising in issues central to an understanding of the "production paradox" (Hopkins et al. 1982). The Beringian environmental synthesis, presented in the concluding chapter of this volume, was compiled largely from the interactions between scientists present at the conference. This paleoecological synthesis is outlined below.

The environment proposed by the "mosaic model" is one of contrasting habitats. The Bering Land Bridge is thought to have been characterised by discontinuously vegetated, barren, upland areas existing amidst more productive, essentially treeless, lowland areas whose vegetation was dominated by graminoid plant species. Hence the "mosaic" analogy.

The interpretation of an environment characterised by local productive regions is based both on studies of mobility, terrain preference, digestive strategy and feeding choice of late Pleistocene ungulates (Redmann 1982; Bliss

and Richards 1982) and on ecological inferences drawn from the dietary requirements and the behavioural repertoires of these ungulates (Guthrie 1982; Olivier 1982; Vereschagin and Baryshnikov 1982).

The presence of mammoth herds in full-glacial Beringia, for example, suggests that patches of concentrated fodder must have been available in close enough proximity to allow the passage of mammoth between feeding sites without excessive weight loss (Hopkins et al. 1982). This principle applies to other Duvanny Yar ungulate species, most of which are interpreted as nomadic and wide-ranging, and as capable of moving significant distances in the course of a year (Hopkins et al. 1982). Mountain sheep and musk ox, however, are relatively sedentary, and tend to cluster in familiar areas. This implies that productive regions able to sustain groups of at least ten to fifteen individuals on an annual basis must have existed in full-glacial Beringia. Hopkins et al. (1982) propose that these areas were up to a few tens of kilometres in diameter. Inferences thus suggest that the Duvanny Yar environment might be envisaged as a mosaic of well dispersed, productive "hot spots". Hopkins et al. (1982) urge that the crux of Beringian ecosystem reconstruction must be an understanding of these patches of significant productivity.

The present thesis contributes to this understanding. The research aims to identify factors which would have been

potentially capable of enhancing the productivity of local areas within the Duvanny Yar environment. The hypothesis, upon which the current thesis is based, stems from the modern analytical phase of paleoecology (Ball 1975) which, in this instance, involves hypothesis generation using the model-building approach (Pirks 1985). This approach provides a basis for comparing observed and predicted patterns and facilitates the generation of hypotheses that can be tested statistically with paleoecological data. The present thesis employs a simplified qualitative ecosystem model (Figure 1.3) which illustrates the probable interactions between seven components of an ecosystem. The model has been applied to Duvanny Yar Beringia by Schweger (1992) and is expounded upon in the following section (2.5).

2.5 Beringian Ecosystem Model

The ecosystem model serves to integrate the various aspects of the Beringian paleoenvironment into a "whole" (Schweger 1992). It illustrates the dynamic equilibrium which exists between each component of the ecosystem and demonstrates that the various factors cannot be considered in isolation of one another. At the same time the model allows for a detailed investigation of each individual component. This section outlines first the climate, second the interaction between the ungulate fauna and third the

edaphic factors within the ecosystem. It is from the edaphic component that the loessal hypothesis, the crux of the present research, stems.

2.5.1 Climate and Microclimate of the Duvanny Yar Interval

At the high latitude of Beringia, incoming solar radiation has fluctuated considerably during the last 40,000 years (Gal-Chen 1982). A summer radiation minimum occurred early in the Duvanny Yar interval, 25,000 years ago, and a peak occurred at the beginning of the Holocene, 10,000 years ago.

Direction of slope exposure is considered the most important microclimatic factor at Beringian latitudes (Barry 1982) as differences in the amounts of radiation received by moderately steep north- and south-facing slopes correspond to "equivalent latitude" differences of about 30 degrees. Consequently, even during the summer minimum of 25,000 years ago the more hilly parts of Beringia would have included significantly warm areas on south- and south-west facing slopes.

The winter-active sand dunes (Hopkins 1982) indicate that many areas of Duvanny Yar Beringia were windy during the winter months, making for a severely cold environment (Hopkins et al. 1982). The Beringian ecosystem, however, was governed less by the prevailing temperatures and more by the duration of the dormant season, accessibility of forage, and

variations in the thickness, density and continuity of the snow cover. These factors are all considered to have influenced the dispersal of the mammal species within the Duvanny Yar landscape (Hopkins et al. 1982).

2.5.2 Interactions between mammoth-steppe fauna

Grazing relationships between herbivorous mammals appear such that each species was able to create and maintain a level of environmental diversity that helped serve the needs of the coexisting species. The animals themselves manured the landscape, and their feeding constantly removed surplus plant production and prevented organic accumulation. Their trampling and feeding sparked graminoid production and augmented the tendency for nutritious, pioneering ruderals to remain prominent in the vegetation.

Cratering of snow especially by bison and caribou was an important mammalian process operating in the Beringian environment (Guthrie 1982, 1990) causing the exposure of patches of bare ground. These bare patches, together with the deposition of windblown sediment on top of the snow, affected the whole ecosystem by altering the albedo of the snow's surface (Hopkins et al. 1982). Reduced albedo in turn hastened the snowmelt and consequently initiated the early onset of spring growth (Guthrie 1982).

This feedback mechanism accounts for "local spring

protein flushes" (Hopkins et al. 1982, p.435) that constitute spring growth as it coincides, over a period of several months, with the melting of snowbanks across the region. Hopkins et al. (1982) postulate that the nomadic Beringian mammoth-steppe fauna which travel between productive patches would have "reenacted a grazing succession in one seasonal (protein-rich) hot spot after another" (p.435).

2.5.3 Edaphic factors: "loessal hypothesis".

Vegetative productivity is closely related to edaphic conditions. Late Pleistocene Beringian soils have been described as nutrient rich, more deeply thawed and of higher pH than those of present-day Beringia (Hopkins et al. 1982). The higher nutrient status of Beringian soils is explained according to various theories. Hopkins et al. (1982), for example, propose that the deeply annually thawed soil layer, the active layer, may have prevented nutrients from being lost to recycling through retention in the permafrost and may have enhanced microbial activity which would in turn have encouraged rapid nutrient turnover within the soil (Hopkins et al. 1982). C.A.S Smith (personal communication 1994), however, is not convinced that deep thawing occurred to any significant extent in the semi-arid late Pleistocene environment. He proposes that present-day soils supporting dry tundra show no evidence of deep thawing and attributes

this to the insulating properties of dry soil. Instead, he maintains that the active layer of the dry Duvanny Yar soils would only have been slightly thicker than the wet tundra soils.

The presence of loess in Beringian soil profiles has also been proposed to explain high edaphic nutrient status. Several researchers (e.g., Clark 1985; Velichko et al. 1984) have noted that loess accumulation greatly enhances the fertility of soils. A contemporary illustration of this phenomeon is the Yellow Plateau in China which comprises loess-rich soils supporting highly productive contemporary grasslands.

The present thesis is based upon the observed links between the presence of loess and grassland nutrient status and productivity. A large number of hypotheses have been put forward and tested regarding loess, its generation, chemistry, transport, distribution and pedogenesis (Schweger 1992). This thesis, however, focuses upon the role of loess in the evolution and functioning of the Beringian ecosystem. The concept, known as the "loessal hypothesis" was developed and qualitatively tested by Schweger (1992). The next chapter expands upon this hypothesis and describes the way in which it is applied and quantitatively tested in the current thesis.

CHAPTER 3: LOESSAL HYPOTHESIS

The "mosaic model" (section 2.4) proposes a full-glacial ecosystem composed of different plant communities rather than a widespread, uniform steppe or tundra. The Duvanny Yar environment would likely have included patches of high productivity that would have supported the diverse Beringian "mammoth fauna" (Hopkins et al. 1982).

Schweger (1992) looks to the edaphic component of the Beringian ecosystem for an explanation of these productive "hot spots". His investigation of Beringian edaphic conditions led him to contrast Cryosols which currently typify the surface of Alaska and Yukon with Beringian Brunisolic-like soils which he suggests were widespread during the Duvanny Yar interval.

Present-day tundra soils have a high moisture content, and are classified as Orthic or Gleysolic Turbic Cryosols. The soils are poorly drained, cold and characterised by a vegetation of ericaceous species, moss and the tussock form of *Eriophorum*. They are generally acid and exhibit very low nutrient status since many of the nutrients are locked up in the organic matter entrapped within the permafrost or surface peat. Low levels of microbial activity due to excess moisture and cold temperatures prevent decomposition of the surface organic layer which in turn insulates the mineral soil and maintains a shallow permafrost table (Schweger

1992).

The Duvanny Yar Beringian soil, on the other hand, is best described as a Brunisolic or Regosolic Static Cryosol. This classification indicates weak soil development and moisture status which precludes cryoturbation, but enables permafrost formation within one metre of the soil surface (C.A.S. Smith personal communication 1994). These soils were thought to have been well drained and vegetated by deeply rooted tundra and steppe species including grasses, *Artemisia*, *Polygonum*, *Chenopodium* and *Plantago*. During summer they were relatively warm, because of their dry condition and minimal organic cover. Bare mineral soil was often exposed and surface accumulation of organic litter was minimal and organic matter accumulated as well-developed humus within the mineral soil. Microbial activity was high, pH was high and evaporation often caused salts to accumulate at the soil surface (Schweger 1992).

Schweger (1992) proposes that these Brunisolic-like soils were sufficiently fertile to sustain a productive Beringian ecosystem. He suggests that the key difference between these soils and present day Cryosols is the incremental deposition of aeolian silt or loess to the soil surface (see Figure 3.1). Schweger (1992) thus proposes the "loessal hypothesis" which states that

the deposition of loess under full glacial conditions was a key factor in maintaining the highly productive ... (Beringian) soils and, ultimately, the Beringian ecosystem (p.41).

Figure 3.1 Hypothetical soil profile contrasting
Orthic/Gleysolic Turbic Cryosol and
Brunisolic/Regosolic Static Cryosol edaphic conditions
(after Schweger 1992, Fig. 2).

According to Schweger (1992), the testing of this hypothesis requires the use of modern analogues since no full glacial paleosol for Beringia has yet been described. Buried paleosols, dating from 17,000 years B.P., however, are currently being studied on the Seward Peninsula. The results are as yet unpublished and were unavailable to Schweger (1992).

Schweger (1992) thus employed three modern literary analogues as qualitative evidence to support the proposal that the "loessal hypothesis" is a possible explanation for the increased productivity of "hot spots" in Duvanny Yar Beringia. Schweger (1992) describes his research as "a generalised and qualitative example of (the ecological) approach (to paleoecology) in identifying and testing the role of loess" (p.44).

In contrast, the current thesis aims to be a detailed and quantitative example of the ecological approach to paleoecology. The primary objective of this thesis is to investigate the extent to which the receipt of loess influences the productivity of contemporary grasslands. Ultimately the thesis employs the principle of uniformitarianism in extending the conclusions realised from the present-day ecosystem backward in time to explain the productivity of the Duvanny Yar ecosystem. In light of this, data collection was undertaken in an environment approximately representing the full-glacial Beringian

ecosystem in southwest Yukon Territory.

The purposes of this chapter are (1) to describe the background of the "loessal hypothesis"; and (2) to explain why the chosen study area in southwest Yukon Territory is an appropriate modified analogue of the Beringian environment and hence for the application of the "loessal hypothesis".

3.1 *Loessal Hypothesis: Background review*

Schweger's (1992) investigation of the literature led him to believe that "(T)hree recent discoveries support the hypothesis that loess was a key factor in soil formation and the maintenance of the Beringian ecosystem" (p.42).

Studies of road dust in northern Alaska constitute the first line of evidence (Walker and Everett 1987). The ecological consequences of road dust from the Dalton Highway and Prudhoe Bay Spine Road simulate the effects of loess fall upon the surrounding forest-tundra vegetation. Schweger (1992) concludes that changes in plant community composition, such as the elimination of ericaceous species and *Sphagnum* moss and the appearance of species better suited to mineral substrates, higher pH, deeper thaw and rapid snow melt (Walker and Everett 1987), in response to the aeolian inputs, are moving the environment towards that which has been hypothesized for the Brunisolic/Regosolic Static Cryosol.

A second line of evidence considered by Schweger (1992) comes from geochemical analyses of Antarctic glacial ice which suggest that glacial ice acts as an atmospheric sink for nitrate and ammonium ions (Zeller et al. 1988) and that ice marginal environments watered by glacial ice melt would be highly productive. Schweger (1992) carries the point a step further, proposing that melt waters rich in phosphate, potassium and fixed nitrogen would also contain rock-flour derived from glacial abrasion, this being the source of the phosphate and potassium. Schweger (1992) suggests that this rock flour could adsorb the nitrates from the glacial ice and upon redeposition as loess would greatly enhance the fertility of soils at considerable distances from the ice margin itself.

The third line of evidence comes from a survey of grazing potential in southern Yukon Territory. Johansen et al. (1989) discovered high forage production and greatest carrying capacity, at least for horses, in grassland/parkland communities dominated by *Artemisia-Festuca*. These communities and their distinctive high pH, high calcium carbonate, well drained loamy soils are "limited to those areas close to a source of windblown loess such as the Donjek River" (Johansen et al. 1989). The 1989 survey thus implies a correlation between soil properties/loess deposition and forage productivity but does not provide any quantitative evidence to substantiate this

claim.

The current thesis investigates field data collected in the same region as the 1989 survey and aims to elucidate evidence pertaining to this soil property/increased productivity claim. The study area is postulated to be a "modified analogue" of the highly productive "hot spots" proposed by Hopkins et al. (1982) for Duvanny Yar Beringia. As a result conclusions drawn from the study area's contemporary grassland ecosystems can be projected on to the late Pleistocene environment. Justification for assuming the Kluane Lake region as a "modified analogue" of full-glacial Beringia is presented in the following section (3.2).

3.2 Kluane Lake Region: A "modified analogue"

Matthews (1982) and Guthrie (1984), amongst others, have concluded that extinction of the Pleistocene large mammal assemblage rules out the possibility of modern analogues. Other authors (e.g., Young 1982; Schweger 1992) believe that "some local environments such as the grazed loessal grasslands of southern Yukon may be close approximations" of modern analogues (Schweger 1992, p.43). The term "modified analogue" is appropriate in this context since the region exists under a temperate, semi-arid boreal environment, rather than under arctic polar desert conditions.

The "modified analogue" that constitutes the study area for this thesis lies within the Greater Kluane region in southwest Yukon Territory. The Greater Kluane region extends eastward from the United States-Canadian border at longitude 141°W to $136^{\circ}15'\text{W}$ and southward from latitude $63^{\circ}40'\text{N}$ to $60^{\circ}35'\text{N}$. The area within which field work for this thesis was undertaken comprises only a small portion of this region. It is confined to the southern edge of Kluane Lake and will be termed the "Kluane Lake region" as opposed to the "Greater Kluane region" as shown in Figure 3.2.

Geist (1978) is convinced that the Greater Kluane region is comparable to the productive periglacial ecosystems of the late Pleistocene. Geist (1978) maintains that this region is "the most representative of all glacial systems for studying periglacial ecology" (p.197) in the context of the "production paradox". He bases this statement on a number of criteria.

First, the periglacial flora of the Greater Kluane region are thought to parallel those of Eurasia during the late Pleistocene (Geist 1978). Of particular relevance are the plants of the Duvanny Yar loess steppe of which a small number still exist in the St. Elias Range. Vegetation of the Greater Kluane region is described in detail in the following chapter (section 4.6).

Second, the large mammal fauna of the Greater Kluane region possess a notably close affinity to the "mammoth

Figure 3.2 Location of Greater Kluane Region and Kluane Lake Region, southwest Yukon Territory (after Johansen et al. 1988).

fauna" of the last glaciation in Eurasia (Vereshchagin 1967). In late Pleistocene times, researchers suggest that fauna of the region comprised almost as many species of large mammals (29) as of small mammals (34). The present day ratio of large herbivores (7) to small herbivores (23) in the St. Elias Range is similar to that of the Great Plains prior to European settlement (5 to 17), despite the better productivity of the Great Plains. It is similar to that of the Eurasian Steppes (7 to 27) and almost mirrors the contemporary trophic structure of some African ecosystems (Geist 1978, from Guilday 1967).

Third, mammals of the Greater Kluane region, in a few species, also appear to attain the maximum phenotypic body size for their species. The largest living bears, the Alaska brown bears (*Ursus arctos middendorfi*), for example, live beside, or maybe even at times on, the glaciers on the oceanic side of the St. Elias Range (Geist 1978). The Alaska moose (*Alces alces gigas*), also found in the Range, is the largest subspecies of moose, but it is not known whether the St. Elias moose exceed other moose in size, since no data are available for comparison. Weights have been recorded for the Dall's sheep in the St. Elias Range, however, and they appear to exceed those of Dall's sheep elsewhere by almost one-third in body weight (Geist 1978).

The mere existence of these larger-bodied species of vertebrates suggests that the Greater Kluane region contains

periglacial ecosystems which are highly productive in comparison to tundra ecosystems at comparable altitudes and latitudes. The standing crop of grassland ecosystems in Kluane National Park, for example, is about 89 kg/km^2 (Hoefs 1973), almost five times that cited for tundra ecosystems (from Petrides and Swank 1965).

The current thesis aims to determine the extent to which increased productivity of grassland communities, analogous to those postulated for the Duvanny Yar Beringian ecosystem, is the result of additions of loess to their environment. It concentrates upon highly productive lowland sites of the Kluane Lake region, not previously considered by Hoefs (1973), as a "modified analogue" of the Duvanny Yar Beringian ecosystem. Indeed, Hoefs (1973) notes that if he had included these sites in his biomass calculations, and had introduced and allowed populations of horse, elk, musk ox and bison to stabilise within the area, the standing crop of the Kluane National Park would probably be close to 175 kg/km^2 in a climatic regime similar to that found today.

The following chapter describes the specific nature of both the Greater Kluane and the Kluane Lake regions and focuses upon the relevance of the regions as "modified analogues" of Duvanny Yar Beringia for the testing of the "loessal hypothesis".

CHAPTER 4: STUDY AREA

This chapter considers the environment of the Greater Kluane and the Kluane Lake regions, and examines various components of the ecosystems, both at a macro- and a micro-scale. At each juncture the chapter elaborates upon the significance of the environment to an interpretation and understanding of the late Pleistocene periglacial ecosystem.

4.1 *Physiographic and Geologic Setting*

The St. Elias Mountains constitute a major portion of the Greater Kluane region. The St. Elias Range belongs to the high-mountain system that borders the Gulf of Alaska and trends through northwestern British Columbia, southwestern Yukon Territory and south-central Alaska. These mountains are geologically and physiographically uniform (Denton 1974) and form a prominent topographic barrier between the northwest Pacific Ocean and the North American continent (Eisbacher and Hopkins 1977). The St. Elias Mountains are subdivided into the Icefield Ranges, the Kluane Ranges, the Alsek Ranges and the Duke Depression (Matthews 1986 - see Figure 4.1).

The Icefield Ranges form the core of the St. Elias Mountains and are covered by ice, with numerous peaks and large areas above 3,000 m elevation. They contain the

Figure 4.1 Physiographic Regions of southwest Yukon Territory (after Matthews 1986).

highest point in Canada, Mount Logan, at an elevation of 5,959m.

The Shakwak Valley forms a sharp boundary between the St. Elias Mountains and the Yukon Plateaus to the northeast (Bostock 1948; Rampton 1971). The Shakwak Valley is 8-14 km wide (Clague 1981) and lies partly along the Denali Fault, and partly along an older (latest Cretaceous - earliest Tertiary) shear zone (Eisbacher and Hopkins 1977). The Denali Fault is a major intra-continental crustal break extending for more than 2,000 km from south-central and southeastern Alaska into British Columbia (Eisbacher and Hopkins 1977).

Alignment of these physiographic units is southeast to northwest (Hoefs et al. 1978). Geologically, the units comprise a eugeosynclinal sequence of rocks. Rampton (1981) dates the sequence from Ordovician to Cretaceous and describes it as "a great thickness of sediments, predominantly argillaceous but containing abundant volcanic rocks, that have accumulated in a deep-water marine environment" (p.1). The landscape has resulted from collision of the Pacific crustal plate with the continental margin of North America. As a consequence of regional compression, the crust has thickened and its surface is rising. This uplift is responsible for the change in the mid Tertiary St. Elias environment from "a rolling upland with wide shallow alluvial valleys and a temperate climate"

(Eisbacher and Hopkins 1977, p.333) to an area of sufficient elevation to support the formation of thick ice sheets by the mid-Miocene (16 Ma).

4.2 Regional Climate

Today there is a marked contrast between the climates on the southwest and northeast flanks of the St. Elias Mountains. This reflects the effectiveness of the St. Elias Mountains and the Coast Mountains as a climatic barrier to the penetration of moist, warm air from the Pacific (Wahl et al. 1987). The climate of the Gulf of Alaska to the southwest is maritime but northeast of the mountains Yukon Territory experiences continental conditions. Taylor-Barge (1969) defined a zone of transition, or climatic divide, separating maritime and continental characteristics 160 km inland from the coast, in the vicinity of the topographic divide of the St. Elias Mountains.

The Greater Kluane region lies to the northeast, in the rainshadow of the St. Elias Mountains, where the climate is classified as approaching semi-aridity (Kendrew and Kerr 1955, Taylor-Barge 1969). Annual total precipitation decreases from up to 4,000 mm on the coast side to under 300 mm in the Shakhwak Valley (Clague 1981; Wahl et al. 1987).

The temperature field is complex due to the proximity

of the Pacific and the extreme range in elevation of the mountain barrier. On an annual basis the mean temperature ranges from $+2.5^{\circ}\text{C}$ at Yakutat on the marine side (C.A.S. Smith personal communication 1994) to -5°C on the northeast side of the transition zone (Hoefs et al. 1978; Wahl et al. 1987). These data are summarised in Table 4.1 using statistics from three locations. Juneau experiences the maritime coastal climate of the Gulf of Alaska; Kluane Lake experiences an arid continental climate in the rain shadow area east of the St. Elias Mountains; and Haines Junction experiences a slightly less arid continental climate in the region south of the St. Elias rain shadow.

The aridity of the Greater Kluane region (234 mm/year) resembles the aridity of Duvanny Yar Beringia (less than 200 mm/yr), caused, at that time, by the Bering land bridge which displaced or even eliminated moisture from the Bering Sea away from interior Beringia. Climatic modelling (e.g., Barnosky et al. 1987) indicates that at approximately 18,000 B.P., the height of the last glacial, the climate of Beringia was influenced by strong anticyclonic circulation and adiabatic warming of air flowing off the ice sheets: processes which led to an overall windy, arid and continental Beringian climate during glacial periods in North America (Schweger 1992).

Table 4.1 Climatic statistics from selected stations in southwest Yukon Territory and Alaska (Data from Kluane Lake and Haines Junction from Environment Canada 1982, data from Juneau from Arctic Environmental Information and Data Centre 1986).

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Annual mean
Monthly mean air temperature (°C)													
Kluane Lake	-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
Haines Junction	-22.9	-15.6	-10	-0.6	5.4	10.3	12.5	10.8	6.2	-1.3	-12.2	-20.5	-3.2
Juneau	-5.4	-2.2	0	4	8.2	11.7	13.2	12.6	9.6	5.4	0.3	-3	4.5
Monthly mean precipitation (mm)													
Kluane Lake	7.2	5.9	5.2	7.9	22.1	32.3	47	34.1	17.2	16.3	17.7	11	233.9
Haines Junction	21.9	15.9	9.5	7.6	14.9	29.1	36.3	28.9	29.4	33.1	34.1	31.8	292.5
Juneau	94.2	91.2	80	71.6	88.1	73.9	106.7	129.5	159.8	188.7	128.3	109	1321.3

4.3 Glaciation

The major snow accumulation zone in the St. Elias Mountains today lies between 1,500 m and 3,000 m. The copious supply of moisture from the Gulf of Alaska is mainly responsible for the extensive network of glaciers in the Icefield Ranges (Wahl et al. 1987). Marcus and Ragle (1970) found that equilibrium line elevations in these mountains average approximately 1,100 m on the marine slope and 2,100 m on the continental side. Valley glaciers extend downslope from accumulation zones between 1,200 m and 900 m above sea level (Wahl et al. 1987).

The largest glaciers are the Lowell, Kaskawulsh, Kluane, Donjek, Walsh, Logan, Seward and Hubbard the majority of which are on the windward, maritime side of the St. Elias Mountains. The Kaskawulsh Glacier is of particular importance to the study area.

4.3.1 Kaskawulsh Glacier and Kluane Lake

The Kaskawulsh Glacier is 73 km long (Denton and Stuiver 1967). The glacier terminates at the junction of the Kaskawulsh and Slims River valleys, which respectively carry the glacial meltwater into the Gulf of Alaska via the Alsek River and into the Bering Sea via the Yukon River drainage. The Slims River Valley, which begins at the terminus of the Kaskawulsh Glacier, traverses the Kluane Range in a

northeasterly direction and opens into the Shakhwak Valley at the southern end of Kluane Lake, approximately 23 km from the glacier (Muller 1967).

Kluane Lake, the largest lake in Yukon Territory, is about 80 km in length (Hoefs et al. 1978). The Slims River, which flows from the western edge of the Kaskawulsh Glacier terminus, is the main source of water. On leaving the lake, water travels about 2,250 km by the Kluane-Yukon river system to the Bering Sea. In contrast, waters from the eastern part of the Kaskawulsh Glacier terminus drain through the Kaskawulsh River to reach the sea in the Gulf of Alaska by way of the Alsek River in about one tenth of the distance.

Bostock (1952, 1969) proposes that Kluane Lake may not always have drained the way it does today. He suggests that after the last major Pleistocene advance (the Kluane Glaciation - see section 4.3.2) the lake may have drained to the Gulf of Alaska through the valleys of the Slims, Kaskawulsh and Alsek Rivers (Figure 4.2). Bostock (1952) maintains that such a course, if formerly open, would have been blocked by the advance of the Kaskawulsh Glacier during the Neoglacial period, at which time the present drainage via the Kluane River would probably have been established.

This process would have led to a reversal in the drainage of the Slims River into Kluane Lake. Bostock (1969) proposes that the level of the lake would consequently have

Figure 4.2 Drainage routes in the area of Kluane Lake, southwest Yukon Territory (Bostock 1969, Fig. 1).

risen rapidly and flooded its basin to 10 m above its present level, before finding an overflow channel to Burwash Creek along the course of the present channel of the Kluane River. It is important to note that Bostock's hypothesis has not been fully accepted (Johnson and Raup 1964, p.26-28).

4.3.2 Glacial Chronology and Stratigraphy

Beringia is the term given to those parts of Yukon Territory, Alaska and central and eastern Siberia that were never glaciated during the Quaternary period. The Kluane Lake region study area is located approximately 25 km to 50 km south of the unglaciated zone (e.g., Tarnocai et al. 1985 - see Figure 4.3). Evidence of past glaciations is found everywhere in the form of moraines, erratics, scouring of bedrock, outwash, drift and loess deposits. Pleistocene events in the southwest Yukon have been described in general terms by Bostock (1952), Kindle (1953) and Muller (1967). Very detailed work has been done on the Kaskawulsh Glacier-Slimes Valley-Shakwak Trench complex by Denton and Stuiver (1966, 1967), and by Borns and Goldthwait (1966).

According to Denton and Stuiver (1966) and Muller (1967), three large glaciations occurred in southwest Yukon and a fourth much smaller one, the Neoglaciation, is still current. Using drift morphology and stratigraphy combined with ^{14}C dates, Denton and Stuiver (1966) worked out the chronology and named the events. Figure 4.4 relates this

Figure 4.3 Glacial limits in southern Yukon Territory (after Tarnocai et al. 1985).

Key:

- Limit of pre Shakwak (pre-Reid) Glaciation
- Limit of Icefield (Reid) Glaciation
- Limit of Kluane (McConnell) Glaciation
- General direction of ice movement

Figure 4.4 A comparison between the nomenclature proposed for late Pleistocene glacial chronology in the northeastern St. Elias Mountains (Denton and Stuiver 1967) and the chronology and nomenclature of the glacial sequence in Yukon Cordillera (Vincent and Klassen 1989).

General chronostratigraphy						Yukon Cordilleran icesheets (O.J. Hughes)	St. Elias Mountains (after Denton and Stuiver 1967)
Time	Period	Epoch	Stage				
		HOLOCENE					
10	Q U A T E R N A R Y	P L E I S T O C E N E	L A T E	W I S C O N S	LATE		Neoglaciation
20							Sims Non-glacial Int.
30					McConnell Glaciation = Macauley Glaciation	Kluane Glaciation	
60							
80				EARLY	Boutellier Non-glacial interval > 37 ka	Boutellier Non-glacial interval > 37 ka	
				SANGAMONIAN			
130							
320				MIDDLE	ILLINOIAN		
						Pre-Reid interglacial	Silver Non-glacial interval
730		EARLY	PRE-ILLINOIAN			Klaza Glaciation and Nansen Glaciation	Shakwak Glaciation

chronology to the glacial sequence in the Yukon Cordillera (Vincent 1989). The dates are modified to correlate the glaciations with results from radiocarbon dating in the more recent literature (e.g. Tarnocai and Smith 1989; Vincent and Klassen 1989).

The Shakwak Glaciation was the oldest and most extensive glacial period dating from before 730 000 years B.P. (Vincent and Klassen 1989). The Shakwak ice-sheet was derived from the Icefield Ranges and it flowed into the Shakwak trench by way of the Slims Valley. The Silver nonglacial interval marked the end of this glacial period, and was subsequently followed by the Icefield Glaciation. During this glaciation, glaciers are believed to have flowed down the Slims, Duke and Donjek Valleys to join a major icefield in the Shakwak trench, where the flow was generally in the northwesterly direction, as indicated by the ice gradient and the alignment of drumlins.

The Boutellier nonglacial interval separated the Icefield Glaciation from the Kluane Glaciation. The Kluane Glaciation was characterised by ice advancing north from the Icefield Ranges. The ice initially entered the Shakwak Trench through the Slims Valley and deposited outwash sediments and tills at its snout (Denton and Stuiver 1966). At the end of the glaciation, warmer conditions caused the ice to retreat southwards exposing active outwash plains of silty material. Winds picked up much of this material and

subsequently deposited it as Kluane loess on the surrounding landscape (Denton and Stuiver 1966).

Kluane loess consists of well-sorted silt with some fine sand. It is composed of a wide range of mineral types, reflecting the complex lithology of the source rocks of glacial sediments in the region (Denton and Stuiver 1966). Kluane loess forms the oldest unit of drift in the study area, and its thickness varies from 0.36 m to 1 m, depending on altitude, aspect and slope (Hoefs et al. 1978).

The Slims nonglacial interval includes the "Hypsithermal interval" as defined by Deevey and Flint (1957). During this relatively warm period the Kaskawulsh Glacier retreated 23 km above the present location of its terminus (Denton and Stuiver 1966). The Slims River valley train, the most important source of loess for the area, became deactivated and covered in vegetation. The subsequent cessation or near cessation of loess deposition exposed the Kluane loess to weathering processes which allowed the Slims soil to form.

This soil was named after the Slims River along whose banks the soil is particularly well exposed (Denton and Stuiver 1966; 1967). The Slims soil comprises an intensely oxidised horizon, completely leached of calcium carbonate and moderate brown (5YR 4/4) in colour (Denton and Stuiver 1967).

The Neoglaciation is defined by Sharp (1960) as "a

short convenient designation for a readvance of ice subsequent to shrinkage during the Hypsithermal interval" (p.321). It resulted in the advance of the Kaskawulsh Glacier to slightly beyond the present location of its terminus which prompted the reactivation of the Slims River valley trains, thereby inducing renewed loess deposition.

This loess is termed Neoglacial loess and forms a horizon up to 25 cm thick with a thin layer of volcanic ash at its base. This ash has been dated at 1 200 years B.P. (Lerbekmo et al. 1975). A thin layer of unweathered grey loess below the ash indicates that the Neoglacial advance had begun before the volcanic eruption (Hoefs et al. 1978). Lack of weathering in this top loess layer indicates that the Slims Valley train has been active ever since. Denton and Stuiver (1966) state that the Neoglacial maximum of the Kaskawulsh Glacier was reached some time before 1865 A.D. and that there have been fluctuating retreats since then.

The profile described above and illustrated in Figures 4.5 and 4.6 is encountered to an elevation of 1,370 m in the study area. Hoefs et al. (1978) note that the thickness of the profile decreases with elevation and is affected by aspect and slope as well as by exposure to wind (Hoefs et al. 1978). They observe, especially at subalpine elevations, that much modification has occurred through erosion, animal activity, vertical soil movement and incorporation of organic as well as colluvial material.

Figure 4.5 Typical loess profile in Slims River valley,
southwest Yukon Territory (Denton and Stuiver 1967,
Fig. 2).

Figure 4.6 Photograph of typical loess profile in Kluane Lake region, southwest Yukon Territory.

4.4 Active Loess deposition

The Slims River delta is formed where the Slims River enters Kluane Lake (Figure 4.7). The delta is relatively large (7 km²) and is comprised primarily of fine sand and silt (Nickling 1978) making up a virtually flat, smooth surface. Geist (1978) describes the formation of such deltas. Small undulations and scour pits have been observed on the surface of the delta and are thought to result from wind erosion (Nickling 1978). Vegetation is sparse, comprising salt-resistant grasses and willows, and it is confined primarily to sediments near the valley walls. The lack of vegetation cover, low annual precipitation and the fine texture of the delta sediments makes this material extremely susceptible to wind erosion (Nickling 1978). The Slims River Valley consequently has frequent dust storms (Figure 4.8) generated by strong off-glacier winds particularly from May to July (Muller 1967, Nickling 1978). During this period, the Slims River is at a relatively low stage, exposing a large area of recently deposited silt and fine sand. Total precipitation during these months is also low and temperatures are sufficiently high to dry the surface of the delta.

Fossil sand dunes (Hopkins 1982) identified throughout Alaska and Yukon Territory are deemed indicative of windy conditions and intense aeolian activity during the Duvanny

Figure 4.7 Photograph of Slims River delta.

Figure 4.8 Photograph of dust storm in Slims River valley

Yar interval. Loess deflation and deposition are thus considered dominant processes within the full-glacial Beringian ecosystem and their relevance to the Greater Kluane region is illustrated in Figure 4.9.

4.5 *Local climatic conditions*

Local climatic conditions cause the climate of the Kluane Lake region to be much modified from the regional outline presented in section 4.2. Differential spatial and temporal freezing of Kluane Lake has a moderating effect on local temperatures. Hoefs et al. (1978) note that the southern end of the lake does not freeze over until late November or early December whereas the more northern, shallower end of the lake freezes in late October. This explains the significantly higher mean November temperatures at the base of Sheep Mountain (-8.6°C) and at the Kluane Lake Station (-9.4°C) in comparison to the temperature at Burwash (-13.8°C), only 12 km farther north.

Sheep Mountain is a prominent landscape feature within the Kluane Lake region. The geographical orientation of this mountain from southwest to northeast is also thought to modify the local climate of the study area (Hoefs et al. 1978). Direct exposure of the large "broadside" of Sheep Mountain to the sun allows it to receive maximum insolation, even when the sun is at a lower angle in the spring, fall

Figure 4.9 Loess deflation and deposition in Kluane Lake region (modified for Kluane Lake from Guthrie 1990).

and late winter. This causes snow to melt and disappear from Sheep Mountain's east, south and west slopes earlier in the spring. In the summer it contributes to the aridity of the local environment.

The proximity of the study area to the Slims River Valley also influences the climate of the local environment. The Slims River valley serves as an effective funnel for katabatic wind, coming from the southwest down the Kaskawulsh Glacier. Hoefs et al. (1978) note that these winds are particularly strong in late winter, spring and early summer. The winds are responsible for the continuing loess deposition described in section 4.4, and are the underlying cause of high evapotranspiration rates on the exposed slopes of Sheep Mountain and the slopes on the southeastern shore of the lake. Observations of an extremely windy and strongly desiccated environment at Cultus Bay in May 1994, support this statement (C.A.S. Smith personal communication 1994). Hoefs et al. (1978) suggest that these evapotranspiration rates are the reason for the predominance of grassland vegetation in the study area.

The interactions between loess, wind, temperature and water are thought to produce an environment of extremes within the Greater Kluane region (Geist 1978). Microclimatic and fertility variations contribute to the formation of highly productive biotic communities supporting a great diversity of plant and animal species. The vegetative and

edaphic nature of the environment is described in the following sections (4.6 and 4.7).

4.6 Vegetation

Despite its northern location the Greater Kluane region is as well known botanically as any other area in Yukon Territory and northern British Columbia. Hoefs et al. (1978) undertook phytosociological work and identified three biogeoclimatic zones in the study area. These are: (1) the boreal (montane) zone from the lowest elevations of the valley floor to an altitude of about 1,160 m; (2) the subalpine zone between 1,160 m and 1,525 m; and (3) the alpine zone above the 1,525 m. Within these zones Hoefs et al. (1978) described thirty-two plant associations, grouped into twenty-three alliances and seventeen orders. The boreal zone is relevant to this thesis.

Hoefs et al. (1978) observed that the distribution of most plant associations can be correlated to factors such as snow depth and duration of snow-cover, soil moisture during the growing season, aspect, slope and other physical characteristics of the soils. The climax vegetation on mesic zonal sites of the boreal zone, for example, is the white spruce forest. Dry sites, however, are occupied by various grassland associations.

Johansen et al. (1989) investigated the grazing

potentials and plant communities of five selected areas within the Greater Kluane region. They conclude that the Kluane Lake region, along Brooks and Talbot Arms, contains the largest area of productive rangeland in the region: the *Artemisia-Festuca* community. The community is associated with both open poplar stands and aspen forest; green up is early in the spring and there is little snow cover during the winter. Table 4.1 shows the dominant plant species, potential domestic forage production and community grazing capacity of the *Artemisia-Festuca* community.

The vegetation cover of the rangelands in the Kluane Lake region resembles that of the Duvanny Yar productive "hot spots" proposed by Hopkins et al. (1982) (see chapter 2) to the extent that the Duvanny Yar environment constituted an open landscape supporting plant communities controlled by ecological gradients of aspect, slope, elevation, moisture and drainage (Schweger 1992). In addition, Schweger (1992) notes that shrub *Betula* (birch) and *Populus* (poplar or aspen) may have been present in the most favourable settings and that taxa such as *Chenopodium* or *Artemisia* may have been more widespread and locally abundant.

Table 4.2: *Artemisia-Festuca* Community in Kluane Lake Region
(after Johansen et al. 1989).

	GRASSLAND PHASE	ASPEN PHASE
TREE		1. <i>Populus tremuloides</i>
SHRUBS	1. <i>Arctostaphylos uva-ursi</i>	1. <i>Salix bebbiana</i> 2. <i>Shepherdia canadensis</i>
FORBS		1. <i>Anemone patens</i> 2. <i>Artemisia frigida</i> 3. <i>Epilobium angustifolium</i>
GRAMINOIDS	1. <i>Festuca saximontana</i> 2. <i>Carex obtusata</i> 3. <i>Bromus pumpellianus</i>	1. <i>Agropyron trachycaulum</i> 2. <i>Poa glauca</i>
FORAGE PROD.	370 kg/ha	450 kg/ha
GRAZING CAP.	15 ha/AUY	12 ha/AUY

4.7 Soil

The *Artemisia-Festuca* communities in the Kluane Lake region are generally located on hummocky to rolling glaciofluvial deposits overlain by windblown loess. These soils are typical of grassland environments found elsewhere in north western Canada (Cannon and Neilsen 1984) and are classified as Melanic and Eutric Brunisols (Canadian System of Classification 1987). They possess high pH, high calcium carbonate content and an organic rich (Ah) surface horizon (Johansen et al. 1989).

It has been observed that the relatively highly productive *Artemisia-Festuca* grasslands in the Kluane Lake region are confined to those soils in areas which receive loess generated from the outwash plains of the Slims and Donjek rivers (Johansen et al. 1989). The areas not receiving loess are dominated by plant communities with lower forage production.

This thesis employs techniques, outlined in chapter 5, to investigate the soil and vegetation of the study area, with the aim of quantifying any correlation which may exist between loess deposition and forage productivity. The results are presented and discussed in chapter 6, and conclusions put forward in chapter 7.

CHAPTER 5 : DATA COLLECTION

This chapter describes the nature of the field and laboratory procedures utilised to quantify the soil properties, and the productivity and nutrient status of the Kluane Lake grassland ecosystem.

5.1 *Sample plot location*

Data collection was undertaken upon the southern shores of Kluane Lake. Fifteen sites were identified around the lake and at each site two sample plots were chosen to produce a data set comprising thirty plots (Figure 5.1). The essential characteristics of a "sample site" were that it: (1) faced south; (2) sloped gently (i.e. <30 degrees inclination); (3) supported the *Artemisia-Festuca* grassland community (cf. Johansen et al. 1989); and (4) had areal dimensions >10 m by 10 m. Figure 5.2 illustrates a typical site.

Accessibility was an additional consideration in the location of sample sites. Twenty of the thirty sample plots were located at approximately 4 km intervals close to a little-used bush road skirting the southeast shore of Kluane Lake between Silver City, (Mile 1053, Alaska Highway) and Cultus Bay. The remaining ten sample plots were located on the southwest shore of the lake, close to the Alaska

Figure 5.1 Map showing location of sample plots around Kluane Lake.

• Location of plots by number

Figure 5.2 Photograph illustrating a typical grassland site in the Kluane Lake region.

CHAPTER 6: RESULTS AND DISCUSSION

This chapter approaches the field and laboratory data from two perspectives. First it considers the "loessal hypothesis" and deals with the premises (6.1) and then it considers the statistical significance (6.2) of the data. The potential relevance of the data to both past and present ecosystems is discussed in chapter 7.

The results comprise a discussion of soil profiles, properties and productivity of the Brunisolic/Regosolic Static Cryosols in the Kluane Lake Region. A typical soil profile (Figures 4.5 and 4.6) comprises an A horizon of Neoglacial loess over a Bm horizon (Slims Soil) developed in Kluane loess (BC horizon) on top of glacial drift (IICca horizon). The following discussion concerns properties of the A horizon which are associated with the productivity of the grasslands.

6.1 *Loessal Hypothesis: Premises*

The "loessal hypothesis" proposes that the active deposition of Neoglacial loess is key to maintaining highly-productive soils of the Kluane Lake region. Quantitative data pertain to three aspects of this hypothesis: (1) the nature, origin and deposition of the Neoglacial loess (A horizon); (2) the nutrient status of the Neoglacial loess;

Highway (see Figure 5.1).

A primary objective underlying the choice of sample site location was to enable data collection along a gradient of active Neoglacial loess deposition. Denton and Stuiver (1966) note that the thickness of Neoglacial loess in Shakwak Trench decreases both east and northwest from the Slims River delta. Data collection for this thesis was based upon the pretext that quantities of active loess deposition decreased with increasing distance from the Slims River delta. This pretext delineated the areal extent of the study area, limiting it to the shoreline of the lake receiving Slims River loess, as opposed to the shoreline further north receiving loess from the Donjek River valley.

At each sample plot a number of procedures were implemented to obtain both soil and vegetation data. The following section considers each set of procedures in turn.

5.2 *Field procedures*

Standard field procedures were implemented, following field sheets, according to the instruction of C.A.S. Smith, Agriculture Canada.

5.2.1 Soil

i) Site properties were recorded for each plot. The slope and aspect of each plot were obtained using a

clinometer/Brunton compass. The sample plot position on the slope and the microtopography of the plot were also noted.

ii) Field properties

At each sample plot a full soil profile description was completed using standard field description documents for Canada Soil Information System (ACECSS 1987) from the Centre of Land and Biological Resources Research, of Agriculture and Agri-food Canada

Data collection involved digging a pit of approximately 0.5 m by 0.5 m, from the ground-surface into the underlying material to at least 20 cm below the Kluane loess. The face of the cut was cleaned as carefully as possible to avoid mixing of the units. The following data were recorded at each pit:

1. Profile depth
2. Individual horizon depth (including maximum and minimum range)
3. Horizon texture
4. Horizon colour
5. Horizon boundary (distinctness and form)
6. Calcium carbonate content (according to HCl effervescence)
7. Root description (abundance and size)

iii) Soil samples were taken from the centre of each soil horizon. Care was taken to avoid admixture of the sedimentary horizon units. The sample was then placed in a plastic bag and labelled according to the location and depth of the sample.

5.2.2 Vegetation

i) Species diversity

A 10 m by 10 m macroplot with 10 randomly selected 0.5 m by 0.5 m microplots was used to record the foliar cover of forbs and graminoids. The microplots were located at 2 m intervals along two 10 m transects normal to the basal axis of the macroplot. The starting point for each transect was at either 2 m, 5 m and/or 7 m along the basal axis. A booking sheet was used to record the identity and percentage cover of the plants found in each microplot.

ii) Forage productivity

Within each 10 m by 10 m macroplot two 1 m by 1 m quadrats were randomly chosen, and the live vegetation (forbs and graminoids) clipped at the base of their stems and collected in sample bags. The exact location of the quadrats was established by projecting the metre rule in a random direction within the macroplot.

5.3 *Laboratory procedures*

5.3.1 Soil

i) Particle-size analysis

Particle-size analysis is a measurement of the size distribution of individual particles in a soil sample. The major features of particle size analysis are the destruction or dispersion of soil aggregates into discrete units by chemical, mechanical, or ultrasonic means and the separation of particles according to size limits by sieving for sand-size material, and sedimentation using the pipette method to sample various fractions of the fine-grained sediments (Sheldrick 1984). Ultrasonic techniques were the primary method of dispersion in the present study.

ii) Organic matter content: loss on ignition

The loss in weight resulting from igniting a soil in contact with air includes that due to combined water in soil colloids, to combustion of organic matter and to decomposition of carbonates. The temperature recommended for determining loss on ignition varies depending upon the information desired. In this case, soil samples were heated to 350°C for eight hours as recommended by J.K. Torrance, Carleton University.

iii) pH.

Soil pH was measured to one decimal place in 0.01 M CaCl_2 using a pH meter (Sheldrick 1984).

iv) Carbon and nitrogen content

A LECO instrument was employed by the Centre of Land and Biological Resources Research of Agriculture Canada to determine the percentages of total carbon and total nitrogen content.

5.3.2 Vegetation

i) Species diversity

The species of the various plants within the microplots were identified, using appropriate reference texts, namely Posilyd and Cody (1980); Trelawny (1988) and Pratt (1991). Species frequency and mean percentage cover are recorded in the appendix).

ii) Forage productivity

The air-dried vegetation samples collected from each quadrat were weighed. The mean mass of the two samples from each site was recorded (g/m^2).

5.4 *Statistical procedures*

Two primary statistical measures exist to discern the

strength, direction and significance of a linear relation between two variables. They are: (1) the Pearson's product-moment correlation coefficient and (2) the Spearman rank correlation coefficient. The Pearson's correlation coefficient is a parametric measure of the relation between two variables on an **interval** scale. The technique assumes that both variables have come from normally distributed populations. The Spearman rank correlation coefficient is a nonparametric measure of the relation between two sets of **ordinal** (ranked) values, not necessarily normally distributed. The data for this thesis fit the criteria only for the Spearman rank correlation coefficient.

Spearman rank correlation coefficients measure the direction and degree of association between two variables using values between -1.0 and 1.0. A value of -1.0 indicates a perfect inverse relation or negative correlation between two variables and a value of 1.0 indicates a perfect direct relation or positive correlation. A complete absence of relation or no correlation is indicated by a coefficient of 0.0 (Ebdon 1985). Spearman rank coefficients also test the significance of a correlation in estimating how probable it is that an observed correlation between two variables represents an extant correlation in the population from which the samples were taken (Ebdon 1985).

This statistical technique was employed to determine the extent to which biomass and species diversity of the

Artemisia-Festuca grasslands is associated with: (a) the addition of loess to the grassland environment; and (b) the properties of the loess/soil in the grassland environment. The results are presented in the next chapter.

CHAPTER 6: RESULTS AND DISCUSSION

This chapter approaches the field and laboratory data from two perspectives. First it considers the "loessal hypothesis" and deals with the premises (6.1) and then it considers the statistical significance (6.2) of the data. The potential relevance of the data to both past and present ecosystems is discussed in chapter 7.

The results comprise a discussion of soil profiles, properties and productivity of the Brunisolic/Regosolic Static Cryosols in the Kluane Lake Region. A typical soil profile (Figures 4.5 and 4.6) comprises an A horizon of Neoglacial loess over a Bm horizon (Slims Soil) developed in Kluane loess (BC horizon) on top of glacial drift (IICca horizon). The following discussion concerns properties of the A horizon which are associated with the productivity of the grasslands.

6.1 *Loessal Hypothesis: Premises*

The "loessal hypothesis" proposes that the active deposition of Neoglacial loess is key to maintaining highly-productive soils of the Kluane Lake region. Quantitative data pertain to three aspects of this hypothesis: (1) the nature, origin and deposition of the Neoglacial loess (A horizon); (2) the nutrient status of the Neoglacial loess;

and (3) the resulting vegetative productivity of the grasslands developed on the loessal sites.

6.1.1 Neoglacial loess

Clarification of three points concerning the Neoglacial loess horizon is necessary. The first deals with the horizon depth and the particle-size distribution of the Neoglacial loess. The second identifies two layers within the Neoglacial loess horizon: an "active loess" layer (ACK horizon) and a "humified loess" layer (Ahk horizon). The third examines the proposition that the amount of loess deposition decreases with increasing distance from the Slims River delta and it constitutes evidence discerning the origin of the silt-sized particles. This third point is critical in validating the study area as a "modified analogue" of the productive "hot spots" in the Beringian Duvanny Yar ecosystem.

a) Properties of Neoglacial loess

Two soil factors examined in this thesis are horizon depth and texture. Horizon depth is controlled in the environment by addition and removal of material to and from the profile. At the sites sampled near Kluane Lake, there was no consistent variation in horizon depth with any of the factors measured, including distance from the Slims River delta. It is, in fact, likely that the slope steepness (between 0 and 30 degrees inclination) of the grassland

sites determines the balance between the input and output of Neoglacial loess within the soil profiles of the Kluane Lake region. Long term studies of Neoglacial loess accumulation and mass budget, however, were not possible in the scope of this work, but are suggested important further research topics (see chapter 7).

The texture was determined using the pipette method (section 5.2.1) and the following grain-size fractions were established according to the Canadian System of Soil Classification (1987) for pedological investigations:

47 μ m	<sand<	2mm
20 μ m	<coarse silt<	47 μ m
5 μ m	<medium silt<	20 μ m
2 μ m	<fine silt<	5 μ m
	clay<	2 μ m

At this juncture it is important to note these grain-size boundaries. From here on the thesis employs the terminology: sand; coarse, medium, fine silt; and clay to describe the grain-size distribution and no further reference is made to the diameter of the soil particles.

The texture of the Neoglacial loess (A horizon) is similar to that of the Kluane loess (BC horizon) - see Table 6.1. The A horizon, however, contains more sand, which may have been blown in from the shores of Kluane Lake. The BC horizon, on the other hand, has a higher clay content. This is likely to be due to the process of clay illuviation, operating over time in the soil profile, resulting in the

Table 6.1 Summary properties of soil horizons averaged over study area.

HORIZON	TOTAL CARBON (%)	TOTAL NITROGEN (%)	ORGANIC MATTER (%)	SAND (%)	SILT (%)	CLAY (%)
ACk	2.86	0.17	5.54	37.4	53.99	1.94
Ahk	3.81	0.23	7.03	50.31	47.33	2.34
Bm	1.77	0.13	4.53	41.33	53.57	5.12
BC			4.45	40.36	54.08	5.56
IICca			3.83	63.47	33.17	3.36

HORIZONS: A = Neoglacial loess (n = 30)

(combination of ACk and Ahk horizons)

ACk = Active Neoglacial loess (n = 15)

Ahk = Humified Neoglacial loess (n = 15)

Bm = Slims soil

BC = Kluane loess

IICca = Kluane drift

accumulation of clay-sized material in the lower horizons (Buol et al. 1980).

b) Active and humified layers

The mineralogy of the Neoglacial loess is quartz-chlorite or quartz-calcite (Nickling 1972). The horizon can be subdivided into two layers: an "active Neoglacial loess" (ACK) layer and a "humified Neoglacial loess" (Ahk) layer (Figure 6.1). It is assumed that the entire study area is actively receiving windblown silt, but the presence of a distinguishable ACK horizon at 15 of the sites (see Figure 6.2) implies a net accumulation of active loess. The Ahk layer represents loess which has been stable in the profile for a sufficiently long time period to accumulate organic matter and thus become humified.

Summary properties of the soil horizons averaged over the study area are presented in Table 6.1. In general the ACK and Ahk horizons differ both in texture and in nutrient status. The ACK horizon has the highest percentage silt content and the lowest percentage sand content of all the horizons. The Ahk horizon appears to be the source of nutrients within the A horizon and has higher available percentage carbon, nitrogen and organic matter contents than the ACK horizon. The two horizons are similar in pH between 6 and 8 and in colour, ranging from 2.5 Y 3,2 to 10 YR 3,2. Both horizons produce an effervescence in the presence of

Figure 6.1 Photograph of soil profile in Kluane Lake region depicting ACK and Ahk horizons.

Figure 6.2 Spatial distribution of plots "WITH ACK" and "WITHOUT ACK" horizons around Kluane Lake.

- ⊙ Plot with a distinguishable ACK horizon
- Plot without a distinguishable ACK horizon

hydrochloric acid, a reaction which indicates carbonate content. This explains the suffix "k" in the labeling of the horizons. In general, the reaction is strongest in the ACK horizon.

c) Source of Neoglacial loess

The research design (section 5.1) for this thesis is based on two pretexts: (1) that the source of the Neoglacial loess is exclusively from the Slims River delta; and (2) that during transport, larger and heavier loess particles are deposited before finer and lighter loess particles. Given these pretexts, it follows that Neoglacial loess at sites further from the loess source will comprise fewer large-grained particles than sites closer to the loess source. The silt-sized grain fraction data from the Kluane Lake region (Table 6.2: initial data set) support this assertion as the proportion of silt in the A horizon decreases with distance from the Slims River delta ($r_s = -0.72$; Figure 6.3). It is puzzling, however, that the percentage sand composition of the A horizons increases with distance from the Slims River delta ($r_s = 0.65$). This result suggests that the source of the sand-sized particles in the A horizon is not the Slims River delta.

The Slims River delta is comprised of both fine sand and silt particles (Nickling 1978), however the sand component tends to move by saltation, rather than deflation, (P.G. Johnson, personal communication 1994). Only the silt

Table 6.2 Initial and recalculated correlation

coefficients demonstrating the variation in soil texture with distance from the Slims River delta (shading implies a significant correlation at the one-tailed 95% confidence level).

HORIZON	GRAINSIZE (%)	SOIL TEXTURE	
		INITIAL DATA SET	RECALCULATED
A	sand	0.65	0.00
	total silt	-0.72	-0.30
	coarse silt	-0.69	0.12
	medium silt	-0.66	-0.10
	fine silt	0.21	0.40
	clay	-0.22	0.30
Ahk	sand	0.68	0.00
	total silt	-0.70	-0.32
	coarse silt	-0.39	0.09
	medium silt	-0.67	-0.15
	fine silt	-0.64	0.14
	clay	-0.37	0.26
ACk	sand	0.66	0.00
	total silt	-0.43	0.09
	coarse silt	-0.32	0.25
	medium silt	-0.34	-0.15
	fine silt	-0.56	0.38
	clay	0.00	0.25

Figure 6.3 Neoglacial loess (A): Scattergraph of percentage silt and distance from the Slims.

-size component is brought into suspension by the wind (Nickling 1978) and deposited as Neoglacial loess on the surrounding grasslands. The paradoxical silt and sand compositions of the A horizons suggest that the grasslands receive inputs of sand-sized sediment from sources other than the Slims River delta, perhaps the shores of Kluane Lake.

In order to identify the source of the Neoglacial loess as the Slims River delta, it was necessary to focus specifically upon the silt-size grain fraction of the A horizons. To achieve this focus, the particle-size distributions were recalculated without the sand-sized fraction (Table 6.2: recalculated data set). This recalculation and recorrelation process elucidated values which support the pretext of an overall decrease in the percentage silt fraction ($r_s = -0.30$) with distance from the Slims River delta. A significant increase in the finest silt size fraction (fine silt: $r_s = 0.41$) with distance from the Slims River delta was also noted. These results, together with mineralogical studies (Nickling 1978), support the hypothesis that the Slims River delta is the source of loess in the study area. Hopkins (1982) proposes that the Duvanny Yar environment was characterised by intense aeolian activity and that various localities within Beringia recieved inputs of loess emanating from glaciofluvial outwash. The silt-sized grain fraction data presented here

strengthen the argument that the grassland ecosystems of the Kluane Lake region are analogous to the loessal environments of Duvanny Yar Beringia.

6.1.2 Nutrient status of Neoglacial loess

Organic matter is the source of a large number of essential plant nutrients. These nutrients include Ca^{2+} , K^+ , Na^+ and Mg^{2+} and are released during the oxidation process when organic matter decays to form humus.

Carbon makes up a large proportion of organic matter and thus close relationships exist between percentage organic matter and percentage carbon content of soils. A fairly close ratio also exists between percentage carbon and nitrogen content (Brady 1990), and Brady (1990) attests that the amount of organic matter and carbon that can be maintained in a soil is largely dependent on the amount of nitrogen present. These relations are exemplified at Kluane Lake in all three horizons (the A; the AC; and the Ah). Table 6.3 illustrates the highly significant positive correlations that exist between carbon, nitrogen and organicmatter. As already mentioned, the "humified loess layer" (Ah) is the main source of the nutrients.

6.1.3 Vegetative productivity of grasslands

Biomass (gm^{-2}) and species diversity are factors

Table 6.3 Correlations between percentage nutrient content of Neoglacial loess horizons.

NUTRIENT CORRELATIONS	HORIZON		
	A	Ahk	ACk
Total carbon (%) v. total nitrogen (%)	0.88	0.80	0.81
Total carbon (%) v. organic matter (%)	0.91	0.94	0.88
Total nitrogen (%) v. organic matter (%)	0.86	0.73	0.81

Correlations between percentage available carbon, nitrogen and organic matter content in each horizon are statistically significant to the 95% confidence level.

applied to determine the forage productivity of the grassland sites. It is a widely-held belief that more diverse communities are associated with higher rates of primary production. Recent experimental data (e.g., Kareiva 1994; Naeem et al. 1994) support this conviction, as do the results from the Kluane Lake region where data show a highly significant correlation between biomass and species diversity in the A horizon as a whole ($r_s = 0.61$) (Figure 6.4) and at those sites with distinguishable ACK horizons ($r_s = 0.56$).

Section 6.1 has established three premises upon which the following discussion of results (6.2) is based. First it has shown the A horizon of soil profiles in the Kluane Lake region to be consistent with the hypothetical loess origin, the Slims River delta, because the grain-size distribution of the silt becomes finer with distance from the Slims. Second, it has demonstrated the close relationship between the percentage available carbon, nitrogen and organic matter contents, and it has shown these values to be highest in the humified loess layer. Third, it has established the link between biomass and species diversity and has thus shown these to be reliable statistical parameters in the prediction of grassland productivity.

Figure 6.4 Neoglacial loess (A horizon): Scatterplot for productivity variables.

6.2 Loessal Hypothesis: Results

A model of the Kluane Lake natural ecosystem (Figure 6.5) constitutes the framework for statistical analysis of the field and laboratory data. The model comprises independent and dependent variables and assumes three constants: aspect; slope; and elevation. There is one independent variable: distance from the Slims River delta; and three groups of dependent variables: soil components (texture and horizon depth); fertility components (available carbon, nitrogen and organic matter content); and vegetation components (biomass and species diversity). Analysis and discussion of data concerning the inter-relations of the environmental variables is presented in this section. At each juncture, the link between active loess deposition and the nutrient status and productivity of the grasslands is examined.

The data are discussed, first as a whole (30 plots), and then as two parts, comprising plots (15) with and plots (15) without net accumulations of active loess. The plots with net accumulations of loess have a distinguishable ACK horizon. Values are taken from the entire A horizon data set, thus plots "WITH ACK" horizons also have an Ahk horizon but plots "WITHOUT ACK" horizons only have an Ahk horizon.

Statistical correlations between variables are

Figure 6.5 Model of Kluane Lake natural ecosystem.

presented in graphs and tables. The critical values expressing the significance of a correlation at the one-tailed 95% confidence level vary between the data sets and the significant variables are thus illustrated by the shading in the tables.

6.2.1 Correlation of soil texture and nutrient status

There is a positive correlation between the percentage silt- and clay-sized particles and the nutrient status (percentage available carbon, nitrogen and organic matter contents) of the A, Ahk and ACK horizons, and a negative correlation between the sand-sized particles and the nutrient status of these horizons (Table 6.4). The highest significant positive correlation is between the percentage coarse silt grain-size fraction and the nutrient status of all three of the horizons. This correlation is mirrored at both sites with and at sites without distinguishable ACK layers. The percentage coarse silt grain-size fraction at sites without accumulations of active loess is significantly correlated with the available carbon ($r_s = 0.65$) as well as the available nitrogen ($r_s = 0.60$) and organic matter ($r_s = 0.70$) contents.

6.2.2 Correlation of soil texture and productivity

There is a statistically-significant positive correlation (Table 6.5) between (1) the percentage coarse

Table 6.4 Correlation coefficients between nutrient status
and soil texture.

HORIZON	SOIL TEXTURE	NUTRIENT STATUS		
	GRAINSIZE (%)	TOTAL CARBON (%)	TOTAL NITROGEN (%)	ORGANIC MATTER (%)
A	sand	-0.43	-0.34	-0.33
	total silt	0.28	0.22	0.12
	coarse silt	0.49	0.42	0.28
	medium silt	0.09	0.09	0.00
	fine silt	-0.16	-0.17	-0.19
	clay	0.26	0.19	0.22
Ahk	sand	-0.29	-0.16	-0.35
	total silt	0.33	0.21	0.25
	coarse silt	0.45	0.36	0.40
	medium silt	0.10	-0.05	0.00
	fine silt	-0.03	-0.12	-0.18
	clay	0.32	0.15	0.23
ACk	sand	-0.14	0.14	0.02
	total silt	0.30	0.22	0.02
	coarse silt	0.52	0.28	0.20
	medium silt	0.18	0.24	-0.06
	fine silt	0.15	0.20	0.03
	clay	0.00	-0.10	-0.25
WITH ACK	sand	-0.50	-0.35	-0.31
	total silt	0.22	0.08	0.02
	coarse silt	0.48	0.32	0.27
	medium silt	0.15	0.10	-0.06
	fine silt	0.21	0.08	0.13
	clay	0.45	0.25	0.37
WITHOUT ACK	sand	-0.39	-0.40	-0.48
	total silt	0.40	0.43	0.50
	coarse silt	0.65	0.60	0.70
	medium silt	0.09	0.12	0.22
	fine silt	-0.40	-0.23	-0.31
	clay	0.18	0.09	0.12

Table 6.5 Correlation coefficients between productivity and soil texture.

HORIZON	SOIL TEXTURE	PRODUCTIVITY	
	GRAINSIZE (%)	BIOMASS (g/m ²)	SPECIES DIV.
A	sand	-0.16	-0.14
	total silt	0.28	0.24
	coarse silt	0.20	0.12
	medium silt	0.03	-0.04
	fine silt	0.20	0.13
	clay	0.07	0.04
Ahk	sand	-0.18	-0.15
	total silt	0.27	0.13
	coarse silt	0.33	0.09
	medium silt	0.09	0.04
	fine silt	-0.15	0.14
	clay	0.25	0.16
ACk	sand	-0.26	0.07
	total silt	0.49	0.18
	coarse silt	0.51	0.25
	medium silt	0.17	-0.11
	fine silt	0.58	0.58
	clay	0.24	0.17
WITH ACK	sand	-0.33	0.19
	total silt	0.52	0.13
	coarse silt	0.47	0.07
	medium silt	0.08	-0.22
	fine silt	0.47	0.26
	clay	0.06	0.03
WITHOUT ACK	sand	-0.10	-0.32
	total silt	0.09	0.34
	coarse silt	0.07	0.23
	medium silt	-0.04	0.20
	fine silt	0.13	0.35
	clay	0.18	0.12

silt grain-size fraction in the humified (Ahk) loess horizon and the biomass of the associated grassland ($r_s = 0.33$), and (2) the total silt, and coarse and fine silt fractions of the active (ACK) loess horizon and the biomass of the grassland ($r_s = 0.49, 0.51$ and 0.58 respectively). The only statistically-significant correlation between species diversity and texture is in the percentage fine silt fraction of the active loess layer ($r_s = 0.58$).

At sites with distinguishable accumulations of active loess, there are statistically significant positive correlations between the percentage silt-sized fractions (total, coarse and fine silt) and the grassland biomass. Correlations are lower, however, between these same variables at sites without distinguishable accumulations of active loess layers.

6.2.3 Summaries of soil texture, nutrient status and productivity correlations

The results presented above indicate that the silt fraction of the A horizon is, statistically, positively correlated with nutrient status and productivity in the grasslands of the Kluare Lake region. The most noteworthy significant correlations are between the silt-sized fraction and (1) the nutrient status of the humified loess (Ahk) and the percentage silt-size fraction of the humified loess, and (2) the productivity of the active loess (ACK horizon) and

the percentage silt-size fraction of the active loess. The presence of active loess accumulation is more strongly associated with increases in the *productivity* (biomass) than with increases in the *nutrient status* of the sites.

The focus upon carbon, nitrogen and organic matter as representative of the nutrient status of the loess, however, may be misleading. The ACK horizon is positively correlated with productivity which suggests that it must contain some degree of nutrient status. In most plant species, growth is limited by three major plant nutrients, potassium, phosphate and fixed nitrogen. Zeller et al. (1988) maintain that glacial margin environments are enriched in both potassium and phosphate, especially in areas where the glaciers have overridden igneous and metamorphic terranes. Mechanical grinding processes along the ice-rock interface beneath the glacier result in chemical bond breakage making these nutrients available for plant uptake (Zeller et al. 1988).

It is thus possible that the ACK horizon might be rich in significant essential nutrients which are readily available to plants without having to undergo the time-dependent pedogenic process of humification (see section 6.2.4).

The silt-size fraction of the A horizon is Neoglacial loess which emanates from the Slims River delta (section 6.1c). It is deposited in largest quantities at sites closest to its source and in smallest quantities at sites

furthest away (section 6.1.1.c). The following sections, (6.2.4 and 6.2.5), employ the variable "distance from the Slims River delta" to investigate whether the quantity of Neoglacial loess input affects the nutrient status and productivity of the grasslands.

6.2.4 Correlation of distance from the Slims River delta and nutrient status

There is a negative correlation between distance from the Slims and nutrient status of the A and Ahk horizons (Table 6.6). This correlation is statistically significant for carbon and organic matter in the Ahk horizon ($r_s = -0.44$ for both variables; Figure 6.6), and at those sites without accumulations of active loess ($r_s = -0.71$ and -0.82 respectively). The correlations between distance from the Slims and percentage total nitrogen content are negligible, as is the correlation between distance from the Slims and nutrient status of the ACK horizon. It has already been observed (section 6.1.2) that the ACK horizon is less rich in nutrients of carbon, nitrogen and organic matter than the Ahk horizon (see Table 6.1). This is possibly because the active loess (ACK) input to the grassland sites has occurred so recently that the nutrient fixing pedogenic process of humification has not yet acted upon the loess.

Table 6.6 Correlations coefficients between distance from the Slims River delta and nutrient status.

NUTRIENT STATUS	HORIZON	DISTANCE FROM SLIMS (km)
TOTAL CARBON (%)	A	-0.30
	Ahk	-0.44
	ACK	-0.01
	WITH ACK	-0.02
	WITHOUT ACK	-0.71
TOTAL NITROGEN (%)	A	-0.18
	Ahk	-0.18
	ACK	0.21
	WITH AC k	0.09
	WITHOUTACK	-0.56
ORGANIC MATTER (%)	A	-0.22
	Ahk	-0.44
	ACK	0.13
	WITH ACK	0.11
	WITHOUT ACK	-0.82

Figure 6.6 Humified loess (Ahk horizon): Scatterplot of total carbon content and distance from the Slims River delta.

6.2.5 Correlations of distance from the Slims River delta and productivity

The correlations between distance from the Slims and total productivity (biomass and species diversity), though negative (Table 6.7), are very low and below statistical significance at the 95% confidence level.

Biomass appears to decrease and species diversity increase with distance from the Slims at those sites with distinguishable accumulations of active loess. The converse is true for those sites without accumulations of active loess. The statistics, however, are not significant at the 95% confidence level.

6.2.6 Summaries of distance from the Slims River delta, nutrient status and productivity correlations

In general the nutrient status of the A and Ahk horizons of sites furthest from the Slims is lower than the nutrient status of the same horizons at sites closer to the Slims. The absence of active loess (ACK) accumulation in profiles further from the Slims is associated with lower levels of nutrient status than at sites closer to the Slims. Overall, however, the ACK horizon has no gradient in nutrient status with distance from the Slims River delta.

The productivity of the three horizons, in contrast, is not statistically-significantly correlated with distance from the Slims River delta. This observation prompts an

Table 6.7 Correlations coefficients between distance from the Slims River delta and productivity.

PRODUCTIVITY	HORIZON	DISTANCE FROM SLIMS (km)
BIOMASS (g/m ²)	A	-0.08
	Ahk	-0.08
	ACK	-0.15
	WITH ACK	-0.24
	WITHOUT ACK	0.33
SPECIES DIVERSITY	A	-0.07
	Ahk	-0.07
	ACK	0.24
	WITH ACK	0.18
	WITHOUT ACK	-0.10

examination of the relation between soil nutrient status and productivity in the study area.

6.2.7 Correlations of nutrient status and productivity

There are positive, though not statistically-significant, correlations between nutrient status (carbon, nitrogen and organic matter) and productivity (biomass and species diversity) in all three horizons (Table 6.8). There is, however, a significant correlation between the percentage total carbon in the Ahk horizon and plot biomass ($r_s = 0.34$).

Productivity is more highly (though not significantly) correlated with percentage available carbon content of profiles containing distinguishable accumulations of active loess than in profiles without these accumulations. The converse is true for nitrogen, and the difference is negligible for the organic matter content.

6.2.8 Data from the east side of Kluane Lake

This final section of results looks specifically at the twenty sites located on the east-side of the lake (Figure 6.2). Special consideration is given to these sites as they appear to be more consistently representative of the Duvanny Yar grassland ecosystem than the western side of the lake which, aside from small grassland patches, largely comprises forested spruce.

Table 6.8 Correlation coefficients between nutrient status and productivity.

NUTRIENT STATUS	HORIZON	PRODUCTIVITY	
		BIOMASS (g/m ²)	SPECIES DIV.
TOTAL CARBON (%)	A	0.3	0.17
	Ahk	0.34	0.23
	ACK	0.36	0.05
	WITH ACK	0.34	0.12
	WITHOUT ACK	0.17	0.1
TOTAL NITROGEN (%)	A	0.25	0.11
	Ahk	0.22	0.21
	ACK	0.1	-0.33
	WITH ACK	0.11	-0.13
	WITHOUT ACK	0.37	0.32
TOTAL ORGANIC MATTER (%)	A	0.22	0.17
	Ahk	0.03	-0.03
	ACK	0.13	-0.03
	WITH ACK	0.28	0.04
	WITHOUT ACK	0.03	0.12

The statistically significant positive correlations between grassland nutrient status and productivity, and the silt-size component of the A and Ahk horizons is shown in Table 6.9. The statistically-significant decrease in nutrient status of the A and Ahk horizons with distance from the Slims, and the decrease in biomass are shown in Table 6.10. An anomalous statistic is the statistically significant correlation between the distance from the Slims and the biomass supported by soils with an ACK horizon ($r_s = -0.96$). This is unexpected since the correlation coefficient of this aspect of the entire data set is not significant (although of the same sign, see Table 6.7). This contrasting result lends support to the hypothesis that soil productivity is linked to total quantity of Neoglacial loess input (Figure 6.7). The positive correlation between nutrient status and productivity is demonstrated in Table 6.11, however there is a high negative statistically-significant correlation ($r_s = -0.69$) between the percentage total nitrogen content in the ACK horizon and the species diversity of the grasslands. The significance of this statistic, however, is not clear at the present time.

In terms of paleoenvironmental reconstruction, however, both the entire data set and the data pertaining specifically to the east side of the lake, support the concept of productivity "hot spots" existing within Duvanny Yar Beringia and constitute quantitative evidence in support

Table 6.9 East side of Kluane Lake: Correlation coefficients between soil texture and nutrient status.

HORIZON	SOIL TEXTURE (%)	NUTRIENT STATUS			PRODUC TIVITY	
		TOTAL CARBON (%)	TOTAL NITROGEN (%)	ORGANIC MATTER (%)	BIOMASS (g/m ²)	SPECIES DIV.
A	sand	-0.43	-0.37	-0.52	-0.24	-0.18
	total silt	0.94	0.26	0.34	0.25	0.36
	coarse silt	0.55	0.50	0.53	0.25	0.15
	medium silt	0.35	0.24	0.33	0.21	0.19
	fine silt	0.03	-0.04	-0.08	0.21	0.40
	clay	0.22	0.22	0.30	0.19	0.00
Ahk	sand	-0.61	-0.55	-0.46	-0.27	-0.17
	total silt	0.61	0.48	0.63	0.25	0.20
	coarse silt	0.74	0.63	0.75	0.31	0.16
	medium silt	0.54	0.36	0.59	0.29	0.22
	fine silt	0.15	0.10	0.21	0.20	0.31
	clay	0.27	0.23	0.30	0.32	0.12
ACK	sand	-0.43	-0.37	-0.37	-0.54	0.17
	total silt	0.47	0.37	0.37	0.54	-0.11
	coarse silt	0.66	0.60	6.00	0.43	-0.23
	medium silt	0.37	0.26	0.26	0.66	0.17
	fine silt	0.26	0.09	0.09	0.21	0.51
	clay	0.60	0.49	0.49	0.54	0.06

Table 6.10 East side of Kluane Lake: Correlation coefficients between distance from the Slims River delta and nutrient status and productivity.

NUTRIENT STATUS	HORIZON	DISTANCE FROM SLIMS (km)
TOTAL CARBON (%)	A	-0.45
	Ahk	-0.67
	ACK	-0.27
TOTAL NITROGEN (%)	A	-0.27
	Ahk	-0.40
	ACK	0.07
ORGANIC MATTER (%)	A	-0.54
	Ahk	-0.48
	ACK	0.01
BIOMASS (g/m ²)	A	-0.17
	Ahk	-0.14
	ACK	-0.98
SPECIES DIVERSITY	A	-0.20
	Ahk	-0.17
	ACK	-0.31

Figure 6.7 East side of Kluane Lake: Scatterplot of biomass and distance from the Slims River delta.

Table 6.11 East side of Kluane Lake: Correlation
coefficients between nutrient status and productivity.

NUTRIENT STATUS	HORIZON	PRODUCTIVITY	
		BIOMASS (g/m ²)	SPECIES DIV.
TOTAL CARBON (%)	A	0.43	0.08
	Ahk	0.46	0.16
	ACk	0.20	-0.46
TOTAL NITROGEN (%)	A	0.31	0.04
	Ahk	0.28	0.12
	ACk	-0.10	-0.69
ORGANIC MATTER (%)	A	0.28	-0.03
	Ahk	0.42	0.19
	ACk	-0.09	-0.66

of Schweger's "loessal hypothesis".

CHAPTER 7: CONCLUSIONS

The potential relevance of the data presented in the previous chapter, to both past and present ecosystems is considered in this chapter. Emphasis is placed upon the reconstruction of productivity "hot spots" in Duvanny Yar Beringia (7.1); brief consideration is given to the management of rangeland ecosystems in the Yukon today (7.2); and avenues for further research are proposed (7.3).

7.1 Paleoenvironmental reconstruction

The reconstruction of the Duvanny Yar ecosystems, in this thesis, relies upon the principle of uniformitarianism which involves extending observations about processes within the present ecosystem backwards in time, thereby using the present to model the past. The Kluane Lake region, as a "modified analogue" of a productive "hot spot" in Duvanny Yar Beringia, constitutes the study area for testing Schweger's (1992) hypothesis that the deposition of loess was the key variable in maintaining these highly productive areas. The following conclusions summarise quantitative evidence, presented in chapter 6, which support Schweger's "loessal hypothesis".

First, the statistical significance of the deposition of finer grained material at increasing distances from the

Slims ($r_s = -0.3$) shows that loess originating from the Slims River delta is an important edaphic factor within the ecosystem.

Second, various criteria indicate that the receipt of loess by the grasslands increases their productivity. These criteria include (1) the statistically significant positive correlations between the total silt and coarse and fine silt fractions of the active (ACK) loess horizon and the biomass of the grassland ($r_s = 0.49, 0.51$ and 0.56 respectively); (2) the statistically significant correlations between total silt, coarse and fine silt, at those sites which have distinguishable accumulations of loess and the biomass of the associated grasslands ($r_s = 0.52, 0.47$ and 0.47 respectively), in comparison to those at sites without distinguishable accumulations of loess ($r_s = 0.09, 0.07$ and 0.13 respectively); and (3) the statistically significant negative correlation between distance from the Slims and biomass supported by soils with an ACK horizon on the east side of Kluane Lake ($r_s = -0.96$).

Third, it is worth noting that the receipt of loess by the entire Kluane Lake region makes it significantly more productive than surrounding regions (Johansen et al. 1989). Its standing crop, for example, is almost five times that cited for tundra environments and its forage productivity comes close to that calculated for the Alberta prairie (Geist 1978) more than 1,600 km to the south and east. The

point is that the Duvanny Yar "hot spots", as represented by the ecosystems in the Kluane Lake region, may have been far more productive than the surrounding tundra areas, at comparable latitudes and altitudes experiencing similar climatic conditions, and that these "hot spots" were capable of supporting a complex trophic structure of large mammals.

7.2 Contemporary rangeland management

Additional to its significance for interpretation of the late Plesitocene environment, this thesis is relevant in the context of the development of rangeland management strategies in southwest Yukon Territory for present day ecosystems. The soil survey information, the nutrient and productivity statistics and the species list (see appendix) may be used for estimating the magnitude of the grazing resource for contemporary regional planning purposes.

7.3 Opportunities for further research

The current study has demonstrated the use of modern environmental analogues as indicators of paleoenvironmental conditions. The quantitative data presented here support the thesis that inputs of windblown silt (loess) to grassland environments are directly associated with increases in nutrient status and productivity of grassland soils. This

conclusion applies both to contemporary environmental conditions and to conditions during the Duvanny Yar interval. It lends support to the hypothetical existence of loess-maintained productivity hot spots, theoretically capable of supporting Beringian mammoth fauna. In this way the thesis contributes to the academic search for a resolution to the full-glacial "production paradox".

Further research is proposed into several aspects of this thesis. First, the replication of the field and laboratory procedures employed in this thesis, within other analogous environments, would establish the validity of the current results.

Second, a more comprehensive investigation of the nutrient status of the loess is proposed, considering the presence of nutrients additional to those quantified in this research. Investigation of loessal potassium and phosphate content, for example might better quantify the link between loess deposition and the "fertility" of the grasslands.

Third, the mass budget of the Neoglacial loess profile in the Kluane Lake region could be considered in more detail. Strategically positioned loess traps around the edge of the lake, for example, would more accurately quantify the extent of active loess receipt by grassland environments than was possible within the scope of this work. In addition, the implementation of identical field procedures at paired grassland sites, one group of sites receiving

controlled artificial applications of loess, and another group of sites, in the same environment, not receiving additional loess inputs is proposed. This would allow more precise quantification of loess input to the grasslands and enable more meaningful statistical inferences to be drawn between the edaphic and vegetative components of the ecosystem.

A final contribution to the current research would involve an extensive Beringian-wide search for the location of the productivity "hot spots". It is possible, for example, that arctic grasslands, identified by C.A.S. Smith (personal communication 1994) in northeast Siberia, might yield further information about Duvanny Yar Beringia. These grasslands, along the East Siberian Sea near the mouth of the Kolyma River, were observed to comprise tussockless tundra which was only slightly hummocky, dominated by grasses and small sedges, but underlain by permafrost at about 50 cm. The annual precipitation for this region is about 150 to 175 mm/year, indicating a very arid climate. The soils have been correlated with those of a paleosol, discovered on the Seward Peninsula, thought to date from full-glacial Beringia, but not yet documented in the literature.

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APPENDIX

List of observed vegetation species

SPECIES	FREQUENCY (no. of plots out of 30)	MEAN % cover at plots where spp. recorded
Common Yarrow <i>Achillea millefolium</i>	5	4
Monkswood <i>Aconitum delphinifolium</i>	1	0.2
Wheat Grass <i>Agropyron sibircum</i>	5	6
<i>Agropyron alaskanum</i>	9	25
Cut-leaf Anemone <i>Anemone multifida</i>	24	12
Narcissus-flowered Anemone <i>Anemone narcissiflora</i>	1	40
Few-flowered Anemone/Windflower <i>Anemone parviflora</i>	1	0.4
Pink Pussytoes/Pink Everlasting <i>Antennaria rosea</i>	1	7
Holboell's Rockcress <i>Arabis holboelli</i>	4	2.5
Kinnikinnick <i>Arctostaphylos uva-ursi</i>	17	60
Alpine Arnica <i>Arnica angustifolia</i>	1	1
Prairie Sagebrush/Frigid Wormwood <i>Artemisia frigida</i>	20	29
Aster <i>Aster</i> spp.	9	3
Milk Vetch <i>Astragalus</i> spp.	3	5
Brome-Grass <i>Bromus ciliatus/Pumpellianus</i>	5	2

Reed Bentgrass		
<i>Calamagrostis canadensis</i>	1	20
<i>Calamagrostis purpurascens</i>	19	12
Paintbrush		
<i>Castilleja</i> spp.	5	3
Sedge		
<i>Carex</i> spp.	22	25
Cnidium Cnidiifolium		
<i>Cnidium cnidiifolium</i>	1	0.2
Northern Comandra		
<i>Geocaulon lividum</i>	2	5
Fleabane		
<i>Erigeron</i> spp.	15	4
Willow Herb		
<i>Epilobium</i> spp.	1	0.2
Fescue		
<i>Festuca ovina</i>	4	11
Northern Bedstraw		
<i>Galium boreale</i>	12	1.5
Wild Sweet Pea/Eskimo Potato		
<i>Hedysarum</i> spp.	2	1
Wild Blue Flax		
<i>Linum perenne</i>	7	4
Northern Oxytrope		
<i>Oxytropis campestris</i>	25	6
Showy Locoweed		
<i>Oxytropis splendens</i>	5	11
Yukon Beardtongue		
<i>Penstemon gormanii</i>	10	12
Cinquefoil		
<i>Potentilla</i> spp.	2	2.5
Pasque Flower/Spring Crocus		
<i>Pulsatilla patens</i>	4	15
Prickly Rose		
<i>Rosa acicularis</i>	9	7

Yellow saxifrage <i>Saxifragia</i> spp.	3	1.5
Canada Goldenrod <i>Solidago canadensis</i>	17	8
American Vetchling <i>Vicia americana</i>	5	3
Moss	20	26
Bareground	30	33
Litter	17	15
Lichen	14	26

END

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