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THE FLORISTICS AND COMMUNITY ECOLOGY OF EXTRAZONAL STEPPE IN THE YUKON AND KOLYMA RIVER DRAINAGES

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THE FLORISTICS AND COMMUNITY ECOLOGY OF EXTRAZONAL STEPPE IN THE YUKON AND KOLYMA RIVER DRAINAGES

A

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By

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ABSTRACT

I studied the ecological controls over the composition of extrazonal steppe vegetation on bluffs in the Yukon and Kolyma river watersheds. I also investigated the biogeographic factors that caused differences in species richness among bluffs in four watersheds in Alaska and the Yukon Territory. An index of solar radiation (equivalent latitude) and elevation were the primary controls over the structure and composition of steppe vegetation. Steppe in topographic positions with cool microclimates contained more species than did steppe in warmer facies, although dominant species occurred over a wide gradient in microclimate. Species richness of a bluff was a function of the habitat heterogeneity found there. Tall bluffs contained a greater variety of microclimatic and edaphic conditions and more species than ones with limited elevational extent. The flora of Yukon River bluffs is particularly rich because of the landscape diversity of the area.

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CHAPTER ONE

RELATIONSHIPS BETWEEN TOPOGRAPHY, SOIL, AND EXTRAZONAL STEPPE VEGETATION IN SUBARCTIC ASIA AND NORTH AMERICA

I. INTRODUCTION

Islands of grassy, treeless vegetation occur in isolated areas across interior regions of the boreal zone of the Russian Far-East and Alaska. These subarctic steppe sites are restricted to localities where ecological conditions are inimical to the establishment of forest (Batten et al. 1979, Edwards and Armbruster 1989, Wesser and Armbruster 1991). In marked contrast to zonal vegetation in the subarctic, these sites are characterized by a relatively high proportion of bare ground and dry soils. This vegetation is dominated by sagebrush (*Artemisia* sp.) and perennial graminoids and forbs.

The flora of subarctic steppe includes groups of species with disparate biogeographic and ecological affinities (Murray et al. 1983). In Alaska, widespread plants common in boreal meadow and woodland habitats (e.g. *Galium boreale* and *Rosa acicularis*) coexist with arctic-alpine xerophytes (e.g. *Potentilla nivea* and *Erigeron compositus*) on slopes dominated by species with temperate steppe affinities (e.g. *Agropyron spicatum* and *Artemisia frigida*). Steppe sites in northern regions of the Russian Far-East harbor populations of plants with different biogeographic distributions including arctic cryophytes (*Dianthus repens*, *Artemisia arctica* and *Oxytropis vassilczenkoi*), widespread steppe elements (*Poa stepposa* and *Galium verum*), and plants from temperate steppe regions of Asia (such as *Thymus serpyllum* and *Clausia aprica*).

Detailed examinations of the community ecology of subarctic steppe and the autecology of its component taxa have been limited to single sites in the eastern interior of Alaska (Edwards and Armbruster 1989, Wesser and Armbruster 1991, Lloyd et al. 1994). The primary focus of these studies has been the ecological factors controlling the ecotone between steppe and neighboring vegetation types, specifically forest and alpine tundra. These studies of within-bluff patterns of vegetation have clarified the controls over the distribution of species at these individual sites.

The purpose here is to describe patterns in the community ecology of subarctic steppe on a wider geographic scale than was done in previous studies. The study design includes a variety of sites over a broad geographic area. I describe the environmental

controls over the distribution of species within this vegetation type itself rather than across an ecotone to a neighboring community, and then test whether the variables that have been identified as important in controlling species composition within sites are important in controlling the composition of steppe between sites.

I use data from quadrat-based sampling to model the response of plant community composition and structure to topographic variables and describe the distribution of the dominant species in relation to these parameters. I then test for differences in the response to environmental gradients of plants with different geographic distributions. I also compare the important community characteristics of subarctic steppe between study areas in the Russian Far-East and Alaska.

I include sites encompassing the whole spectrum of topographic situations that support this vegetation and a broad geographic area. My reasons for doing so are two-fold. First, the potential for bias in evaluating the ecological preferences of a species is high when data from a only a single locality are used. Secondly, including greater variation in topography maximizes the length of the environmental gradients within the data set, and therefore allows for a more complete description of the synecology of this community and the autecology of its members in relation to environmental factors.

Extrazonal steppe has been suggested as a possible analogue for a component of the zonal vegetation of continental areas of the Bering Land Bridge and adjacent unglaciated parts of Asia and North America (Beringia) during full glacial periods (Young 1976, Edwards and Armbruster 1989, Lloyd et al. 1994). This contention has been disputed by some palynologists who interpret the pollen record from late-glacial Beringia as consistent with sparse fellfields or discontinuous tundra (Ritchie and Cwynar 1982).

What separates these two assessments are different hypotheses about factors that limit distribution of steppe on the current landscape. One hypothesis holds that subarctic steppe is primarily composed of thermophilic plants limited to small islands of habitat on southerly exposures by their physiological intolerance of cold soil temperatures (Ritchie and Cwynar 1982). The distribution of such plants would clearly have been even more restricted in Beringia during the Pleistocene, a period much colder than today.

An alternative hypothesis (Edwards and Armbruster 1989) holds that the restriction of these plants is a function of biotic interactions, not inherent physiological tolerance. These authors suggest that the current distribution of steppe species is a

function of their inability to compete for light in mesic localities occupied by boreal forest. According to this formulation, steppe plants would have occupied a much wider segment of the full glacial landscape than they do at present, because they would not have been displaced by forest vegetation.

Examinations of the factors that control the ecotone between steppe and neighboring habitats have generally supported the second hypothesis (Wesser and Armbruster 1992, Lloyd et al. 1994). The array of biogeographic distributions exhibited by species associated with subarctic steppe, however, suggests that component species probably have various and even contradictory responses to environmental and competitive factors. Presumably, coexistence of the species within steppe vegetation depends upon the partitioning of resources (such as light, nutrients, and moisture) along environmental gradients. In other words, both of the above hypotheses could be valid, but for different components of the vegetation (Lloyd et al. 1994).

In a sense, the surfaces presently supporting subarctic steppe represent "holes" in the fabric of zonal vegetation types that dominate the landscape of present day Beringia. Conditions in these areas are markedly atypical compared with those occurring on most surfaces in the biome, and zonal species are unable to persist there. These surfaces, then, provide refuges for species mostly excluded from zonal plant communities.

The ecological properties of steppe sites are variable, and are controlled by the topographic position of a particular site. Steep, south-facing slopes at low elevation are hotter and drier than high-elevation sites (due to the environmental lapse rate) and ones receiving less solar energy because they are less steep, less south-facing, or both. Because it is likely that xeric, treeless surfaces have persisted in continental regions of Beringia throughout the Quaternary, additions and subtractions to this flora must have occurred throughout this period (Murray et al. 1983).

Might not the ecological distribution of different floristic components within the vegetation of subarctic steppe reflect the environmental conditions that resulted in their addition to the flora of these sites? Perhaps amphiberingian taxa present in North American steppe associations migrated to these areas during glacial stages (periods colder than today). Species with amphiberingian distributions should therefore increase in importance in colder facies (higher elevation or less south-facing) of modern steppe at both ends of Beringia. Similarly, if continental North American taxa arrived in interior Alaska during a warmer, xeric interval of the Holocene, as has been suggested by Murray

et al. (1983), these taxa should be more abundant in warmer steppe facies. Little is known about the ecology of the endemic component of the steppe flora, and the response of these taxa to environmental gradients could provide insights into the origin of this unique flora.

I examined the response of members of the major biogeographic groups in the steppe flora to environmental gradients to test whether these groups of plants show consistent responses within the groups and if so, whether these responses differ significantly among groups. Taxa were assigned to a group based on their distribution (Table 1; Hultén 1968, Czerapanov 1995).

II. METHODS

STUDY AREAS

Yukon River Study Area

Physiography

The upper Yukon River valley is located in east-central Alaska, and is bordered to the south by the Yukon-Tanana Upland and to the north by the Ogilvie Mountain Range. Where the river cuts through upland areas the terrain is steep; mountainous stretches are interspersed with low-lying, rolling topography and extensive areas of floodplain. This region, largely unglaciated throughout the Quaternary, lies at the eastern edge of Beringia, the vast, mostly ice-free zone that during the full-glacial stretched from interior Yukon Territory across the Bering Land Bridge into the upper reaches of the Indigirka and Yana rivers in northeastern Asia. The area included in this study extends northwest from Dawson City, Yukon Territory (64° N, 139°18' W) along the Yukon River corridor to Eureka Creek bluff, above Circle City, Alaska (65°50' N, 144°03' W) (Fig. 1).

The Tintina fault is a defining element of the geology of this area. This fault separates the metamorphic rock units of the Yukon-Tanana Upland from the relatively unmetmorphosed sediments occurring north of the river. As much as 420 kilometers of right-lateral displacement has been estimated along this ancient fault zone that connects with the Rocky Mountain trench to the south (Roddick 1967). The Yukon River mostly parallels the Tintina fault zone throughout the study area, but the river diverges from the zone at Eagle, flowing north of the Tintina trench. The principal rock units south of the

Table 1. Definition of biogeographic categories for two study areas in Alaska and the Russian Far-East.

Study area	Biogeographic category	Current distribution
Yukon River	Widespread	Circumpolar/boreal or present on three circumpolar continents
	Amphiberingian	Range centered on Beringia and present on both sides of the Bering Strait
	North American	Restricted to North America
	Alaska-Yukon Endemic	Restricted to Alaska and the Yukon Territory
Kolyma River	Widespread	Circumpolar or widespread throughout Russia and in Europe
	Amphiberingian	Range centered on Beringia and present on both sides of the Bering Strait
	Siberian	Primarily restricted to Siberia and the Russian Far-East

fault are the metamorphic gneiss, mica-schist, phyllite, and related strata that comprise the geologic units of the Yukon-Tanana Upland (Brabb and Churkin 1969, Foster 1976). North of the river the geology is a complex of interbedded siltstone, mudstone and conglomerates of Pliocene origin alternating with exposures of lower Cretaceous argillite, graywacke, and shale. The Ogilvie Mountains are composed of older dolomite, shale, and limestone units.

The Tatonduk and Kandik rivers flow into the Yukon from the north, the Charley and Seventymile and Fortymile rivers enter from the south. The Tatonduk watershed includes several of the highest limestone peaks and ridges of the western Ogilvie Mountains, whereas the Kandik flows out of the low hills at the north-westernmost extent of this range. The Charley River is a deeply incised stream that flows into the Yukon from its headwaters near the crest of the western Yukon-Tanana Upland.

Fluvial processes over-steepen slopes of friable and unconsolidated bedrock throughout the area. These processes are particularly active on south-facing features where aridity precludes the development of a closed canopy and the consequent stabilizing influence of tree roots and dense cover of vegetation . This dynamic edaphic environment markedly affects the development of vegetation on river bluffs and the distribution of species in steppe habitats.

Climate

The climate of the upper Yukon River valley is strongly continental with long, cold winters and short but hot summers. Variation in climatic variables is relatively minor. For example, between Dawson and Eagle the difference in mean yearly precipitation is just 6.5 mm (314.5 and 308 mm/yr, respectively). Mean annual temperature is -5°C at Dawson and -4°C at Eagle. The mean temperature in July is 15° C at both stations. The entire study area falls between the heating-degree-day isolines of 8,500 and 9,000 Celsius (Wahl et al. 1987).

Vegetation

The upper Yukon drainage lies within the northern boreal-forest biome. Taiga ecosystems dominate this area. Open muskegs of *Picea mariana* occupy low-lying terrain and areas underlain by permafrost . Closed *Picea glauca* and mixed *Picea-Betula* forests occupy the well drained facies. Drier and warmer south-facing slopes and

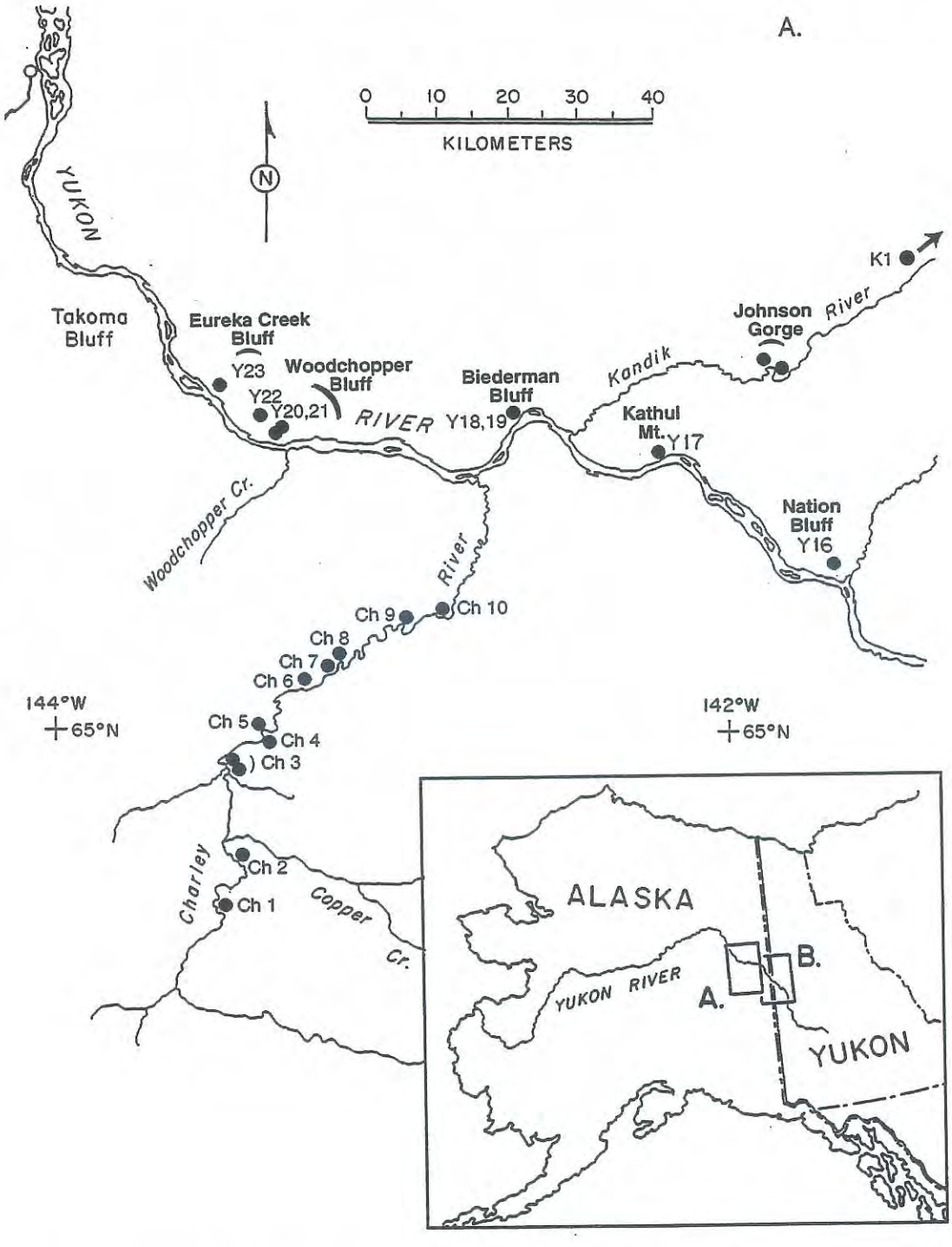


Fig. 1. Map of the Yukon River study area. This map includes sites on the Yukon River discussed in Chapter 1 and sites on the Charley, Kandik, and Tatonduk, Rivers discussed in Chapter 2.

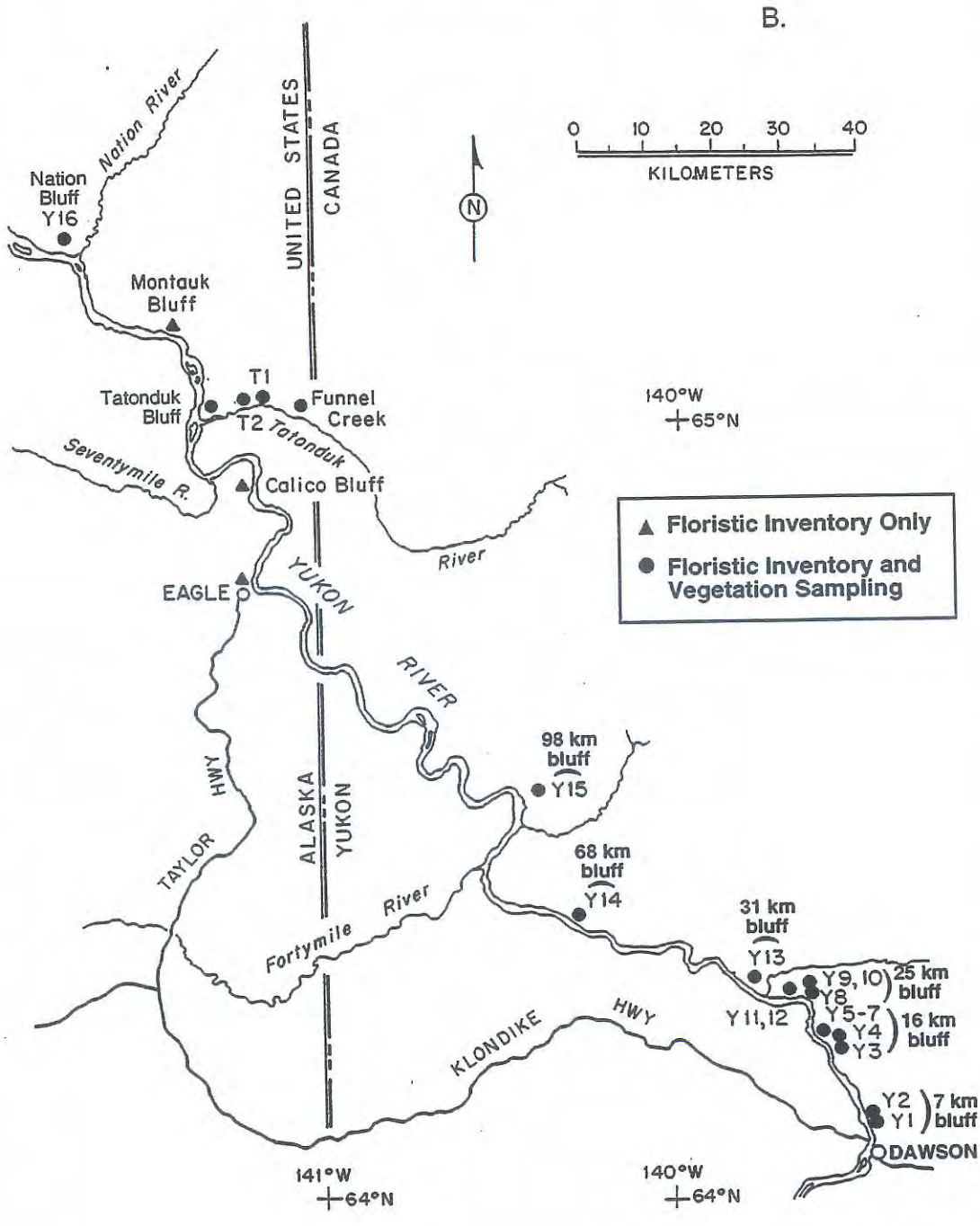


Fig. 1 (continued). Map of the Yukon River study area.

recently burned areas are occupied by *Populus tremuloides* woodland and open patches of steppe vegetation. Floodplains support *Populus balsamifera* and *Alnus* thickets, which grade into *Picea glauca* forest on older surfaces.

Large bluffs along the Yukon River represent the largest islands of habitat for steppe species west of Dawson City and east of the Kolyma River in Russia. On long stretches, where this huge river flows east to west, large south-facing riverside bluffs have been steepened by the erosive action of the river to the degree that the dry, disturbed environment precludes the establishment of forest communities. Fields of steppe vegetation occupy these sites.

I established 25 sites for vegetation sampling on 12 major bluffs. Two of these fields were subsequently excluded from the vegetation analyses because they were heavily dominated by the creeping shrub *Arctostaphylos uva-ursi* and were judged to represent a separate, nonsteppe community. The farthest upriver site was located seven km west of Dawson on Fourth Creek bluff, the most downriver site was located on the bluff at Eureka Creek, almost 400 river km downstream, 40 km east of Circle City. Fieldwork was conducted during summer 1991-93.

Kolyma River Study Area

Field work in the upper Kolyma River of the Russian Far-East was conducted near the "Aborigen" field station of the Institute for Biological Problems of the North, 61.5° N 149.49° E. The climate of this area is strongly continental with long, extremely cold winters and warm, dry summers. Annual precipitation is 286 mm; 40 % of this falls as snow during the cold months of October through April. Mean annual temperature is -12° C; mean July temperature is 15.5° C. The frost-free period lasts from 50 to 60 days in June and July. Major climatic variables in the study area closely approximate those of the upper Yukon River.

The study area is located near the western edge of Beringia (Fig. 2). The landscape of this part of north Asia is dominated by taiga ecosystems in the lowlands and tundra at elevations above 1,000 m. The dominant vegetation in the vicinity of the field sites is *Larix dahurica* woodland with an understory of *Pinus pumila*, *Betula nana*, and *Alnus fruticosa* and an ericaceous dwarf shrub layer. Well-drained facies and burned sites are occupied by *Populus tremula* woodland. Exposed ridges and rocky sites support scattered *Pinus pumila* thickets. Steppe vegetation in the upper Kolyma is

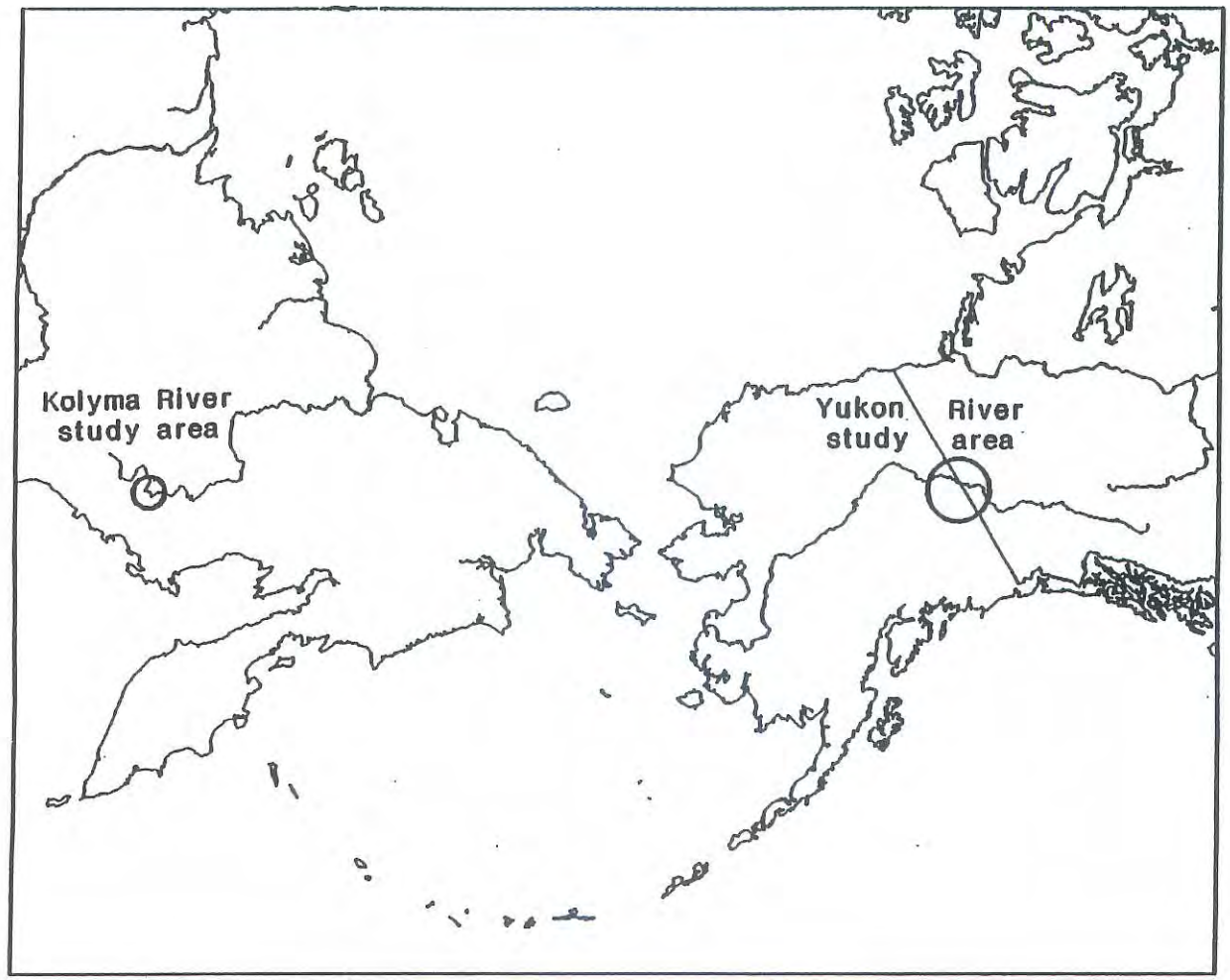


Fig. 2. Map of Beringia showing the location of the Yukon and Kolyma River study areas.

mostly restricted to south-facing slopes where high evapotranspiration and rapid runoff exclude tree species (Yurtsev 1982, Alfimov and Berman 1992). One exception is a large northerly exposed hillside with steppe vegetation, dominated by *Festuca brachyphylla* and a diverse mixture of forbs with both steppe and dry tundra affinities. The uncharacteristic presence of steppe on these north-facing slopes has been attributed to the removal of much of the snow cover by winter wind (D. I. Berman pers. comm.); redistribution of snow results in greater aridity on these surfaces compared with other north-facing slopes.

Field work in Russia was conducted during the first 3 weeks of July 1992. I chose two steppe areas in close proximity to one another for the large span of aspect that they encompassed and their similarity with regard to topographic and vegetation variables. Sites 1 through 3 were located on a large north-facing hill that supported steppe on surfaces facing between north-northwest (340°) and east-northeast (50°). Sites 4 and 5 were located on an adjacent west-facing slope. Sites 6 and 7 were situated on a south-facing bluff approximately 6 km from sites 1 through 5. At this site, steppe slopes a ranged in aspect between 130° and 235°.

FIELD METHODS

Site selection

To sample the vegetation, soil, and topographical characteristics of these sites I delimited and measured discrete steppe fields and then created a sampling grid within each one for the random placement of vegetation quadrats and soil-sampling points. A steppe field consisted of an uninterrupted patch of steppe vegetation.

I identified potential sites using topographic maps and aerial photographs. Final determination was made in the field, based on the following criteria: 1) the virtual absence of tree cover; 2) open vegetation generally free of woody plants; and 3) dominance of indicator taxa. At sites in North America, indicator taxa included the sagebrushes *Artemisia frigida* and *A. alaskana*, the grasses *Agropyron spicatum* and *Calamagrostis purpurascens*, the sedges *Carex supina* and *C. obtusata*, and several forbs including *Potentilla hookeriana, P. pennsylvannica*, *Penstemon gormanii*, and *Pulsatilla patens*. Indicator taxa in the Kolyma river area included *Carex argunensis*,

Dracocephalum palmatum, Elytrigia villosa, Festuca brachyphylla, Galium verum, Pulsatilla patens, and *Thymus serpyllum.*

Due to time constraints, I did not sample the vegetation of all fields on a particular bluff. When it was necessary to choose between fields, I chose the field that contained the most complete representation of the bluff flora. In practice, this often was the largest field on the bluff. On bluffs where significant variation existed between fields (either in vegetation or topography), an effort was made to include this variability. For example, on a bluff with steppe fields located at elevations of 300, 500 and 700 m, I sampled each of these three fields rather than sampling only the field at 500 m.

A primary criterion for site selection in the upper Kolyma River was the inclusion of fields on surfaces with the greatest variation of aspect with minimal variation in elevation, tree cover, and geology. Seven sites between 500 and 650 m in elevation within the two study areas were chosen, representing a spectrum of aspects from due north to nearly due south.

Vegetation sampling

Sampling of steppe

Sampling points were located at random in each field. Each point determined the lower left-hand corner of a sampling frame. This frame delimited a 4 m^2 patch of ground within which vegetation and topographical variables were recorded. Sampling intensity at a site was based on the size of the field, the variability in it, and the time available. No site had fewer than five quadrats and the largest site contained 20.

I estimated the percent cover of each vascular plant species within each quadrat. Cover of litter, bare ground, rock, lichens (as a class), and bryophytes (as a class) were also estimated. I recorded five topographical variables: slope (in degrees), aspect (corrected for declination), elevation, drainage (whether the plot was situated in a concavity or convex area of the slope) and the degree of geomorphic disturbance of the substrate. Soil depth was determined at each plot by inserting a metal probe at each corner of the quadrat. I also estimated the percent of the southern hemisphere of the sky shaded by trees.

Soil disturbance was quantified on a scale of 1 to 5, 1 representing an undisturbed soil surface, and 5 signifying a fresh slide scarp. I assessed the drainage characteristics of a site by assigning a score between -3 and +3: 0 represented a flat slope cross section, -3

meant the quadrat was located on the summit of a convex ridge within the field; +3 represented a quadrat situated in the bottom of a substantial slope concavity or gully.

I also collected soil samples at each site. At randomly selected quadrats, I took two soil cores from the upper 10 cm of soil and combined them to form the soil sample for the quadrat. Soil was sampled from two quadrats at each site on the Yukon River. Within each of the seven sites on the Kolyma River, a random subset of quadrats was selected for soil sampling (between 40 - 50 % of quadrats were sampled at each site). Soil samples were placed in paper bags in the field, air dried, and analyzed in the laboratory.

Sampling of ecotones

I established transects across the steppe-aspen forest ecotone at three sites on the Yukon River where steppe vegetation graded evenly into aspen forest. Ecotone transects were sampled at Nation, Woodchopper and Eureka Creek bluffs. Although these sites are widely separated geographically, they were similar in both topography and vegetation. To quantify changes in species composition between steppe and neighboring forest understory the location of the ecotone transect was determined at random. A measuring tape was laid out from the randomly chosen start of the transect (in steppe) and directed into the forest. The transects were terminated at a point when extending them further would not increase canopy cover (that is, in full forest). Sampling stations were placed at 5 m intervals along this transect beginning with two quadrats in full steppe at the start of the transect. At each sampling station a second tape was laid parallel to the ecotone transect, extending 5 m on each side. Two sampling points placed at each station were randomly situated within this 10 m span. Quadrat sampling at these points followed the protocol outlined previously for steppe quadrats.

Each ecotone transect had a minimum of four stations (eight quadrats). I averaged topographic and vegetation variables within each station for the ecotone transects. Due to the similarities in important vegetation and topographic parameters mentioned previously, I treated the transects as replicates and analyzed the data from these transects as though they spanned a single ecotone. For purposes of data analysis, then, the thirteen stations were used as independent observations of vegetation. Sample size for individual transects would have been too small for analysis.

LABORATORY METHODS

In the laboratory, I sieved soil samples to obtain < 2 mm particles. Percent organic matter and pH were determined for each sample. I determined soil pH using a 1:1 soil to water slurry, which was thoroughly mixed and allowed to equilibrate for 1 h. Percent organic matter was determined as the fraction of soil weight lost on ignition at 500° C for 10 h. I used the micropipette technique developed by Miller and Miller (1987) to determine soil texture.

On soils from the Kolyma River sites, I also performed laboratory incubations of rewetted soils and determined available nitrogen, rate of potential net nitrogen mineralization, and rate of soil respiration for each sample. Rates of net nitrogen mineralization and soil respiration were determined on 15 g (dry weight) of soil which was brought to 60 % of water holding capacity in gas-impermeable jars fitted with rubber septa and incubated in the dark for 30 days at 15° C. Respiration rates were obtained by periodically analyzing 10 ml of jar atmosphere for CO_2 with a Shimadzu GC-8A gas chromatograph. Following the 30-day incubation period, I extracted available N from the samples using 50 ml of 2 M KCl solution. Initial nitrogen concentrations were obtained by extraction with 2 M KCl from 10 g subsamples of the original soil samples. Extractions were analyzed for NH4 and NO3 using a Lachat Quickchem Autoanalyzer.

ANALYTICAL METHODS

Equivalent latitude

Equivalent latitude is an index of potential solar radiation for a topographic surface; it varies as a function of slope angle, aspect, and latitude (Lee 1962). This variable has been used to predict the distribution of plant communities and permafrost in taiga ecosystems of Alaska (Dingman and Koutz 1974). The equivalent latitude of a plot represents the latitude at which a level surface would receive the equivalent amount of potential solar energy as the sloped surface in question. The equivalent latitude (EQ) for a site is calculated with the following equation:

$$EQ = \arcsin[(\sin K * \cos H * \cos L) + (\cos K * \sin L)]$$

(where... K = slope in degrees, H = deviation from true north, L = latitude)

I calculated values of EQ for each quadrat sampled. The mean of the quadrat scores was used as the EQ value for the site. These values were used as an independent variable in regression models to predict soil and vegetation characteristics.

Characterization of vegetation

The fundamental sampling unit for the analyses of vegetation was the 4 m^2 quadrat. I ordinated data on plant cover using detrended correspondence analysis (DCA, Hill 1979). For each site on the Yukon River, I averaged data to obtain mean percent cover by species. These composite scores were then ordinated. At the Kolyma River area, cover data from individual quadrats were used in the ordinations. Scores from the first two DCA axes were then used as dependent variables in simple and multiple regressions to assess the relationship between topographic variables and vegetation. At Yukon River sites, the means of environmental parameters were used as independent variables, whereas individual values for quadrats were used for the Kolyma River sites.

The different analysis of the two data sets reflects the different geographic scale inherent within them. Using values for individual quadrats the analysis of the Yukon River data would have been inappropriate because of the geographic clustering and potential lack of independence of the quadrats measured within a bluff. Sites at the Kolyma River, on the other hand, were confined to a much smaller area and sampling was designed to minimize variation in site attributes other than aspect. For this reason, I assumed that the quadrats were reasonably independent with regard to important variables. This assumption was validated by performing regressions on segments of the gradient, which yielded similar results to the entire data set.

Another method I used to analyze responses of vegetation to topography was by an estimation of species richness and dominance. The two indices I used were: 1) the number of vascular plant species per quadrat (S) and 2) Simpson's index of dominance concentration (C). Simpson's index (C) is defined by the following equation:

$$C = \Sigma\, p_i^2 \quad \text{where } p_i = \text{relative cover values of each species (as decimal fractions)}$$

Simpson's index expresses, for a patch of vegetation, the distribution of "importance" among the component species of the vegetation. The higher the value of

C, the greater the dominance by a few species. For instance, in a quadrat with only one plant species, *C* would equal 1.0. In a quadrat with 10 species of equal cover it would equal $[(.1^2) * (10)]$ or 0.1. This value was computed separately for every quadrat recorded in this study.

Characterization of the biogeography of component species

I tested whether groups of species with similar biogeographic distributions showed consistent responses to the major environmental variables controlling steppe vegetation. Twenty-four species from the Yukon River sites were selected for these analyses based on their importance within the vegetation (frequency and cover). Nineteen of these were prominent throughout the drainage; five were very prominent at the 14 most upriver sites, but absent downstream. The 40 most common species (those occurring in ≥ 10 quadrats) from the Kolyma River area were used in these analyses. Taxa from both study areas were classified into biogeographic categories (Table 1).

Characterization of the autecology of component species

Single-factor gradient analysis

I used gradient analysis to characterize the response of steppe species to topographic and environmental variables. I partitioned the total number of quadrats into three segments along each environmental gradient, based on the value of the environmental variable. The criterion I used to partition the gradient was maximization of evenness of sample size (number of quadrats) among the segments. Cover of each species was averaged within each of these segments. For example, the gradient for EQ at the Yukon River sites was partitioned into three segments containing the quadrats on surfaces of < 30° EQ, those between 30° and 36° EQ, and those on surfaces > 36°EQ. Percent cover for a species was then averaged over all quadrats within each of these segments to obtain the mean cover of the species for each portion of the gradient.

The large number of quadrats sampled and the extensive geographic area covered by the Yukon River fieldwork allowed me to examine the response of these taxa to both EQ and elevation. The unique feature of the Kolyma River area, on the other hand, was the unusually large span of EQ of surfaces occupied by steppe vegetation. I selected sites such that differences in elevation between sites were minimized. Consequently, the

autecology of species in the Kolyma River study area were examined only with regard to EQ.

Two-factor gradient analysis

The diversity of slope, aspect, elevation, and drainage of the surfaces sampled on the Yukon River allowed for the simultaneous consideration of the effect of several environmental factors on the abundance of a species. Two-factor gradient analysis enabled me to construct response surfaces for steppe species to the most important variables affecting species distributions within this community.

Two-factor gradient analysis is similar to single-factor gradient analysis except that each cell represents the quadrats that meet two sets of conditions, instead of one. Two gradients are partitioned into segments and a matrix consisting of cells describing all of the combinations of these segments is constructed. Cover of a species is averaged for all quadrats within a cell and the results are presented as a three-dimensional bar graph.

Statistical Methods

Tests of association

Formal tests of the association between membership in the biogeographic groups and specific responses to environmental gradients were performed. First, I tested whether species showed significant responses to the gradients in question by subjecting the cover data from the cells at the two extremes of the gradient to one-tailed t-tests. If the test showed a significant difference, the species was classified as having a positive or negative response to this variable, depending on whether it increased or decreased in abundance with higher levels of the environmental factor. If the test showed no detectable difference, the response was considered neutral.

The number of significant responses of each type was tallied for each biogeographic category. These results were then placed in contingency tables. Because there were two possible significant responses (either positive or negative) to a gradient and two gradients were examined (EQ and elevation), four contingency tables were analyzed for the Yukon River area. The two columns in these tables represent the number of taxa showing a significant response versus the number not showing this response. The rows of the table represent the biogeographic categories. These data were then subjected to a G-test of independence (Sokol and Rohlf 1981). The endemic

category was dropped from this analysis because of the small number of taxa (three) present in sufficient abundance to characterize their gradient responses.

Analysis of data from the Kolyma River was identical to that from the Yukon River area except that only two contingency tables were analyzed because only the gradient in EQ was considered. A final contingency table was constructed combining the number of significant responses from both study areas to EQ by members of these groups.

Vegetation and environment relationships

I used stepwise multiple regression to identify significant relationships between the vegetation scores and other biotic variables to environmental variables (MINITAB statistical software was used for all regression analyses). The criterion of maximum F-statistic was used to determine those variables to be included in the models. Data were assessed for conformity to assumptions, and variables were log transformed when required to meet the assumption of equal variances. The relationship between soil variables and topography also was analyzed using linear regression. Soil parameters were averaged by site and used as dependent variables in regression models.

III. RESULTS

YUKON RIVER STUDY AREA

Abiotic Environment

Slopes at the Yukon River sites were generally steep (mean inclination = 34.4°; Table 2) and south-facing (mean aspect = 193°). The range of slope angles observed was 27° to 42°, and aspects ranged between east-south-east and west-south-west. Mean EQ on these slopes was 32.93°, with a range of 24.46° to 43.13° (Table 2), suggesting that the solar radiation load there was similar to level surfaces of considerably lower latitude. Site elevations ranged from 265 to 880 m with a mean of 481 m.

Steppe slopes on the Yukon River are typically convex or flat in cross section, as reflected in mean drainage index of -0.06. These fields, however, are commonly dissected by gullies and smaller drainage features formed by the erosive action of channelized slope wash. This fluting pattern results in a mosaic of relatively more mesic

Table 2. Physical variables recorded at 23 sites on the Yukon River.

	Slope (degrees)	Aspect (degrees)	Azimuth (degrees)	EQ (degrees)	Elevation (meters)	% Rock	% Bare	Disturb Index	Drainage Index
Mean	**34.35**	**193**	**28.17**	**32.93**	**481**	**2.5**	**11**	**2.60**	**-0.06**
Std. Error	1.07	6.53	3.78	5.11	39	0.37	2.34	0.15	0.06
Min.	27.2	120	5	24.46	265	0.10	0	1.19	-0.50
Max.	42.3	237	60	43.13	880	6.10	46.5	3.75	0.50

Table 3. Soil properties of 23 sites on the Yukon River.

	soil pH	% organic	% sand	% silt	% clay
Mean	**6.99**	**6.34**	**50**	**44**	**6**
Std. error	0.08	0.43	2.60	2.40	0.63
Range	6.2-8.0	3.5-11.9	24-69	28-74	0.5-10

and drier areas within steppe because areas occupying gully bottoms receive additional moisture from the convex areas.

Geomorphic disturbance in these fields is variable, depending upon several topographic variables, principally slope angle. The average value for the disturbance index at the Yukon sites was 2.64 (Table 2). There was an average of 11 % bare ground and 2.5 % rock cover per quadrat. Tree cover within the fields was generally minimal, averaging 2.6 percent canopy cover of the ground surface. Isolated stands of trees encroach into steppe fields, however, particularly in swale features.

Soils at the Yukon sites were silty loams and loams of neutral to basic reaction (mean pH = 6.99; Table 3). With few exceptions, there was generally low organic matter accumulation in these soils. Mean soil organic matter was 6.34 % with a range of 3.5 to 11.9 %.

There were strong correlations between topography and soil variables at sites within the Yukon River drainage (Table 4). Soil pH and disturbance were negatively correlated with EQ. Slope angle was correlated with the degree of geomorphic disturbance and soil pH. Geomorphic disturbance was positively correlated with the amount of bare ground at a site and its mean soil pH. Disturbance was negatively correlated with organic matter content of soil.

Soil pH was also negatively correlated with soil organic matter. Low pH was associated with high organic-matter concentrations in these soils. This is likely due to the formation of weak organic acids during organic matter decomposition. Soil pH also was related to soil texture. This variable was positively correlated with silt content and negatively correlated with sand content. Percent bare ground was positively correlated with geomorphic disturbance and negatively correlated with soil organic matter.

Vegetation

Artemisia frigida, *Calamagrostis purpurascens*, *Pulsatilla patens* and *Androsace septentrionalis* were common at all study sites on the Yukon River. *Agropyron spicatum* was absent from only one high-elevation site. Other common taxa were *Bupleurum triradiatum*, *Carex supina* ssp. *spaniocarpa*, *Epilobium angustifolium*, *Galium boreale*, *Juniperus communis*, *Minuartia yukonensis*, *Penstemon gormanii*, *Potentilla hookeriana*. *Potentilla pennsylvannica*, *Rosa acicularis*, *Saxifraga reflexa*, *Solidago multiradiata* and *Zygadenus elegans*. Structure and composition of the vegetation of

Table 4. Correlation matrix of physical and soil variables for 23 sites on the Yukon River . Number given is simple coefficient of correlation between the two variables. Linear regression determined the statistical significance of the relationship between the variables. Column headings are as follows: Sl=slope, Azi=azimuth off 180°, Dist=disturbance, Drn=drainage, %Rk=rock cover, %Bg=bare grd., %TC=tree cover, %O=soil organic matter, %Cl=clay, %Slt= silt, %Snd =sand. Levels of significance: * = $p<0.05$, ♦ = $p<0.01$, ♣ = $p<0.001$

	Sl	Azi	EQ	Elev	Dist	Drn	%Rk	%Bg	%TC	pH	%O	%Cl	%Slt
Azi	0.10												
EQ	-0.86	0.40											
Elev	-0.26	0.14	0.26										
Dist	0.66	-0.09	-0.67	-0.17									
Drn	0.07	0.24	0.09	-0.13	-0.17								
%Rk	0.31	0.20	-0.24	0.05	-0.06	0.01							
%Bg	0.18	-0.20	-0.30	0.36	0.55	-0.33	-0.07						
%TC	0.32	0.03	-0.31	-0.40	0.33	-0.22	-0.40	-0.18					
pH	0.45*	0.13	-0.41*	0.12	0.66	-0.13	0.28	0.38	0.18				
%O	-0.31	0.22	0.44*	-0.14	-0.59	0.24	-0.08	-0.63	-0.18	-0.62			
%Cl	-0.30	0.14	0.38	-0.03	-0.18	0.10	-0.08	-0.29	0.19	-0.27	0.55		
%Slt	0.01	-0.19	-0.05	-0.13	-0.19	0.16	-0.21	-0.25	0.02	-0.43*	0.36	0.15	
%Snd	0.06	0.13	-0.13	-0.03	0.22	-0.17	0.21	0.31	-0.06	0.47*	-0.47*	-0.38	-0.97

these sites is a continuum with key taxa present at all sites. Dominance by component taxa, however, was variable among the sites. There were 55 species that occurred in the quadrats (Table 5).

Vegetation variables differed among sites (Table 6). Mean number of vascular plant species per quadrat ranged between 4.6 and 16.6 with a mean of 9.0. The range in values of Simpson's index was 0.18 to 0.91 with a mean of 0.34. Although aspen and other tree species do encroach onto steppe, tree shading of steppe fields is minimal except near the ecotone with neighboring forest communities. The mean amount of southern sky obscured by trees was 2.6 %.

There also was considerable variation in the importance of moss and lichen cover among Yukon River sites. A few sites were carpeted with a relatively thick layer of bryophytes or fruticose and foliose lichens, whereas others had virtually no mosses and only a thin layer of crustose lichens on the soil surface. Moss cover averaged 19 % and mean lichen cover was 39 %. Total cover of vascular plants per site averaged of 26 %, with an average of 41 % litter cover.

Several of the biotic variables were intercorrelated (Table 7). Simpson's index is mathematically related to species richness, so the strong correlation between *S* and *C* is not surprising. Moss cover is negatively correlated with the amount of litter at a site, and lichen cover is negatively correlated with high cover of vascular plants.

Relationships Between Topography and Vegetation

A few important variables were strong predictors of the variation in the vegetation among steppe sites on the Yukon River: EQ, elevation, shading, soil organic matter content, and texture are the strongest predictors of community composition within the study area (Table 8). Hot and dry south-facing sites at low elevation were characterized by low species richness and dominance by the large-statured bunch grasses *Calamagrostis purpurascens* and *Agropyron spicatum* and the sagebrush *Artemisia frigida.* Only a few xerophytic perennials (such as *Potentilla pennsylvanica* and *Pulsatilla patens*) and few mosses or foliose lichens persist on these surfaces. Sites at higher elevation or with high EQ support populations of these plants, along with a suite of generally restricted herbaceous taxa (such as *Bupleurum triradiatum*, *Minuartia yukonensis*, *Papaver nudicaule* ssp. *americanum*, and *Saxifraga reflexa*). The vegetation of such sites is characterized by small-statured plants, high cover of mosses

Table 5. Vascular plant species occuring in quadrats sampled at 23 sites on the Yukon River. Species are ranked according to their score on DCA axis 1.

Taxon	Score on DCA-1	Score on DCA-2
Potentilla nivea L.	402	-18
Artemisia alaskana Rydb.	384	231
Gentiana propinqua Richards.	384	231
Rubus idaeus L.	384	231
Zygadenus elegans Pursh.	380	191
Epilobium angustifolium L.	362	44
Hedysarum alpinum L.	361	200
Dryopteris fragrans (L.) Schott	352	-78
Polemonium pulcherrimum Hook.	352	-78
Senecio ogoturukensis	337	-6
Saxifraga tricuspidata Rottb.	335	65
Festuca altaica Trin.	303	-12
Cerastium beeringianum Cham. & Schlecht	294	-24
Draba murrayi	294	200
Bupleurum triradiatum L.	290	-103
Erysimum angustatum Rydb.	288	-44
Poa glauca M. Vahl	282	125
Alyssum americanum Greene	262	-137
Mertensia paniculata (Ait.) G. Don	259	-1
Papaver nudicaule L.	259	-4
Minuartia yukonensis Hult.	258	-99
Potentilla hookeriana Lehm.	249	61
Solidago multiradiata Ait.	242	246
Achillea borealis Bong.	239	330
Bromus Pumpellianus Scribn.	236	41
Erigeron compositus Pursh	236	41
Cnidium cnidiifolium (Turcz.) Schischk.	235	550
Podistera yukonensis Math.& Const.	234	-192

Table 5, continued.

Taxon	Score on DCA-1	Score on DCA-2
Antennaria spp.	231	-88
Saxifraga reflexa Hook.	221	-64
Galium boreale L.	207	215
Dodecatheon frigidum Cham.	200	284
Arctostaphylos uva-ursi (L.) Spreng.	187	499
Pulsatilla patens (L.) Mill.	180	101
Calamagrostis purpurascens R. Br.	166	135
Erigeron caespitosus Nutt.	153	-13
Aster sibiricus L.	150	189
Campanula aurita Greene	121	-59
Arabis Holboellii Hornem.	116	285
Androsace septentrionalis L.	112	69
Potentilla pennsylvanica L.	101	66
Agropyron spicatum	91	-41
Rosa acicularis Lindl.	51	248
Halimolobus mollis (Hook.) Rollins	36	88
Penstemon Gormanii Greene	25	70
Silene menziesii Hook.	13	118
Artemisia frigida Willd.	-33	52
Amalanchier alnifolia (Nutt.) Nutt.	-61	165
Smilacina stellata (L.) Desf.	-61	165
Linum perrene L.	-93	168

Table 6. Biotic variables recorded at 23 sites on the Yukon River. *S* is the number of vascular plant species per quadrat, *C* is Simpson's Index of dominance concentration.

	S	C	% vascular plant cover	% moss cover	% lichen cover	% litter cover	% sky shaded
Mean	**9**	**0.34**	**26.0**	**19.0**	**39.0**	**41.0**	**2.6**
Std. error	0.6	0.03	1.4	4.6	4.4	6.0	0.5
Min.	4.6	0.18	11.5	0.3	5.8	22.0	0.0
Max.	16.6	0.91	45.8	73.0	75.6	99.0	8.6

Table 7. Correlation matrix for biotic variables for 23 sites on the Yukon River. Number given is simple coefficient of correlation between the two variables. Level of significance was determined using linear regression.

	Total vascular plant cover	% Moss cover	% Lichen cover	% Litter	% sky shaded	*S*
% Moss cover	-0.42					
% Lichen cover	-0.56♦	0.33				
% Litter cover	0.35	-0.55♦	-0.39			
Tree shade	0.17	-0.22	-0.43*	0.61♦		
S	-0.14	-0.07	0.27	0.17	-0.18	
C	0.13	0.01	-0.42*	0.04	0.37	-0.79♣

S = Number of vascular plant species per quadrat *C* = Simpson's index of dominance concentration. Levels of significance: * = $p<0.05$, ♦ = $p<0.01$, ♣ = $p<0.001$

Table 8. Multiple regresion relationships between vegetation variables and topographic and soil variables at 23 sites on the Yukon River. SS is type III sums of squares for each independent variable.

Dependent variable	R^2	Error d.f.	F	Independent variable	b	SS	t	p
DCA-1	.80	18	23.3	EQ	9.24	60096	6.36	<.001
				Percent sand	-2.04	10881	-3.45	.003
				Elevation	0.093	5677	2.27	.035
DCA -2	.80	19	38.9	Tree Cover	17.1	27732	7.77	<.001
				% O-Matter	14.2	17197	5.48	<.001
S	.62	20	16.1	EQ	0.33	85.89	3.86	.001
				Elevation	0.002	39.64	3.11	.006
C	.63	19	16.3	EQ	-.012	0.103	-4.50	<.001
				Elevation	-.0001	0.020	-2.28	.034
Moss cover	.63	20	16.7	Disturbance	-19.5	5790	-4.27	<.001
				Litter cover	-0.35	945	-2.16	.043
Lichen cover	.56	20	12.6	Disturbance	-16.0	4590	-3.24	.004
				Plant cover	-1.04	901	-2.04	.055
Plant cover	.19	21	5.05	EQ	-0.59	198	-2.25	.035

and lichens and less bare ground than at the warmest sites. Hence, the number of vascular plant species per quadrat (*S*) was strongly positively correlated with EQ and elevation ($r^2 = 0.64$, $p < 0.001$; Figs. 3 and 4).

Species richness per 4 m^2 quadrat was not necessarily indicative of overall species richness for a field. The correlation of species richness with EQ may be simply an artifact of smaller plant size with a fixed quadrat size. To assess whether overall species richness also was correlated with site EQ, I compared species-area curves for sites with differing mean EQ values. This was done by dividing the sites into three classes of EQ (< 30°, between 30° and 36°, and > 36°) and plotting species-area curves for the first eight quadrats at all sites. I then calculated the mean species richness for each incremental increase the area sampled for all sites within each EQ class. The same procedure was performed for the relationship between elevation and species-area curves. There was a positive relationship between overall species richness and both of these variables (Figs. 5 and 6); both per plot and total species richness are positively correlated with EQ and elevation.

Whereas species richness declined with decreasing EQ, mean cover of vascular plants was weakly positively correlated with EQ ($r^2 = 0.18$, $p = 0.05$). As a result, values for Simpson's index (*C*) for these sites were strongly negatively correlated with EQ and elevation ($r^2 = 0.63$, $p < 0.001$) reflecting the trend of increased dominance by a few important species at the most xeric lowland sites.

Increases in the elevation, EQ, and shade at a site results in corresponding changes in structure and composition of the vegetation. These changes are reflected in the site scores on the first two DCA axes. Most of the variance in site scores on the first DCA axis (eigenvalue = 0.37) is explained by EQ of the site ($r^2 = 0.63$, $p < 0.0001$; Fig. 7). Variables that significantly add to the explanatory power of this model are elevation and soil texture (r^2 for full model = 0.80, $p < 0.001$; Table 8). The model including mean tree cover and percent soil organic matter is a powerful predictor of variation in the second DCA axis (eigenvalue = 0.25), explaining 80.4 % of the variance in DCA-2.

These ordination scores reflect two major trends in the vegetation. First, cooler sites at higher elevations tend to contain populations of tundra plants such as *Lloydia serotina* and *Arnica frigida* in addition to the lowland elements. Widespread xerophytes such as *Carex supina* and *Potentilla nivea* are also more common in these situations. Secondly, particularly in shaded situations, but also in drainage areas and on aspects

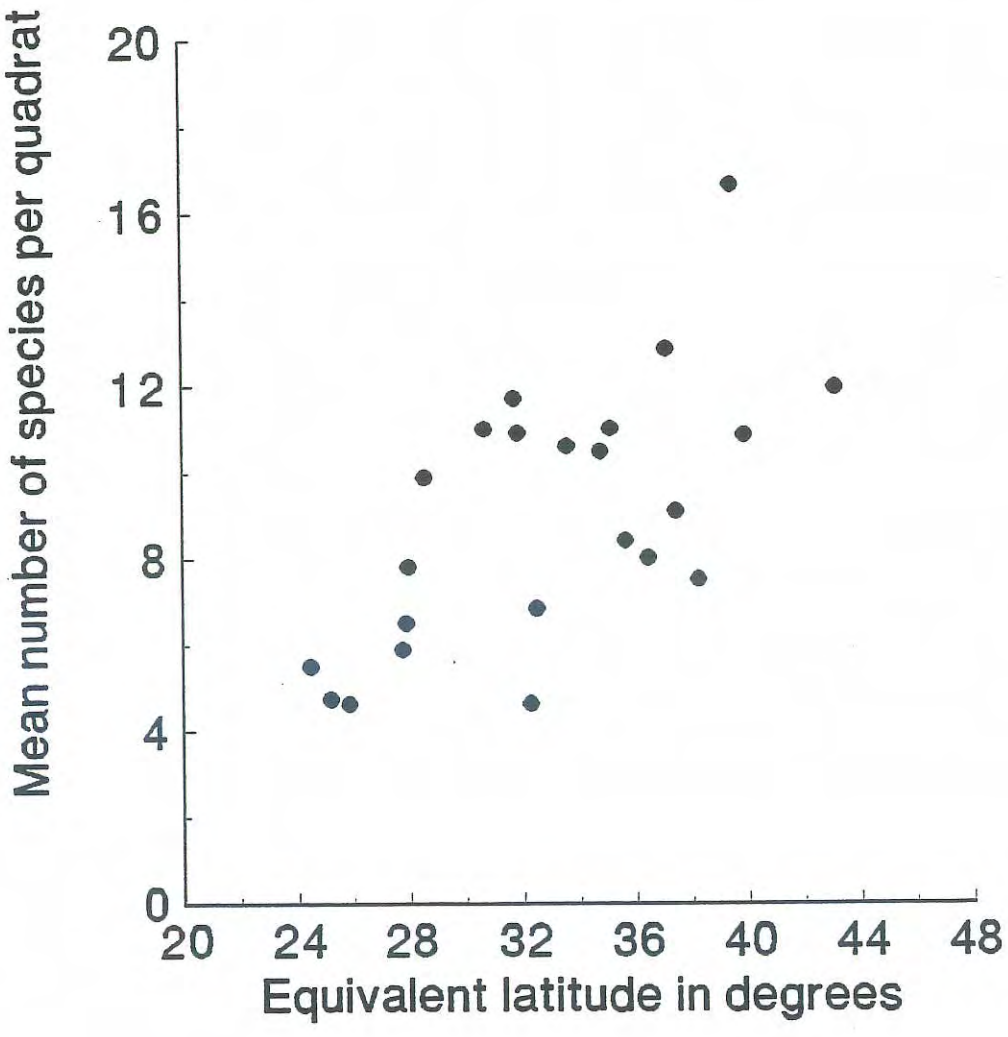


Fig. 3. Mean number of species per quadrat in relation to EQ at 23 sites on the Yukon River.

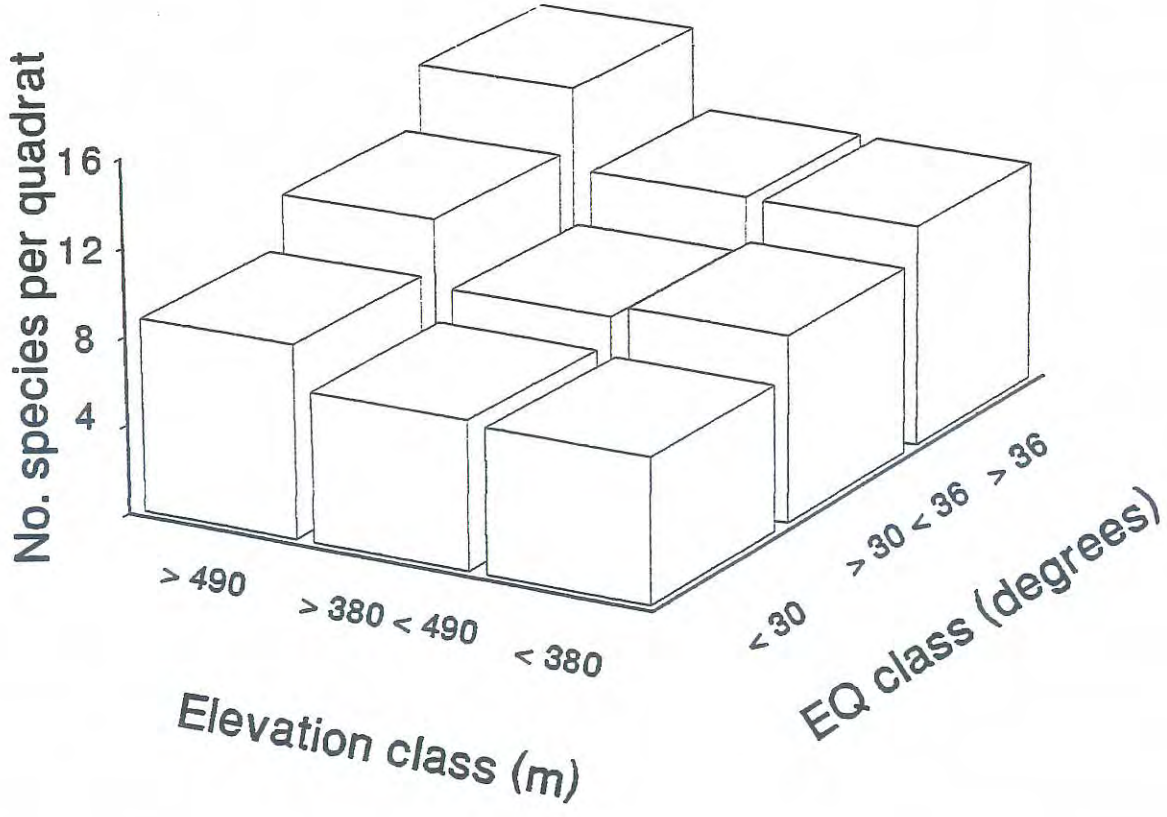


Fig. 4. Mean number of species per quadrat in relation to EQ and elevation within steppe vegetation of 23 sites on the Yukon River.

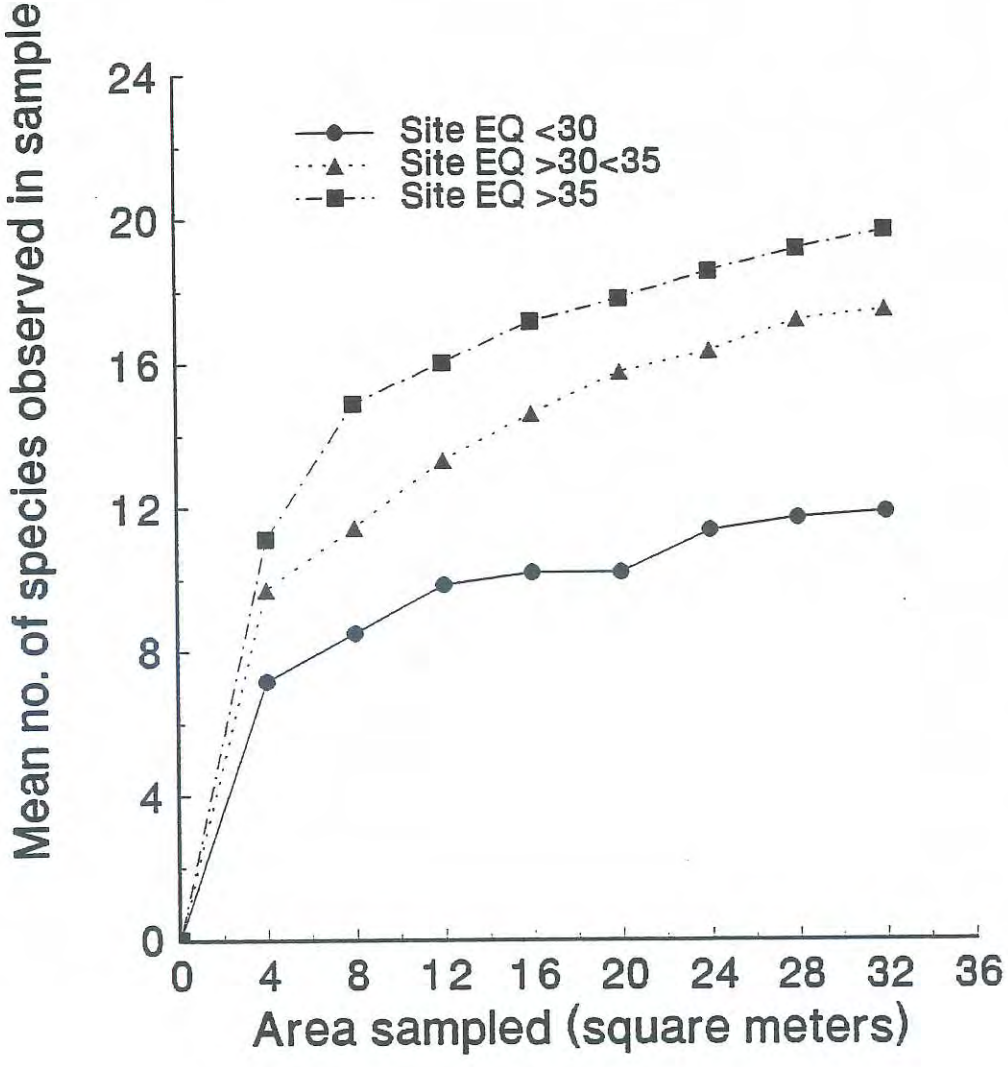


Fig. 5. Mean species-area curves for sites in three categories of EQ in the Yukon River study area.

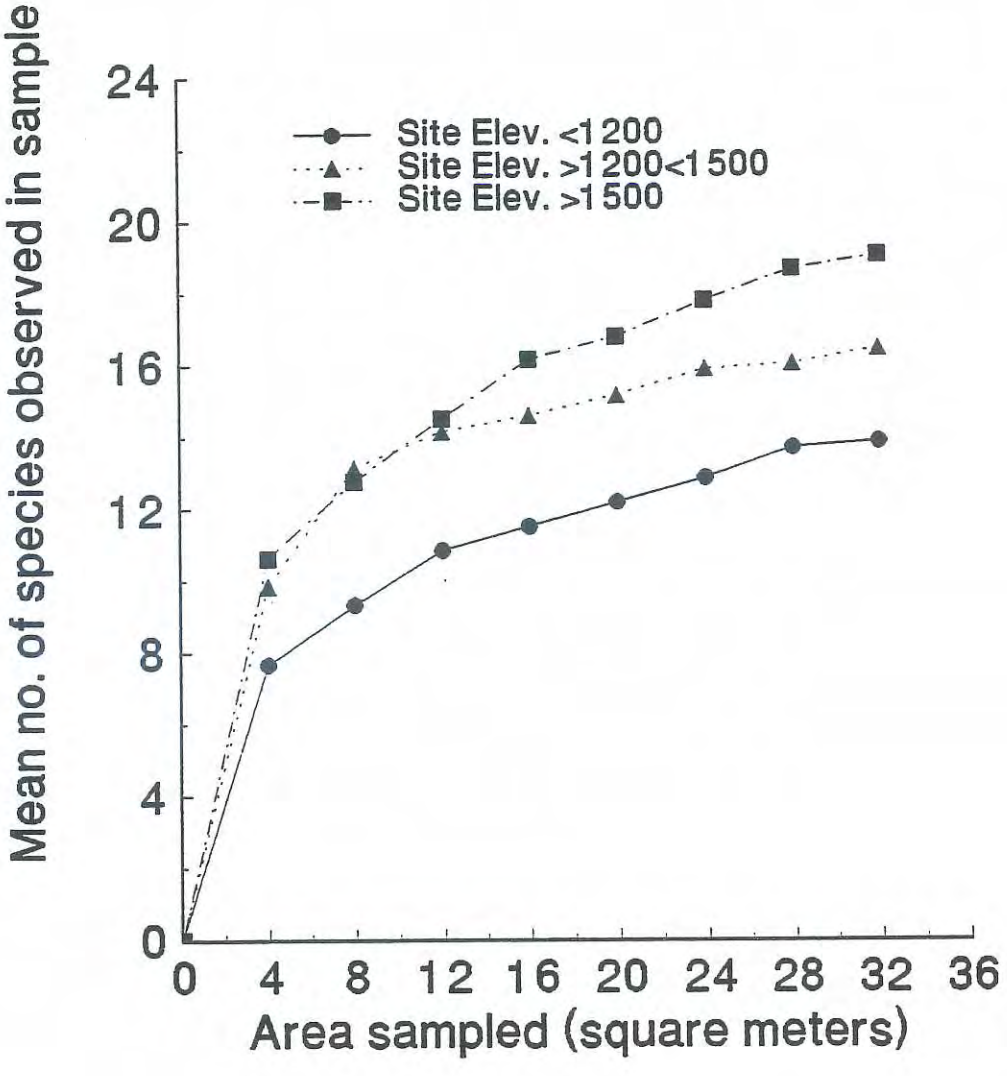


Fig. 6. Mean species-area curves for sites in three categories of elevation in the Yukon River study area.

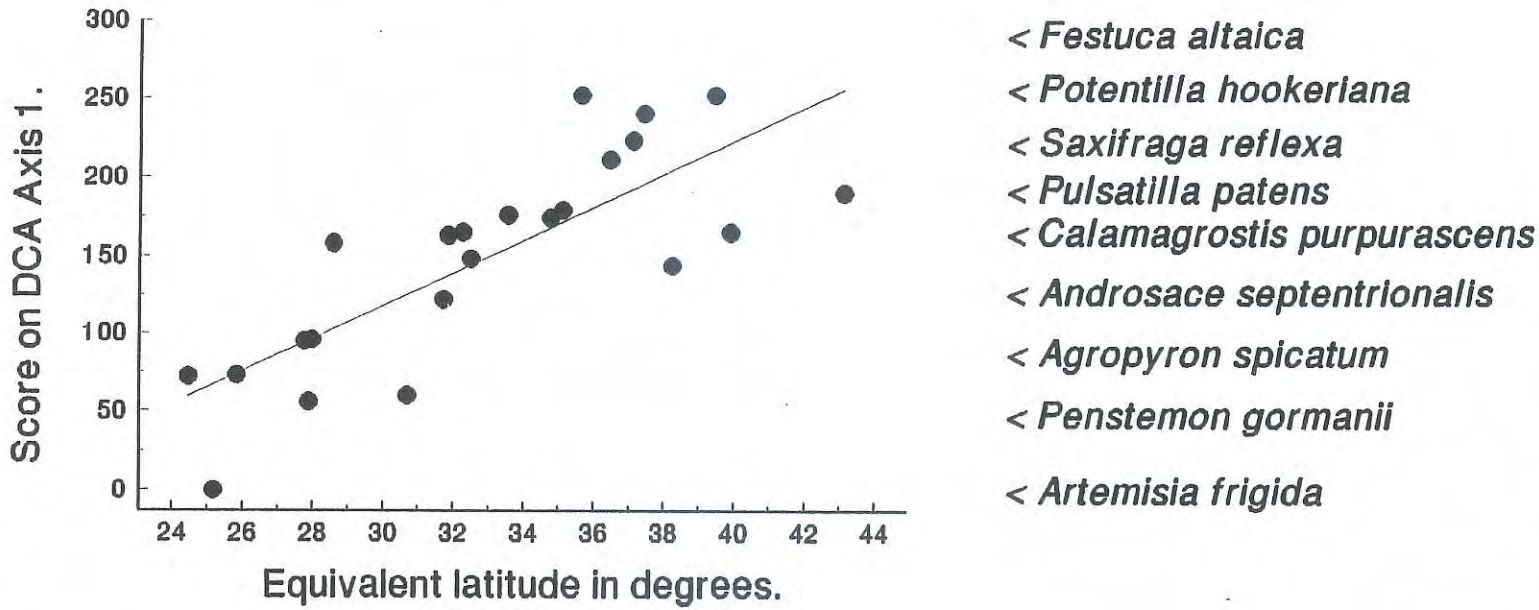


Fig. 7. Vegetation score on DCA-1 as a function of EQ for 23 sites on the Yukon River. Selected species scores (on DCA-1) are included at right.

other than due south, a variety of boreal woodland and meadow plants occurred in steppe (e.g. *Zygadenus elegans*, *Solidago multiradiata* and *Galium boreale*). In both situations, lowland steppe species, notably the dominants *Agropyron spicatum* and *Artemisia frigida*, were displaced to varying degrees.

The vegetation of high-elevation steppe areas was low-statured. This type consisted of more numerous, but smaller, plants. These sites tend to have an important lichen component and resemble graminoid-herbaceous tundra occurring on well-drained ridges in the Ogilvie Mountains and Yukon-Tanana Upland. High-elevation steppe vegetation contains plants with tundra affinities and has high cover values for nonvascular plants.

Soil disturbance also affected the vegetation directly in several ways including species composition at steppe sites. Disturbance exposes mineral soil for colonization by seedlings, removes soil organic matter and the alters the competitive balance in favor of faster growing, more readily dispersed plants. Increase in the amount of exposed soil surface also resulted in higher soil temperature, increased runoff, and less moisture retention by the soil.

The cover of both mosses and lichens, relatively slow-growing organisms, was particularly negatively affected by geomorphic disturbance. The best model predicting lichen abundance at Yukon River sites includes disturbance and total cover of vascular plants ($r^2 = 0.59$, $p < 0.001$; Table 8). Cover of bryophytes also appeared to be negatively affected by both disturbance and litter cover. The relationship between the bryophyte cover I collected and these variables does not meet the assumptions of regression analysis, due to the large number of zero values in these data.

Ecotone transects

Aspen forest often occupies the relatively well-watered swales in southerly exposed slopes that otherwise support steppe on Yukon River bluffs. Two of the ecotones sampled here appeared to be associated with increasing slope concavity (Fig. 8). The transition from steppe to forest along the transect at Woodchopper bluff, on the other hand, paralleled increasing westerly aspect of the slope (Fig. 9). This may be due the summit of this large bluff shading westerly exposures in the area during the latter part of the day. Easterly exposed slopes there do not have an equivalent obstruction and therefore receive more total radiation.

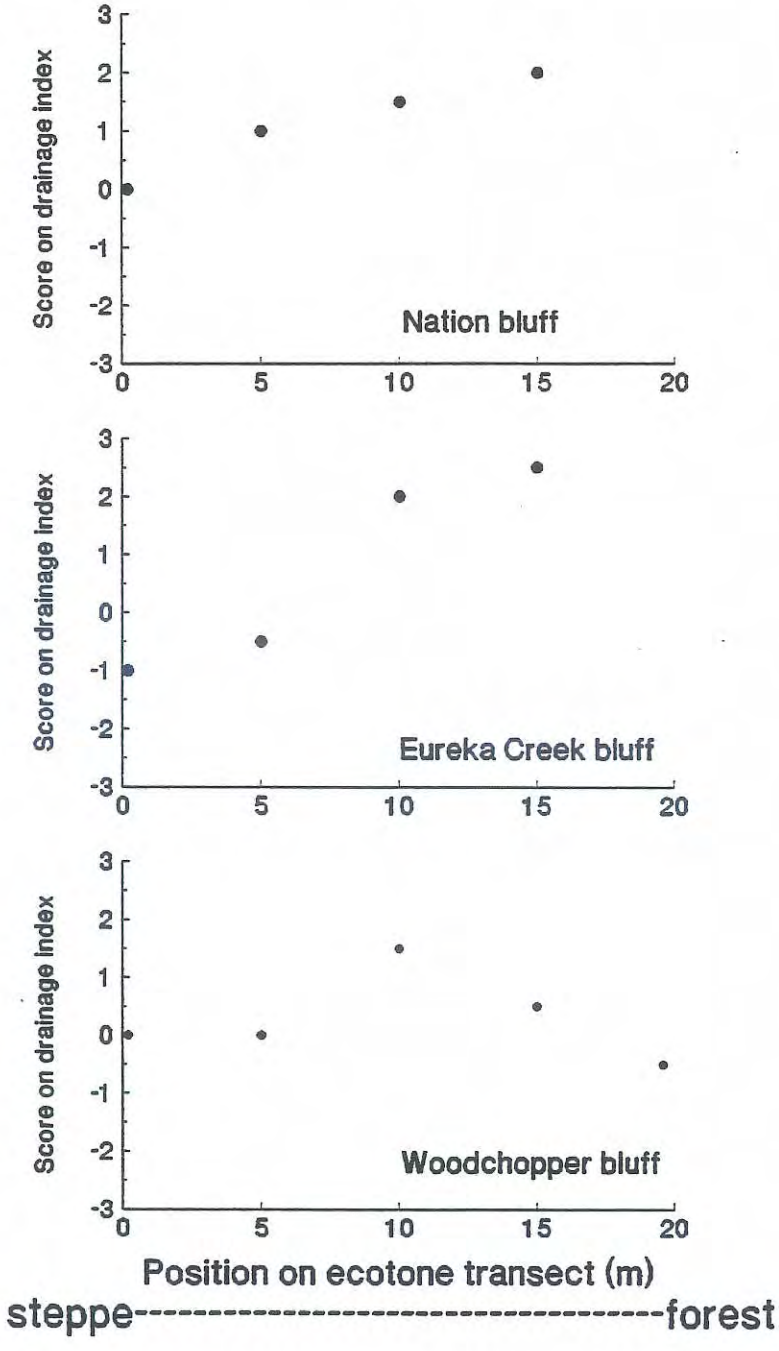


Fig. 8. Scores on the drainage index for stations along three ecotone transects on the Yukon River.

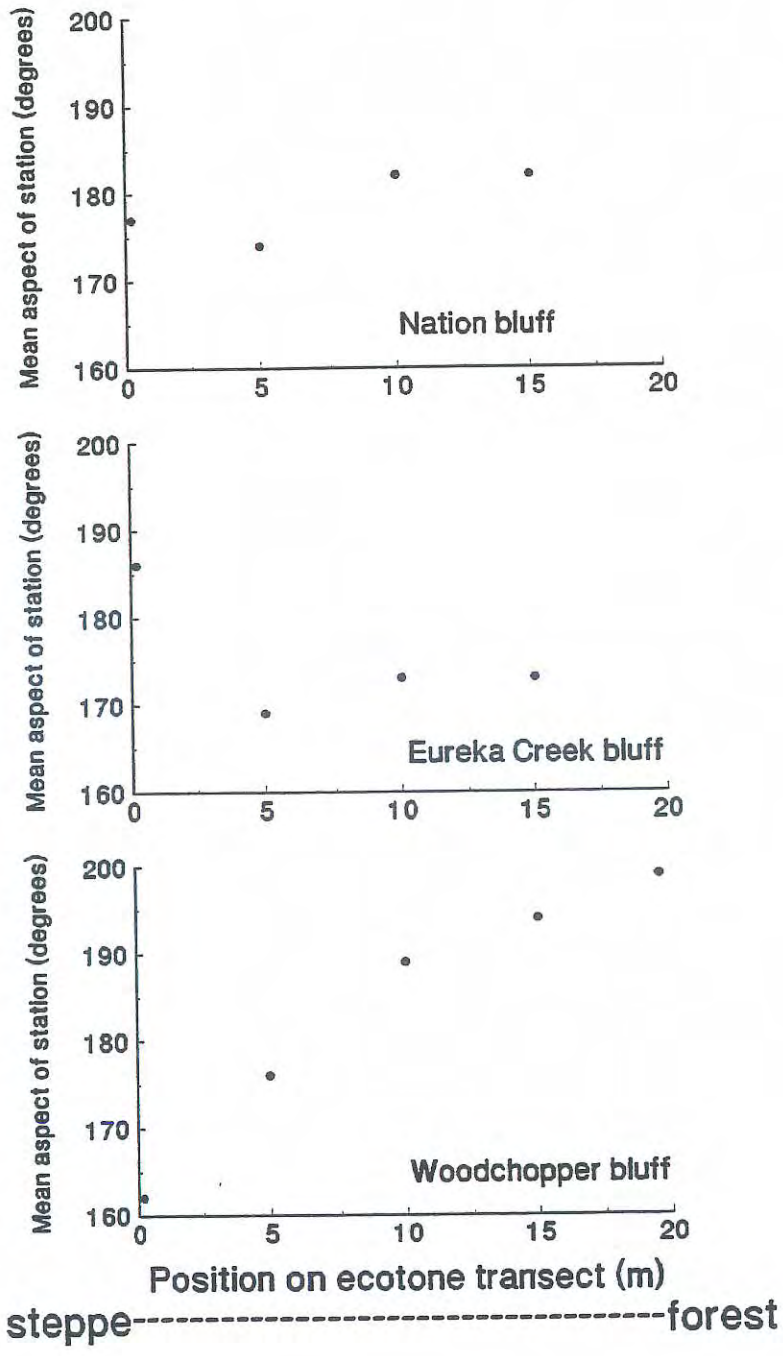


Fig. 9. Aspect of stations along three ecotone transects on the Yukon River.

Ordination of cover data from 13 vegetation stations sampled on the ecotone transects resulted in a strong first axis of variation. The first DCA axis (eigenvalue = 0.786) separated forest, edge, and steppe quadrats. The cover data entered into this analysis were for nonarboreal species in the 2 m above the ground. Shrubs typical of the forest understory such as *Viburnum edule* and *Sheperdia canadensis* scored high on this axis along with forest floor species such as *Linnaea borealis* and *Moeheringia laeteriflora*. Scoring low on the gradient were endemics such as *Penstemon gormanii* and *Draba murrayi* and the dominant steppe taxa *Agropyron spicatum*, *Artemisia frigida* and *Pulsatilla patens*. Boreal species typical of forest edges and canopy gaps such as *Rosa acicularis*, *Galium boreale* and *Solidago multiradiata* had intermediate scores on this axis.

A pronounced shift in both the structure and composition of the vegetation correlates with the change from unshaded steppe vegetation to forest understory. Dominance shifted from nonwoody forbs and graminoids in steppe areas to woody shrubs at the forested end of the ecotone (Fig. 10). Stepwise regression identified percent of sky shaded as the strongest predictor of the variation on this axis ($r^2 = 0.76$, $p < 0.0001$; Fig. 11). This simple linear model represented the best fit for the variation on DCA-1

Typical steppe species showed sharp declines in abundance along the short length (15 m) of these transects . Gradient analyses of steppe dominants *Agropyron spicatum*, *Pulsatilla patens*, *Calamagrostis purpurascens* and *Artemisia frigida* showed steep reductions in cover that parallel increases in shading by trees (Fig. 12). The shrubs *Sheperdia canadensis* and *Viburnum edule*, on the other hand, have much higher cover values in these shaded areas (Fig. 13).

The position of the ecotone (i.e. where trees are on the landscape) was controlled by different factors among these three bluffs (Figs. 8 and 9). The nature of the understory vegetation, conversely, is most strongly affected by factors associated with how much light penetrates to the ground (Fig. 11).

Effect of fire on the distribution of steppe

The ecotone between aspen forest and steppe is a dynamic one, and with time many of these open patches of vegetation undergo succession into forest. At each site visited, I searched for surficial charcoal, snag trees and fire scars on living trees. All sites

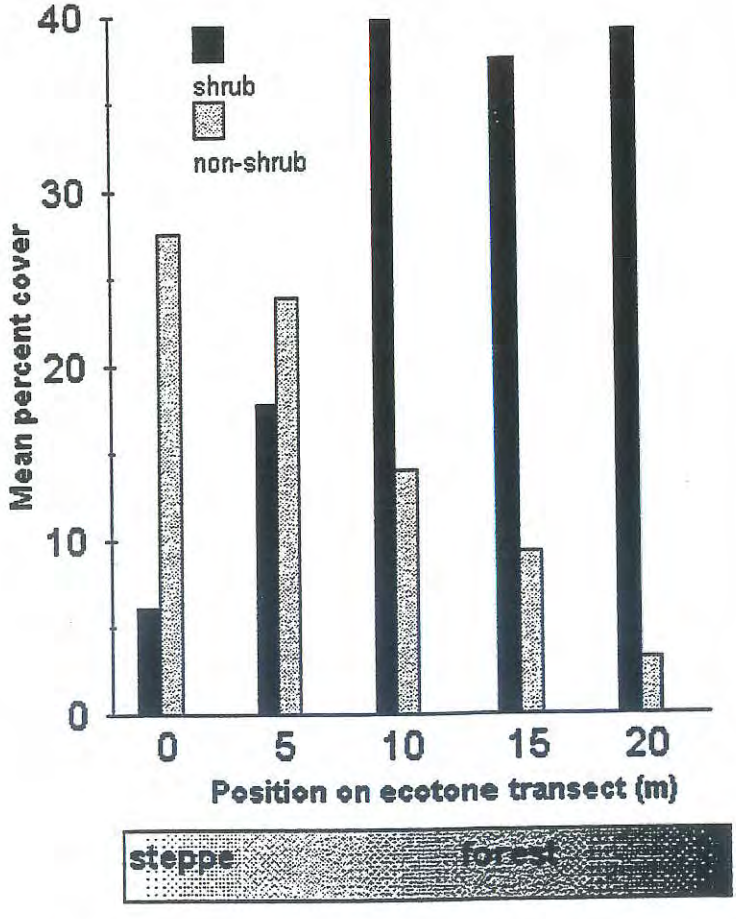


Fig. 10. Cover of shrub and non-shrub elements across all stations on three ecotone transects on the Yukon River.

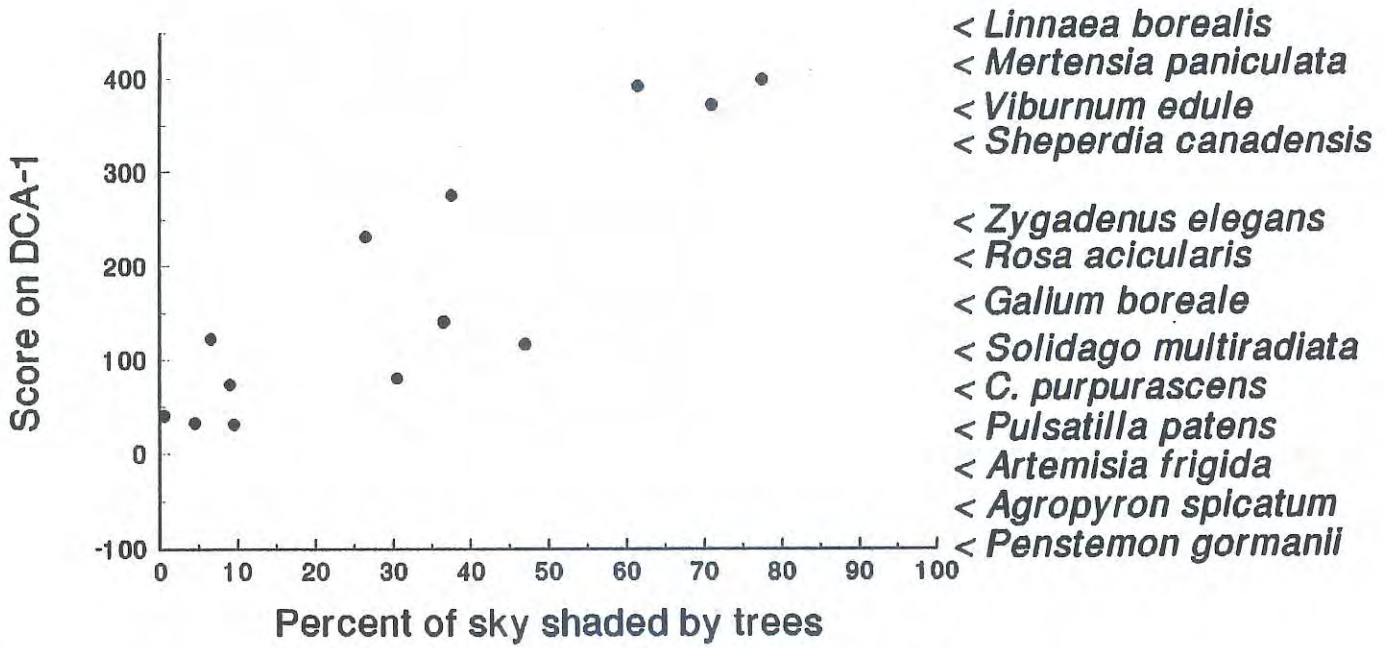


Fig. 11. Vegetation score on DCA-1 as a function of shading for 13 stations on three ecotone transects on the Yukon River.

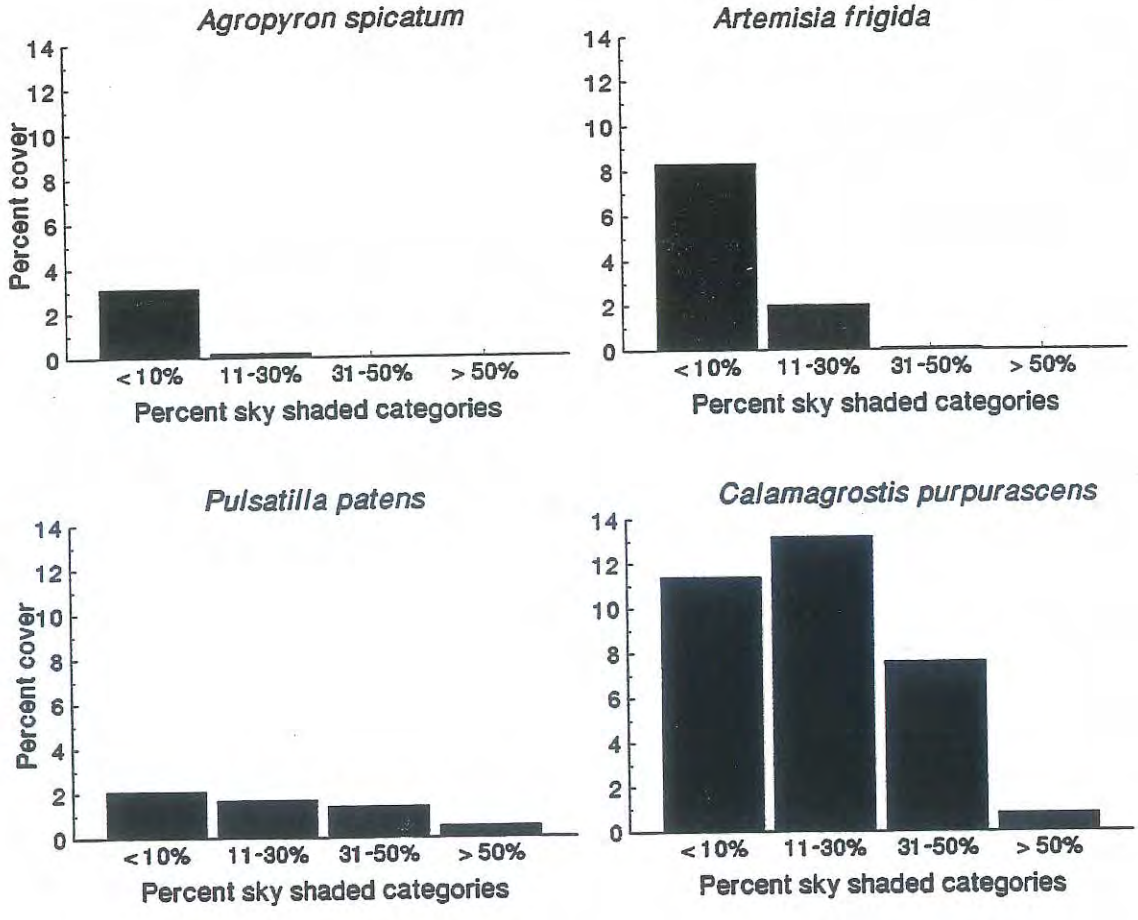


Fig. 12. Gradient analysis of cover of four steppe plants in relation to the amount of shade along three ecotone transects on the Yukon River.

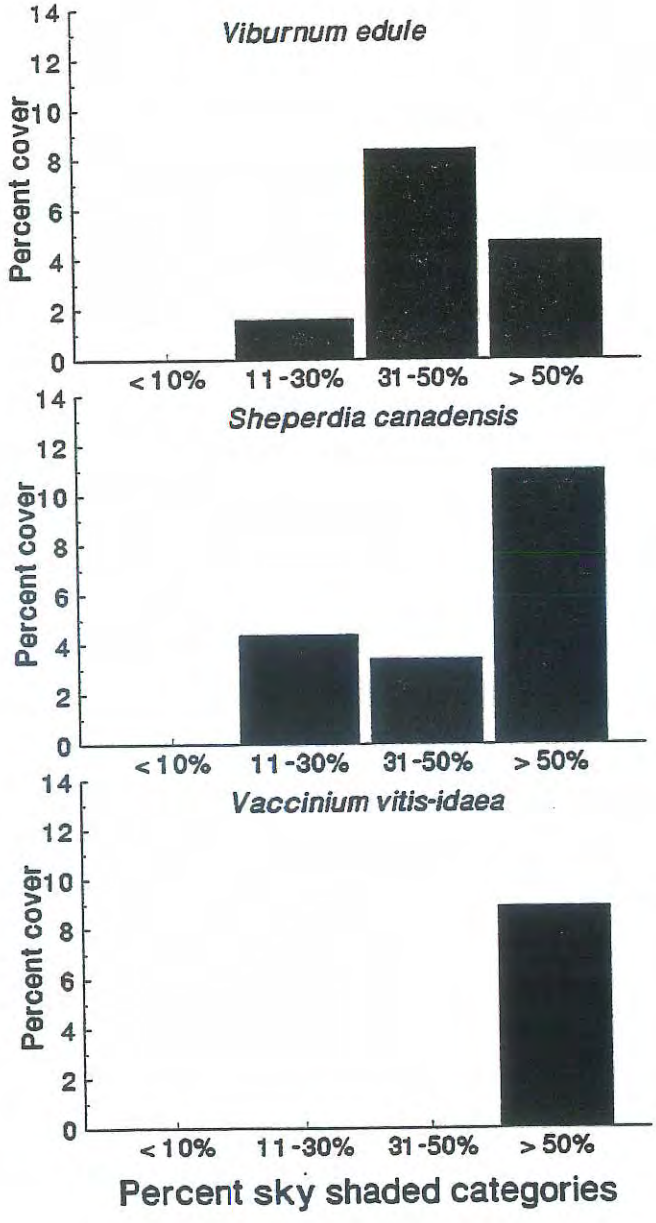


Fig. 13. Gradient analysis of cover of three forest understory plants in relation to the amount of shade along three ecotone transects on the Yukon River.

outside of a narrow range in aspect around due south (approximately 160° to 210°; Fig. 14) contained evidence of fire. Fires apparently served to increase available habitat on river bluffs in interior Alaska for the shade-intolerant steppe taxa.

Patterns of species distribution

The nature of the steppe community that develops on a surface in the upper Yukon River is in large part determined by a few important variables. EQ and elevation have similar effects on the composition of this vegetation throughout the study area. These factors strongly controlled the composition of steppe vegetation within the study area.

The strong trends in the vegetation identified by the first two DCA axes provide a conceptual framework within which to consider the ecological distribution of distinct groups of component species. Plotting the position of component species based on their scores on these axes yields informative patterns in the distribution of species groups in relation to environmental gradients.

Axis 1 was strongly related to EQ and elevation. Sites with high scores on this axis were, on average, higher in elevation and less south-facing than sites with low scores. Research at Kathul Mountain strongly suggests that the variation in vegetation reflected by this axis parallels the transition from steppe into dry tundra facies (Edwards and Armbruster 1989, Lloyd et al. 1994). The second axis is predicted by soil organic matter content and percent of sky shaded by trees. Wesser and Armbruster's (1991) work at Eagle bluff suggests that the variation in vegetation reflected by this axis parallels the transition from steppe into neighboring forest where the herbaceous vegetation meets with more favorable moisture conditions but also with greatly reduced availability of light.

I plotted the position of component taxa within the coordinate grid described by these two axes. For simplicity, I centered the partitions at the half-way point of each DCA axis. General habitat characteristics of the four quadrants described by this partition were inferred from the relationships between each axis and environmental characteristics identified by the regression analyses of site scores (Fig. 15).

Boreal meadow and woodland taxa were in the most mesic quadrant 2 (Fig. 16), which was characterized by surfaces of high EQ, elevation and increased soil organic

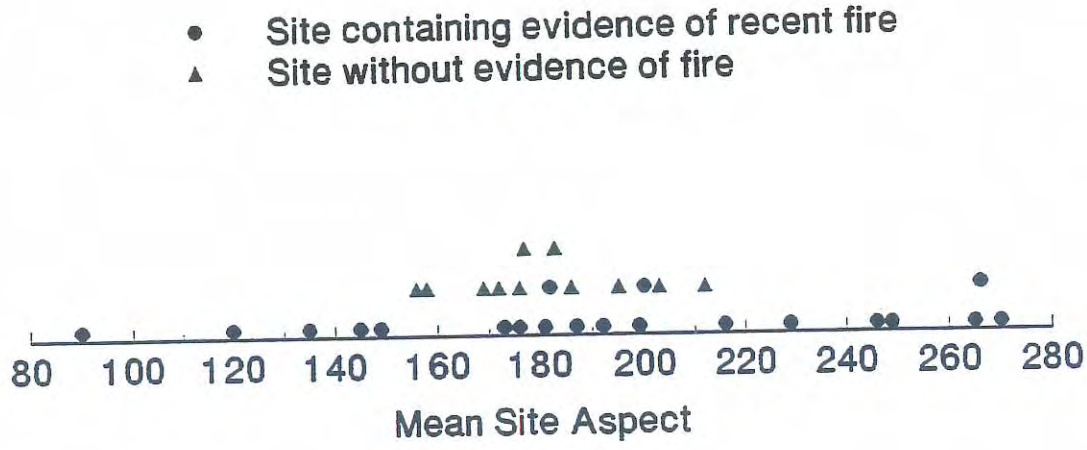


Fig. 14. Evidence of recent fire in steppe fields in relation to aspect at sites on the Yukon, Charley, Kandik, and Tatonduk Rivers.

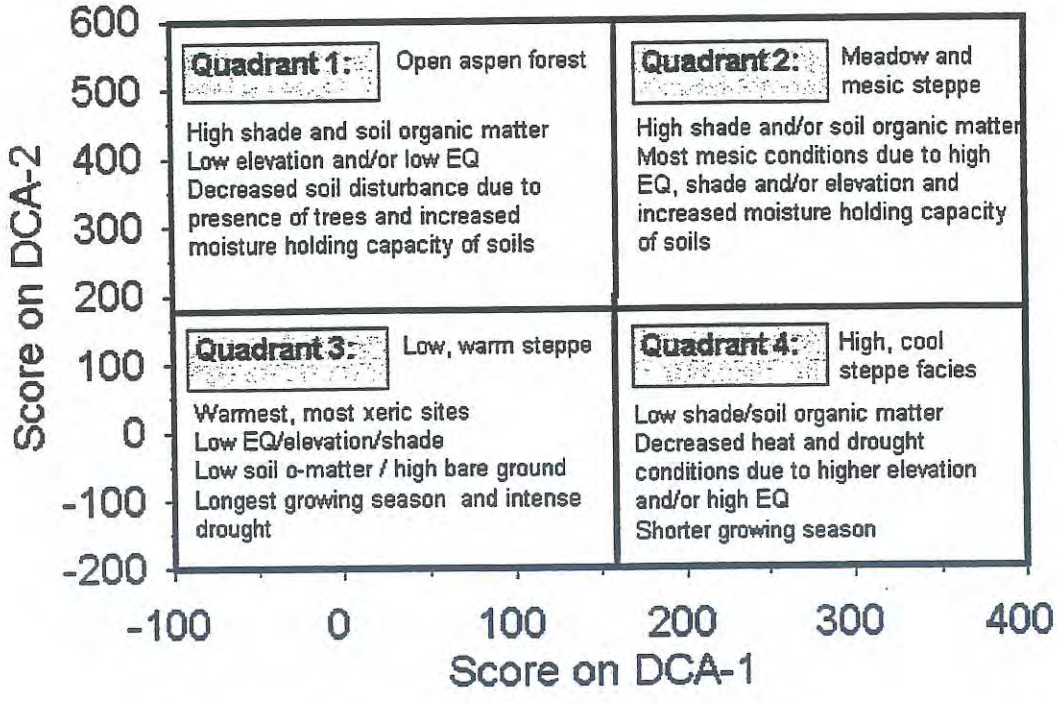


Fig. 15. Habitat characteristics of quadrants within coordinate grid described by DCA axes 1 and 2. Data are from for 23 sites on the Yukon River and these characteristics are inferred from regression analyses of site scores on environmental variables.

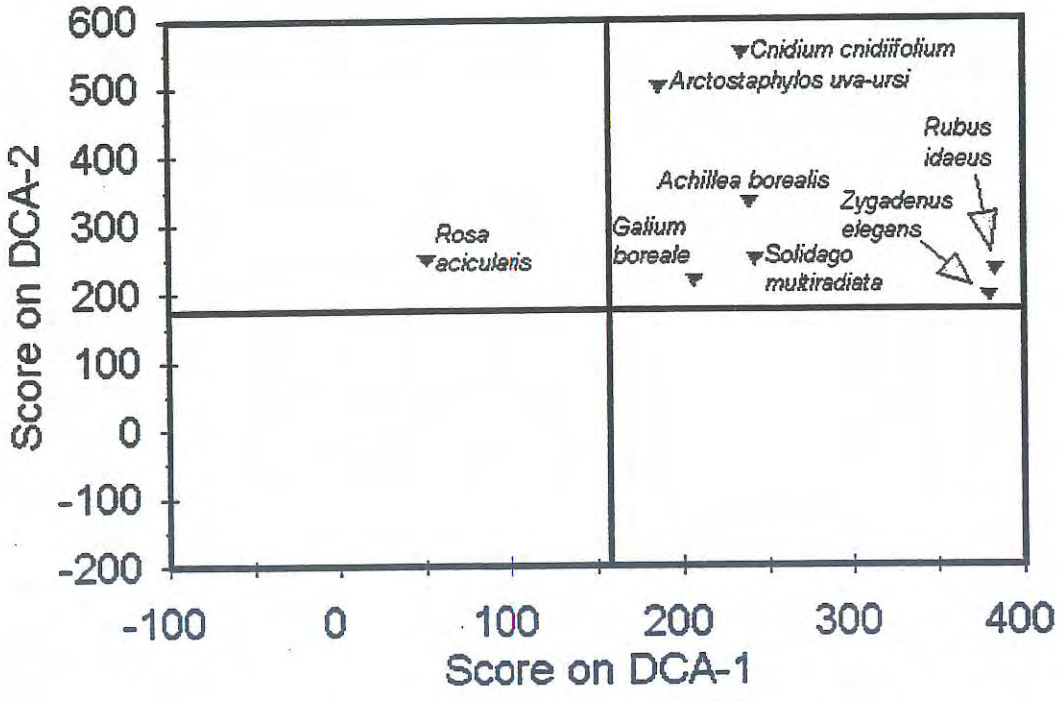


Figure 16. Ordinated location of common boreal species in the Yukon River steppe flora. Location is determined by species scores on DCA axes 1 and 2 for 23 sites on the Yukon River.

matter content and shade. Plants that have strong temperate steppe affinities clustered in quadrant 3 (Fig. 17); the most xeric sites with high radiation loads and little or no shade.

The disjunct amphiberingian taxa clustered high on DCA-1 and low on DCA-2 (see Fig. 18). The environment described by this quadrant was one of high light (little shade) and low soil organic matter but cooler soil temperatures. The amphiberingian taxa also showed a strong degree of separation from temperate steppe species in this ordination. Interestingly, there was substantial ecological overlap between the endemic component of the flora and the disjunct amphiberingian taxa (Fig. 19). This consonance suggests that the ecological situations that favor the disjunct Asian flora also favor the endemic component. Species from neither group (save the endemic *Penstemon gormanii*) appears to be ecologically linked to the most warm and xeric conditions within steppe dominated by the primary indicator taxa (*Artemisia, Agropyron, Calamagrostis*).

Arctic-alpine species with both North American and widespread biogeographic distributions are clustered in a position intermediate of the niche space containing the taxa of boreal meadows and the areas occupied by members of the endemic flora (Fig. 20).

KOLYMA RIVER STUDY AREA

Abiotic environment

The physical environment of sites 1 through 3 was characterized by moderately steep, north-facing slopes at elevations between 480 - 550 m (Table 9). These areas were treeless and bordered by open larch forest and rubble slopes with little vegetative cover. Sites 4 and 5 faced just south of due west. In this area steppe graded into open stands of *Pinus pumila* on slopes and *Larix* forest on level terrain. The elevation at sites 4 and 5 was between 540 and 585 m. Steeper slopes and deeper soils on the south-facing sites (6 and 7) resulted in generally higher levels of small scale geomorphic disturbance there. The elevation at sites 6 and 7 ranged between 488 - 550 m. These sites occupied the corner of a terrace with aspects spanning east-southeast to west-southwest (130° - 235°). Open steppe was bordered by small stands of *Populus tremula* on the slopes and closed mixed *Betula* and *Larix* forest on adjacent level terrain.

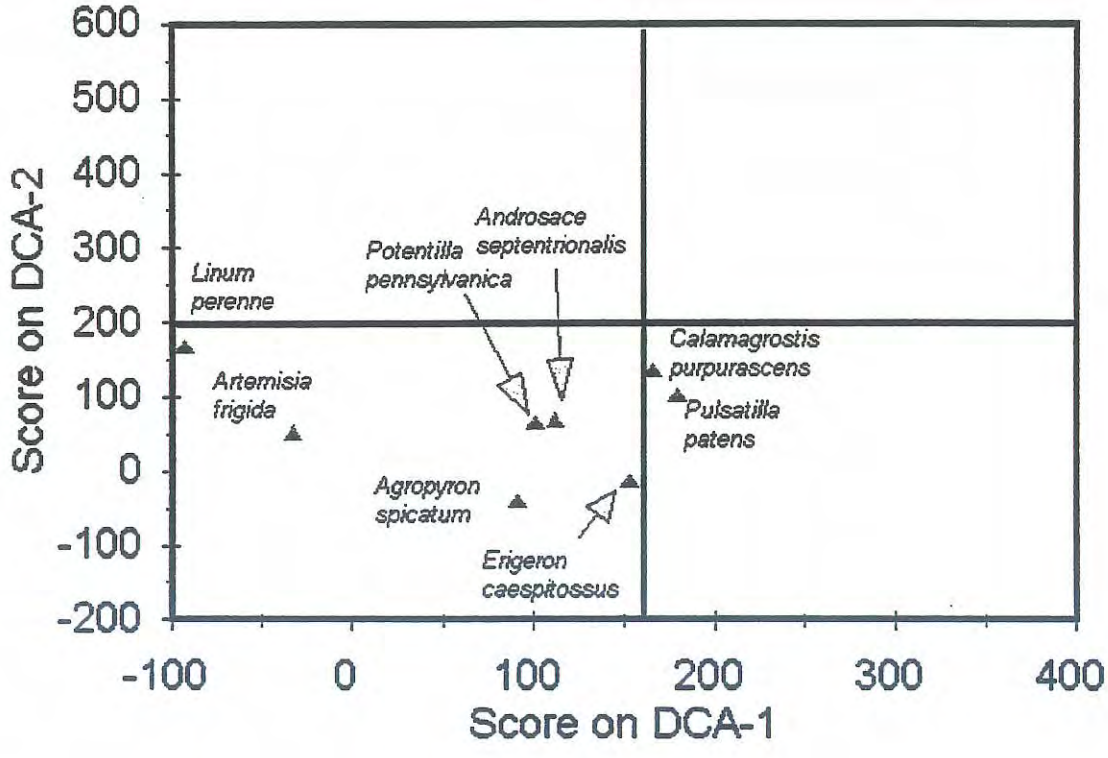


Figure 17. Ordinated location of plants with temperate steppe affinities in the Yukon River steppe flora. Location is determined by species scores on DCA axes 1 and 2 for 23 steppe sites on the Yukon River.

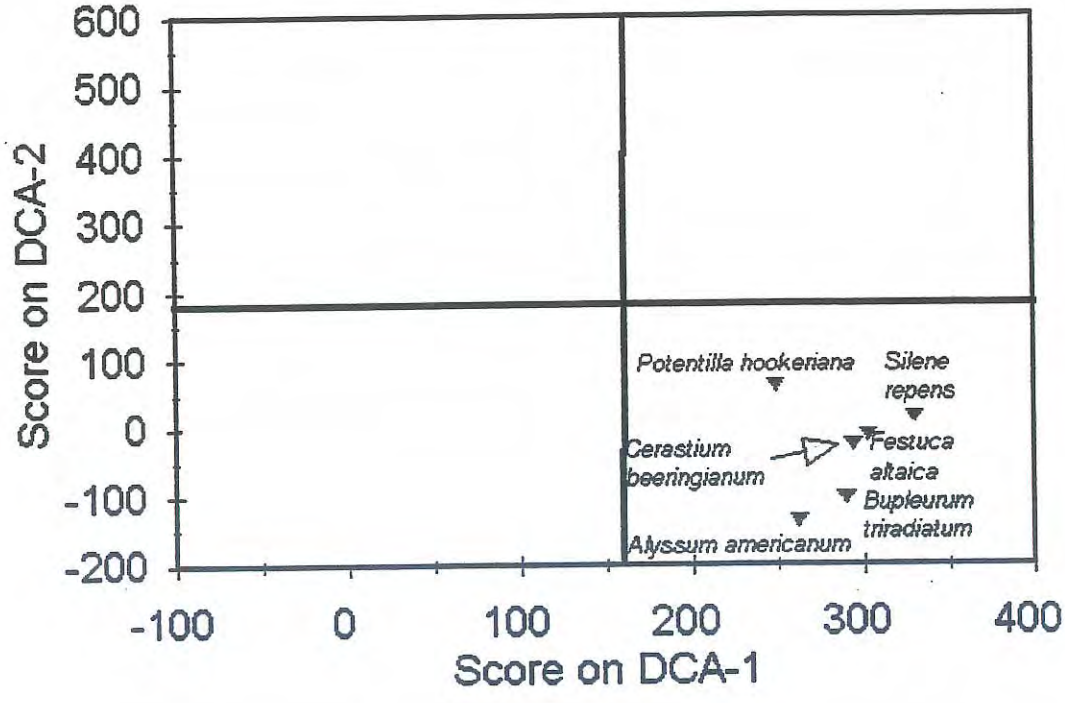


Fig. 18. Ordinated location of common amphiberingian steppe taxa in the Yukon River steppe flora (except *Artemisia frigida*). Location is determined by species scores on DCA axes one and two for 23 sites on the Yukon River.

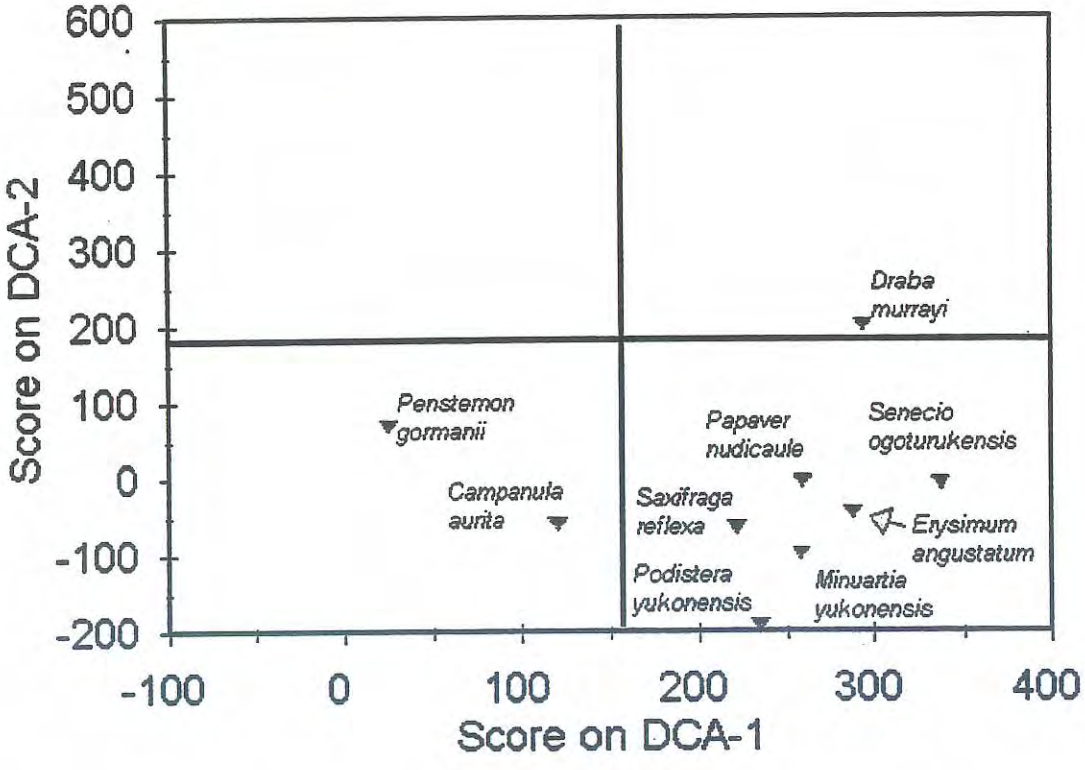


Fig. 19. Ordinated location of endemic taxa in the Yukon River steppe flora. Location is determined by species scores on DCA axes 1 and 2 for 23 steppe sites on the Yukon River.

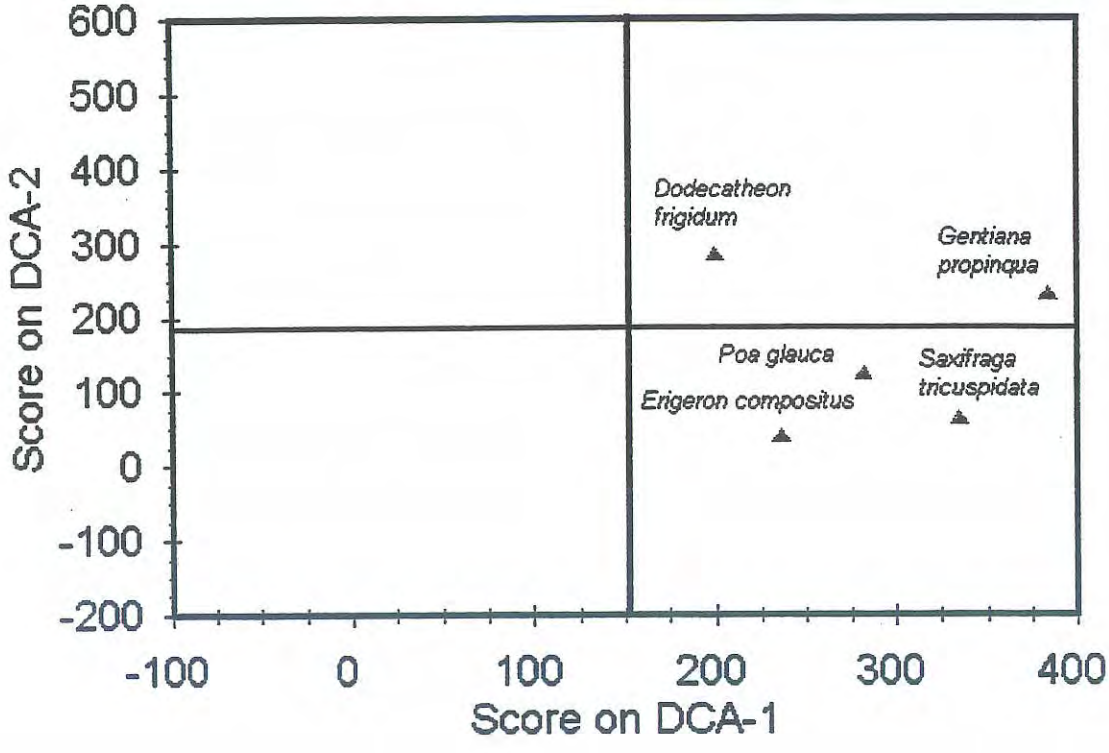


Fig. 20. Ordinated location of common arctic-alpine species in the Yukon River steppe flora. Location is determined by species scores on DCA axes 1 and 2 for 23 steppe sites on the Yukon River.

Table 9. Physical variables recorded at seven sites on the Kolyma River. Values are mean ± standard error.

Site	(n)[1]	Slope (degrees)	Aspect (degrees)	Azimuth (degrees)	EQ[2] (degrees)	% Rock	% Bare	Disturbance Index	Drainage Index
1	20	23.6 ± 0.8	9 ± 2.1	172 ± 1.7	82.8 ± 0.7	2 ± 0.3	36 ± 3.3	2.6 ± 0.2	-0.30 ± 0.22
2	15	26.9 ± 0.6	326 ± 0.7	146 ± 0.7	74.2 ± 0.3	7 ± 1.5	8 ± 2.4	2.0 ± 0.1	0.00 ± 0.22
3	8	24.1 ± 1.3	53 ± 3.4	127 ± 3.4	66.3 ± 1.6	1 ± 0.3	35 ± 5.8	3.0 ± 0.3	0.25 ± 0.16
4	18	24.1 ± 0.7	261 ± 0.8	81 ± 0.8	50.6 ± 0.6	1 ± 0.3	21 ± 7.1	2.9 ± 0.2	-0.50 ± 0.17
5	9	27.3 ± 1.0	258 ± 27.3	78 ± 1.8	47.4 ± 0.9	1 ± 0.2	19 ± 7.4	3.3 ± 0.2	-0.22 ± 0.28
6	18	32.5 ± 0.6	237 ± 1.9	57 ± 1.9	37.0 ± 0.5	2 ± 0.7	8 ± 2.9	3.4 ± 0.1	±0.06 ± 0.21
7	8	37.2 ± 1.3	151 ± 2.3	29 ± 2.3	26.7 ± 1.1	1 ± 0.3	19 ± 9.2	4.0 ± 0.3	0.38 ± 0.13

[1](n) = no. of quadrats at site [2]EQ = equivalent latitude

Soil

Soil attributes differed significantly between sites (Table 10). Mean soil pH of sites at high EQ was lower than at sites of low EQ ($r^2 = 0.85$, $p < 0.001$; Fig. 21). At south-facing sites white carbonate crusts were evident on surface rocks, and small concretions of carbonates were visible in the soil. Conversely, soil organic matter content was positively correlated with site EQ ($r^2 = 0.86$, $p < 0.001$; Fig. 22). As a consequence of higher organic matter content, available nitrogen also was higher in soils at the high EQ areas than warm, south-exposed sites. With increasing southern exposure, soils tended to be deeper and less rocky, apparently with a higher proportion of fines compared with the coarse-grained, rocky soils of sites at high EQ. North-facing soils appeared to have undergone less mineral weathering than those from intermediate and south-facing areas.

Clear patterns also emerged from the soil respiration/N-mineralization incubations. As expected, soil organic matter content was highly predictive of respiration rate over the course of the incubation ($r^2 = 0.895$, $p < 0.0001$). Similarly, the rate of net nitrogen mineralization was positively correlated with initial organic matter content when expressed as micrograms nitrogen mineralized per gram of total soil dry weight ($r^2 = 0.85$, $p < 0.0001$). In terms of the total soil, then, there was a close correlation between microbial activity in the incubations and availability of mineralizable substrate. Although there was considerable variability within sites, mean site EQ was highly predictive of mean potential microbial activity at a site due to the close correlation of EQ with total organic matter content. The regression relationships between mean rates of respiration and mineralization in the incubations and site EQ are highly significant ($r^2 = 0.79$, $p = 0.01$, and $r^2 = 0.63$, $p = 0.03$, respectively; Fig. 23).

If the observed rates of microbial activity are corrected using the organic matter fraction of the soil rather than its total dry weight, however, there is no correlation between topographic position and potential microbial activity. Rates of microbial activity per gram of organic matter present in the soil remained virtually the same across the topographical gradient. Whereas total soil respiration and net mineralization were significantly positively correlated with EQ, the ratio of carbon respired to nitrogen mineralized in the incubations was unrelated to topography ($p = 0.80$). If the nitrogen status of the plants on the north slope were significantly better than that of those on south slopes, an increase in organic matter quality would be one likely result. Although

Table 10. Soil properties of seven sites on the Kolyma River. Values are means ± standard error. [1] number of soil samples taken at site [2] mg mineral N per gram of soil (dry weight).

Site	(n)[1]	pH	% Organic	Avail.N[2]	Soil Depth
1	6	5.07 ± 0.11	16 ± 4	21.07 ± 7.59	12.0 ± 2.2
2	6	5.43 ± 0.16	18 ± 3	28.34 ± 4.81	12.4 ± 1.6
3	4	5.47 ± 0.12	17 ± 5	29.80 ± 7.34	5.8 ± 1.4
4	8	5.57 ± 0.06	8 ± 1	13.32 ± 2.28	17.2 ± 1.2
5	4	6.02 ± 0.21	10 ± 2	22.40 ± 5.95	12.6 ± 3.5
6	8	6.45 ± 0.06	8 ± 1	16.46 ± 2.36	22.9 ± 2.1
7	6	6.23 ± 0.14	5 ± 1	8.67 ± 3.97	26.0 ± 2.8

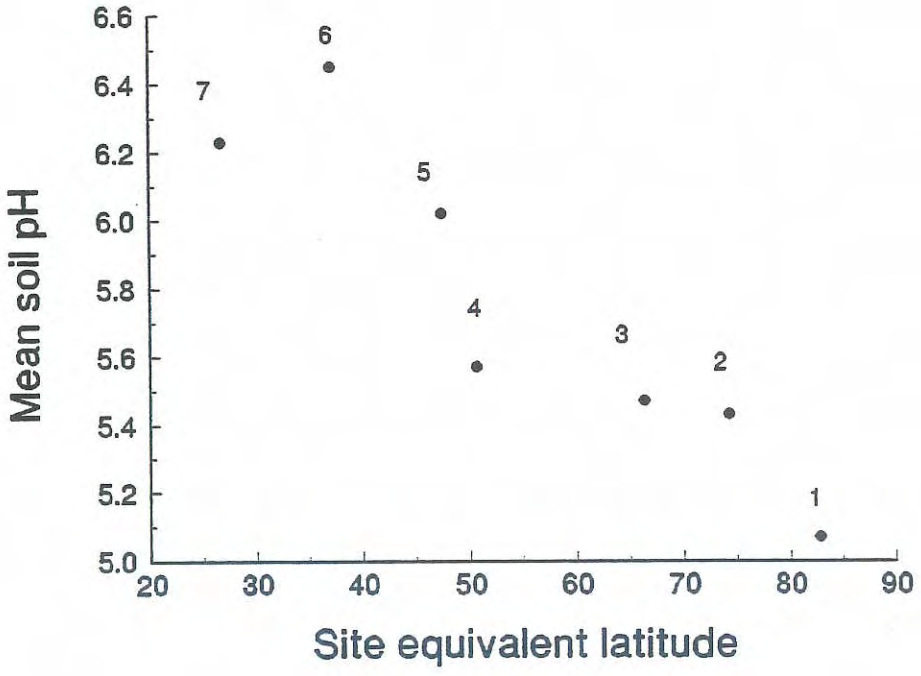


Fig. 21. Soil pH as a function of EQ at seven sites on the Kolyma River.

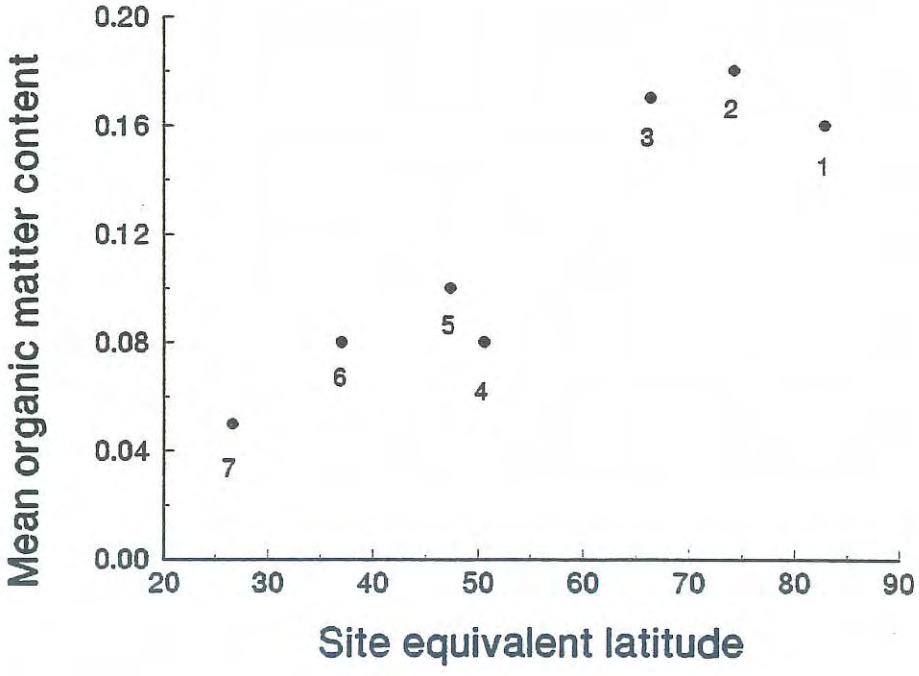


Fig. 22. Soil organic matter content as a function of EQ at seven sites on the Kolyma River.

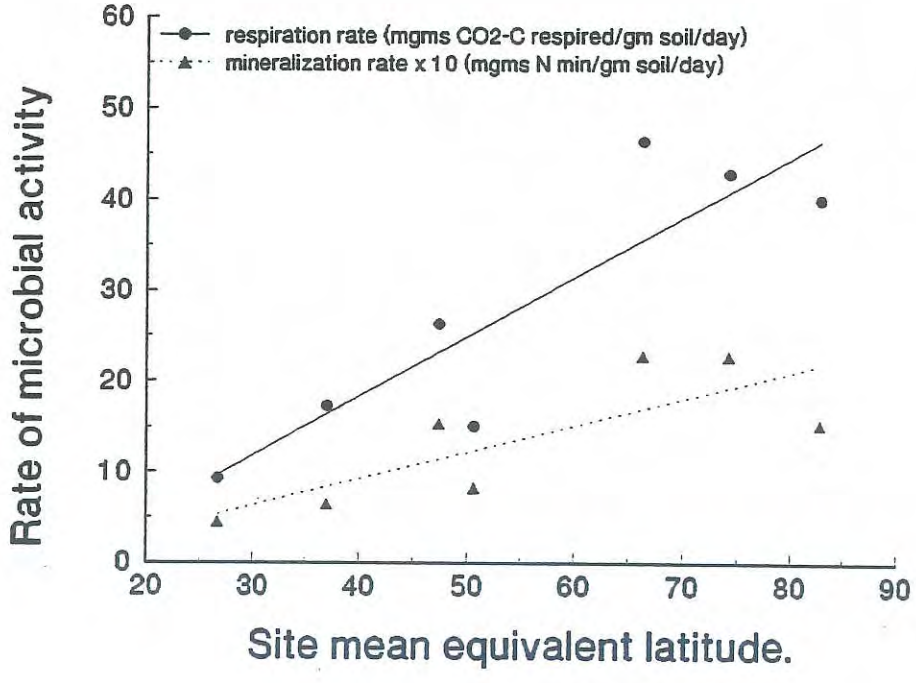


Fig. 23. Soil mineralization and respiration rates as a function of EQ at seven sites on the Kolyma River.

the quantity of substrate certainly differs between these soils as a function of topographical position, the quality of the substrate may not.

Vegetation

North-facing steppe contained a mix of steppe and tundra taxa (Table 11). This vegetation includes xerophytes also occurring at steppe sites along the Yukon River such as *Potentilla nivea*, *Pulsatilla patens*, and *Silene repens* growing alongside common amphiberingian tundra taxa such as *Artemisia arctica*, *Androsace chamaejasme* and *Bistorta plumosa*. The structure of the vegetation on these north-facing sites resembles the highest elevation sites at Kathul Mountain in Alaska. These sites have organic-rich, yet coarse-grained soils, high cover of lichens, a prominent tufted fescue component, and a species-rich herbaceous flora including plants with tundra affinities. Dominant vascular taxa on the north-facing steppe included the tufted *Festuca brachyphylla*, *Oxytropis vassilczenkoi* and *Dianthus repens*. The spike moss *Selaginella sibirica* was very abundant on north-facing surfaces along this gradient.

South-facing slopes supported larger plants and lower species richness. Dominant taxa on these surfaces were *Dracocephalum palmatum*, *Elytrigia villosa*, *Thymus serpyllum*, *Saxifraga multiflora* and *Vicia* sp. (Table 11). Although abundance of dominant species shifted along the gradient and some species only occurred at one extreme, several species occupied the entire gradient, and many occurred along more than one-half of it.

Relationships between vegetation and topography

Ordination of plant abundance values results in a powerful first DCA axis (eigenvalue = 0.656) suggesting a high degree of ordering of these data. EQ was strongly predictive of the variation along this axis ($r^2 = 0.875$, $p < 0.0001$; Fig. 24).

Community structure varied as a function of EQ, as was also the case at the Yukon River sites. Specifically, species richness per quadrat and lichen and bryophyte cover increased with EQ whereas total herbaceous cover, concentration of dominance (Simpson's index), and amount of litter cover decreased with EQ. In other words, surfaces of low EQ supported a less diverse vegetation containing more vascular plant cover, and dominance concentrated in a few important species (Fig. 25). Mean species-

Table 11. Distribution of species among seven sampling sites on the Kolyma River. Column numbers represent sites. '1' indicates presence of species in quadrats at site, '-' indicates absence from quadrats. DCA-1 is species-score on DCA-1.

Taxon	1	2	3	4	5	6	7	DCA-1
Galium boreale L.	-	-	-	-	-	1	-	484
Sedum sp. 1	-	-	-	-	-	1	1	483
Campanula sp.	-	-	-	-	-	-	1	476
Poa sp.	-	-	-	-	-	1	1	458
Potentilla Hookeriana Lehm.	-	-	-	-	-	1	1	457
Thymus serpyllum L.	-	-	-	-	-	1	1	456
Androsace septentrionalis L.	-	-	-	-	-	1	-	452
Arabis sp.	-	-	-	-	-	1	1	450
Clausia aprica (Steph) Korn.-Tr.	-	-	-	-	-	1	1	426
Castelleja sp.	-	-	-	-	-	1	-	419
Sedum sp. 2	-	-	-	-	-	1	-	417
Elytrigia villosa (Drabov) Tzvelev	-	1	1	1	1	1	1	324
Saxifraga multiflora Ledeb.	1	1	1	1	1	1	1	323
Dracocephalum palmatum Steph.	-	1	-	1	1	1	1	322
Artemisia sp. 1	-	-	-	1	1	-	-	309
Vicia sp.	-	1	-	1	1	1	1	301
Epilobium angustifolium L.	1	-	-	1	1	1	-	251
Rosa acicularis Lindl.	-	-	-	1	1	1	-	222
Pulsatilla patens (L.) Mill.	1	1	1	1	1	1	1	207
Allium strictum Schrad.	1	1	1	1	1	1	1	202
Carex pediformis C.A. Meyer	1	1	-	-	-	1	1	202
Arenaria tschuktorum Regel	1	-	-	1	1	1	1	191
Gypsophila violacea (Ledeb.) Fenzl.	-	1	1	1	1	-	-	170
Galium verum L.	1	1	1	1	1	1	1	161
Potentilla nivea L.	1	1	1	1	1	-	-	147
Poa stepposa (Krylov) Roshov.	-	-	-	-	-	1	1	146

Table 11, continued

Taxon	1	2	3	4	5	6	7	DCA-1
Silene repens Patrin	-	1	1	1	1	1	-	142
Scorzonaria radiata Fisch. ex Ledeb.	1	1	1	1	1	-	-	137
Carex argunensis Turcz. ex Trev.	1	1	1	1	1	-	-	134
Astragalus sp.	-	1	-	1	-	-	-	131
Phlojodicarpus villosa Turcz.	1	1	1	-	1	-	-	102
Astrocodon expansus (J. Rudolph) Fed.	1	1	1	1	1	-	-	75
Erysimum Pallasii (Pursh) Fern.	1	1	1	1	1	-	-	60
Taraxacum sp.	-	1	-	-	-	-	-	57
Aster alpinus L.	1	1	1	1	-	-	-	54
Calamagrostis purpurascens R. Br.	1	1	1	1	-	-	-	54
Artemisia sp. 2	-	1	-	-	-	-	-	34
Androsace chaemejasme Host	-	-	1	-	-	-	-	25
Stellaria jacutica Schischk.	1	1	1	1	1	-	-	22
Festuca brachyphylla Schult.	1	1	1	1	1	0	0	16
Oxytropis sp. 2	-	1	1	-	-	-	-	9
Buplurum triradiatum Adams	1	1	1	1	-	-	-	7
Orostachys spinosa (L.) C.A. Meyer	-	1	-	-	-	-	-	6
Oxytropis vassilczenkoi Jurtz.	1	1	1	1	-	-	-	1
Patrinia sibirica (L.) Juss.	1	1	1	-	-	-	-	1
Artemisia arctica Less.	1	1	1	-	-	-	-	-1
Dianthus repens Willd.	1	1	1	-	-	-	-	-11
Dryopteris fragrans (L.) Schott	1	1	1	-	-	-	-	-15
Selaginella sibirica (Milde) Hieron.	1	1	1	1	1	1	1	-15
Papaver nivale Tolm.	1	1	1	-	-	-	-	-25
Silene stenophylla Ledeb.	1	1	1	-	-	-	-	-28
Polygonum bistorta L.	1	1	1	-	-	-	-	-31
Hierochloe alpina (Sw) Roem.&Schult	1	1	1	-	-	-	-	-34
Polygonum sp.	1	-	-	-	-	-	-	-50
Polemonium boreale Adams	1	-	-	-	-	-	-	-61

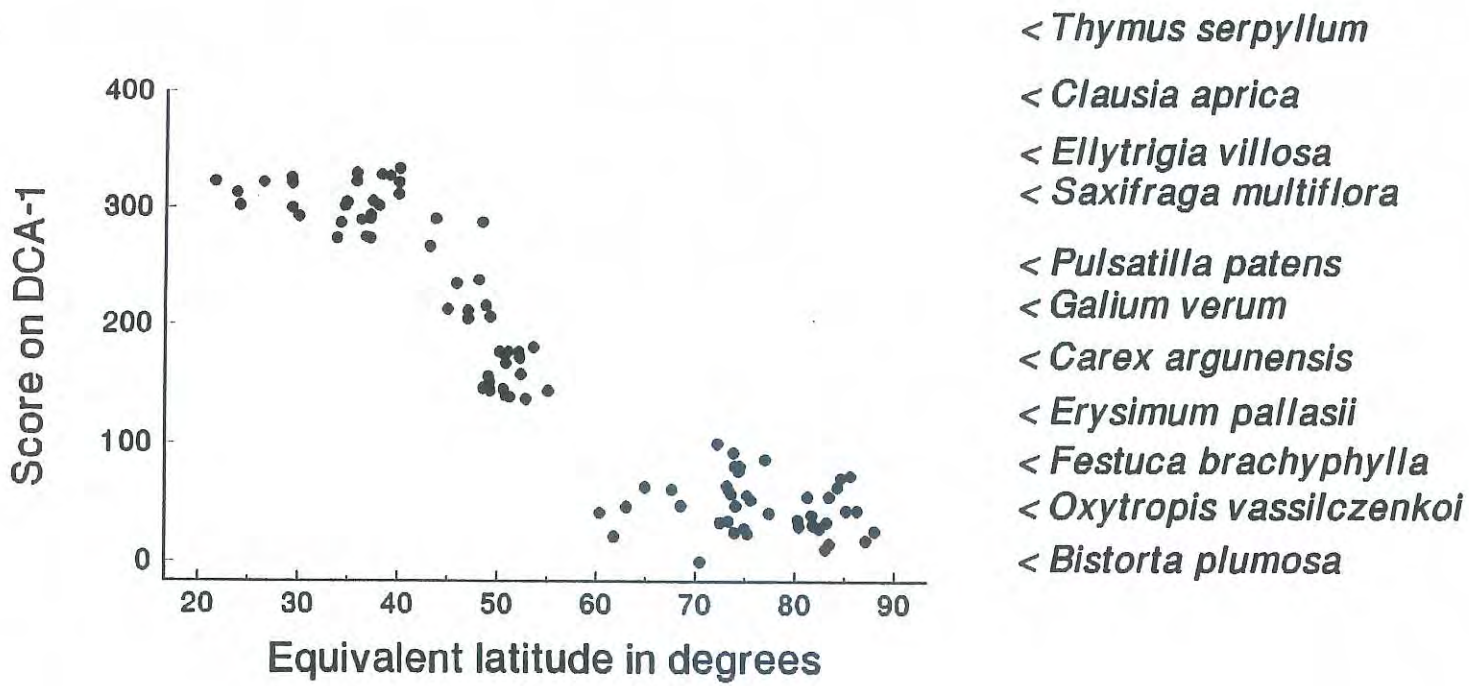


Fig. 24. Vegetation score on DCA-1 as a function of EQ for 96 quadrats at steppe sites on the Kolyma River. Selected species scores (on DCA-1) are included at right.

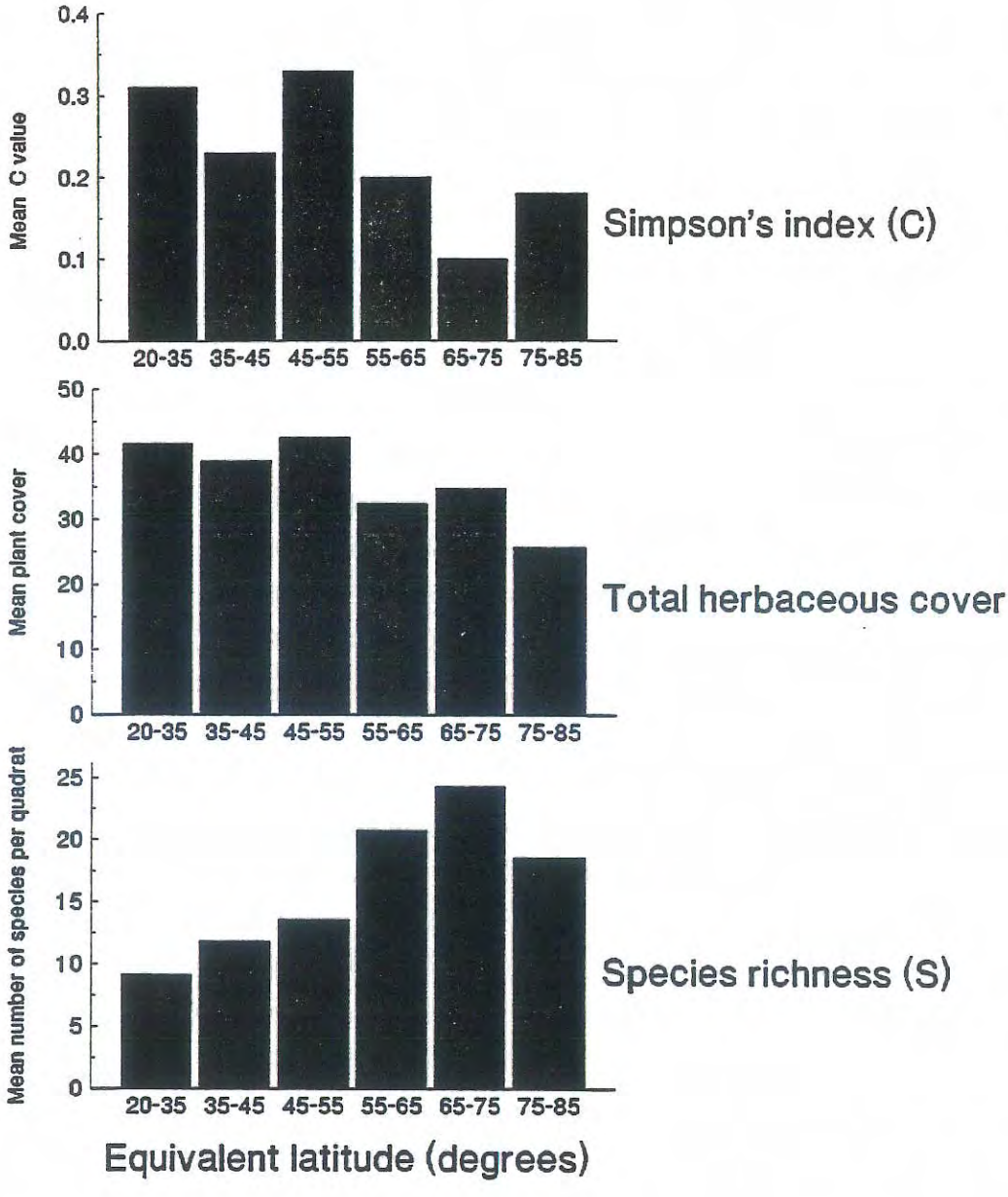


Fig. 25. Gradient analyses of three community parameters in relation to EQ in steppe vegetation at sites on the Kolyma River

area curves for sites with different values of EQ (Fig. 26) show that total species richness for a site correlated well with species richness per quadrat.

Disturbance was also negatively correlated with DCA-1, species richness, and both lichen and bryophyte cover. Total herbaceous cover increased with increased concavity of the slope, suggesting a beneficial increase in soil moisture in even small swales.

Although the number of vascular plant species per quadrat decreased by more than one-half over the course of this gradient, there is no parallel decline in total vascular plant cover. In fact, total vascular plant cover tended to increase with decreasing EQ ($r^2 = 0.20$, $p < 0.001$). Indeed, this resulted in a weak inverse correlation between herbaceous cover and species number in a quadrat ($r = -0.17$).

The cover of lichens and bryophytes was much reduced on south-facing slopes (Fig. 27). Highest lichen abundance was observed at plots between 55° and 75° EQ. Lichen cover at the south-facing sites was restricted to crustose forms. Mosses were more prominent in sheltered areas and slope depressions on the mid and high EQ areas. Vascular plant cover exceeded bryophyte cover in low EQ areas.

Patterns of species distribution

Interestingly, plants that increase in abundance on the most xeric, south-facing surfaces tend to be broadly distributed within steppe habitat, whereas plants dominant at high EQ are frequently absent or nearly so from the sites of lowest EQ (Fig. 28). The south-slope dominants, *Elytrigia villosa* and *Saxifraga multiflora* persist across the entire gradient, whereas the cold steppe taxa *Festuca brachyphylla* and *Oxytropis vassilczenkoi* are absent from the lowest EQ areas (Fig. 28).

AUTECOLOGY AND BIOGEOGRAPHY OF STEPPE PLANTS

Yukon River study area

Two factor gradient analysis

The persistence of south-slope dominants throughout the available habitat was noted for both the Kolyma River and Yukon River steppe floras. The response surface elucidated by two-factor gradient analyses of species abundance provides a more complete picture of the character of species responses to a suite of environmental variables.

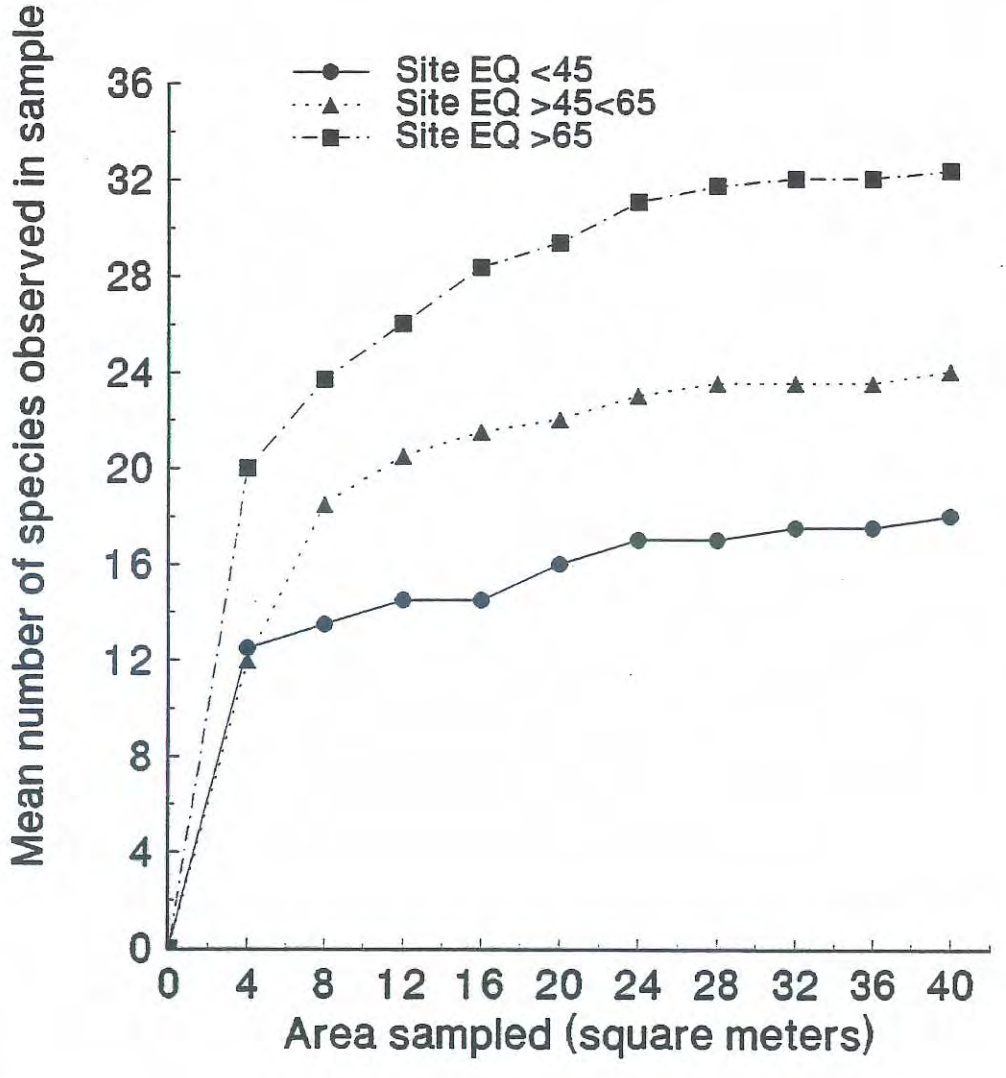


Fig. 26. Mean species-area curves for sites in three categories of EQ on the Kolyma River.

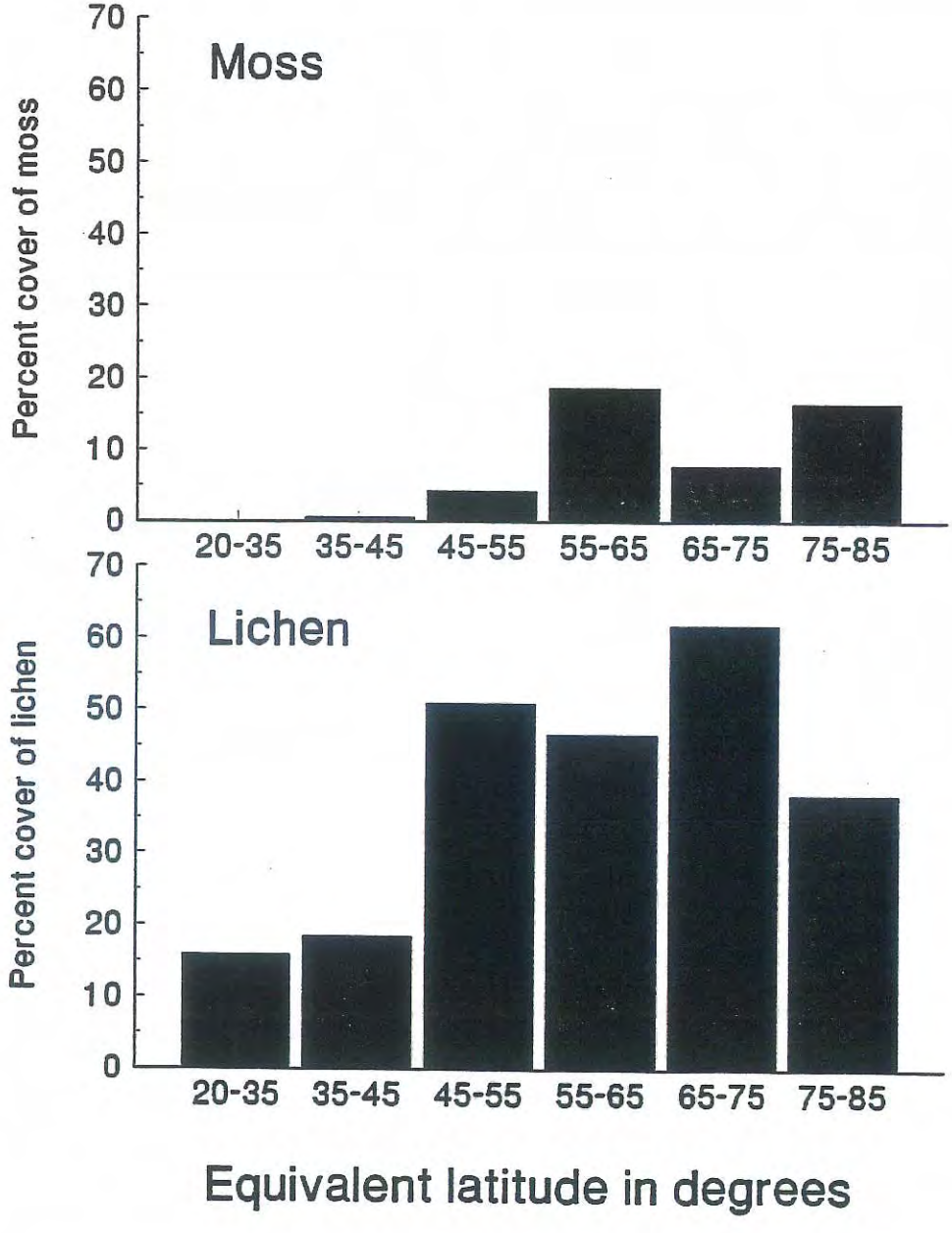


Fig. 27. Gradient analyses of moss cover and lichen cover in relation to EQ in steppe vegetation at seven sites on the Kolyma River.

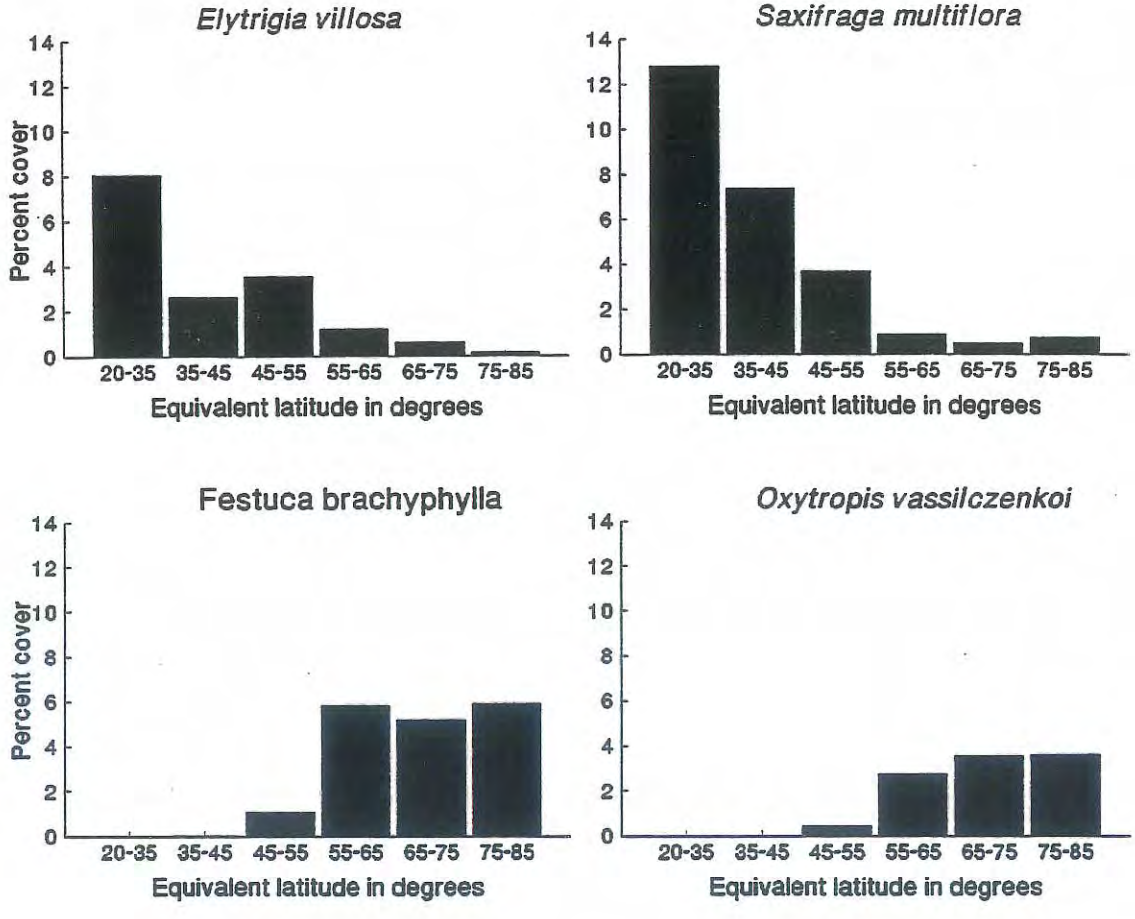


Fig. 28. Gradient analyses of cover of two warm steppe dominants (*E. villosa* and *S. multiflora*) and two cold steppe dominants (*F. brachyphylla* and *O. vassilczenkoi)* in relation to EQ in steppe vegetation on the Kolyma River.

The three most abundant taxa on the low EQ facies of Yukon River steppe sites, *Calamagrostis purpurascens*, *Agropyron spicatum*, and *Artemisia frigida* display broad ecological amplitudes (Figs. 29 through 31). Although both the direction and magnitude of their responses to the variables differ, these xerophytic taxa appear capable of growth and reproduction under an array of ecological conditions. Thus the contrast with the ecological distributions of *Minuartia yukonensis* and *Dodecatheon frigidum* is marked (Figs. 32 and 33). *Minuartia* is entirely absent in quadrats below 380 meters in elevation and *Dodecatheon* is virtually absent from quadrats in the low EQ category, regardless of the levels of other factors. The pronounced increase in *Dodecatheon* cover in concave slope areas is characteristic of several species whose abundance in steppe is greatly increased in relatively well-watered slope depressions and gully features within hot and dry facies on low EQ slopes.

Association between geographic distribution and ecological response

Twenty four prominent steppe taxa from Yukon River sites were categorized into biogeographic classes (Table 12). The same categorization was performed for 40 taxa from the Kolyma River sites (Table 13). In both study areas, species more abundant on surfaces of high EQ far outnumbered those that were more abundant at low EQ (Fig. 34).

There is a strong degree of association between a positive response to elevation and membership in the biogeographic groups at Yukon River sites ($p = 0.0001$; Fig. 35). Nearly one-half of the widespread species are more abundant at low elevation than high elevation, whereas none showed an increase in abundance at high elevation. The group of species with an amphiberingian distribution, on the other hand, showed a marked tendency toward increasing abundance with increasing elevation. Only the common steppe plant in this category, *Artemisia frigida,* showed increased abundance at low elevation. Species restricted to North America were unresponsive to the gradient in elevation with only one species increasing in abundance with elevation and none showing the opposite response.

The responses of these taxa to EQ showed a similar trend: amphiberingian species were more likely to show a significant increase in abundance with increased EQ than members of the other groups (Table 14). These differences, however, were not statistically significant.

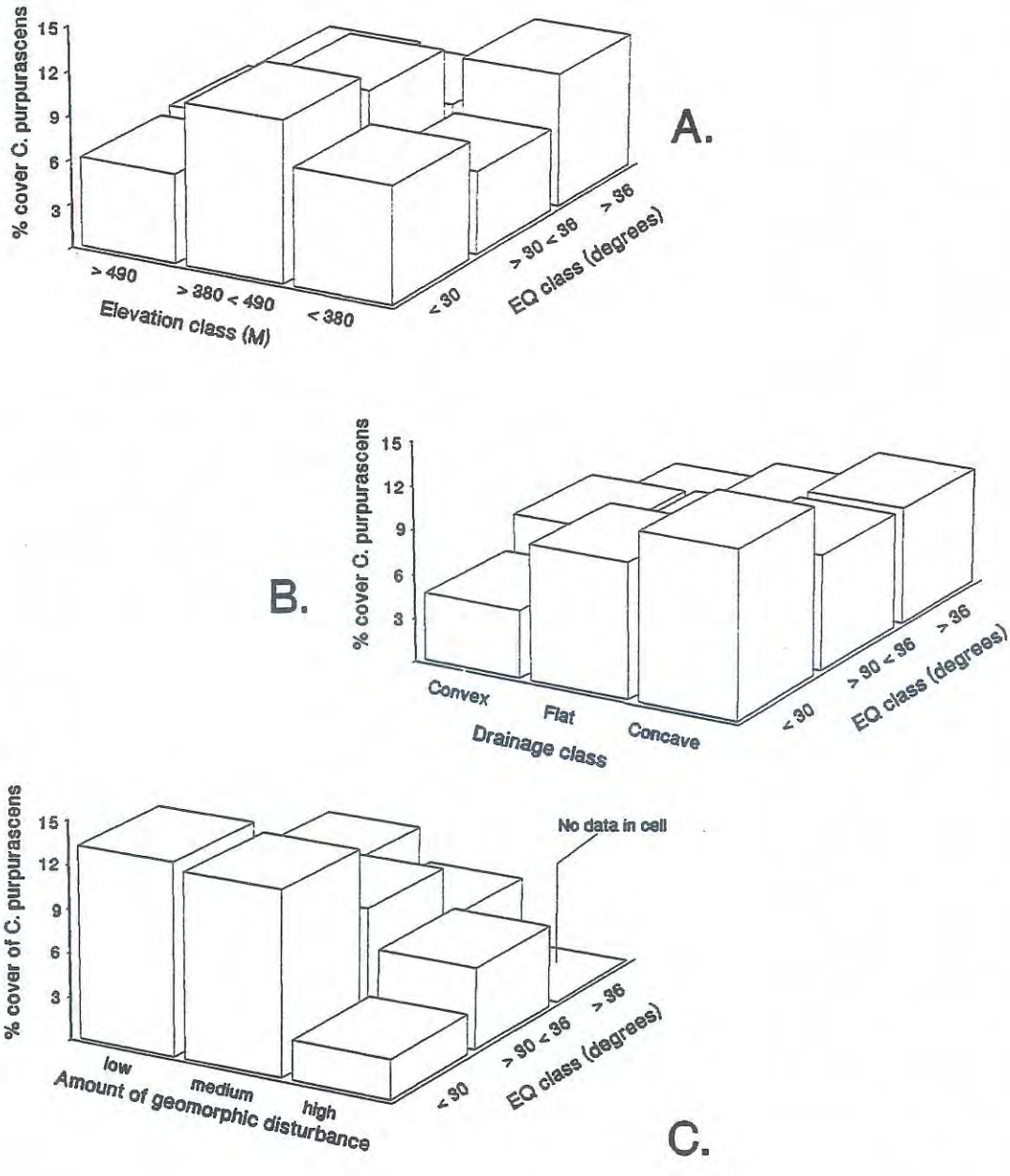


Fig. 29. Two-factor gradient analyses for *Calamagrostis purpurascens* cover in the Yukon River study area. Habitat variables are: (A) EQ and elevation, (B) EQ and drainage and (C) EQ and disturbance.

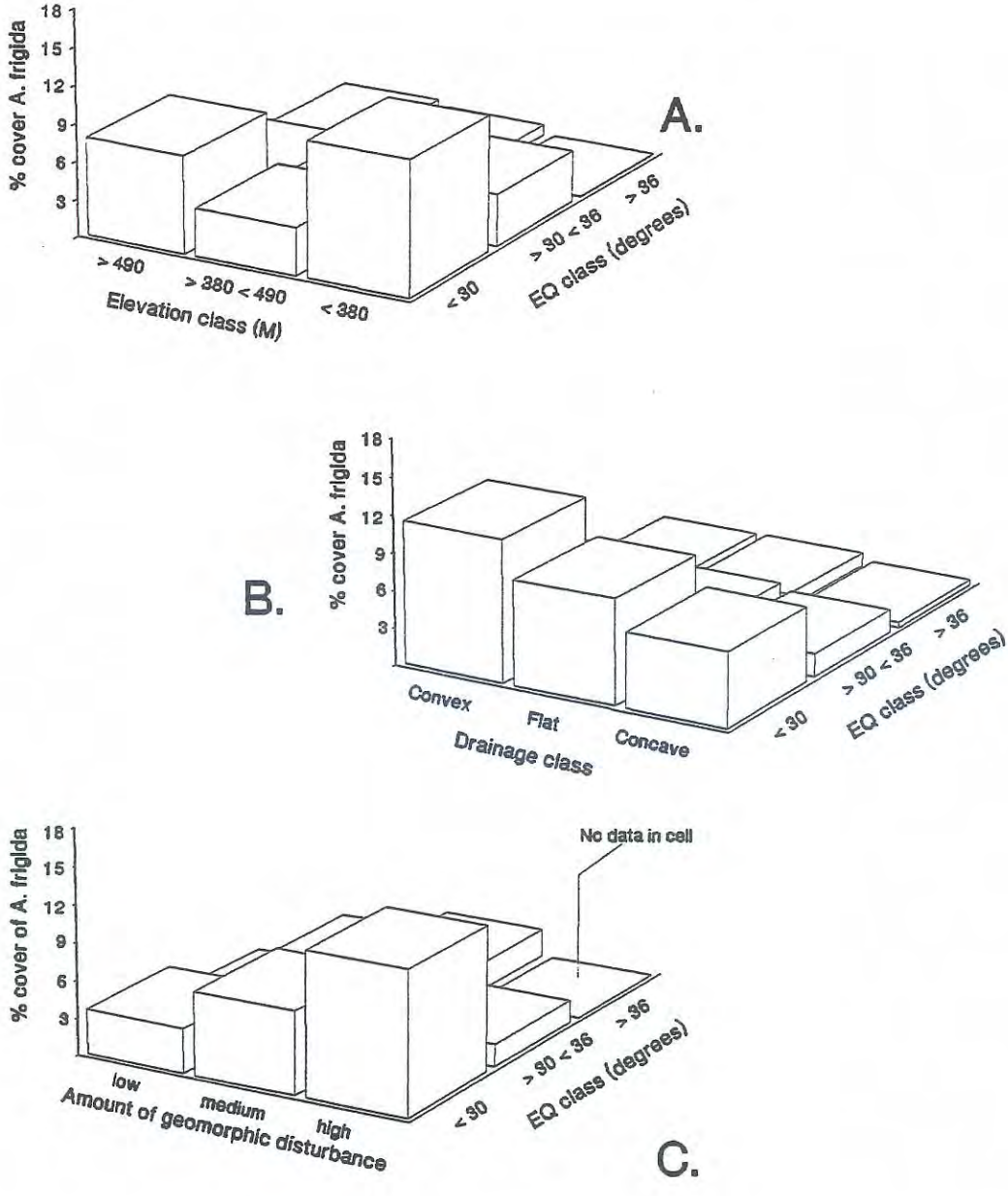


Fig. 30. Two-factor gradient analyses of *Artemisia frigida* cover in the Yukon River study area. Habitat variables are: (A) EQ and elevation, (B) EQ and drainage and (C) EQ and disturbance.

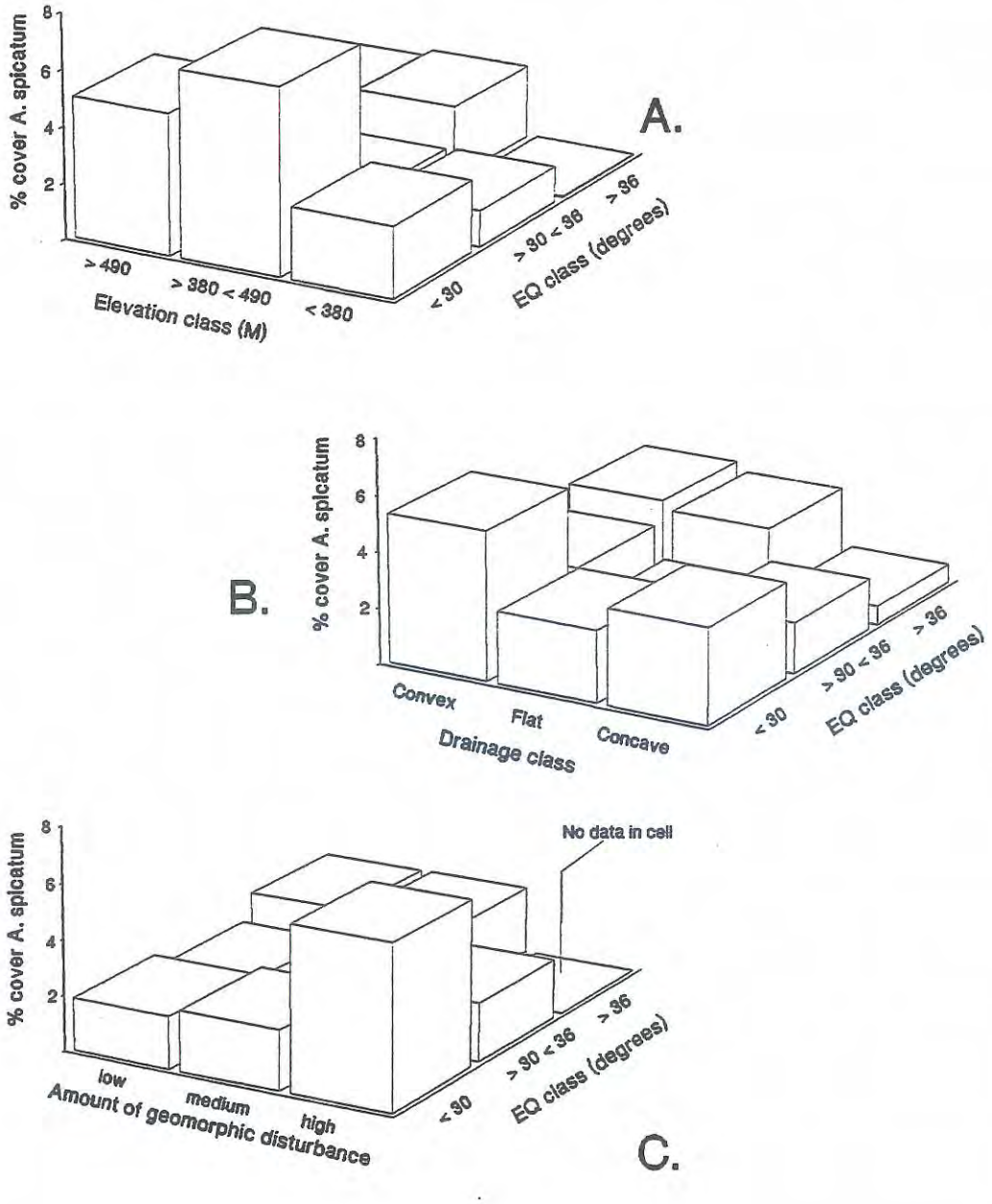


Fig. 31. Two-factor gradient analyses of *Agropyron spicatum* cover in the Yukon River study area. Habitat variables are: (A) EQ and elevation, (B) EQ and drainage and (C) EQ and disturbance.

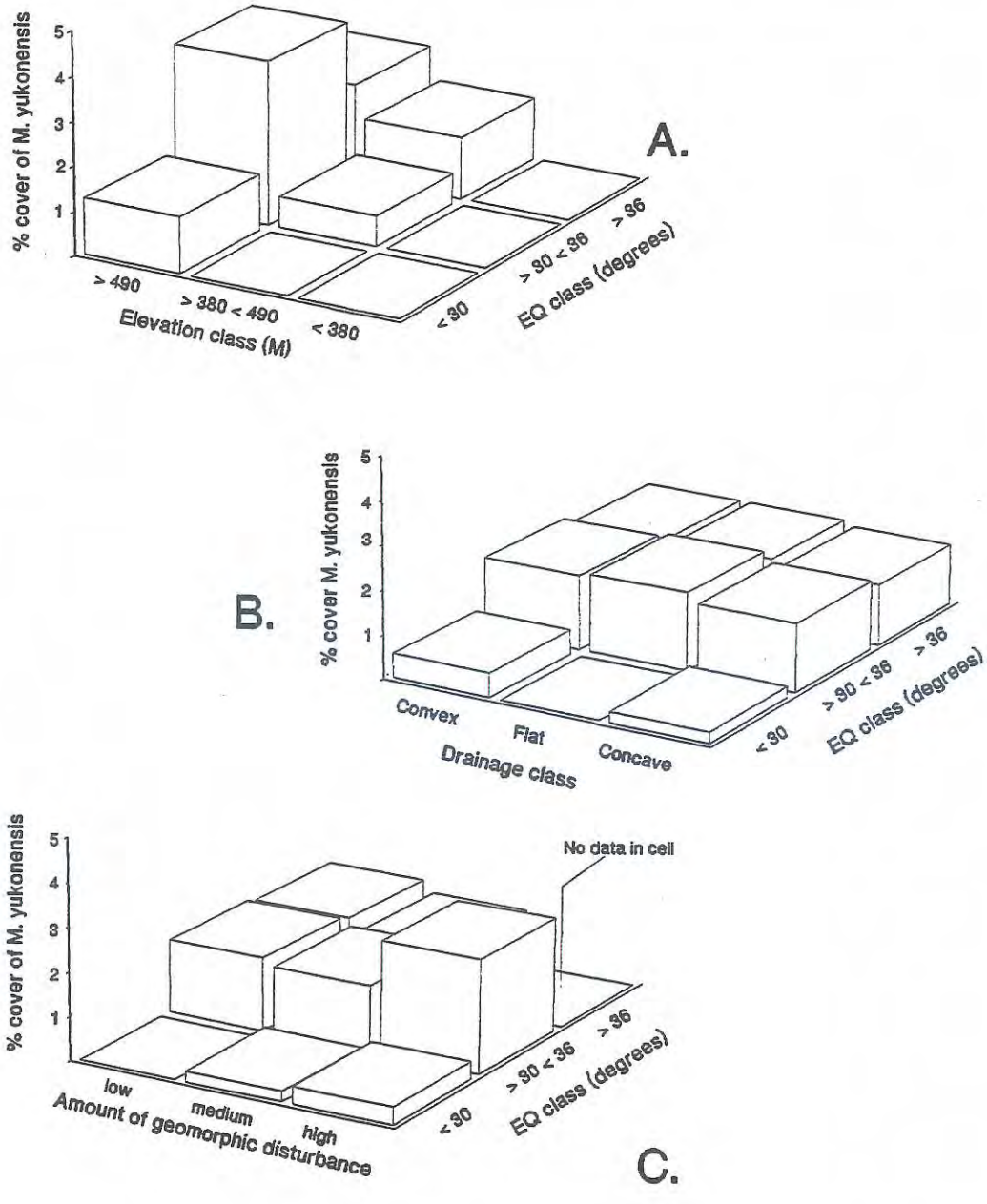


Fig. 32. Two-factor gradient analyses of *Minuartia yukonensis* cover in the Yukon River study area. Habitat variables are: (A) EQ and elevation, (B) EQ and drainage and (C) EQ and disturbance.

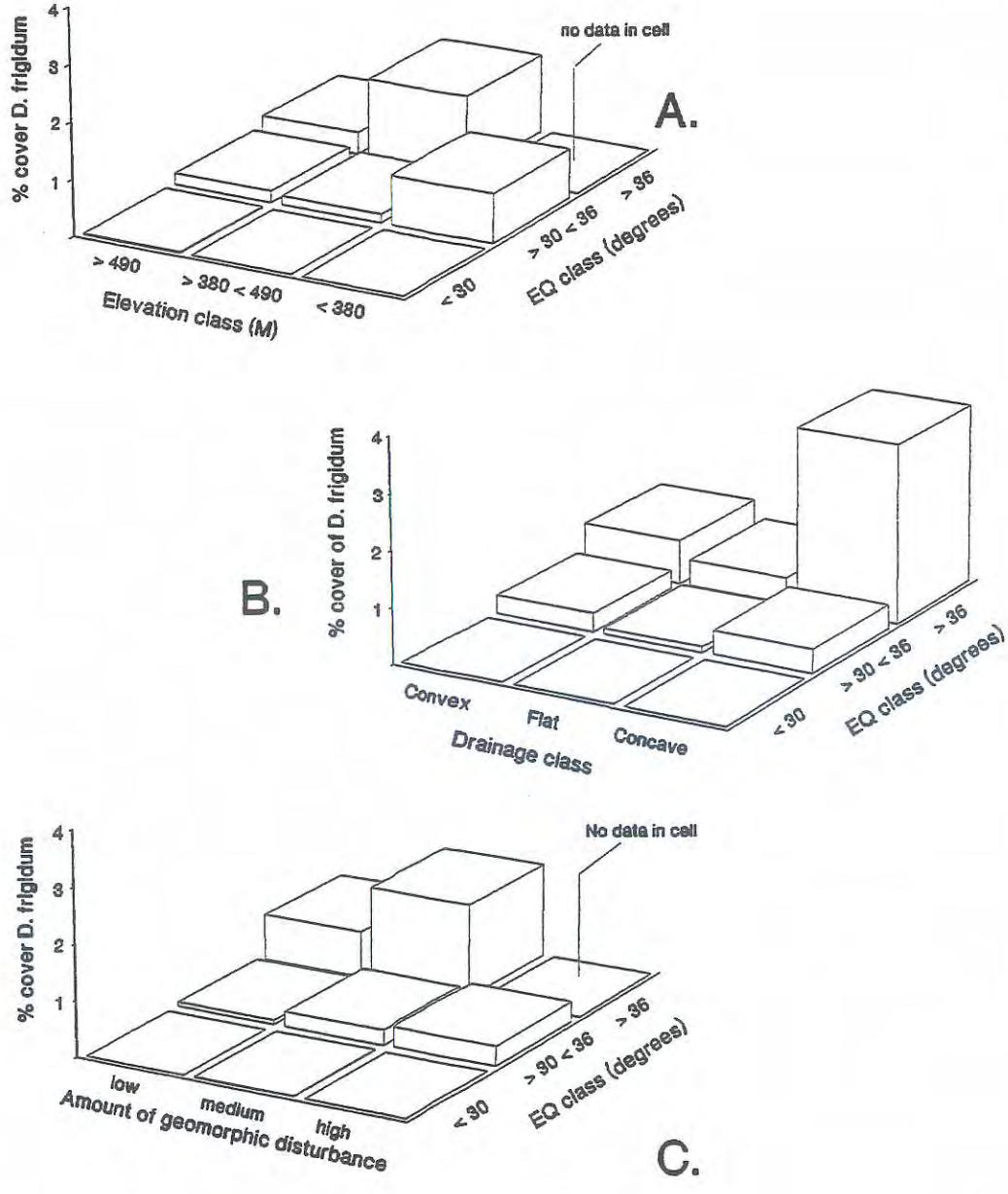


Fig. 33. Two-factor gradient analyses of *Dodecatheon frigidum* cover in the Yukon River study area. Habitat variables are: (A) EQ and elevation, (B) EQ and drainage and (C) EQ and disturbance.

Table 12. Distribution of 24 selected species from Yukon River sites among four biogeographic groups.

Widespread	North American	Amphiberingian	Endemic
Androsace septentrionalis	*Agropyron spicatum*	*Alyssum americanum*	*Minuartia yukonensis*
Carex supina	*Erigeron caespitosus*	*Artemisia frigida*	*Podistera yukonensis*
Calamagrostis purpurascens	*Potentilla pennsylvanica*	*Bupleurum triradiatum*	*Saxifraga reflexa*
Epilobium angustifolium	*Saxifraga tricuspidata*	*Cerastium beeringianum*	
Galium boreale	*Solidago multiradiata*	*Dodecatheon frigidum*	
Pulsatilla patens	*Zygadenus elegans*	*Festuca altaica*	
Rosa acicularis		*Potentilla hookeriana*	
		Silene repens	
7 species	6 species	8 species	3 species

Table 13. Distribution of 40 taxa occuring in ≥ 10 quadrats in the Kolyma River study area among three biogeographic groups.

Widespread	Amphiberingian	Siberian
Allium strictum	*Artemisia arctica*	*Arenaria kamtschatika*
Aster alpinus	*Bupleurum triradiatum*	*Astrocodon expansus*
Calamagrostis purpurascens	*Dianthus repens*	*Carex argunensis*
Dryopteris fragrans	*Bistorta plumosa*	*Carex pediformis*
Erysimum pallasii	*Potentilla hookeriana*	*Clausia aprica*
Festuca brachyphylla	*Selaginella sibirica*	*Dracocephalum palmatum*
Galium verum	*Silene repens*	*Elytrigia villosa*
Hierochloe alpina		*Gypsophila violacea*
Potentilla nivea		*Orostachys spinosa*
Pulsatilla patens		*Oxytropis vassilczenkoi*
Rosa acicularis		*Papaver cf. nivale*
Thymus serpyllum		*Patrinia sibirica*
		Phlojodicarpus villosa
		Poa stepposa
		Saxifraga multiflora
		Scorzonaria radiata
		Silene stenophylla
		Stellaria jacutica
12 species	7 species	18 species

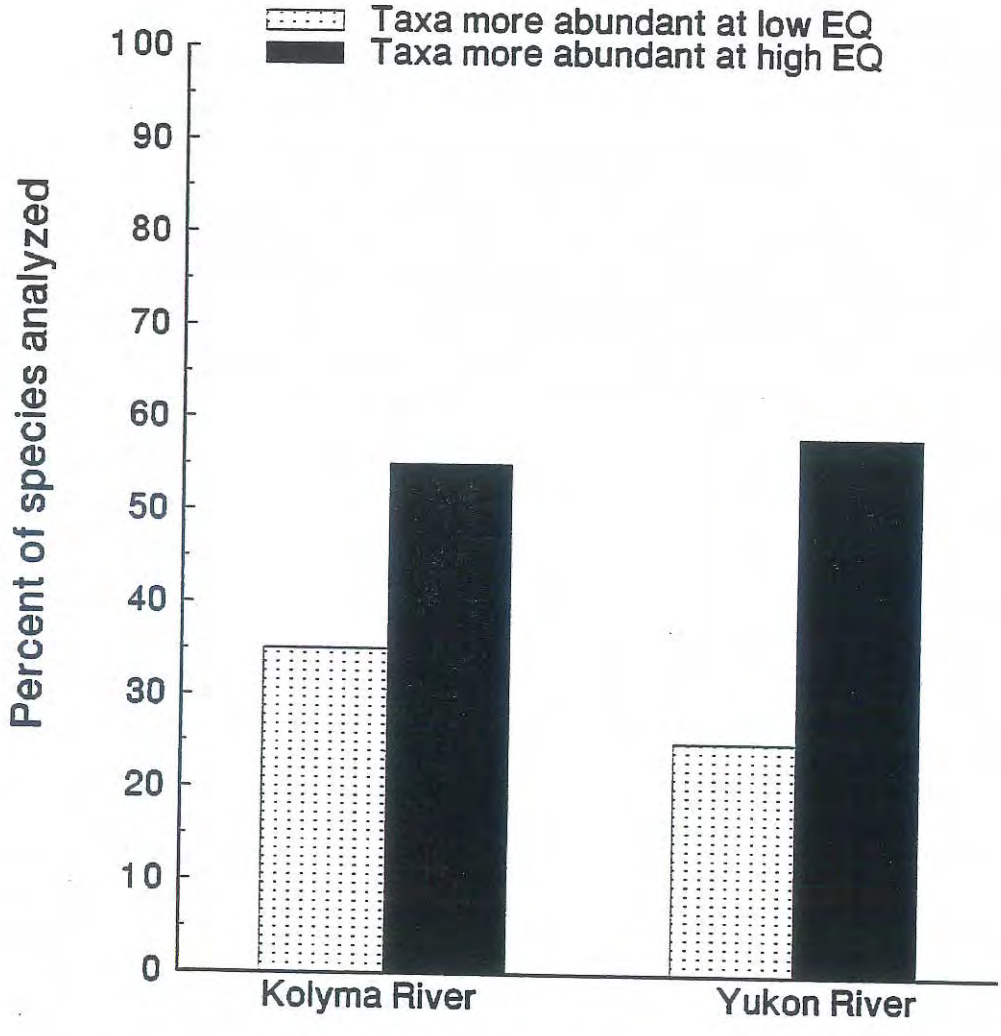


Fig. 34. Proportion of prominent species showing two different responses to EQ in steppe vegetation in the Yukon and Kolyma River study areas.

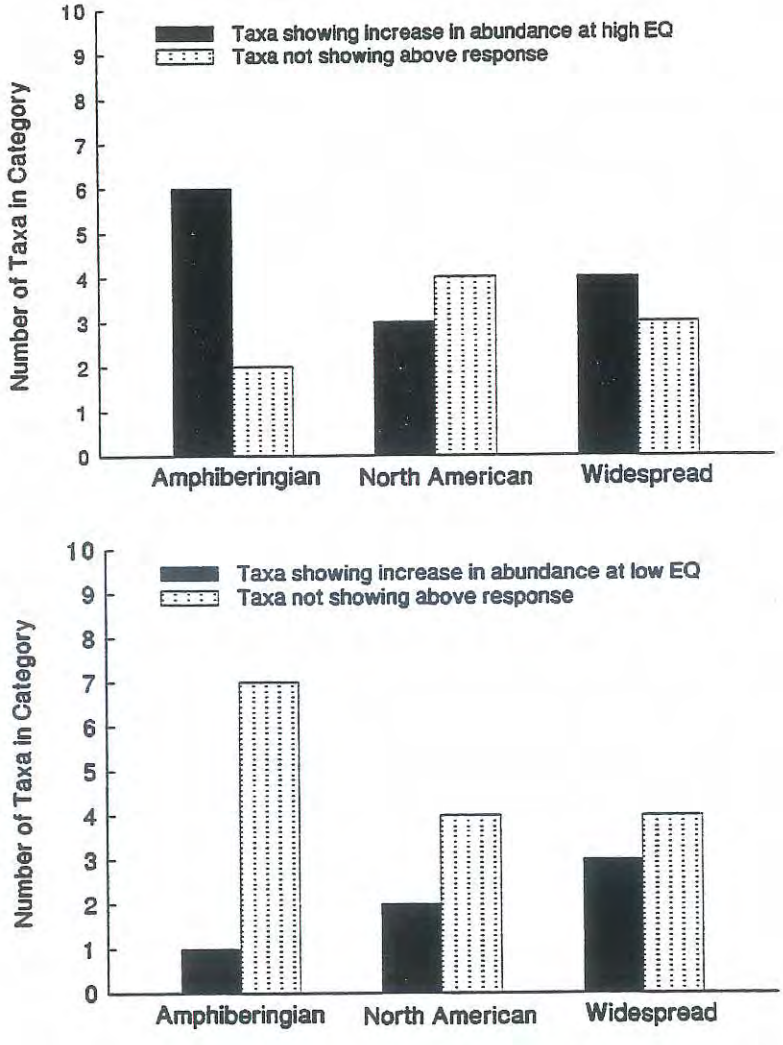


Fig. 35. Number of prominent species showing two different responses to elevation in steppe vegetation in the Yukon River study area.

Table 14. Number of taxa in biogeographic groups showing different responses to the gradient in EQ in the Yukon River study area.

	Species showing increased abundance at low EQ	Species showing decreased abundance at low EQ
Widespread	3	4
Amphiberingean	1	7
North American	2	4
Total	7	15

Table 15. Number of taxa showing different responses to gradient in EQ in continental and amphiberingean groups in the Yukon and Kolyma River study areas combined.

	Species increasing in abundance at low EQ	Species increasing in abundance at high EQ
Amphiberingean	2	9
Restricted to continent	11	13
Total	13	22

Kolyma River study area

Forty species occurred in ≥ 10 of the 97 quadrats at the Kolyma River sites. Of these, almost twice as many species were more abundant at high EQ than those that increased abundance at low EQ.

Contingency tables were constructed based on the gradient responses of these taxa to EQ. These analyses showed that amphiberingian taxa were more numerous than expected in the positive response to high EQ category and less common than expected in the positive response to low EQ category (Fig. 36). None of these differences, however, was statistically significant.

Yukon and Kolyma River study areas combined

To assess this trend of enrichment of the vegetation of the warmest, most xeric sites with species restricted to their respective continents, and the converse tendency of species with amphiberingian distributions to show increased abundance on high EQ surfaces, I constructed a contingency table combining the species from both Asian and North American sites. The columns represent number of species significantly increasing at high EQ or low EQ. I limited the rows to the two biogeographic groups of particular interest, species with restricted to continent and those with amphiberingian distributions (Table 15). Although the G-test on these data yields a nonsignificant association ($p < 0.105$), a real pattern may exist.

IV. DISCUSSION

ECOLOGY OF STEPPE IN TWO STUDY AREAS

Ecotone between steppe and forest

My results substantiate the observation that the maintenance of subarctic steppe on the landscape of continental areas of both eastern Alaska and western Siberia is strongly controlled by environmental variables correlated with the inclination and azimuth of a slope. The mean aspect of the sites within the Yukon River study area was nearly due south with a steep average inclination. The anomalous presence of the steppe vegetation on the north-facing slope in the Kolyma River study area notwithstanding, this vegetation type is generally restricted sites of high insolation within both of these landscapes.

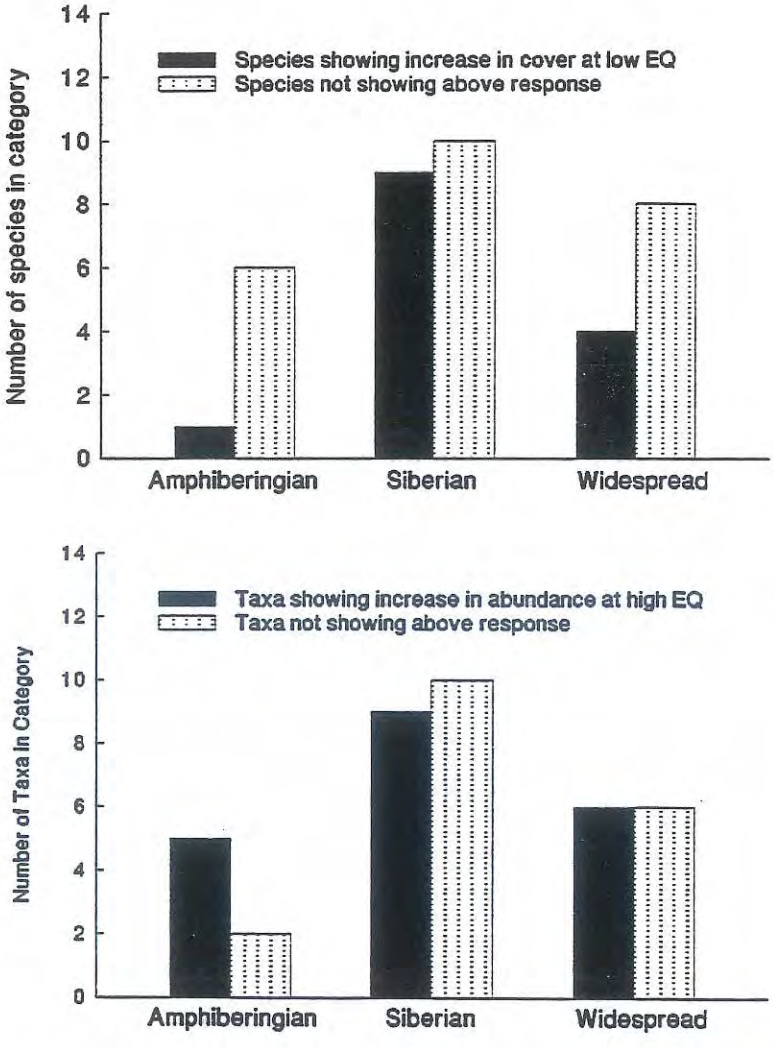


Fig. 36. Number of prominent species showing two different responses to EQ in steppe vegetation in the Kolyma River study area.

Data from ecotone transects on the Yukon River suggest that minor changes in slope morphology increasing the amount of moisture received by a site can result in a major shift in the vegetation from steppe to forest. Steppe plants are generally excluded from shaded areas under the forest canopy. These plants are replaced by woody shrubs such as *Viburnum edule* and *Sheperdia canadensis* that have broad distributions throughout boreal North America.

The observations mentioned above are congruent with an earlier conclusion that low soil moisture restricts tree growth on south-facing bluffs and that low light conditions preclude steppe plants from growing under the forest canopy (Wesser and Armbruster 1991). Several stations along the ecotone transects that support forest occupy facies with EQ values that support steppe in other areas. This suggests that the ecotone between steppe and neighboring aspen forest on any given surface is a dynamic one. The location of this ecotone is likely controlled by an interaction between local characteristics such as soil depth and texture, disturbance events, and periodic variation in precipitation.

Personal observation of well-developed aspen forest on very steep, directly south-facing slopes on several bluffs suggests that given enough time (i.e. lack of disturbance events) aspen forest may be able to propagate itself across most south-facing bluff surfaces. The encroachment of trees into steppe results in increased shading and reduced bare ground there. This in turn alters the evapotranspiration regime of these areas. This amelioration of conditions in steppe close to forest in turn allows further encroachment of aspen into steppe, and so on. Given the cloning habit of this plant, it is intriguing to consider the possibility that reciprocal subsidization may be occurring between plants in different topographic positions. That is, aspen ramets in well-watered gullies may exchange water with ramets on xeric facies in return for solutes from ramets in high radiation facies.

Evidence of recent fire within several of the steppe fields I visited provides additional evidence that steppe species are "fugitive" on the landscape. In some areas, it was clear that a slope that presently supported well-developed steppe (sometimes including populations of several of the endemic and disjunct taxa) had at one time been completely forested. The evidence for this was the presence of large, burnt trees.

Community ecology of subarctic steppe in two study areas

Landscape scale patterns in vegetation ecology

A major goal of this study was to determine whether factors identified as important in controlling species composition within two single bluffs (Eagle Bluff and Kathul Mountain) also control species composition among a variety of widely separated sites. In other words, are these local patterns discernible at the scale of the landscape? Regression analysis of the ordination scores from 23 widely separated Yukon River sites shows that the environmental factors controlling the two major axes of variation within this vegetation broadly coincide with those that have been identified in earlier studies at single sites. Specifically, the radiation regime of a site (here approximated by EQ), its elevation, and the amount of shade it receives from trees, are strongly predictive of the vegetation of a site. Soil variables correlated with moisture-holding capacity and soil fertility significantly refine the models predicting species composition on the regional scale.

At both Eagle Bluff and Kathul Mountain, a primary determinant of the variation in steppe vegetation was the amount of solar radiation received by a site (estimated by slope-aspect interaction) (Edwards and Armbruster 1889, Wesser and Armbruster 1991). EQ was a more powerful predictor of vegetation than slope-aspect interaction in this data set. My interpretation is the same, however; variation in steppe community composition is strongly related to the radiation regime of the surface it occupies, which is controlled by its topographic position. This relationship appears to hold over a wide geographic area and regardless of variation in a variety of edaphic and ecological conditions, as demonstrated by the strong prediction by EQ of both Yukon and Kolyma river study area vegetation scores.

The overriding importance of EQ in controlling species composition among steppe sites in two such distant regions of the subarctic means that this is likely a general trait of open habitats at this latitude. The importance of slope characteristics such as aspect and slope to the radiation characteristics of a site are exaggerated at high latitudes (Lieffers and Larkin-Lieffers 1987, Walker et al. 1992). The conspicuously uneven distribution of solar radiation at high latitude allows for significant variation in the habitat attributes of a site on bluffs on both sides of the Bering Strait.

Responses of community structure to topography also show a high degree of similarity in the widely separated Yukon and Kolyma river watersheds. Species richness,

concentration of dominance and the relative importance of vascular versus nonvascular plant cover all show similar responses to topographic variables (principally EQ) at both Asian and American sites.

The variation in the composition of the vegetation within the Kathul Mountain steppe community is largely a function of microclimatic effects of elevation (Edwards and Armbruster 1989, Lloyd et al. 1994). Results of my study show that these habitat characteristics also order the composition of the vegetation of steppe sites at the scale of the landscape. Regression of DCA-1 scores of 23 Yukon River sites on elevation yielded a significantly positive association. Furthermore, the direction of the response of the vegetation score to increasing EQ and increasing elevation is the same. This outcome is likely due to the fact that decreasing the radiation load and increasing the elevation of a surface have certain parallel effects on microclimate. A decrease in soil temperature and yearly sums of evapotranspiration would be expected in both instances. This would result in less prolonged drought and heat stress, and decreased losses of fixed carbon due to photorespiration for these plants.

Soil texture significantly increases the fit of the regression predicting variation in DCA-1 for the Yukon River sites. Increased sand content of steppe soils results in increased drainage and a reduced capacity for retaining moisture within the soil. This outcome could explain why soil texture influences the composition of the vegetation on these moisture-limited sites.

Wesser and Armbruster (1991) showed that the single best predictor of the character of low elevation steppe vegetation at Eagle Bluff was the amount of photosynthetically active radiation (PAR) intercepted at ground level. In turn, the variable most predictive of PAR was the amount of tree shading of steppe plots. Additionally, soil from their forest plots had a significantly higher organic matter content than soils from open steppe areas (Wesser and Armbruster 1991). Similarly, variation in the DCA-2 ordination scores for Yukon River sites was predicted by the amount of shade cover and soil organic matter. Minor decreases in light intensity from the limited shading of the ground within steppe has substantial effects on the character of the vegetation.

A particularly valuable aspect of the data set gathered in this study is that it contains the most important trends present in subarctic steppe vegetation: those that occur in response to EQ, elevation and shading. It is conceptually valuable to view the

two DCA axes as representative of the two principal interfaces of steppe with other vegetation types. Axis 1 represents the interface between very warm and dry steppe areas and cooler, less moisture-stressed facies supporting this vegetation. Species situated high on this axis such as *Potentilla nivea*, *Senecio ogoturukensis* and *Festuca altaica*, among others, have ecological distributions that include tundra and associated alpine plant communities. Axis 2 represents the tension between open steppe habitats and neighboring forest areas. Species high on axis 2 such as *Achillea borealis*, *Rubus ideaus* and *Rosa acicularis* are common components of the understory of boreal forest areas in the interior. Dominants of low elevation steppe with distributions including temperate steppe tend to cluster low on both of these axes.

Both of the ordination axes of the vegetation in the Yukon River study area are likely correlated with moisture gradients to varying degrees. This is because of the correlation of both sand content and organic matter content of a soil with its capacity to hold moisture. Similarly, less radiation is received at ground level in high EQ and at shaded sites, although for very different reasons. Several species, particularly meadow plants such as *Cnidium cnidiifolium* and *Dodecatheon frigidum* score high on both of the axes. These taxa represent the most mesophytic elements within this flora.

Trends in species richness

Another general trend, on both sides of the Bering Strait, is a significant reduction in species richness on the warmest, most xeric steppe facies. The model that included EQ and elevation predicted 63 % of the variation in the number of species per quadrat at Yukon River sites. Similarly, EQ predicted 56 % of the variation in this variable at Kolyma River sites and species richness declined from 17.70 at the most north-facing site to 7.75 at the most south-facing site. A parallel trend was observed in the autecology of component species. Many more species at both study areas were more abundant on surfaces of high EQ (and elevation) than vice versa. Therefore, dominance within the vegetation of warm, xeric slope facies is concentrated in a few species with high relative cover.

This suggests that only a few drought and heat tolerant taxa are physiologically capable of growth and reproduction on the surfaces at the low end of the moisture gradient. The increased abundance of other taxa on increasingly more mesic and cooler surfaces results in increased competition in these areas and hence in decreased abundance

of the warm steppe dominants. The positive response of several warm steppe dominants to increased geomorphic disturbance, another factor that reduces vegetative cover, suggests that these species are intolerant of competition. Indeed, experimental work has demonstrated the poor competitive ability of *Agropyron spicatum* (Eissenstat and Caldwell 1987).

Experiments in grassland ecosystems support the hypothesis that it is drought that decreases species richness on these sites. Tilman and El Haddi (1992) reported that species richness in a grassland system was severely curtailed by episodic drought. They noted that in a severe drought year their sites experienced a loss of 37 % of the species and 47 % of the above-ground biomass. These sites remained floristically depauperate despite quickly returning to normal plant biomass in subsequent years. Their work showed that, even in a region of continuous grassland, some sites remained recruitment-limited for many years following a drought.

The high potential evapotranspiration of subarctic steppe sites with southerly aspect causes increased frequency and intensity of drought on these sites in comparison with less southerly exposures (Wesser and Armbruster 1991). Greater water loss from plant tissues also would result from higher heat loads. Drought, therefore, would periodically winnow all but the most stress-tolerant taxa from these facies. In the fragmented, discontinuous subarctic steppe plant community, limited recruitment following extirpation of a population would be expected to be even more severe than at the station investigated by Tilman and El Haddi (1992). This is because source populations are often at a great distance are likely much smaller than in areas of continuous grassland.

Tilman and El Haddi (1992) also reported that the probability of a species being lost from a site was inversely related to its pre-drought biomass. That is, they observed that dominant species showed higher rates of survival in drought stressed communities than species with low cover values (Tilman and El Haddi 1992). This outcome also could help explain the positive relationship between dominance and decreasing EQ found at both Yukon and Kolyma sites.

Importance of vascular vs. nonvascular plants

In addition to shifts in dominance among species of vascular plants along the topographic gradients within subarctic steppe, there was a concomitant shift in the

overall importance of the nonvascular biota. The hot and dry facies at low EQ were often largely free of foliose lichens and moss cover. The spaces between the clumps of sagebrush and bunch grasses in these areas were occupied by bare ground and some crustose lichens. This increase in bare ground likely resulted in higher soil temperatures and rapid evaporation from the soil surface.

On high elevation sites and on slopes with aspects other than due south, there was a greater cover of bryophytes and lichens. In exceptional cases, steppe plants protruded through a rich ground cover of mosses and foliose and fruticose lichens. Vascular plant cover was lower in such areas. Where lichens and mosses abounded, bare ground was reduced and the soil surface receives a measure of insulation. High disturbance at sites with steep slopes reduces nonvascular plant cover. The moisture and temperature regimes of the warmest sites also probably restrict the distribution of many nonvascular taxa, particularly mosses, which require free moisture for reproduction.

The increased importance of nonvascular plants and concomitant decrease in bare ground on some steppe sites must exert an influence on the character of the vascular plant community. The reduction in the amount of bare soil available for colonization and the modulation of extremes in soil temperature brought about by the insulation of the soil surface might result in reduced cover of the dominant steppe taxa. These taxa are favored in the warmest, generally more disturbed sites where competition is reduced.

Many of the most species-rich and floristically interesting subarctic steppe sites occupy relatively stable slope facies containing high cover of foliose and fruticose lichens. This could be due older, more stable surfaces collecting more species over time and also developing substantial lichen and moss cover. It could also reflect a more decisive role of lichen cover in maintaining open areas of vegetation. The role of nonvascular plants in organizing plant community structure is unstudied. Nonvascular plants, however, probably have important effects on the community ecology of subarctic steppe.

Autecology of steppe plants

Responses of subarctic steppe taxa to landscape variables do not support the hypothesis that these taxa have restricted distributions because of their intolerance of cool soil conditions (Ritchie and Cwynar 1982). At both the Yukon and Kolyma River study areas, only a fraction of the flora showed marked increases in abundance on the

warmest topographic surfaces. These south-slope dominants, however, tended to be present throughout the available habitat. They are present even in areas very atypical of subarctic steppe, such as the north-facing slopes in the Kolyma River area and high elevations on Kathul Mountain and other localities in eastern Beringia.

The responses of the Kolyma warm steppe dominants *Elytrigia villosa* and *Saxifraga multiflora* to EQ demonstrate this pattern. These species were present at sites throughout the entire gradient, showing that even such extreme variation in microclimate and soils does not exceed their physiological tolerances. Although their abundance is substantially higher at the warmest sites, these plants are not excluded from the coldest areas. Similarly, *Agropyron spicatum*, *Artemisia frigida* and *Calamagrostis purpurascens*, the three most prominent taxa in warm steppe on the Yukon River, are present throughout the wide geographic and habitat variation sampled there.

Although it is evident that some of these taxa were substantially more abundant on warm slope facies, it is unclear whether this is because of a release from competition in these floristically depauperate facies or because microclimatic conditions there are closer to their physiological optima. Both of these factors likely contribute to these trends. The increase in abundance at high levels of geomorphic disturbance of *Artemisia frigida* and *Agropyron spicatum* suggests that competitive release may be an important factor for these taxa.

That a large number of the plants generally restricted to steppe showed increases in abundance on cooler facies within steppe makes it difficult to conclude that the distribution of these plants reflects their physiological requirement for the warmest available facies. It is much more likely that given a treeless landscape, many of the plant species that are restricted to steep, south-facing sites under the present climatic regime would have substantially increased ranges. Indeed, the mixing of steppe and tundra taxa at the exceptional north-facing site in the Kolyma drainage demonstrates the considerable ecophysiological overlap between xerophytic steppe and tundra plants. Steppe and tundra plants also mingle on high elevations of bluffs rising into the alpine in the Yukon River area.

BIOGEOGRAPHY OF STEPPE SPECIES

Species scores in ordination analysis

The niche spaces defined by DCA-1 and DCA-2 ordination axes of Yukon River steppe vegetation makes it possible to evaluate the characteristics of biogeographically informative groups of component taxa. The clustering of most amphiberingian taxa high on DCA-1 and low on DCA-2 (with the notable exception of the relatively widespread steppe plant *Artemisia frigida*) shows that these taxa are associated with cooler facies within steppe occurring at relatively high elevation and with high values of EQ. This cluster is separated from the dominant warm steppe elements such as *Artemisia frigida* and the dominant grasses. The ordinated position of amphiberingian taxa low on DCA-2 further suggests that these taxa are usually associated with unshaded, high light environments. Their separation from the boreal taxa clustered above them on axis 2 shows that they are displaced by these taxa in relatively shaded sites within steppe.

These results are parallel to those of Lloyd et al.(1994) who reported that the cooler facies of steppe at high elevation on Kathul Mountain are relatively enriched by taxa with Asian affinities as compared with warmer, low elevation sites. This pattern generally supports the hypothesis that the presence of Asian taxa on Yukon River bluffs is attributable to their migration across a dry and treeless full glacial landscape.

That the endemic taxa (except for *P. gormanii*, which typically inhabits hot, dry and disturbed localities) clustered in a similar position to amphiberingian species suggests ecological similarities between these floristic components. The separation of most of the endemic taxa from species with temperate steppe affinities is consonant with their geographic distribution in arctic and subarctic environments. Perhaps more intriguing, this result suggests a link between the ecological preferences of these taxa and conditions conducive to the migration of the Asian taxa. The existence of the relatively rich endemic flora in continental areas of Alaska is a reflection of the existence of dry, ice-free refugia in Beringia during glacial advances. The ecological preferences of these plants suggests that they may have evolved under the climatic regime of the full-glacial periods.

Association between ecology and biogeography of component species

At the Yukon River sites, there was a significant association between membership of a species in a biogeographic group and its response to elevation. Except for *Artemisia frigida*, the amphiberingean taxa showed a uniform tendency to increase in abundance at

high elevation steppe sites whereas the members of each of the other groups showed a much lower than expected tendency to increase in abundance at high elevation. Interestingly, the three endemic taxa whose gradient responses were examined, also increased in abundance at high elevation sites.

The EQ gradient analyses of the species from the Yukon River sites were less conclusive. These analyses showed that amphiberingean taxa displayed a tendency toward increased abundance on high EQ surfaces, although the deviation from the other two groups was not significant. Most of the taxa from the other groups that showed this response (such as *Epilobium angustifolium*, *Galium boreale*, *Zygadenus elegans*, and *Saxifraga tricuspidata*) are not generally restricted to steppe sites, and their distribution in these communities likely represents the extreme of their ecological tolerance for aridity. Most amphiberingean taxa, on the other hand, are generally restricted to these sites, thus the pattern they display of increasing abundance with increasing EQ likely is truncated by the abrupt transition into forest habitats where conditions are inimical to the establishment of these plants.

The difference with regard to the strength of the association between the biogeographic groups and elevation and EQ is interesting. In addition to the confounding effect of greater ecological specificity of generally restricted species mentioned previously, this difference is at least partially related to biogeographic factors associated with the nonrandom distribution of steppe species richness between bluffs. Bluffs with little elevational extent tend to harbor fewer total species than those spanning a large elevational gradient. Therefore, populations of some amphiberingian taxa are absent from fields situated on bluffs of limited elevation regardless of whether the field is of low or high EQ. In some instances, this may obscure the connection between their ecology and biogeographic distribution.

One-half of the Siberian taxa and a third of the widespread taxa at the Kolyma River sites increased in low EQ sites. In contrast, only one of seven amphiberingian taxa showed this response. This degree of association between gradient response and biogeography is not statistically significant, however ($p = 0.21$).

In the analysis that included sites on both sides of the Bering Strait, only 14 % of 14, amphiberingian taxa increased in abundance on surfaces of low EQ. This suggests these species were particularly prone to occupying cooler than average facies on subarctic steppe bluffs. In contrast, 11 of 23, or 46 percent, of species restricted to their

respective continents increased on low EQ surfaces. Although not significant at the 0.05 level ($p = 0.105$), these trends are suggestive of the presence of a "filter" effect in the amphiberingean flora of subarctic steppe.

The hypothesized relationship between the North American biogeographic subgroup and dominance on low elevation and low EQ sites was not supported. This is at least partially due to three of the most prominent North American taxa on Yukon River sites not being restricted to subarctic steppe. The boreal species *Solidago multiradiata* and *Zygadenus elegans* and the common subarctic and arctic plant *Saxifraga tricuspidata* are common in a variety of habitats in the study area other than steppe. The abundance of these taxa does not increase on the most xeric facies because their habitat volume in steppe represents the extreme of their ecological distribution with regard to drought and heat tolerance. A variety of North American taxa with continental steppe affinities such as *Linum lewisii* do appear to increase on low EQ surfaces but were not present in a sufficient number of quadrats to reasonably assess their gradient response.

This points out a limitation of the landscape approach taken in this study. In any study design, there is a tradeoff between sampling intensity and extent of the sampling area. To visit the large number of sites over the wide geographic area encompassed in this study, the sampling intensity at one site could not be as great as if I had concentrated on a single bluff. Therefore, simply by chance, the rare species within a field were sometimes not present within sampling quadrats. By compiling floristic inventories of each bluff, however, I was able to quantify the distribution of rare species between bluffs. The results of analysis of those patterns will be presented in the next chapter.

Another factor complicating the biogeographic analyses is the presence of plants with cold steppe and tundra distributions that are restricted to either continent. For instance, *Stellaria jacutica* and *Astrocodon expansus* are cryophytes restricted to northern Asia. These taxa showed a strong increase in abundance on cold facies of Kolyma River steppe. That these continental taxa are tallied in the high EQ category results in a greater likelihood of rejecting the hypothesis that amphiberingean plants are more likely to increase on cold facies than expected in relation to other groups.

Clearly, a variety of factors other than the ecological response of a taxon would have dictated whether the species migrated across the Pleistocene landbridge and whether, once arriving, populations would have survived until the present. These factors

include breeding system, dispersal ability, minimum viable population size, intrinsic rate of population growth, and response to stochastic events. The presence of a substantial group of cryophytes restricted to Asia does not argue against the hypothesis that the amphiberingian steppe taxa of Alaska are the result of late glacial floristic exchanges. Thus, the contingency table analyses are arguably overly conservative tests of this hypothesis.

SOIL-ENVIRONMENT RELATIONSHIPS

Soil characteristics varied significantly with topography; their differences in relation to EQ were particularly evident over the wide gradient investigated at the Kolyma River sites. Available nitrogen, organic matter content, and potential respiration were all higher at high EQ whereas pH and soil depth decreased with EQ. North-facing soils tended to consist of coarse-grained mineral fragments in a matrix of decomposing organic matter whereas south-slope soils were generally fine-grained mineral soil low in organic matter. These patterns in soil characteristics were paralleled by the patterns in vegetation and floristic composition. As such, it is difficult to disentangle the contributions of microclimate and soil qualities in producing the trends described within the vegetation. Variation in soil, however, is largely a function of soil microclimatic variables that consistently covary with landscape factors such as EQ or elevation. In other words, the nature of the soils of a slope is largely inseparable from their topographic position.

Lloyd et al. (1994) observed trends in soils along an elevational gradient from warm steppe to cold steppe and tundra on Kathul Mountain similar to those described here for the transition along a gradient of EQ. Coupled with strong similarities in the structure and composition of the vegetation, the covariation in these patterns strongly suggests identical controls over vegetation and soil processes at the two sites at opposite ends of Beringia. Specifically, the role of soil temperature and depth of the thawed layer may be particularly important in regulating physical weathering of soil particles and rates of organic matter mineralization at both sites.

In extensive measurements of the soil microclimate on the same set of slopes I investigated at the Kolyma River sites, Alfimov and Berman (1992) reported that total soil degree days above 0° C were significantly higher on south-facing slopes than on north-facing ones. These differences were 2.5 fold at the surface, 3.6 fold at 5 cm depth

and 400 fold at 20 cm below the surface. On average, north-facing soils remained cooler throughout the growing season (Alfimov and Berman 1992).

The accumulation of soil organic matter on north-facing slopes is likely a result of the shorter span of time that these soils are thawed and experience active decomposition of organic matter. Soil on the north-facing sites may be frozen ≤ 2 months longer per year than the soil on the south-facing slopes (Alfimov and Berman 1992). Additionally, rates of nutrient turnover may be slower in the cooler soil microclimate at high EQ. Increased levels of erosion and small-scale slope failures on the steepest sites also diminish the amount of soil organic matter.

Although the quantity of available nitrogen and soil organic matter varied significantly with EQ, organic matter quality did not. Variation in the amount of available nitrogen between sites suggests that the nitrogen nutrition of plants growing in high EQ sites is better than for those in low EQ sites. There are four reasons that these data may be misleading with regard to the actual nitrogen uptake by the vegetation:

1) The analysis was carried out on the fine fraction of soil which represents a smaller percentage of the coarser soils of the north-facing sites.

2) If rates of turnover are slower due to cold soil temperatures, as hypothesized, pool sizes would not be indicative of total N flux over the growing season. Nonetheless, intermittent bouts of accelerated mineralization in favorable conditions could result in temporary high N availability (Burke 1989).

3) Higher concentration of H^+ ions in the more acidic soil of north-facing areas could impede nitrogen uptake by plants on those sites.

4) Deeper solum and thaw depths on south-facing slopes allow for a greater volume of root colonization and perhaps diminished below-ground competition.

HOLOCENE EXTRAZONAL STEPPE AND DUVANNY-YAR STEPPE TUNDRA

Debate concerning the vegetation of full-glacial Beringia

Young (1976) suggested subarctic steppe as an analogue for segments of the zonal vegetation of continental areas of Beringia during the Duvanny Yar interval, the last phase of Pleistocene glacial advance. This hypothesis has caused debate among Quaternary scientists interested in the character of the flora and fauna of landbridge Beringia (see Young 1976 and 1982, Matthews 1982, Ritchie and Cwynar 1982). Two

separate questions are involved in this debate. The first concerns whether steppe or steppe-like vegetation constituted an important component of the landscape of full-glacial Beringia. The second concerns whether the plant communities on river bluffs today bear a resemblance to the hypothetical full-glacial vegetation type.

According to some authors, interior regions of Beringia during Pleistocene glacial maxima were characterized by xeric landscapes dominated by a cold steppe, or "steppe-tundra" vegetation mosaic (Giterman et al. 1982, Guthrie 1968, 1982, 1985, 1990, Matthews 1982, Young 1982, Yurtsev 1982).

Evidence supporting the presence of steppe-tundra landscapes in Pleistocene Beringia includes the following observations:

1. Vertebrate fossils dating to the full glacial period that indicate the presence of a relatively diverse mammalian fauna adapted to grazing and dry, firm soil conditions (Guthrie 1968, 1982, 1990, Matthews 1982).
2. Assemblages of invertebrate fossils dating to the full-glacial that contain dryland and steppe indicator taxa such as members of the genera *Harpalus* and *Morychus* (Giterman et al. 1982, Matthews 1982).
3. Disjunctions in the distribution patterns of xerophytic plants associated with modern extralimital steppe communities in east and west Beringia. These patterns are inferred to be the result of contractions in the ranges of steppe taxa during the Holocene (Murray et al. 1983, Young 1982, Yurtsev 1964, 1972, 1982).
4. Fossil pollen spectra dating to the full-glacial that contain relatively high percentages of herb, graminoid and *Artemisia* pollen. These spectra have been interpreted as consistent with a treeless landscape dominated by steppe-tundra (Guthrie 1992, Young 1982).

Many authors have written that Pleistocene steppe-tundra is without analogue on the current landscape (Giterman et al. 1982, Guthrie 1982, 1992, Mattews 1982). On the other hand, Yurtsev (1982) has proposed that the closest living approximation of this vegetation type may occur on Wrangel Island, where a relatively diverse complement of cold-hardy xerophytes coexist in a vegetation without analogue on either mainland. Young (1982) hypothesized that the vegetation that developed in the highly continental, semiarid climate of south-central Beringia "had the general aspect of an open, rather

thinly vegetated steppe" dominated by bunch grasses such as *Agropyron* sp., *Calamagrostis purpurascens*, *Elymus innovatus* and *Festuca altaica*. He suggested that the dominant *Artemisia* species in this area would have been *A. alaskana*, *A. arctica*, *A. borealis*, or *A. furcata*.

Some palynologists have disputed the idea that steppe vegetation existed in Beringia during the cold, dry Duvanny Yar interval (Colinvaux 1964, Ritchie and Cwynar 1982, Eisner and Colinvaux 1990). Ritchie and Cwynar (1982) have interpreted the low influx rates and taxonomic composition of fossil pollen samples contained in cores dating to this period as consistent with an entirely different type of vegetation. They suggest that sparse fellfield and tundra plant communities predominated during this period. They proposed that the closest analogues to full-glacial vegetation types exist today in the high arctic and at high elevation farther south where short growing seasons and intense cold limit plant growth and the formation of a continuous ground cover. Important species in their reconstruction of the vegetation of continental Beringia during the Pleistocene include *Alopecuris alpinus*, *Artemisia arctica*, *Dryas* sp. *Salix polaris*, and *Eriophorum* sp.

Two very different pictures of the vegetation of the full-glacial landbridge emerge from these alternative interpretations of the fossil data. Inherent in these different versions are assumptions about the ecophysiology of plants that constitute extrazonal steppe assemblages today. Ritchie and Cwynar (1982) argued that modern steppe is composed of plants that require a deep active layer and are limited to areas with high net radiation due to a requirement for warm growing season temperatures. They state that "such a soil environment, reconstructed zonally, would imply a thermal regime totally incompatible with the regional paleoclimates suggested by all other evidence" from the Duvanny Yar period.

An alternative hypothesis (Edwards and Armbruster 1989) recognized the restriction of these assemblages to areas with high net radiation, but proposes that this is a not the result of physiological intolerance of cold soil temperatures or a need for deep active layer on the part of subarctic steppe species. They suggested that the geographic limitation of steppe species is a function of their inability to compete for light in the topographic positions occupied by boreal forest on the current landscape. According to this formulation, steppe plants could have occupied a much wider segment of the full

glacial landscape than they do at present, because they would not have been displaced by forest vegetation.

Results of this study contribute to this debate in three principal ways:

1. These data do not support the idea that the majority of plants that inhabit extrazonal steppe require high heat or a deep active layer.
2. Subarctic steppe has a variety of expressions on the current landscape, that are not equally useful as structural analogues for steppe-tundra vegetation.
3. The dynamic nature of the vegetation on south-facing bluffs and the limited extent of steppe in eastern Beringia suggests that a significant degree of "sorting" of these communities has occurred over the course of the Holocene. This sorting includes the extinction of component species from habitat islands and successional change within the vegetation there. Hence, it is highly unlikely that patches of steppe vegetation extant today represent actual relicts of full-glacial vegetation.

Results from the Kolyma River area clearly showed that a variety of plants predominant in the warm, dry environment on southerly exposures, such as *Pulsatilla patens*, *Elytrigia villosa*, and *Dracocephalum palmatum*, also inhabited areas with low radiation receipts, hence cool soil temperatures, and a thin active layer. Similarly, the dominant plants in the Yukon River area showed broad environmental tolerances. Although several of the dominant plants are most abundant in the warmest facies (*Agropyron*, *Artemisia*), these taxa persist across the environmental gradient spanned by steppe. Indeed, most common steppe species, such as *Carex supina*, *Bupleurum triradiatum* and *Minuartia yukonensis* increase in abundance in cooler, less insolated facies. Furthermore, almost all of the amphiberingian plants analyzed from the Yukon River study area showed a positive response to increased elevation, a factor correlated with lower soil temperatures. These findings are consistent with the idea that a variety of species inhabiting subarctic steppe would have occupied a wider segment of the landscape of Pleistocene Beringia.

It is especially probable that relatively widespread and amphiberingean xerophytic species such as *Calamagrostis purpurascens*, *Carex supina*, *Festuca lenesis*, *Potentilla hookeriana*, and *Pulsatilla patens* would have played considerably more important roles in the full-glacial vegetation than they do at present. Not only are these species abundant

in subarctic steppe on both sides of the Bering Strait, they occur in the dry and cold landscapes of Wrangel Island and several constitute an important component of xerophytic vegetation on Greenland (Yurtsev 1982). Their geographic and ecological distributions do not support the idea that they require high temperatures and a deep active layer to grow and reproduce.

As Lloyd et al.(1994) pointed out, discussions of subarctic steppe among paleoecologists have neglected the variable nature of this vegetation in their analysis of its environmental constraints and utility as an analogue of full-glacial vegetation. Subarctic steppe plant communities in the Yukon and Kolyma river areas are composed of species with an array of limiting factors and responses to environmental conditions. Radiation load, soil factors, disturbance, microtopography and elevation were all found to affect the distribution of steppe species in different ways and to varying degrees. Therefore, it is erroneous to attribute the control over the distribution of plants within this community to any single limiting factor. However, a common requirement for most, but not all, of the species that inhabit these sites is an absence of a closed forest canopy (Edwards and Armbruster 1989, Wesser and Armbruster 1991).

A result of shade intolerance is that the distribution of subarctic steppe is primarily determined by topography. Topographic positions that preclude the development of forest because of aridity or frequent disturbance provide habitat for a suite of species that are essentially fugitive on the current landscape. Secondarily, fire plays a role by creating openings in the boreal forest that blankets these regions. Steppe assemblages also form in xeric facies of such openings.

I have shown that the nature of the vegetation that develops on one of these surfaces is determined by its topographic position (slope, aspect, elevation). The vegetation that occupies the very high radiation and warm environment of south-facing, low elevation sites of river bluffs is likely a poor analogue for Pleistocene steppe-tundra. The vegetation of these sites is characterized by large-statured plants, low diversity, and dominance by plants with temperate steppe affinities. This is not to say that the flora that comprises this vegetation would have been precluded from steppe-tundra, only that the structure of the vegetation that results from this environment is unlikely to have been widespread under an intensely cold regional climate. These sites appear to have a diminished component of amphiberingian and endemic plants in comparison with cooler facies of subarctic steppe.

The coldest facies in both the Yukon and Kolyma River areas harbor a mixture of plants with both tundra and steppe affinities. At exceptional sites, such as the north-facing steppe on the Kolyma River, there is a gradual transition between steppe and tundra. Given cold and dry microclimatic conditions, these distinct vegetation types intermingle. The plant community that results from these local conditions may represent a third vegetation type altogether; one extremely limited on the current landscape but potentially more widespread under colder and drier climatic conditions.

Amphiberingian species showed a significantly positive response to increasing elevation within Yukon River steppe communities. This supports the idea that these plants are favored in cooler soil temperatures relative to other members of this flora. Most of the species inhabiting subarctic steppe in both the Kolyma and Yukon River areas decrease in abundance in the warmest topographic positions. Species that inhabit subarctic steppe usually are more abundant on surfaces of higher than average EQ or elevation. Species such as *Minuartia yukonensis* and *Bupleurum triradiatum* in the Yukon River study area and *Erysimum palasii* and *Phlojodicarpus villosus* in the Kolyma River study area are absent from the warmest topographic positions, yet they inhabit communities that are demonstrably steppe.

Lloyd et al.(1994) suggested that the plant community that occupies the highest slopes of Kathul Mountain represented a potential structural analogue for parts of the steppe-tundra landscapes of continental Beringia during the Duvanny Yar interval. The strong resemblance between the vegetation and soil characteristics of north-facing slopes in the Kolyma River study area and the high elevation slopes on Kathul Mountain adds a measure of support to this proposition. The transition in this vegetation parallels a cline in elevation at Kathul Mountain and a cline in radiation (EQ) on the Kolyma River. Common denominators associated with both of these gradients are decreased length of growing season and lower mean soil temperature.

The limited areal extent of subarctic steppe on the current landscape must strongly influence both the type of plants that persist there and the species richness of individual bluffs. Data presented here suggest that, under current conditions, the probability of extinction of populations of steppe plants on a given bluff may be high for two reasons. First, the balance between the amount of open and forested areas on a bluff may shift over relatively short time scales. For instance, a series of wet years could allow the expansion of forest across all but the most south-facing bluff surfaces, severely

limiting the amount of open habitat on a bluff. Secondly, severe drought and the warm soils that characterize many of these sites must periodically winnow species from them. That low EQ surfaces are very species-poor attest to the importance of this phenomenon.

Young (1982) remarked that the fragmentation of the vegetation that occurred as a result of the "rapid shift from a highly continental climate associated with the vast land areas of the Bering Land Bridge to a more maritime climate caused by the expansion of the seas" would have resulted in diminution of floristic diversity among the xerophytic groups that predominated under the continental climatic regimes of the glacial period. If such a process of fragmentation occurred, the steppe communities that persist today have undergone even greater changes since that time. The stressful nature of the habitats to which they have been confined (i.e. pronounced drought concomitant with high soil temperatures, relatively frequent soil disturbance and small area of suitable habitat due to encroachment by taiga ecosystems) has presumably resulted in the loss of the more "K-selected" elements of this flora. Hence the modern complement of amphiberingian steppe taxa present in Alaska probably represent a nonrandom sample of a full glacial xerophytic flora with regard to life history traits and ecophysiological adaptations. Surviving taxa must represent the more disturbance-tolerant and dispersal-adapted, ecological generalists of a once more species-rich community.

The repeated "sorting" of these communities that presumably occurs with the contraction and expansion of available habitat on river bluffs is reason for extreme caution in interpreting the vegetation patterns on these sites as closely analogous to zonal vegetation types. Without all the pieces, it is difficult to accurately reconstruct all but the outlines of the entire puzzle. Indeed, Murray et al. (1983) suggested that "the flora of these steppes is ancient, but the communities they form are not necessarily relicts of any one specific period".

There is an additional aspect of this study worth mentioning in the context of the history of these assemblages. Because steppe vegetation only occurs in small and relatively isolated patches (on the scale of the landscape), the potential for bias in evaluating the ecological factors limiting the distribution of plant species within an individual site is high. For instance, the distribution of a species may be restricted to one area of a single bluff for several reasons, only one of which is that the ecological conditions there are particularly favorable for its growth and development. Stochastic events such as recent colonization of the bluff, successional patterns or population

fluctuations unrelated to microclimate might result in a spurious relationship between the abundance of a species and an environmental parameter at a single site. Similarly, covariation in site characteristics may obscure the real limiting factors on species distributions.

For instance, Lloyd et al. (1994) suggested that *Arabis holboelii* and *Androsace septentrionalis* may be restricted to sites of low elevation due to their observed distribution on Kathul Mountain. These species, however, inhabit very disturbed, silty soils across a broad spectrum of elevations, if one considers all Yukon River sites. I have collected *A. septentrionalis* in high elevation alpine situations in central Alaska. The fact that the soil conditions these species prefer are much more prevalent at lower elevations on Kathul Mountain results in a potentially spurious relationship between elevation and the distribution of these taxa. Similarly, *Podistera yukonensis*, while most abundant on low elevation rubble slopes on Kathul Mountain is most often associated with rubble slopes in high elevation and alpine situations in east-central Alaska and Yukon Territory.

The design employed in this study, which incorporates a wide variety of topographic and geographic situations, may provide a more accurate picture of the response of the common constituent taxa to environmental gradients. Although still subject to some biases, the importance of local site differences such as the ones cited above are minimized by the inclusion of greater geographic variability.

SUMMARY

The vegetation of Beringia has alternated between a forested and a treeless condition during the Quaternary (e.g. Hamilton and Ashley 1993, Edwards and Barker 1994, Matthews 1982, Ritchie and Cwynar 1982, Young 1976), and the flora of subarctic steppe bluffs provides a unique window on the biogeographic history of this area (Murray et al. 1983). Treeless areas of large bluffs accommodate taxa with ranges that have been fragmented by the expansion of forest and shrub tundra across the landscape of Alaska and the Russian Far-East during the Holocene.

Discussing the large number of close relationships between the floras of Asian steppes and North American prairies, Yurtsev (1964) wrote that "In the cryophilous steppic group, the case of specific identity of American and Siberian forms is a rule" and further that "the exchange of steppe plants between Siberia and North America could take place only through the continental area of the Bering Land [Bridge] during the time

when the present continental shelf was not covered by the sea". It is incontrovertible that cold-hardy steppe plant species of Asian origin arrived in continental areas of eastern Beringia during glacial stages, as Yurtsev suggested.

Data presented here show that autecological responses of a plurality of taxa that inhabit modern extralimital steppe in east and west Beringia are consistent with a wider distribution during dry and cold glacial epochs. The wide ecological tolerances of these species is evidence that their limited geographic distribution on the current landscape does not necessarily reflect a requirement for warm edaphic conditions, as has been suggested (Ritchie and Cwynar 1982). My observations agree with previous studies at single sites (Edwards and Armbruster 1989, Wesser and Armbruster 1991, Lloyd et al. 1994).

The principal contribution of this study is the extension of these earlier observations to a broader geographic scale. Patterns in community ecology and species distribution within a single site may be influenced by a variety site-specific factors such as differences in soil, slope morphology and successional history within a site. The influence of these local factors is minimized with the inclusion of geographic replication in the study design. Averaging community and species responses to environment over a broad geographic area decreases the bias inherent in these estimates and increases our confidence in their accuracy.

An unexplored facet of the floristics of subarctic steppe sites is the distribution of species richness and floristic composition among bluffs and among watersheds. In this chapter, I limited my discussion of species distribution to the vegetation of 23 individual facies sampled on 12 different bluffs on the Yukon River. I also completed floristic inventories of these bluffs and those in three tributary watersheds supporting steppe in Alaska. These inventories catalog the flora resident in a variety of different facies beyond those intensively sampled for the vegetation analyses. I discuss the patterns of species richness and floristic composition among bluffs in the following chapter.

CHAPTER TWO

FLORISTICS AND SPECIES RICHNESS OF SOUTH-FACING BLUFFS IN FOUR DRAINAGES OF THE UPPER YUKON RIVER IN ALASKA AND CANADA

I. INTRODUCTION

In the first chapter, I used data from quadrat-based sampling to model the relationship between the composition of subarctic steppe vegetation and topography. The composition of this vegetation is strongly controlled by a few important landscape variables. Specifically, factors affecting the solar radiation regime of a surface, such as its slope and aspect, exert strong influences on species richness and the composition of the vegetation.

In the Yukon River drainage, steppe is restricted to south-facing river bluffs. These bluffs are islands of suitable habitat for many of the species in this community, which are excluded from most of the landscape by boreal forest. Certain bluffs within a drainage have high species richness while others harbor relatively few species. On a larger spatial scale, certain drainages can be characterized as enriched or relatively depauperate. In this chapter, I will use floristic data on south-facing bluffs to explore the patterns in plant distribution and species richness within and among drainages in interior Alaska.

The goal of this study is to address the following questions:

1) What geographic variables best predict the patterns of species richness among bluffs within the study area? Further, do all floristic elements within this flora show similar responses to these variables or are there different responses among floristic groups?

2) Can the variables referred to also explain differences in species richness and floristic composition among drainages or are these differences due to other factors?

3) Can the models fitted to answer question (1) help us understand the biological processes responsible for the variation in species richness observed both within and between drainages in the study area?

4) What conclusions regarding the history and unique biogeographic character of these assemblages (such as its high rate of endemism) are suggested by the fitting of these models?

The biogeography of subarctic steppe in North America

Hansford Shacklette, a geologist, was the first to report the presence of the unique association of plants occurring on Yukon River bluffs (Shacklette 1966). He proposed that the high endemism in the flora of Eagle Bluff was a result of phytotoxic elements contained in the greenstone bedrock there. He proposed that the plants in open habitats on Eagle Bluff are tolerant of high levels of these elements (barium, nickel and zinc) and thus benefit from reduced competition with more "aggressive" but less chemically tolerant zonal plant species (Shacklette 1966).

Since Shacklette's work on Eagle Bluff, however, populations of these plants have been found on sites of variable soil chemistry, but similar topographic position in steep, disturbed, and southerly exposed facies. Studies have shown that the xeric nature of these habitats, and not soil toxicity, is responsible for the diminution of competition with zonal species on these slopes (Batten et al. 1979, Edwards and Armbruster 1989, Wesser 1990, Wesser and Armbruster 1991).

Additional plant collections made in the upper Yukon River have revealed that the flora described by Shacklette is not restricted to Eagle bluff (Young 1976, Batten et al. 1979, Murray et al. 1983, Howenstein 1994). Indeed, the system of bluffs in the upper Yukon River valley is part of a unique botanical province centered in the eastern interior of Alaska. The attributes of this province include: 1) a small group of narrowly endemic taxa; 2) a suite of species disjunct from the dry interior of north Asia; and 3) isolated populations of disjuncts from temperate steppe areas of continental North America.

Populations of these plants occur within a xeric habitat mosaic that includes low and high elevation subarctic steppe, rubble slopes, rock outcrops, and open aspen forest. While populations of these biogeographically interesting plants are associated with the islands of grassy steppe vegetation that dot these bluffs, many are often found in their greatest numbers in rubble slopes or rock crevice habitats. The flora I will be considering in this chapter is the bluff flora, in the broad sense, which includes, but is not limited to, the steppe flora.

This flora has a relatively large number of endemic plants, some of which have narrow distributions in Alaska. Four taxa of bluff plant communities are designated as candidates for protection under the Endangered Species Act. The endemic species *Cryptantha shackletteana*, *Draba murrayi*, and *Podistera yukonensis* and the endemic

variety *Eriogonum flavum* var. *aquilinum* are all category 2 species under the provisions of the act (Murray and Lipkin 1987). Category 2 status means that more information is needed concerning the distribution of a taxon before it is listed as threatened or endangered. A number of other plants occurring in these communities such as *Douglasia arctica*, *Erysimum asperum* var. *angustatum*, *Papaver nudicaule* ssp. *americanum* and *Phacelia mollis* are endemic taxa with relatively few known populations. In fact, these bluffs support the greatest concentration of rare and endemic taxa of any plant association in Alaska.

Murray et al. (1983) and others have suggested that the upper Yukon River valley has the richest south-facing bluff flora in Alaska. The major tributaries of the upper Yukon River in Alaska such as the Kandik, Charley and Tatonduk Rivers, and the Yukon River bluffs downstream of Dawson City, Yukon Territory, have not been inventoried by botanists. As a result, both the full extent of this unique flora and the distribution of taxa among the available sites are incompletely known.

Effect of area on patterns of species richness in island biotas

The biological significance and causal factors of patterns in species richness among areas of different sizes have been extensively explored and debated in the ecological literature (e.g. Preston 1962, MacArthur and Wilson 1967, Brown 1971, Simberloff 1972, Connor and McCoy 1979, Riebesell 1982, Soule et al. 1988, Kadmon and Pulliam 1993). Three main hypotheses have been advanced to account for the observed positive correlation between species richness and area in a variety of both oceanic and habitat-island systems:

1) Species richness is controlled by passive sampling from a regional species pool. Larger areas contain more species because they contain effectively larger samples from this pool than do small areas (Connor and McCoy 1979).
2) The "area per se" hypothesis is derived from the equilibrium model of island biogeography. This hypothesis holds that differences in species number among larger or smaller islands accrue from the balance between rates of extinction and immigration on each island. Immigration to an island is a function of its distance from sources of potential immigrants. Larger islands accommodate larger populations of a given species, and therefore suffer lower rates of extinction than

smaller islands. The equilibrium between immigration and extinction stabilizes at a higher level of species richness for large islands than for small ones (MacArthur and Wilson 1963,1967).

3) The habitat diversity hypothesis suggests that the number of habitats on an island, which is positively correlated with island size, is primarily responsible for the higher species richness of large islands. Essentially, it says that, because more niches are available on large islands, more organisms can coexist there than on small islands with fewer niches (Williams 1964).

I agree with Connor and McCoy that the best null hypothesis for any system is hypothesis 1. The conclusion that species-area patterns are a result of biological processes such as immigration and extinction (hypothesis 2) or habitat diversity (hypothesis 3) should be made only after having rejected the null hypothesis that the patterns are simply due to chance sampling of a regional species pool by different sized local areas.

The conspicuously island-like nature of open south-facing bluff habitats in interior Alaska stimulates the question of whether there are species-area relationships in this system. I compiled floristic information from bluffs in the study area and then tested the ability of six separate geographic variables from three categories (two area measures, two elevational measures, and two isolation measures) to account for the observed variations in species richness. Using the best individual predictors from each of these categories, I employed path analysis to evaluate the relative contribution of habitat area, elevationally determined habitat heterogeneity, and isolation to the patterns of species richness at several spatial scales. I used the results of these analyses to evaluate the ability of each of the three hypotheses presented previously to explain patterns of species richness in this study system.

II. METHODS

STUDY AREAS

Yukon River

The Yukon River study area is the same as that described in Chapter One (see Fig. 1 for the location of study sites). Floristic data from previous studies of Yukon River bluffs by Batten et al. (1979), Edwards and Armbruster (1989), Wesser and Armbruster (1991) and Howenstein (1994) were added to data collected in this study.

Charley River

The Charley River flows into the Yukon from the south, 152 kilometers downstream from Eagle, Alaska. The headwaters of the Charley River drain the north side of the peaks dividing the Charley, Fortymile and Salcha watersheds. The river flows northeast through the mountainous terrain known locally as the Charley River Mountains.

The channel of the Charley River is deeply incised along parts of its length where bands of steep and rocky bluffs rise from the narrow valley floor. In the middle reaches of the watershed, these bluffs are close to alpine areas and provide winter and summer range for Dall's sheep. The sheep travel between alpine grazing areas and the safety of the steep cliffs along the river. Sheep grazing affects the vegetation of these bluffs, resulting in more bare ground and increased soil perturbation.

Unlike the rest of the study area, the geology of the Charley River watershed is composed of highly metamorphosed units of mica-schist, gneiss, adamyllite and phylite (Brabb and Churkin 1969). The slopes are steep and the soils derived from them are coarser than soils derived from the rock units north of the Yukon River. Floristic data from ten separate bluffs, from 33 km to 124 km upstream from the confluence with the Yukon River, will be considered in this chapter (see Fig. 1).

Kandik River

The Kandik River enters the Yukon River from the north between Kathul Mountain and Biederman Bluff, 122 km downstream from Eagle. This is the westernmost river drainage in the Ogilvie Mountains. The Kandik River is a slow moving, widely meandering stream that occupies a wide valley flanked by low hills. The terrain is mostly gentle and rolling. The river is only enclosed by steep walls in the vicinity of Johnson Gorge where most of the steppe in the Kandik River drainage occurs.

The bedrock of the Kandik sites is dominated by the Graywacke of the Kathul Mountain syncline and argillite (Brabb and Churkin 1969). The valley floor is overlain by extensive alluvial terraces of Quaternary origin. The Kandik valley is occupied by extensive *Picea mariana* muskegs in low lying areas and closed *Picea glauca* forest on well-drained sites. The north-facing slopes of the valley walls support open muskeg whereas south-facing sites have mixed *Betula resinifera* and *Picea glauca* forest.

One site was located on a small bluff about 87 river kilometers from the confluence of the Kandik and Yukon Rivers. Two sites were located in Johnson Gorge, which is 49 km upstream from the confluence with the Yukon (Fig. 1).

Tatonduk River

The Tatonduk River drains the high peaks of the western Ogilvie Mountains, and flows into the Yukon River at Miller's Camp, 40 km downstream from Eagle. The gradient is steep and the river is relatively fast-flowing. The terrain surrounding the Tatonduk River is steep and rugged. Large limestone bluffs and cliffs rise from the floodplain of the river along much of its length. These bluffs are connected to ridges that ascend into alpine areas of the Ogilvie Mountains.

The geology of the of the Tatonduk River bluffs is dominated by the limestone and dolomite units of the Ogilvie Mountain Range (Foster 1976). The geomorphology there is similar to that of the Charley River in that there are bands of cliffs adjacent to the river.

Three sites for vegetation sampling were located on the Tatonduk River. The upriver site was located at the mouth of Funnel Creek near the Canadian border, about 24 km upstream from the confluence with the Yukon; the other two sites were located at 7 and 3.6 km upstream from the confluence with the Yukon River (Fig. 1).

FIELD METHODS

Floristic data were collected in conjunction with the vegetation sampling plan described in Chapter One. Site selection criteria are outlined in the methods section of that chapter. Upon completion of vegetation sampling, a species list was compiled from a survey of all accessible steppe fields for each bluff. The list included plants occurring in treeless habitats including steppe and rubble slopes. Collections and voucher specimens are deposited in the Yukon-Charley Rivers National Preserve herbarium and at the Herbarium of the University of Alaska Museum (ALA).

To minimize differences in sampling intensity among study sites, data analysis was restricted to those sites where vegetation sampling was performed. Because the digitized topographic data used to compute potential habitat area were available only for sites in Alaska, detailed modeling of species richness data was performed only for those sites.

LABORATORY METHODS

Habitat area measurements

Populations of steppe plants are mostly confined to steep, southeast to southwest facing slopes below 950 m. Because these topographical variables define potential habitat for this flora, it was possible to generate a digitized map outlining polygons of potential steppe on the landscape of Yukon-Charley Rivers National Preserve and neighboring areas. The National Park Service's Regional Geographic Information Office in Anchorage produced a G.I.S. data layer based on digitized 1:64,360 topographic data (S. Wesser, pers. comm.). Topographic surfaces that met the criteria presented in Table 16 were designated as potential steppe habitat.

The results of these geographic analyses were printed on a series of 1:63,360 scale plots. Areas that met the topographic criteria outlined previously were designated by shaded polygons. Potential steppe habitat was then quantified by measuring the map area enclosed in these polygons. Total polygon area was then summed to yield total potential habitat for each bluff. I used Sigma-scan software with a personal computer digitizing board to accomplish these measurements.

Distance measurements

Two distance measures were used to estimate bluff isolation. The first measure ("distance-1") was the distance from a bluff to the closest bluff with a minimum potential area of 350,000 m^2. This size was selected because bluffs with a smaller habitat-area were very species-poor and were unlikely to represent a source of propagules for most taxa. The second measure ("distance-2") was the shortest distance to either Kathul Mountain or Eagle bluff, the two richest sites encountered in the study area. These measurements were made from edge to edge of bluff polygons using 1:63,360 scale maps.

Elevation measurements

Two measures of elevation also were used to model patterns of species richness. The first metric was simply the maximum elevation of steep, south-facing terrain on a bluff (as identified by the potential area plots). The second measurement is the elevational extent of steep, south-facing terrain. This value is obtained by subtracting the

Table 16. Range of values used for identification of potential habitat of bluff flora in Alaska.

Topographical variable	Minimum value	Maximum value
Slope (degrees)	28.8	45.0
Aspect (degrees)	120	255
Elevation (meters)	None	861

elevation of the base of the slope from its maximum elevation; it represents the amount of elevation spanned by steep south-facing terrain on a bluff.

ANALYTICAL METHODS

Biogeographic affinity

The bluff flora was grouped into biogeographic categories based on the definitions presented in Table 1. The range maps of Hulten (1968) were used to categorize species distributions. One additional distribution category was "generally restricted" (GR). A generally restricted plant is one that occurs almost exclusively in open, xeric and generally treeless facies. I have followed the definition of Murray et al. (1983) for the GR flora.

Statistical methods

Linear regression was used to model the relationship between the geographic variables and species richness (MINITAB statistical software was used for all statistical analyses). All variables were assessed for conformity with assumptions of linear regression. I analyzed six aspects of species richness: (1) total species richness (all bluff taxa); (2) generally restricted (GR) plants; (3) widespread plants; (4) plants with North American distributions; (5) amphiberingian species; and (6) Alaska-Yukon endemics.

Simple linear regression of these dependent variables on the geographic predictor variables identified the most significant determinants of species richness. I then formulated a hypothetical causal model to assess both the relative and overall strength of the three most powerful variables controlling species richness in this system.

Path analysis is a multiple regression technique (Asher 1983) in which all variables are standardized prior to analysis. Explicit assumptions concerning the direction of causal linkages between variables are made. I assumed that geographic variables affected species richness and not vice versa. In the path diagram, the affect of one variable on another is depicted as a one-headed arrow, and the magnitude of the path coefficient (standardized regression coefficient) indicates the influence this variable has on the dependent variable in a multiple regression. Correlations among the independent variables are symbolized by dashed lines. The path representing the unexplained variance in the model has a magnitude of $(1-R^2)^{1/2}$, where R^2 is the coefficient of multiple

determination for the full model. No problems with multicollinearity were identified using variance inflation factors.

First I analyzed the control of species richness among bluffs within a watershed only for the Yukon and Charley River data sets because the Kandik and Tatonduk Rivers had low sample sizes. I then analyzed the data set containing all 24 bluffs in Alaska to determine whether the factors that control the patterns of species richness within a watershed also control the distribution of species richness among watersheds. I used analysis of variance to analyze differences in species richness among the four study watersheds.

III. RESULTS

FLORISTIC COMPOSITION OF STUDY WATERSHEDS

Yukon River

Excluding tree taxa, 93 species of vascular plants form the bluff flora of the Yukon River. Of these plants, 56 are considered generally restricted in the current study. There was an mean of 40 species per bluff on the Yukon River (SE = 4.1; Table 17). The mean number of GR taxa was 22.7 per bluff (SE = 2.6).

Several species were present at all of the Yukon River bluffs visited. *Artemisia frigida*, *Androsace septentrionalis*, *Calamagrostis purpurascens*, and *Solidago multiradiata* occurred at all sites, and *Agropyron spicatum* was absent from only one. Other species commonly present on Yukon River bluffs include *Arabis holboellii*, *Bupleurum triradiatum*, *Carex supina* ssp. *spaniocarpa*, *Galium boreale*, *Juniperus communis*, *Minuartia yukonensis*, *Poa glauca*, *Potentilla hookeriana*, *Potentilla pennsylvannica*, *Pulsatilla patens*, *Silene repens*, and *Solidago decumbens*.

Species composition data for bluffs on the Yukon River are presented in two separate tables. Floristic data from the bluffs in Alaska are compiled from this study and from those of others (Batten et al. 1979, Edwards and Armbruster 1989, and Howenstein 1994). Because floristic information for these bluffs is available elsewhere, I have listed only the GR taxa (Table 18). Floristic data for bluffs surveyed in the Yukon Territory are unavailable elsewhere, hence all species occurring at these sites are presented here (Table 19).

Table 17. Mean species richness of open habitats on bluffs in four study watersheds. Standard error is given in parenthesis.

Study area	Sample size	Mean number of species	Mean number of GR species
Yukon River	15	40.0 (± 4.12)	22.7 (± 2.6)
Charley River	10	23.3 (± 1.6)	14.7 (± 1.3)
Kandik River	2	32.5 (± 7.5)	16.0 (± 4.0)
Tatonduk River	3	25.7 (± 6.9)	18.0 (± 5.1)

Table 18. Distribution of the generally restricted flora among nine study bluffs on the Yukon River in Alaska. Range is given in column two (Wide =widespread, NA = North American, AB = amphiberingian, End = endemic to Ak.).

Taxon	Range	EAGLE	CALICO	TATONDUK	MONTAUK	NATION	KATHUL	BIEDERMAN	WOODCHOP	EUREKA CRK
APIACEAE										
Bupleurum triradiatum	AB	1	1	0	0	0	1	1	1	1
Podistera yukonensis	End	0	0	0	0	0	1	0	1	0
ASTERACEAE										
Artemisia alaskana	End	1	1	0	0	0	1	1	1	1
Artemisia borealis	Wide	1	1	0	0	0	1	0	0	0
Artemisia laciniata	AB	0	0	0	0	0	1	0	0	0
Artemisia frigida	AB	1	1	1	1	1	1	1	1	1
Artemisia furcata	AB	0	0	0	0	0	1	0	0	0
Aster commutatus	NA	0	0	0	1	0	0	0	0	0
Erigeron caespitossus	NA	0	0	0	0	0	1	0	0	0
Erigeron compositus	NA	1	1	0	0	0	1	0	0	0
Senecio hyperborealis	NA	0	0	0	0	0	1	0	1	0
Senecio ogoturukensis	End	1	0	0	0	0	1	0	1	1
BORAGINACEAE										
Cryptantha shackletteana	End	1	1	0	0	0	0	0	0	0
Eritrichium aretoides	AB	0	0	0	0	0	0	0	1	0
Eritrichium splendens	End	1	0	0	0	0	0	0	0	0
BRASSICACEAE										
Arabis divaricarpa	NA	0	0	0	0	0	1	1	0	0
Arabis hirsuta	NA	1	0	0	1	1	0	0	0	0
Arabis holboellii	NA	1	0	0	1	1	1	1	0	1
Braya humilis	NA	1	1	0	0	0	0	0	1	0

Table 18 continued.

Taxon	Range	E	C	T	M	N	K	B	W	E
BRASSICACEAE										
Draba murrayi	End	1	0	1	1	1	1	1	1	1
Erysimum asperum	End	1	1	0	1	0	1	1	1	1
Erysimum inconspicuum	NA	1	1	0	0	0	1	0	0	0
Lesquerella arctica	NA	0	1	0	0	0	0	0	0	0
CARYOPHYLLACEAE										
Arenaria capillaris	AB	0	0	0	0	0	1	1	0	0
Minuartia yukonensis	End	1	0	0	0	0	1	1	1	1
Silene menziesii	End	1	0	0	0	1	1	1	0	1
Silene repens	AB	1	0	0	1	1	1	1	1	1
CUPRESSACEAE										
Juniperus communis	Wide	1	1	1	0	1	1	1	1	1
CYPERACEAE										
Carex obtusata	Wide	0	0	0	0	0	1	0	0	1
Carex rossii	NA	0	0	0	0	0	1	0	0	0
Carex supina	Wide	1	1	0	1	1	1	1	1	0
FABACEAE										
Astragalus aboriginum	Wide	1	0	0	1	1	1	1	1	1
Oxytropis campestris	Wide	1	0	0	0	1	1	0	0	0
Oxytropis splendens	NA	1	0	0	0	0	1	0	0	0
HYDROPHYLLACEAE										
Phacelia sericea	NA	1	0	0	0	0	1	1	0	0
LILIACEAE										
Smilacina stellata	NA	0	0	0	1	1	1	0	1	0
LINACEAE										
Linum lewisii	NA	1	1	0	0	0	1	1	1	1
PAPAVERACEAE										
Papaver nudicaule	End	0	0	0	0	1	1	0	0	1

Table 18 continued:

Taxon	Range	E	C	T	M	N	K	B	W	E
PLANTAGINACEAE										
Plantago canescens	AB	0	0	0	0	0	0	1	0	0
POACEAE										
Agropyron spicatum	NA	1	1	1	1	1	1	1	1	1
Festuca lenensis	AB	0	0	0	0	0	1	0	0	0
POLEMONIACEAE										
Phlox hoodii	NA	1	0	0	0	0	0	0	1	0
POLYGONACEAE										
Eriogonum flavum	End	1	1	0	0	0	1	0	1	0
PRIMULACEAE										
Androsace chamaejasme	AB	0	0	0	0	0	1	0	0	0
Androsace septentrionalis	Wide	1	1	1	1	1	1	1	1	1
Douglasia arctica	End	0	0	0	0	0	1	1	0	0
RANUNCULACEAE										
Pulsatilla patens	Wide	1	1	1	1	1	1	1	1	1
ROSACEAE										
Chamaerhodos erecta	AB	1	0	0	0	0	1	0	0	1
Potentilla hookeriana	AB	1	0	0	0	0	1	0	1	1
Potentilla nivea	Wide	1	1	0	0	1	1	0	1	0
Potentilla pennsylvannica	NA	1	1	1	1	1	1	1	1	1
SAXIFRAGACEAE										
Saxifraga reflexa	End	1	1	0	0	1	1	1	1	1
SCROPHULARIACEAE										
Penstemon gormanii	End	1	1	1	1	1	1	1	1	1
SELAGINELLACEAE										
Selaginella sibirica	AB	1	0	0	0	0	1	1	1	1

Table 19. Distribution of plant species found on six Yukon River bluffs in the Yukon Territory, Canada. Generally restricted plants are marked GR. Range categories are the same as for Table 3.

			Location in km downstream from Dawson City, Y.T.					
Taxon	Range	Restriction	7 km	16 km	25 km	31 km	68 km	98 km
APIACEAE								
Bupleurum triradiatum	AB	GR	0	1	1	1	0	0
Cnidium cnidiifolium	AB		1	1	1	1	0	0
Podistera yukonensis	End	GR	0	0	1	0	0	0
ASPIDIACEAE								
Dryopteris fragrans	Wide		0	1	1	0	0	0
ASTERACEAE								
Achillea borealis	NA		1	1	1	0	1	1
Antennaria rosea	NA		1	1	1	1	0	0
Artemisia alaskana	End	GR	0	1	1	0	0	0
Artemisia frigida	AB	GR	1	1	1	1	1	1
Erigeron caespitossus	NA	GR	0	1	1	1	0	0
Erigeron compositus	NA	GR	0	0	1	0	0	1
Senecio ogoturukensis	End	GR	0	1	1	1	0	1
Solidago decumbens	NA		1	1	1	1	0	1
Solidago multiradiata	NA		1	1	1	1	1	1
BORAGINACEAE								
Mertensia paniculata	NA		0	0	1	0	0	0
BRASSICACEAE								
Alyssum americanum	AB	GR	0	0	1	0	0	1
Arabis holboellii	NA	GR	1	1	1	1	1	1
Draba nemorosa	Wide		0	1	0	0	0	0
Erysimum asperum	End	GR	0	1	1	0	0	0

Table 19, continued.

Taxon	Range	Restriction	7	16	25	31	68	98
BRASSICACEAE								
Erysimum inconspicuum	NA	GR	0	1	1	0	0	0
Halimolobis mollis	NA	GR	0	1	0	0	1	0
CAMPANULACEAE								
Campanula aurita	End		0	1	1	0	1	1
CARYOPHYLLACEAE								
Cerastium beeringianum	AB	GR	1	1	1	1	0	0
Minuartia yukonensis	End	GR	0	0	1	0	0	1
Silene menziesii	End	GR	0	0	0	0	0	1
Silene repens	AB	GR	1	1	1	1	1	1
CUPRESSACEAE								
Juniperus communis	Wide	GR	1	1	1	1	0	1
CYPERACEAE								
Carex obtusata	Wide	GR	0	1	1	0	0	1
Carex supina	Wide	GR	1	1	1	1	1	1
ELAEAGNACEAE								
Sheperdia canadensis	NA		1	1	1	0	1	1
ERICACEAE								
Arctostaphylos uva-ursi	Wide		1	1	1	1	0	1
FABACEAE								
Astragalus aboriginum	NA	GR	0	0	1	0	0	0
Hedysarum alpinum	Wide		0	1	0	0	0	0
Lupinus arcticus	NA		0	1	1	0	0	0
HYDROPHYLLACEAE								
Phacelia sericea	NA	GR	0	0	1	0	0	0

Table 19, continued

Taxon	Range	Restriction	7	16	25	31	68	98
LILIACEAE								
Lloydia serotina	Wide		0	0	1	0	0	0
Zygadenus elegans	NA		0	1	1	0	0	1
LINACEAE								
Linum lewisii	NA	GR	0	0	0	0	1	0
ONAGRACEAE								
Epilobium angustifolium	Wide		1	1	1	1	1	1
PAPAVERACEAE								
Papaver nudicaule	End	GR	0	0	1	0	0	0
POACEAE								
Agropyron spicatum	NA	GR	1	1	1	1	1	0
Bromus pumpellianus	Wide		1	0	1	0	1	1
Calamagrostis purpurascens	Wide		1	1	1	1	1	1
Festuca altaica	AB		1	1	1	1	1	1
Poa glauca	Wide		1	1	1	1	0	1
POLEMONIACEAE								
Polemonium pulcherimum	NA		1	1	1	0	1	0
PRIMULACEAE								
Androsace septentrionalis	Wide	GR	1	1	1	1	1	1
Dodecatheon frigidum	AB		1	1	1	1	0	0
RANUNCULACEAE								
Anemone narcissiflora	NA		0	0	1	0	0	0
Pulsatilla patens	Wide	GR	1	1	1	1	1	1
ROSACEAE								
Amelanchier alnifolia	NA		0	0	1	0	0	0
Chamaerhodos erecta	AB	GR	0	0	1	0	0	0
Dryas drummondii	NA		0	0	1	0	0	0

Table19, continued.

Taxon	Range	Restriction	7	16	25	31	68	98
ROSACEAE								
Potentilla arguta	NA		0	1	0	0	0	0
Potentilla hookeriana	AB	GR	1	1	1	1	1	1
Potentilla nivea	Wide	GR	0	0	1	0	0	0
Potentilla pennsylvannica	NA	GR	1	1	1	1	1	1
Rosa acicularis	Wide		1	1	1	1	1	1
Rubus idaeaus	NA		1	1	1	0	1	0
RUBIACEAE								
Galium boreale	Wide		1	1	1	1	1	1
SAXIFRAGACEAE								
Saxifraga reflexa	End	GR	1	1	1	1	1	1
Saxifraga tricuspidata	NA		1	1	1	1	1	1
SCROPHULARIACEAE								
Penstemon gormanii	End	GR	1	1	1	0	1	0
SELAGINELLACEAE								
Selaginella sibirica	AB	GR	0	1	1	0	0	1

New locations for several plants of restricted distribution were found in the inventories of bluffs in the Yukon Territory, Canada. Three species were added to the list of plants reported from Yukon River bluff associations. A new location for the rare endemic *Podistera yukonensis* occurred on the upper slopes of the large bluff 25 km. downstream from Dawson City (64°15'41" N, 139°36'13" W). Several large populations of this plant were located both in steppe and on rubble slopes on the upper elevation surfaces of this bluff. Three new sites for the disjunct *Phacelia sericea* were found on bluffs downstream from Dawson. *Erysimum asperum* var. *angustatum* was also located at several bluffs there. The collection of *Chamaerhodos erecta* on the bluff 25 km downstream from Dawson connects the Eagle Bluff collection by Shacklette to the range for the species published by Hulten (1968). *Potentilla arguta* ssp. *convallaria*, a plant with a continental North American distribution and disjunct populations in Alaska and Yukon was found on a bluff 16 km downstream from Dawson City (64°12'16" N, 139° 35' W). Although this is within its known range, this species has not been reported previously from Yukon River bluffs. *Draba nemorosa* and *Draba hirta* also occurred on Yukon Territory bluffs.

Although the flora of the bluffs in Alaska and the Yukon Territory are similar, there are some differences worth noting. *Draba murrayi*, an endemic species common and even abundant on some Yukon, Kandik and Tatonduk river bluffs, was not found on the sites in Canada. *Alyssum americanum*, on the other hand, is absent from the Alaskan study sites but common on the larger bluffs in the Yukon Territory. Likewise *Halimolobus mollis* has not been found on Yukon River bluffs in Alaska, but was an occasional component of the vegetation of several of the Yukon Territory sites.

The two largest biogeographic categories in the flora of the Yukon River bluffs are North American (34 species or 36.6 %; Table 20) and widespread (26 species or 27.9 %); (Table 20). Twenty percent of the flora (18 species) is amphiberingian and 16 % (15 species) are endemics. Data from Douglas (1974) are included in Table 20 for comparison (his work summarizes the floristic composition of the Alsek River watershed, southeast of the Yukon River study area).

Charley River

Fifty four plant species were recorded from open habitats on Charley River bluffs; 27 of these were GR species (Table 21). Fifty one of these species are included in Table

Table 20. Percentage of bluff floras of four study drainages in four biogeographic categories. Data from Porcupine and Tanana Rivers from Howenstein. (1994)
[1] data from Douglas (1974) included for comparison.

	Widespread	North American	Amphi-beringian	AK-YK Endemic
Yukon River	28.3	35.9	19.6	16.3
Charley River	40.7	33.3	11.1	14.8
Kandik River	36.4	27.3	15.9	20.5
Tatonduk River	33.3	31.1	15.6	20.0
Porcupine R.	31.5	39.7	20.5	8.2
Tanana River	41.5	34.0	17.0	7.5
Douglas[1]	43.0	31.0	17.0	5.0

Table 21. Distribution of plant species found on Charley River bluffs. Locations of bluffs are given in river kilometers from confluence with the Yukon River. Range categories are from Table 1.

			Distance of Site from Yukon River									
Taxon	Range		33 km	43 km	63 km	66 km	72 km	85 km	86 km	97 km	112 km	124 km
APIACEAE												
Bupleurum triradiatum	AB	GR	0	1	1	1	0	0	0	1	0	1
ASPIDIACEAE												
Dryopteris fragrans	Wide		0	1	0	0	0	0	1	1	0	1
ASTERACEAE												
Artemisia alaskana	End	GR	0	1	1	1	0	0	0	1	1	1
Artemisia frigida	AB	GR	1	1	1	1	1	1	1	1	1	1
Erigeron compositus	NA	GR	0	0	0	0	0	0	0	0	0	1
Senecio ogoturukensis	End	GR	1	1	0	0	0	0	0	1	0	1
Solidago multiradiata	NA		1	1	1	1	1	1	1	1	1	1
Taraxacum ceratophorum	Wide		0	0	0	0	0	0	1	1	0	1
BORAGINACEAE												
Eritrichium splendens	End	GR	0	0	0	0	0	0	0	0	0	1
Mertensia paniculata	NA		0	0	0	0	0	1	0	1	0	0
BRASSICACEAE												
Arabis hirsuta	NA	GR	0	0	0	0	0	1	0	0	0	0
Braya humilis	NA	GR	1	1	0	0	1	0	1	1	0	0
Draba cana	Wide		0	0	0	0	0	0	0	1	1	1
Draba nemorosa	Wide		0	0	0	0	0	0	0	1	0	1
Halimolobus mollis	NA	GR	0	0	0	0	0	0	0	1	0	1
CAMPANULACEAE												
Campanula aurita	End		1	1	1	1	1	0	1	0	0	0

Table 21 continued.

Taxon	Range		33 km	43 km	63 km	66 km	72 km	85 km	86 km	97 km	112 km	124 km
CARYOPHYLLACEAE												
Minuartia arctica	AB		0	0	1	1	0	0	0	0	0	1
Silene menziesii	End	GR	0	0	1	1	0	0	1	1	0	1
Silene repens	AB	GR	1	0	1	1	1	1	1	1	1	1
CHENOPODIACEAE												
Chenopodium album	Wide		0	0	0	0	0	0	1	1	0	0
CUPRESSACEAE												
Juniperus communis	Wide	GR	1	1	1	1	1	1	1	1	0	1
CYPERACEAE												
Carex obtusata	Wide	GR	1	0	0	0	0	0	0	0	1	1
Carex supina	Wide	GR	0	0	0	1	1	1	0	0	1	0
ELAEAGNACEAE												
Sheperdia canadensis	NA		0	1	0	0	0	1	0	0	0	0
ERICACEAE												
Arctostaphylos uva-ursi	Wide		0	0	1	1	0	1	0	0	0	1
FABACEAE												
Astragalus aboriginum	NA	GR	0	0	0	1	0	0	0	0	0	1
Hedysarum alpinum	Wide		1	0	0	0	0	0	0	0	0	0
Lupinus arcticus	NA		0	0	0	0	0	1	0	0	0	0
Oxytropis campestris	Wide	GR	0	1	1	1	1	0	1	1	0	1
LILIACEAE												
Zygadenus elegans	NA		0	1	0	1	1	1	0	0	0	1

Table 21 continued

Taxon	Range		33 km	43 km	63 km	66 km	72 km	85 km	86 km	97 km	112 km	124 km
LINACEAE												
Linum lewisii	NA	GR	0	0	0	0	0	0	1	1	0	0
ONAGRACEAE												
Epilobium angustifolium	Wide		0	1	0	0	0	1	1	0	0	0
PAPAVERACEAE												
Papaver nudicaule	End	GR	0	1	0	1	0	0	0	0	0	0
PLANTAGINACEAE												
Plantago canescens	AB	GR	0	0	0	0	1	0	0	0	0	0
POACEAE												
Agropyron spicatum	NA	GR	1	1	1	1	1	1	1	1	1	1
Bromus pumpellianus	Wide		0	0	0	0	0	1	0	0	0	0
Cala. purpurascens	Wide		1	1	1	1	1	1	1	1	1	1
Poa glauca	Wide		1	0	0	0	0	1	1	1	0	1
PRIMULACEAE												
Androsace septentrionalis	Wide	GR	1	0	1	0	0	0	1	1	1	1
RANUNCULACEAE												
Delphinium glaucum	NA		0	0	0	0	0	1	0	0	0	0
Pulsatilla patens	Wide	GR	1	0	1	1	1	1	1	1	1	1
ROSACEAE												
Chamaerhodos erecta	AB	GR	0	0	0	1	1	0	0	0	0	0
Potentilla nivea	Wide	GR	0	0	1	1	0	0	1	1	0	1
Potentilla pennsylvannica	NA	GR	1	0	1	1	1	1	1	1	1	1
Rosa acicularis	Wide		1	1	0	0	1	1	0	0	1	1
Rubus idaeaus	Wide		1	0	0	0	0	0	0	1	0	0

Table 21, continued.

Taxon	Range		33 km	43 km	63 km	66 km	72 km	85 km	86 km	97 km	112 km	124 km
RUBIACEAE												
Galium boreale	Wide		1	1	1	1	1	1	1	1	1	1
SAXIFRAGACEAE												
Saxifraga reflexa	End	GR	1	1	0	0	0	1	1	1	1	1
Saxifraga tricuspidata	NA		1	1	1	0	1	1	1	1	0	1
SCROPHULARIACEAE												
Castilleja raupii	NA		0	1	0	0	0	0	0	0	0	0
Penstemon gormanii	End	GR	1	0	1	1	1	1	0	1	0	0

21; *Arabis holboellii*, *Astragalus alpinus* and *Erigeron caespitosus* were each collected at sites where vegetation sampling was not performed, thus these species are not included in this table.

The Charley River flora is for the most part a subset of the Yukon bluff flora. All of the GR species occurring there are present in the Yukon River flora. *Castilleja raupii*, *Chenopodium album*, and *Draba cana* are the only species present on the Charley River bluffs that are absent from the Yukon River sites. Charley River bluffs were species poor compared with Yukon River bluffs both in the total number of species in the watershed and in species richness per bluff. There was an average of 22.8 species per bluff (SE = 1.59; Table 17). Mean GR species richness was 13.1 (SE = 1.0; Table 17). Mean species richness there is several standard errors lower than mean richness on Yukon River bluffs.

The dominant plants in this study area are the same as in other watersheds; *Agropyron spicatum*, *Artemisia frigida*, *Calamagrostis purpurascens*, *Galium boreale*, and *Solidago multiradiata* were found at all 10 sites, whereas *Juniperus communis*, *Potentilla pennsylvannica*, *Pulsatilla patens*, and *Silene repens* were absent from only one site each. Other common plants were *Androsace septentrionalis*, *Oxytropis campestris*, *Saxifraga reflexa* and *Saxifraga tricuspidata*.

There were a few noteworthy new locations for biogeographically interesting plants in this study area. *Papaver nudicaule* ssp. *americanum*, *Chamaerhodos erecta* and *Halimolobus mollis* were each collected at stations on the Charley River. *Eritrichium splendens*, an endemic plant was found at the farthest upriver site. Eagle Bluff is the only other south-facing bluff locality in this area.

Although the character of the vegetation and the floristic composition of a site is largely unrelated to its position along the Charley River corridor, several endemic species appear to be limited to the bluffs of the middle Charley and below, suggesting that dispersal from Yukon River bluffs into this corridor may be occurring. *Penstemon gormanii*, a steppe endemic, was found on the bluff at the mouth of Crescent Creek (km 97) and all but two of the sites below it. Similarly, *Campanula aurita* was found on all but one bluff below the Crescent Creek site. Both of these plants are absent from Salcha and Tanana River bluffs, across the Yukon-Tanana drainage divide. *Papaver nudicaule* ssp. *americanum*, an endemic found on several Yukon River bluffs and one that has been

reported from Salcha River bluffs, was observed at four sites between km 43 and km 74 on the Charley River.

Kandik River

A total of 44 species occurred at the two bluffs visited on the Kandik River; 21 were categorized as GR (Table 22). The flora of this watershed was primarily a subset of the plant species found on Yukon River bluffs; however it is a different subset from the Charley River sites. Most notably, two of the narrowly endemic taxa occurred there. The category 2 plant *Draba murrayi* was found in abundance in a variety of open habitats including steppe, rock crevices, rubble slopes, and open aspen woodland. *Erysimum asperum* var. *angustatum* also was abundant at the Johnson Gorge sites. These are the northernmost collection localities for these rare taxa, which have not been found on sites on the Porcupine River (Howenstein 1994). Additionally, large populations of *Phacelia mollis*, an endemic species previously known only from south of the Yukon River, were located on both bluffs in the Kandik River drainage. The most upriver collection is a range extension of approximately 175 km to the north from the nearest collection near Chicken, Alaska.

Mean species richness was 33.5 (SE = 10.5) at Kandik River sites with an average of 14.0 GR taxa (SE = 4.5; Table 17). This places these variables within two standard errors (SE) of mean richness for Yukon River bluffs. In comparison, total richness on Charley River bluffs was more than four SE less and GR richness was slightly more than three SE less than the mean of these variables on the Yukon (Table 17).

Tatonduk River

Forty-five plant species (excluding trees) occurred on the three bluffs; 28 of these being GR (Table 23). This flora also represents a subset of the Yukon River bluff flora. Although the geology and site characteristics are very different from those of the Kandik River, there are marked similarities between the floras of the two watersheds. For example, populations of the narrowly distributed plants *Draba murrayi* and *Erysimum asperum* var. *angustatum* were found at sites in both drainages. *D. murrayi* was particularly abundant at the Funnel Creek site. This species occurred in several habitats including limestone rock crevices, heavily-grazed turfy benches, grassy steppe, and forest-edge. This site has the highest population density of this plant I have seen

Table 22. Distribution of plant species found on two Kandik River bluffs. Range and restriction categories the same as in Table 4.

Taxon	Range		Kandik 1	Johnson Gorge
APIACEAE				
Bupleurum triradiatum	AB	GR	0	1
ASPIDIACEAE				
Dryopteris fragrans	Wide		1	1
ASTERACEAE				
Achillea borealis	NA		0	1
Artemisia alaskana	End	GR	1	1
Artemisia frigida	AB	GR	0	1
Senecio ogoturukensis	End	GR	1	1
Solidago decumbens	NA		0	1
Solidago multiradiata	NA		1	1
BORAGINACEAE				
Mertensia paniculata	NA		1	1
BRASSICACEAE				
Arabis hirsuta	NA	GR	1	1
Draba murrayi	End	GR	1	1
Erysimum asperum	End	GR	0	1
Erysimum inconspicuum	NA	GR	1	1
CAMPANULACEAE				
Campanula aurita	End		0	1
CARYOPHYLLACEAE				
Cerastium beeringianum	AB	GR	0	1
Silene menziesii	End	GR	0	1
Silene repens	AB	GR	1	1
CUPRESSACEAE				
Juniperus communis	Wide	GR	1	1

Table 22 continued.

Taxon	Range		Kandik 1	Johnson Gorge
CYPERACEAE				
Carex obtusata	Wide	GR	0	1
ELAEAGNACEAE				
Sheperdia canadensis	NA		0	1
ERICACEAE				
Arctostaphylos uva-ursi	Wide		0	1
Vaccinium vitis-idaea	Wide		0	1
FABACEAE				
Astragalus alpinus	Wide		0	1
Hedysarum alpinum	Wide		1	1
GENTIANACEAE				
Gentiana propinqua	NA		1	1
HYDROPHYLLACEAE				
Phacelia mollis	End	GR	1	1
ONAGRACEAE				
Epilobium angustifolium	Wide		1	1
PAPAVERACEAE				
Papaver nudicaule	End	GR	1	1
POACEAE				
Agropyron spicatum	NA	GR	1	1
Bromus pumpellianus	Wide		0	1
Calamagrostis purpurascens	Wide		1	1
Festuca altaica	AB		0	1
Poa glauca	Wide		0	1

Table 22 continued.

Taxon	Range		Kandik 1	Johnson Gorge
PRIMULACEAE				
Androsace septentrionalis	Wide	GR	1	1
RANUNCULACEAE				
Aconitum delphinofolium	AB		0	1
Delphinium glaucum	NA		0	1
Pulsatilla patens	Wide	GR	0	1
ROSACEAE				
Potentilla pennsylvannica	NA	GR	0	1
Rosa acicularis	Wide		1	1
Rubus idaeaus	Wide		1	1
RUBIACEAE				
Galium boreale	Wide		1	1
SAXIFRAGACEAE				
Saxifraga reflexa	End	GR	1	1
Saxifraga tricuspidata	NA		1	1
SELAGINELLACEAE				
Selaginella sibirica	AB	GR	0	1

Table 23. Distribution of plant species found on three Tatonduk River bluffs. Range and Restriction categories are the same as in Table 4.

Taxon	Range		Tatonduk Site 2	Tatonduk Site 1	Funnel Creek
APIACEAE					
Bupleurum triradiatum	AB	GR	0	1	1
ASPIDIACEAE					
Dryopteris fragrans	Wide		0	0	1
ASTERACEAE					
Artemisia alaskana	End	GR	1	0	1
Artemisia frigida	AB	GR	1	1	1
Erigeron compositus	NA	GR	0	1	1
Senecio ogoturukensis	End	GR	0	0	1
Senecio cf. *yukonensis*	End		0	0	1
Solidago decumbens	NA		0	0	1
Solidago multiradiata	NA		1	1	1
BORAGINACEAE					
Mertensia paniculata	NA		0	0	1
BRASSICACEAE					
Arabis hirsuta	NA	GR	1	1	1
Braya humilis	NA	GR	0	1	1
Draba murrayi	End	GR	1	1	1
Erysimum asperum	End	GR	1	0	1
Erysimum inconspicuum	NA	GR	1	0	1
CARYOPHYLLACEAE					
Minuartia yukonensis	End	GR	0	0	1
Silene repens	AB	GR	0	0	1
CUPRESSACEAE					
Juniperus communis	Wide	GR	1	1	1

Table 23 continued.

Taxon	Range		Tatonduk Site 2	Tatonduk Site 1	Funnel Creek
CYPERACEAE					
Carex supina	Wide	GR	1	1	1
ELAEAGNACEAE					
Sheperdia canadensis	NA		1	0	0
FABACEAE					
Hedysarum alpinum	Wide		0	0	1
Oxytropis campestris	Wide	GR	0	0	1
LILIACEAE					
Lloydia serotina	Wide		0	0	1
Zygadenus elegans	NA		0	0	1
LINACEAE					
Linum lewisii	NA	GR	0	0	1
ONAGRACEAE					
Epilobium angustifolium	Wide		1	1	1
PAPAVERACEAE					
Papaver nudicaule	End	GR	0	0	1
PLANTAGINACEAE					
Plantago canescens	AB	GR	0	0	1
POACEAE					
Agropyron spicatum	NA	GR	1	1	1
Calamagrostis purpurascens	Wide		1	1	1
Festuca lenensis	AB	GR	0	0	1
Festuca altaica	AB		1	0	1
Poa glauca	Wide		0	0	1
POLEMONIACEAE					
Phlox hoodii	NA	GR	0	0	1

Table 23 continued.

Taxon	Range		Tatonduk site 2	Tatonduk site1	Funnel Creek
PRIMULACEAE					
Androsace septentrionalis	Wide	GR	1	1	1
RANUNCULACEAE					
Pulsatilla patens	Wide	GR	1	1	1
ROSACEAE					
Potentilla hookeriana	AB	GR	0	0	1
Potentilla nivea	Wide	GR	0	0	1
Potentilla pennsylvannica	NA	GR	1	0	1
Rosa acicularis	Wide		1	1	1
Rubus idaeaus	Wide		0	0	1
RUBIACEAE					
Galium boreale	Wide		1	1	1
SAXIFRAGACEAE					
Saxifraga reflexa	End	GR	1	0	1
Saxifraga tricuspidata	NA		1	0	1
SCROPHULARIACEAE					
Penstemon gormanii	End	GR	1	0	1

anywhere and it does well in the calcium-rich soils derived from the limestone bedrock.

There are several differences between the flora of the Kandik and Tatonduk River bluffs, particularly with regard to the endemic component. *Phacelia mollis* was absent from Tatonduk River sites although it occurred in abundance on the Kandik River. Conversely, *Minuartia yukonensis* and *Penstemon gormanii* were present on Tatonduk bluffs but absent from the Kandik. In the amphiberingian category, *Festuca lenensis*, *Plantago canescens* and *Potentilla hookeriana* were present on the Tatonduk River but absent from Kandik River bluffs.

Mean species richness on the Tatonduk River bluffs was 26.7 species per site (SE = 8.4; Table 17)) with 16.7 of these being GR species (SE = 4.7). Species richness was concentrated at Funnel Creek, just as it was concentrated at Johnson Gorge on the Kandik River. The two smaller sites investigated on the Tatonduk contained subsets of the relatively rich flora of the Funnel Creek bluff.

Comparisons of floristic composition among study watersheds

Charley River

There are two notable differences in the relative importance of the biogeographic groups within the flora of the Charley River as compared to the Yukon River bluffs (Fig. 37). This flora is relatively enriched in widespread species and depauperate in Amphiberingean species. Forty-one percent of the species in the flora of the Charley River bluffs have widespread distributions, as compared to 28 % of the Yukon River flora. On both a percentage and absolute basis, there are fewer species with an amphiberingean distribution in this flora than in the Yukon River flora. Although the numbers of both endemic and North American taxa are much lower in this watershed, they contribute only a slightly smaller percentage to the total flora than they do at Yukon River sites.

The Charley River flora is notably impoverished in rare and sensitive plant species. None of the category 2 taxa was found in this drainage. Similarly, the endemic component (14.8 %) is primarily represented by species with relatively wide distributions in Alaska such as *Artemisia alaskana*, *Saxifraga reflexa*, and *Senecio ogoturukensis*. None of the taxa with distributions widely disjunct from the intermountain west was found on Charley River bluffs.

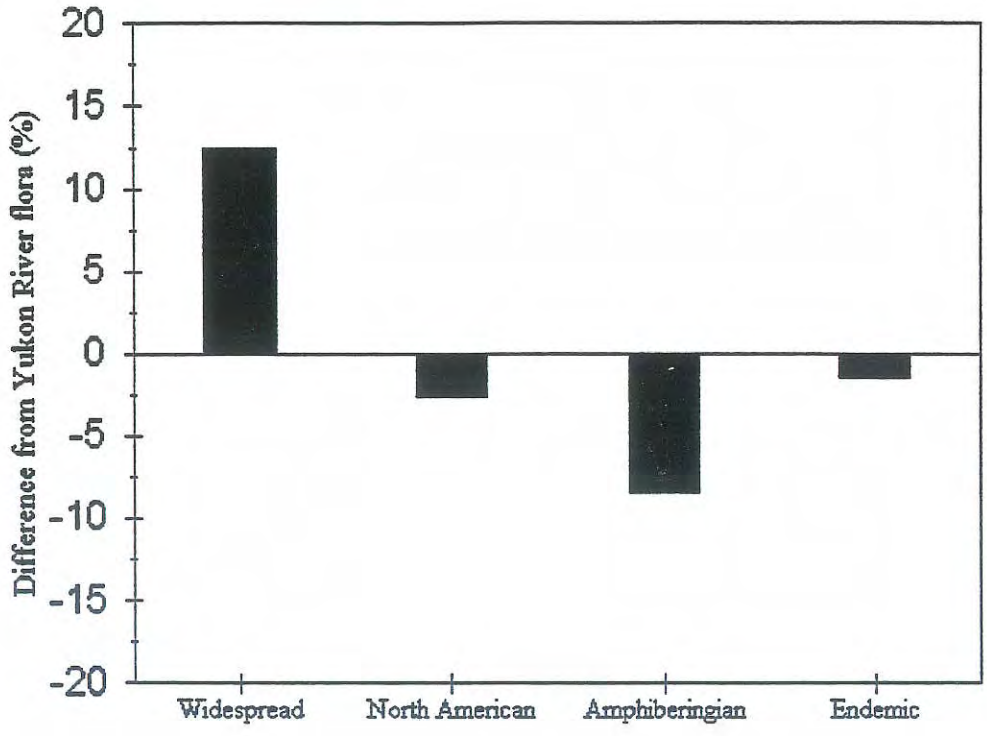


Fig. 37. Difference in the percentage of four biogeographic groups in the Charley River flora in comparison to the Yukon River flora.

Kandik River

There was a less pronounced increase in the importance of species with widespread distributions in the Kandik flora relative to the Yukon flora than was the case for Charley River bluffs. Thirty-six percent of the Kandik flora (16 species) are widespread species. Also in contrast to the Charley River flora, the percentage of endemic plants within the Kandik flora is somewhat higher than in the Yukon River bluff flora (Fig. 38). Amphiberingean taxa constitute 16 % of the Kandik River bluff flora compared to almost 20 % of the Yukon River flora. Plants with North American distributions contribute 27 % of the flora of the Kandik River bluffs. This category represents 34 % of the Yukon River flora (Table 20).

Tatonduk River

The contribution of the four biogeographic subgroups to the total flora in the Tatonduk drainage closely parallels that described for Kandik River sites (Table 20). Species with widespread distributions composed 33.3 % of the Tatonduk flora; 15.6 % are Amphiberingean taxa and another 20 % are endemic to Alaska. North American species make up the remaining 31.1 % of this flora. Like the Kandik River bluffs, the Tatonduk River sites were relatively enriched (on a percentage basis) in the endemic component as compared with Yukon River bluffs (Fig. 39).

Porcupine and Tanana Rivers

Floristic inventories of south-facing bluffs of the Porcupine and Tanana Rivers allow for comparisons with the Yukon River bluff flora (Howenstein 1994). The Porcupine River flora is second only to the Yukon River in the number of total plant taxa and biogeographically interesting plant species (Howenstein 1994). Excluding trees, Howenstein reported finding 77 species of vascular plants at sites on the Porcupine; 41 of these plants were GR.

Although *Eriogonum flavum* var. *aquilinum* is the only category 2 plant present on Porcupine River bluffs, these bluffs have most of the GR taxa present on the Yukon River and a complement of plants with disjunct distribution patterns that have not been found on the bluffs of the Yukon River or its tributaries. *Townsendia hookeri*, a plant disjunct from continental areas of western North America, and an undescribed species of *Erigeron*, are the most noteworthy of this group. In contrast to the Charley, Kandik and

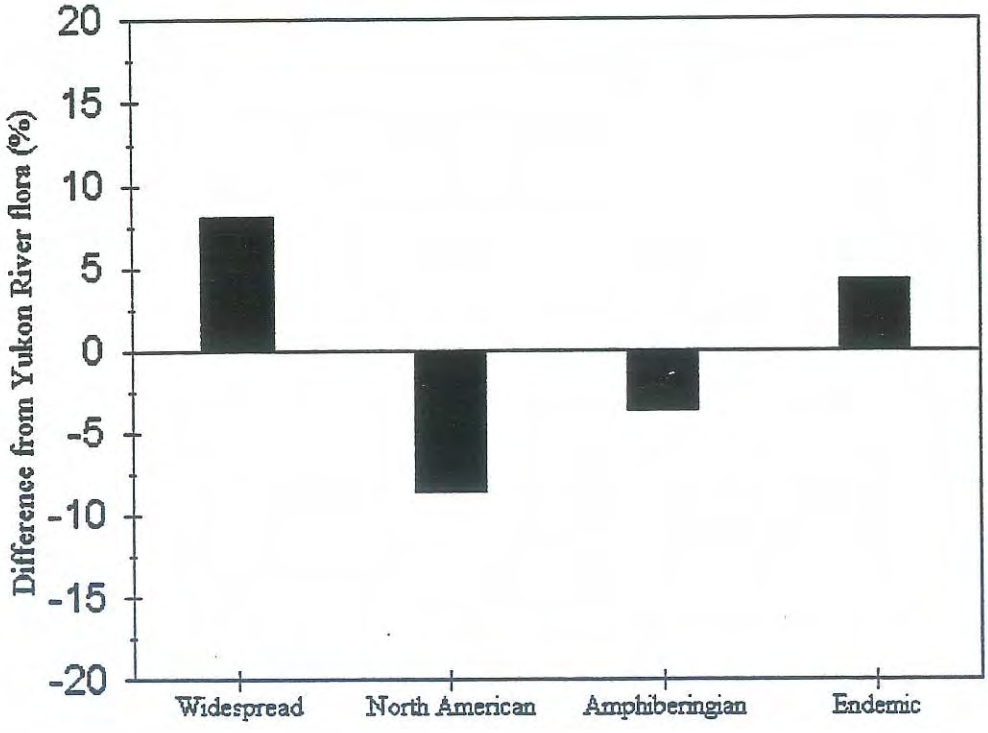


Fig. 38. Difference in the percentage of four biogeographic groups in the Kandik River flora in comparison to the Yukon River flora.

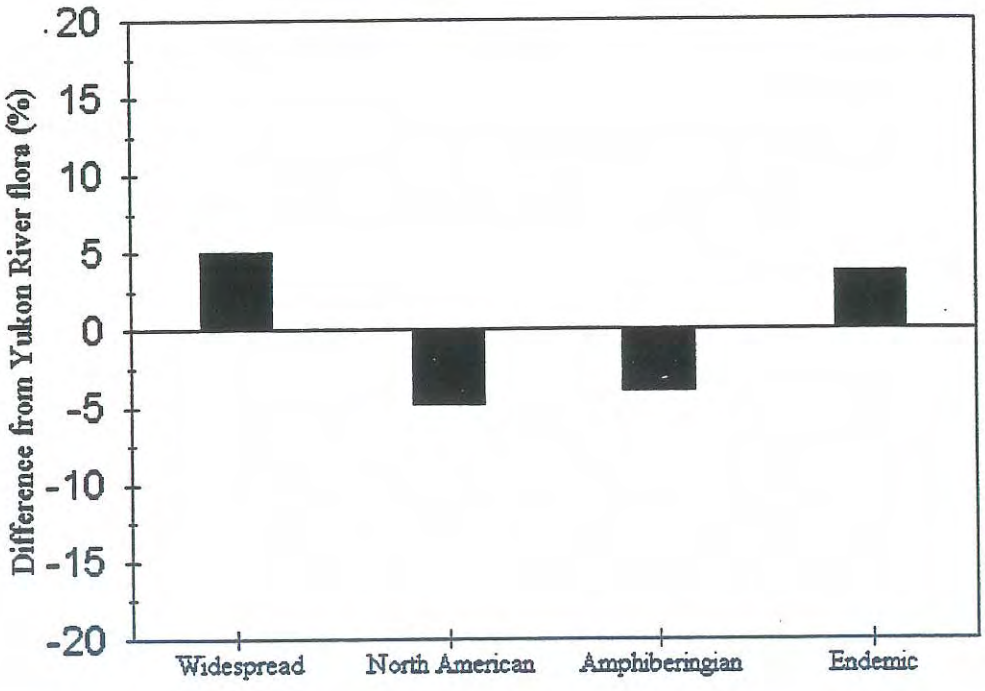


Fig. 39. Difference in the percentages of four biogeographic groups in the Tatonduk River flora in comparison to the Yukon River flora.

Tatonduk, then, the Porcupine River bluff flora was not strictly a subset of the species present on the Yukon River.

There are differences in the relative importance of plants from two of the four biogeographic groups within the flora of the Porcupine as compared with the Yukon River (Fig. 40). There are only six species (or 8 %) endemic to Alaska in the Porcupine River flora compared to 15 (or 16 % of the total) that occur on Yukon River bluffs. Although the Porcupine River flora has fewer North American species (29 vs. 34) in absolute terms, this group makes up a slightly greater percentage (39.7 vs. 35.9; Table 20) of the flora of the Porcupine as compared to the Yukon River. The absolute number of plant species in the widespread and amphiberingian distribution categories are higher in the Yukon River flora, although these groups make up an almost identical percentage of the two floras (see Table 5) .

The bluff flora that Howenstein (1994) reported for the Tanana River is made up of 53 species, exclusive of trees. In addition to having many fewer total species than both the Yukon and Porcupine River bluffs, this flora is relatively depauperate in the rare elements of the bluff flora and in endemic plants. It is composed of a subset of the plants that are found on Yukon River bluffs, except for four graminoid taxa with relatively wide distributions: *Carex filifolia*, *Elymus innovatus*, *Hierochloe odorata*, and *Koeleria gracilis*.

There are just four (or 7.5 % of the total) endemic plants reported for the Tanana River bluffs (Table 20). Except for *Papaver nudicaule* ssp. *americanum* these are all plants with broad distributions in Alaska and the Yukon Territory; none are restricted to the Tanana drainage. *Artemisia alaskana, Saxifraga reflexa*, and *Silene menziesii* ssp. *williamsii* have each been collected over most of the latitudinal and longitudinal extent of the state. The flora of the Tanana River is relatively enriched in plants with widespread distributions in comparison with the Yukon River flora (Fig. 41). In several respects, this flora is similar to the flora of the Charley River.

PATTERNS OF SPECIES RICHNESS AMONG BLUFFS IN A WATERSHED

Yukon River bluffs

Best single predictors of species richness

There are large differences in geographic characteristics (Table 24) and species richness values (Table 25) among the nine bluffs on the Yukon River in Alaska. Kathul

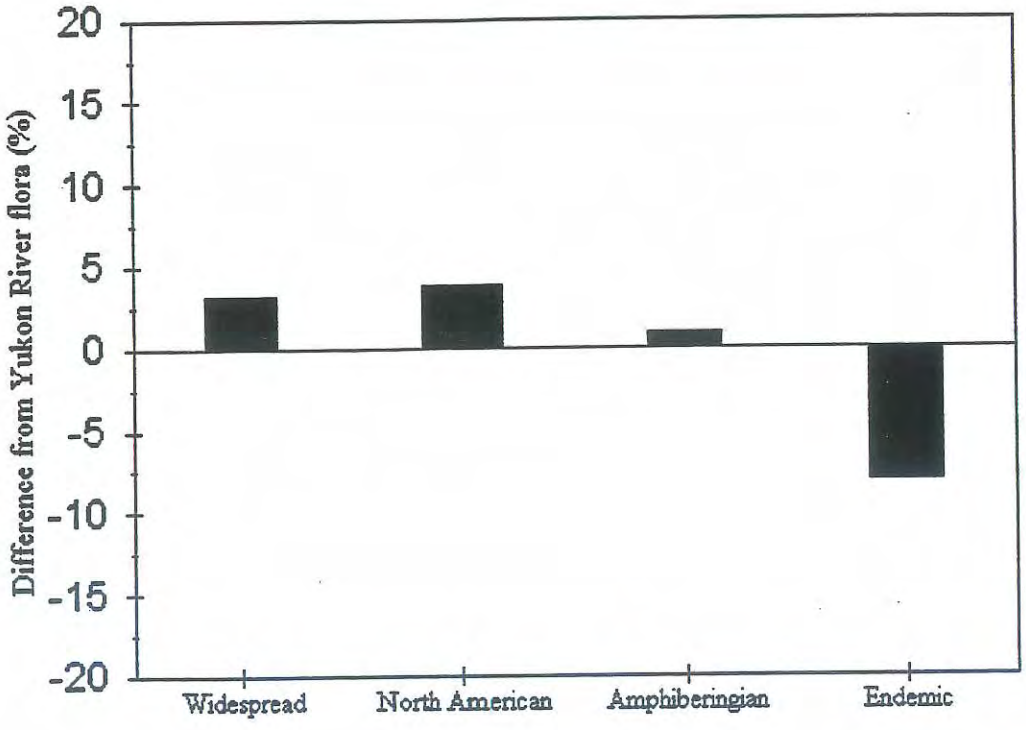


Fig. 40. Difference in the percentages of four biogeographic groups in the Porcupine River flora in comparison to the Yukon River flora.

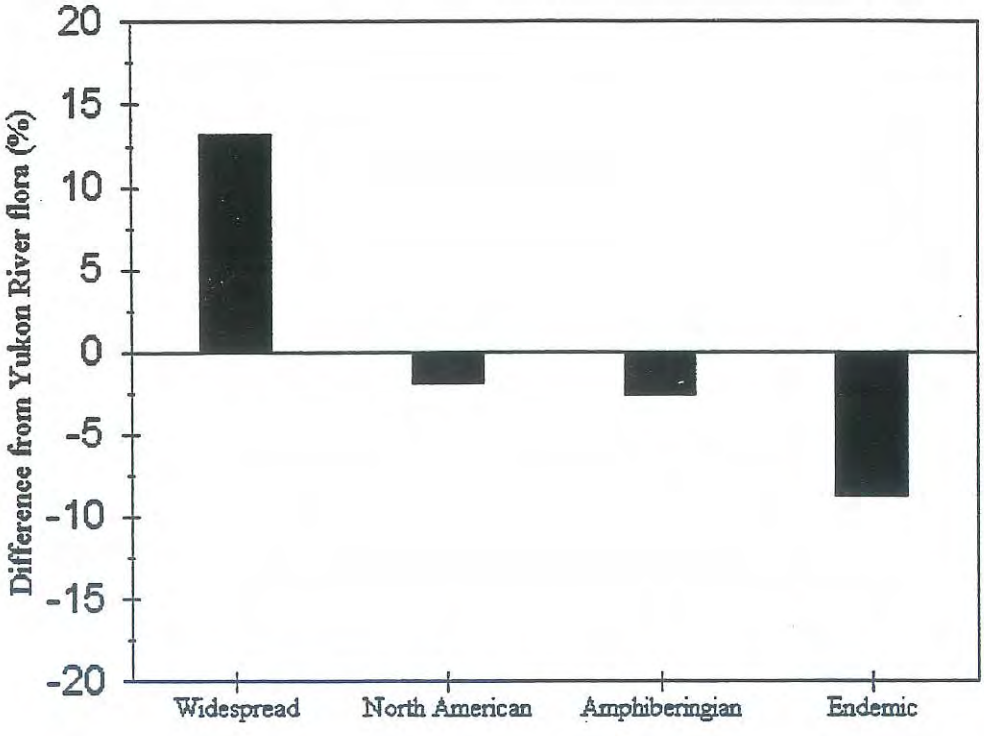


Fig. 41. Difference in the percentages of four biogeographic groups in the Tanana River flora in comparison with the Yukon River flora.

Table 24. Values of geographic variables measured for 24 bluffs in 4 study watersheds in Alaska.

Bluff	Elev. extent (m)	Max. elevation (m)	Area (sq. m)	Log area	Distance 1 (km)	Distance 2 (km)
Eagle	441	685	718415	13.4848	11.5	0
Calico	274	518	430790	12.9734	11.5	11.5
Tatonduk	85	366	37539	10.5331	12	23.5
Montauk	244	472	257594	12.4591	24.5	36
Nation	351	579	351829	12.7709	23.8	23.8
Kathul Mtn.	716	952	1027009	13.8422	12.8	0
Biederman	433	646	1233343	14.0252	12.8	12.8
Woodchopper	335	549	376423	12.8385	5.3	62.8
Eureka Creek	351	564	1543232	14.2494	5.3	68
Kandik # 1	91	457	256299	12.4541	23	39
Johnson Gorge	305	671	648515	13.3824	16	16
Funnel Creek	305	671	528908	13.1786	1.8	36
Taton. Riv. #1	91	427	37539	10.5331	4.8	29
Taton. Riv. #2	91	381	205816	12.3347	7.8	26
Charley bluffs:						
124 Km	305	1006	205056	12.2310	26	149
112 Km	152	762	87387	11.3781	14	137
97 Km	305	823	389886	12.8736	14	122
86 Km	122	610	34173	10.4392	11	111
85 Km	91	518	68317	11.1319	2	110
72 Km	91	485	13971	9.5447	25	97
66 Km	107	488	13971	9.5447	31	91
63 Km	122	503	13971	9.5447	34	87
43 Km	168	457	13971	9.5447	32.5	67
33 Km	107	427	157896	11.9697	27.5	57

Table 25. Species richness data for 24 bluffs in four study watersheds in Alaska. (Second four columns correspond to biogeographic categories: WS = widespread, NAM = North American, AB = amphiberingian, End = endemic).

Bluff	No. WS taxa	No. NAM taxa	No. AB taxa	No. End taxa	GR species richness	Total species richness
Eagle	19	18	10	12	36	59
Calico	12	10	3	7	21	32
Tatonduk	7	5	1	2	8	15
Montauk	9	10	2	3	15	24
Nation	13	10	2	5	19	30
Kathul Mtn.	21	22	14	12	44	69
Biederman	16	12	10	8	25	46
Woodchopper	17	15	7	9	28	48
Eureka Creek	14	12	11	9	24	46
Kandik # 1	9	7	1	6	12	23
Johnson Gorge	16	12	7	9	21	44
Funnel Creek	15	13	7	9	26	44
Taton. Riv. #1	8	5	2	1	11	16
Taton. Riv. #2	8	7	2	5	13	22
Charley bluffs:						
124 Km	15	8	4	5	19	32
112 Km	8	3	2	2	10	15
97 Km	14	8	3	5	17	30
86 Km	12	6	2	3	13	23
85 Km	9	10	2	2	10	23
72 Km	7	6	4	2	12	19
66 Km	8	5	5	5	16	23
63 Km	8	4	4	4	13	20
43 Km	7	7	2	5	10	21
33 Km	10	5	2	4	11	21

Mountain is the most species rich site with 69 species of plants recorded from open habitats. The bluff west of the mouth of the Tatonduk River is the least species rich site with 15 species.

The best single predictor for every class of species richness is the elevational extent of a bluff (Table 26). The amount of potential habitat area is the second best individual predictor (Table 27). These data show that south-facing bluffs with high relief and those with greater area have significantly higher species richness than smaller bluffs and those spanning a limited amount of elevation (Figs. 42 and 43).

Multiple regression models of species richness; path analyses

The relationship between the three predictor variables and each class of species richness is highly significant for the Yukon River data set. Almost all of the variation in the total number of species and in the number of GR species present on a bluff was explained by these models (r^2 of 0.94 and 0.95, respectively). The effects of elevational extent and distance to the closest bluff were significant in both models (Figs. 44 and 45). Increases in the elevational extent of a bluff result in increases in species richness, whereas increasing the isolation of a bluff decreases both the total and GR species richness. Although potential habitat area alone is correlated with total and GR species richness in simple linear regression models, it had a low path coefficient and did not explain significant additional variance in these models (Table 28).

There were differences in the response of the four biogeographic groups to the individual geographic predictor variables. Elevational extent was the only significant variable in the model for the widespread and North American floristic components (Figs. 46 and 47); there were no significant distance or area effects. Models of amphiberingian and endemic species richness, on the other hand, both contained significant distance effects (Figs. 48 and 49). Increasing isolation of a bluff had a negative influence on the number of amphiberingian and endemic species among these nine bluffs. Potential habitat area explained a significant amount of variation in amphiberingian species number, in contrast to other classes of species richness.

Stepwise regression identified elevational extent as the sole predictor of widespread, and North American species richness. In contrast, distance was included in the best model of total and endemic species richness. Elevational extent, area

Table 26. Results of simple linear regression analyses of six aspects of species richness on elevational extent for nine Yukon River bluffs in Alaska.. All variables were standardized prior to analysis.

Floristic component	R^2	R^2 adj.	B	SS	F	p
Total species richness	0.831	0.806	0.859	.7383	34.31	< 0.001
Number of GR species	0.873	0.855	0.881	.7764	48.30	<0.001
Number of widespread taxa	0.818	0.792	0.853	.7268	31.40	< 0.001
Number of N. American taxa	0.811	0.784	0.849	.7210	30.06	< 0.001
Number of AB taxa	0.706	0.663	0.792	.6271	16.77	0.005
Number of endemic taxa	.681	.635	.778	.6051	14.93	0.006

Table 27. Results of simple linear regression analyses of six aspects of species richness on potential habitat area for nine Yukon River bluffs in Alaska. Area measure used is the natural log of the planimetrically determined potential habitat area (in square meters). All variables were standardized prior to analysis.

Floristic component	R^2	R^2 adj.	B	SS	F	p
Total species richness	0.592	0.534	0.770	.5265	10.17	0.015
Number of GR species	0.501	0.429	0.708	.4451	7.02	0.033
Number of Widespread taxa	0.531	0.464	0.729	.4723	7.93	0.026
Number of N. American taxa	0.431	0.349	0.656	.3828	5.29	0.055
Number of AB taxa	0.636	0.585	0.798	.5658	12.26	0.010
Number of Endemic taxa	0.597	0.539	0.773	.5305	10.36	0.015

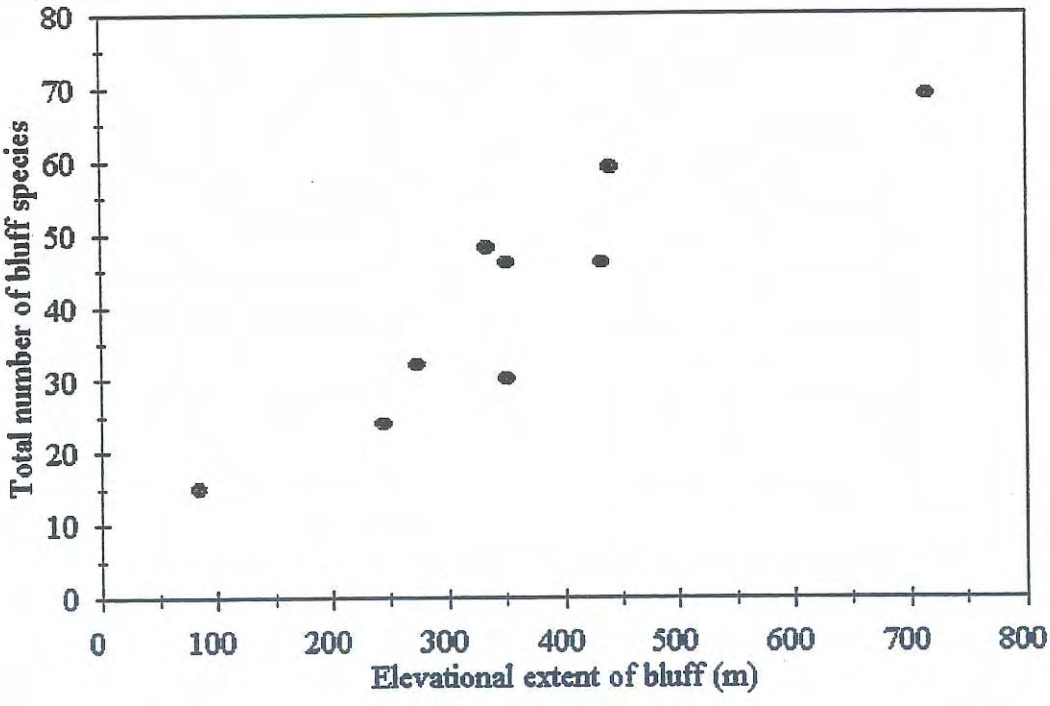


Fig. 42. Total number of species as a function of elevational extent for nine Yukon River bluffs in Alaska.

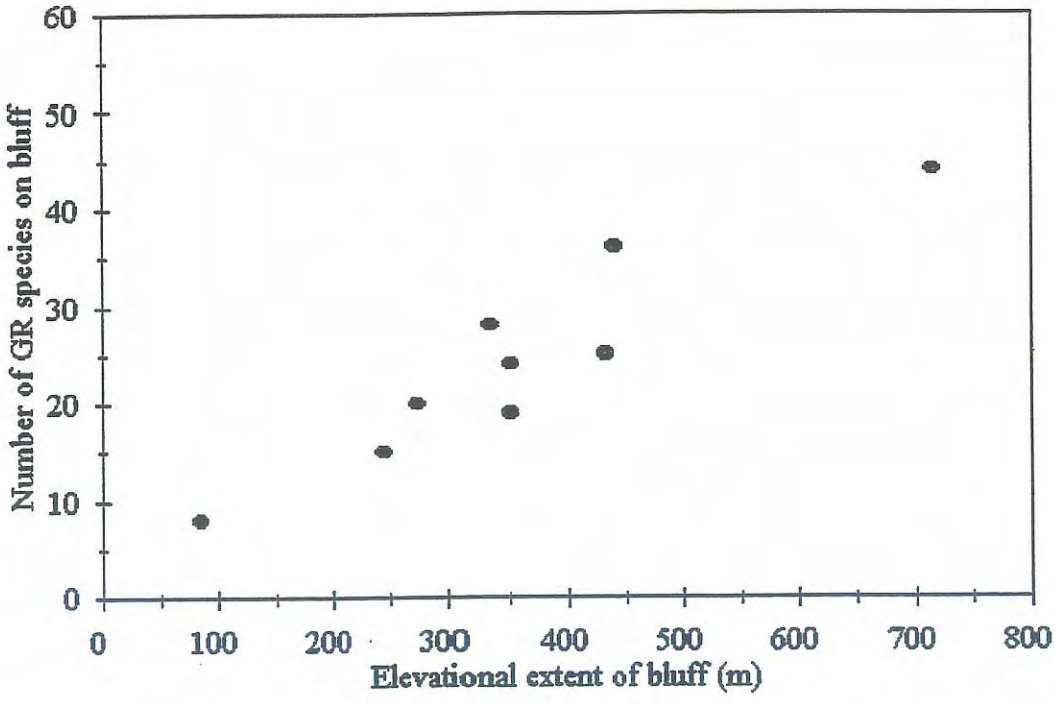


Fig. 43. Number of GR species as a function of elevational extent for nine Yukon River bluffs in Alaska.

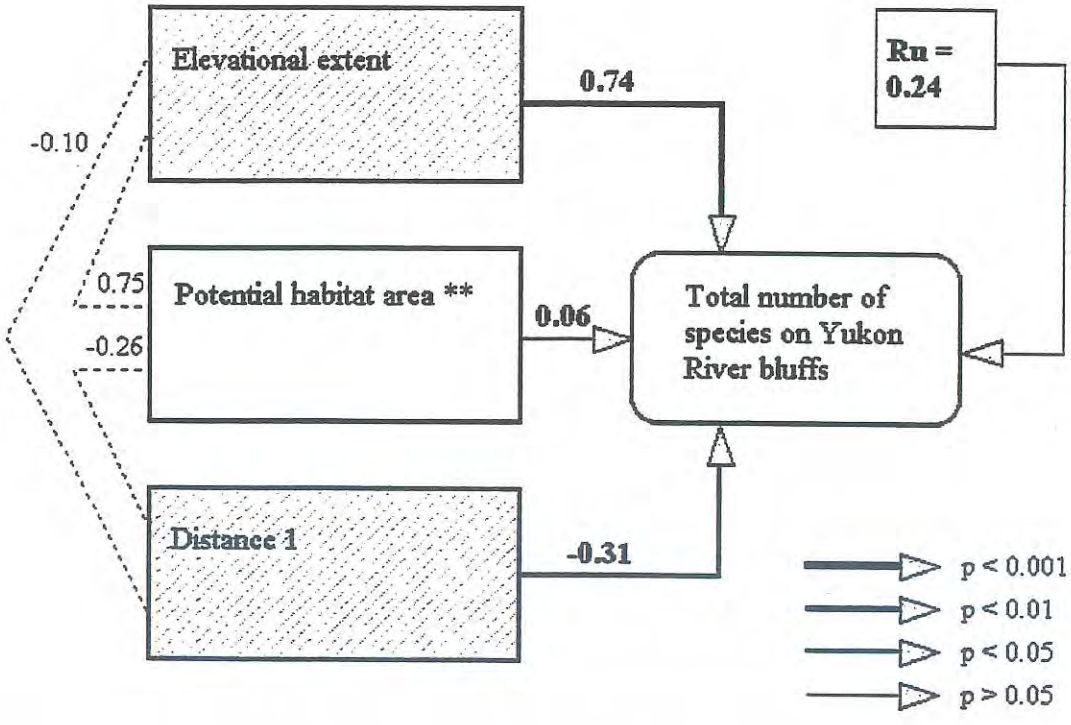


Fig. 44. Path diagram showing the relative strengths of three geographic factors influencing the total number of species among nine Yukon River bluffs. Cross-hatched causal variables boxes indicate that the variable was included in the best model by stepwise regression procedure. Numbers associated with causal arrows are path coefficients. Residual path (Ru) is equal to $(1 - R^2)^{1/2}$. Dashed lines between causal variables represent partial correlation coefficient between two variables. ** log transformed variable.

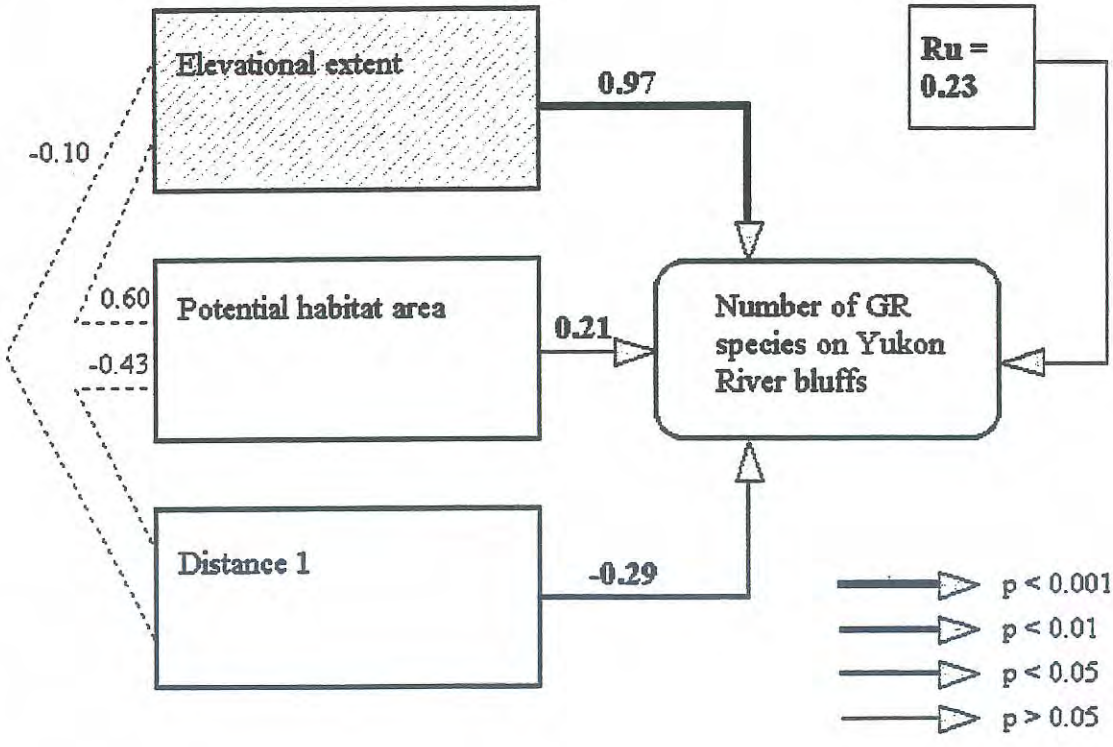


Fig. 45. Path diagram showing the relative strengths of three geographic factors influencing the number of GR species among nine Yukon River bluffs. Cross-hatched causal variable boxess indicate that the variablr was included in the best model by stepwise regression procedure. Numbers associated with causal arrows are path coefficients. Residual path (Ru) is equal to $(1 - R^2)^{1/2}$.

Table 28. Multiple regression equations from seperate path analyses of six components of species richness for nine Yukon River bluffs in Alaska.

Dependent variable	R^2	Error d.f.	Independent variable	B	Seq. SS	Type III SS	F	p
Total species richness	0.94	5	Full model				27.89	0.002
			Elev. extent	0.74	0.74	0.26		0.004
			Habitat area	0.06	0.02	<0.01		0.718
			Distance 1	-0.31	0.09	0.09		0.033
GR species richness	0.95	5	Full model				30.04	0.001
			Elev. extent	0.97	0.78	0.58		0.001
			Habitat area	0.21	0.02	<0.01		0.195
			Distance 1	-0.29	0.06	0.06		0.046
Widespread		5	Full model				14.80	0.008
			Elev. extent	0.91	0.73	0.29		0.013
			Habitat area	0.01	0.01	<0.01		0.97
			Distance 1	-0.25	0.06	0.06		0.16
N. American	0.89	5	Full model				13.83	0.007
			Elev. extent	1.00	0.72	0.61		0.002
			Habitat area	-0.30	0.01	0.05		0.18
			Distance 1	-0.28	0.06	0.06		0.14
AB	0.95	5	Full model				34.36	0.001
			Elev. extent	0.57	0.63	0.19		0.005
			Habitat area	0.33	0.16	0.05		0.053
			Distance 1	-0.29	0.07	0.07		0.037

Table 28 continued.

Dependent variable	R^2	Error d.f.	Independent variable	B	Seq. SS	Type III	F	p
Endemic	0.89	5	Full model				13.90	0.007
			Elev. extent	0.61	0.61	0.16		0.034
			Habitat area	0.17	0.05	0.01		0.470
			Distance 1	-0.39	0.14	0.14		0.042

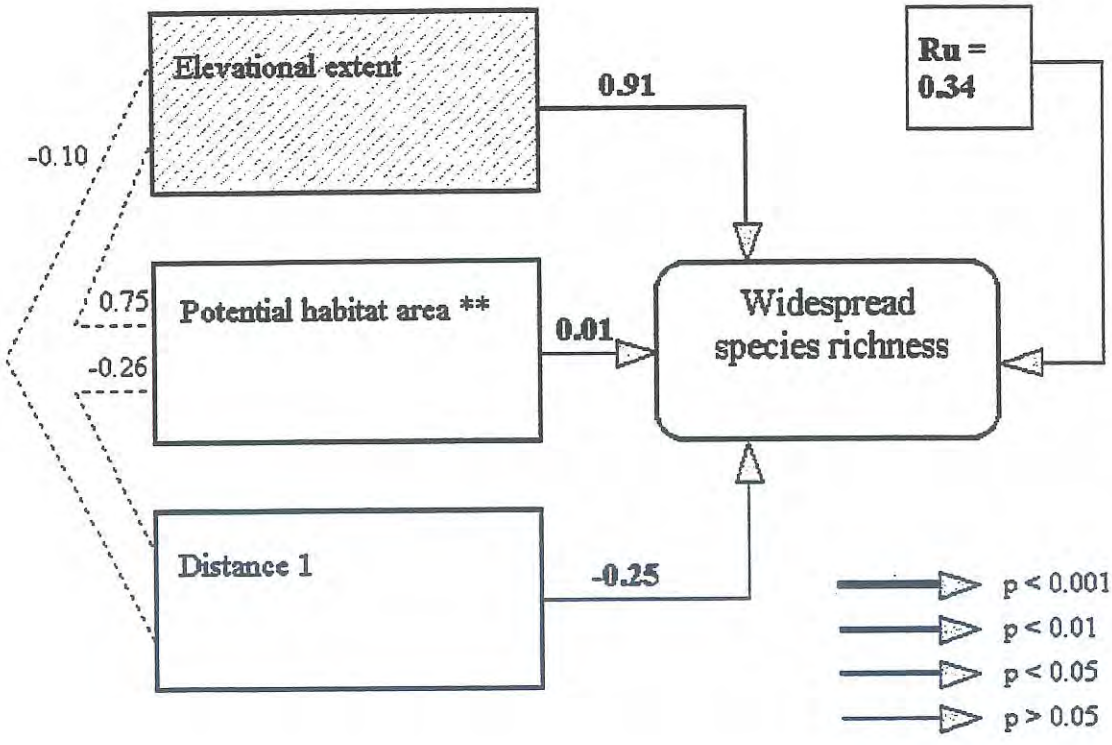


Fig. 46. Path diagram showing the relative strengths of three geographic factors influencing the number of widespread species among nine Yukon River bluffs in Alaska. Cross-hatched causal variable boxes indicate that the variable was included in the best model by stepwise regression procedure. Numbers associated with causal arrows are path coefficients. Residual path is equal to $(1 - R^2)^{1/2}$. Dashed lines between causal variables represent partial correlation coefficient between two variables. ** log transformed variable

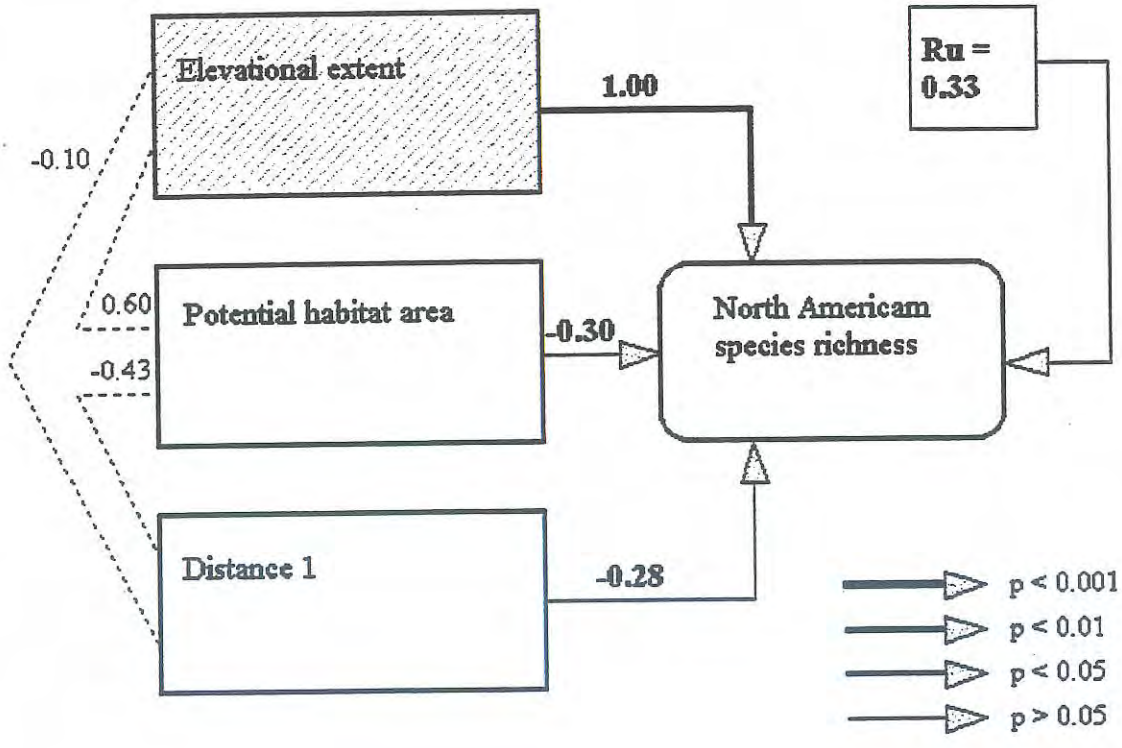


Fig. 47. Path diagram showing the relative strengths of three geographic factors influencing the number of North American species among nine Yukon River bluffs in Alaska. Cross-hatched causal variable boxes indicate that the variable was included in the best model by stepwise regression procedure. Numbers associated with causal arrows are path coefficients. Residual path (Ru) is equal to $(1 - R^2)^{1/2}$.

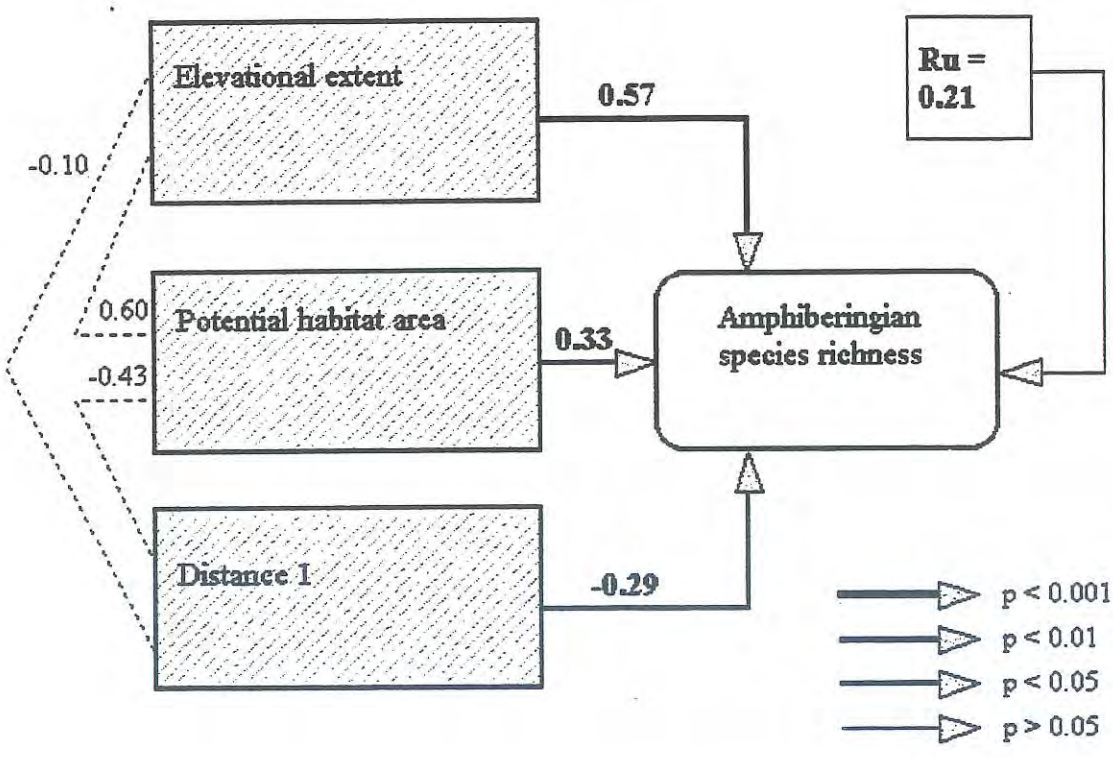


Fig. 48. Path diagram showing the relative strengths of three geographic factors influencing the number of Amphiberingian species among nine Yukon River bluffs in Alaska. Cross-hatched causal variable boxes indicate that the variable was included in the best model by stepwise regression procedure. Numbers associated with causal arrows are path coefficients. Residual path (Ru) is equal to $(1 - R^2)^{1/2}$.

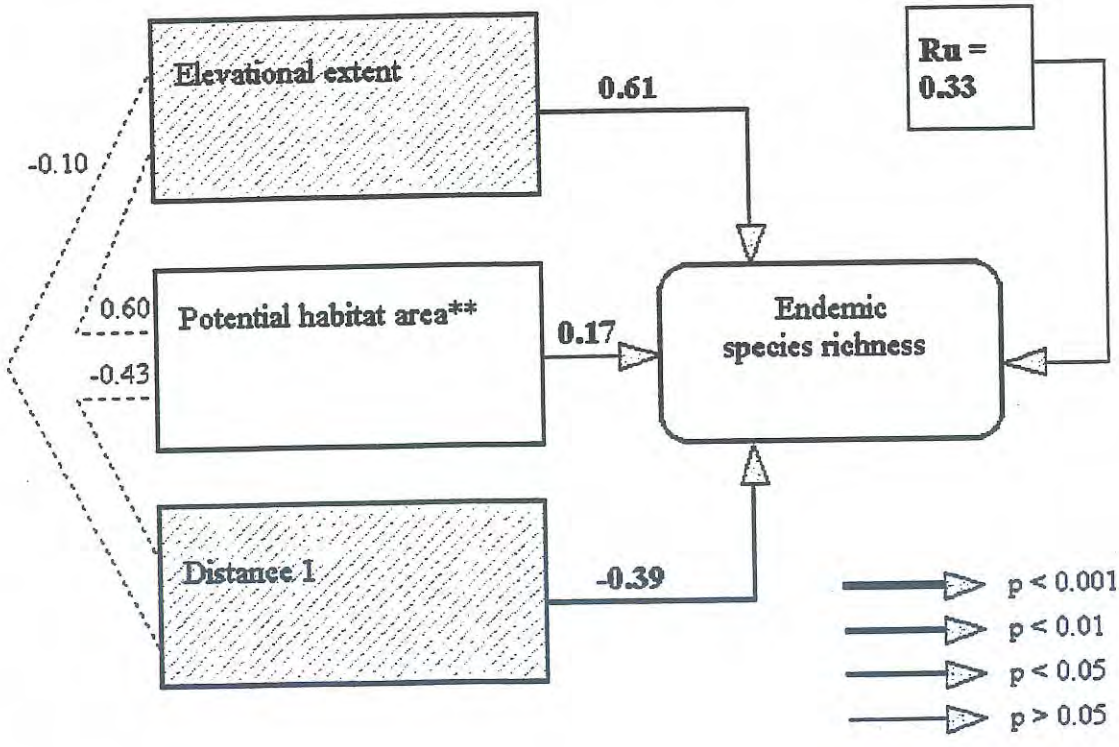


Fig. 49. Path diagram showing the relative strengths of three geographic factors influencing the number of Endemic species among nine Yukon River bluffs in Alaska. Cross-hatched causal variables boxes indicate that the variable was included in the best model by stepwise regression procedure. Numbers associated with causal arrows are path coefficients. Residual path (Ru) is equal to $(1 - R^2)^{1/2}$. Dashed lines between causal variables represent partial correlation coefficient between two variables. ** log transformed variable.

and distance were all contained in the best model for amphiberingian species richness at the nine Yukon River bluffs.

Charley River bluffs

The physiographic properties of the bluffs along the Charley River are different from those in the other study watersheds in several important ways. Although south-facing features are fairly numerous along the river, particularly in its middle reaches, they are generally lower in elevational extent and small in total area, as compared with bluffs in the other drainages (Table 25). Charley River bluffs are also somewhat steeper on average and even dominated by cliff formations in several cases. The bluffs on the Charley River support fewer species, on average, than those in the other watersheds (Table 17).

The strong relationships between geographic factors and species richness variables observed among the Yukon River bluffs are not as evident in the Charley River data set (Figs. 50 and 51). The two bluffs with the largest elevational extent also have the largest area of potential habitat. These two bluffs also have the highest species richness in the watershed. This pattern is similar to trends seen in the other study areas.

Regression of total and GR species richness on the three geographic variables for all 10 sites reveals no significant relationships (Table 29). Simple linear regression identified a significant relationship between elevational extent and these two species richness variables. If the two largest bluffs are removed from the analysis, however, there is no correlation between elevational extent and species-richness. Due to the inappropriateness of these models for the Charley River sites, path diagrams for this watershed were not constructed.

Yukon , Charley, Kandik, Tatonduk River Sites Pooled (24 bluff data set)

Species richness is strongly correlated with the elevational extent of south-facing terrain on a bluff for sites across all four watersheds surveyed in this study (Figs. 52 and 53). The level of significance in simple linear regression of total and GR species richness on this variable is exceedingly high ($F= 122.99$ and $F= 140.15$, respectively). This relationship, then, is a general one that applies throughout the study area. The general nature of this relationship provides a means to examine the differences in species richness between watersheds (see Figs. 52 and 53).

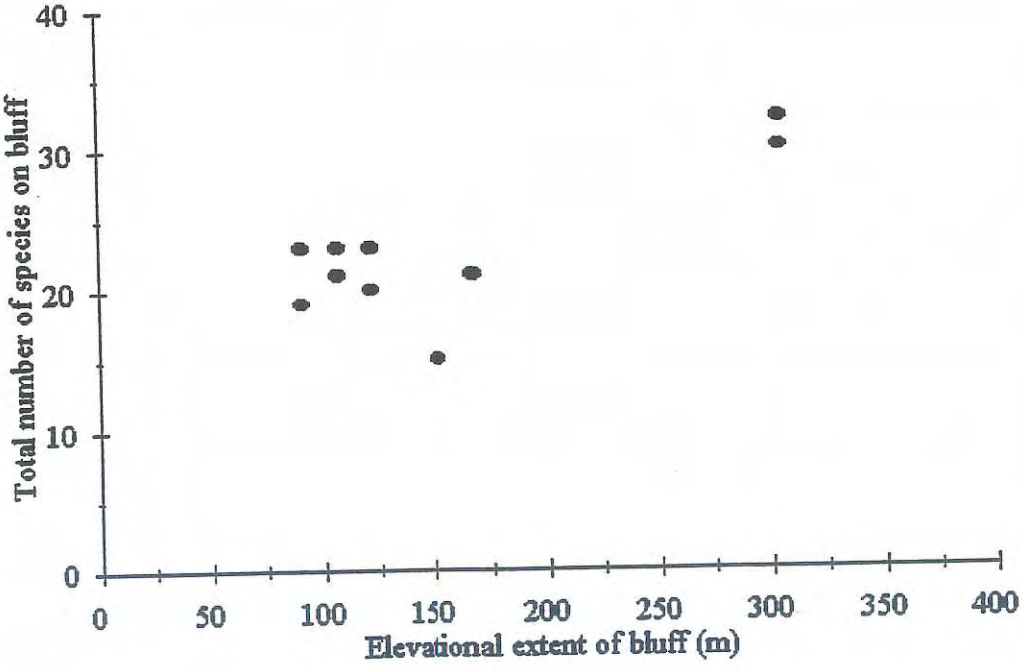


Fig. 50. Total number of plant species as a function of elevational extent for 10 Charley River bluffs in Alaska.

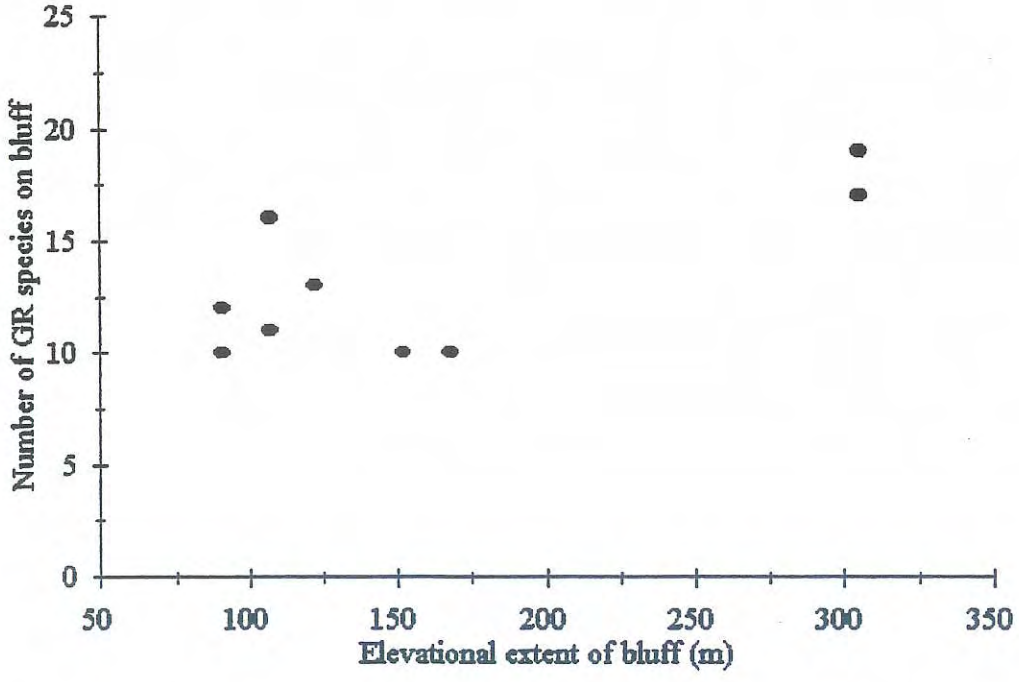


Fig. 51. Number of GR species as a function of elevational extent at 10 Charley River bluffs in Alaska.

Table 29. Multiple regression equations from separate path analyses of two components of species richness for 10 bluffs on the Charley River in Alaska.

Dependent variable	R^2	Error d.f.	Independent variable	B	Seq. SS	Type III SS	F	p
Total species richness	0.61	6	Full model				3.06	0.113
			Elev. extent	0.66	0.60	.14		0.197
			Habitat area	0.14	0.01	.01		0.785
			Distance 1	-0.03	<0.01	<0.01		0.907
GR species richness	0.54	6	Full model				2.38	0.171
			Elev. extent	0.67	0.50	0.14		0.229
			Habitat area	0.06	<0.01	<0.01		0.916
			Distance 1	0.21	0.04	0.04		0.524

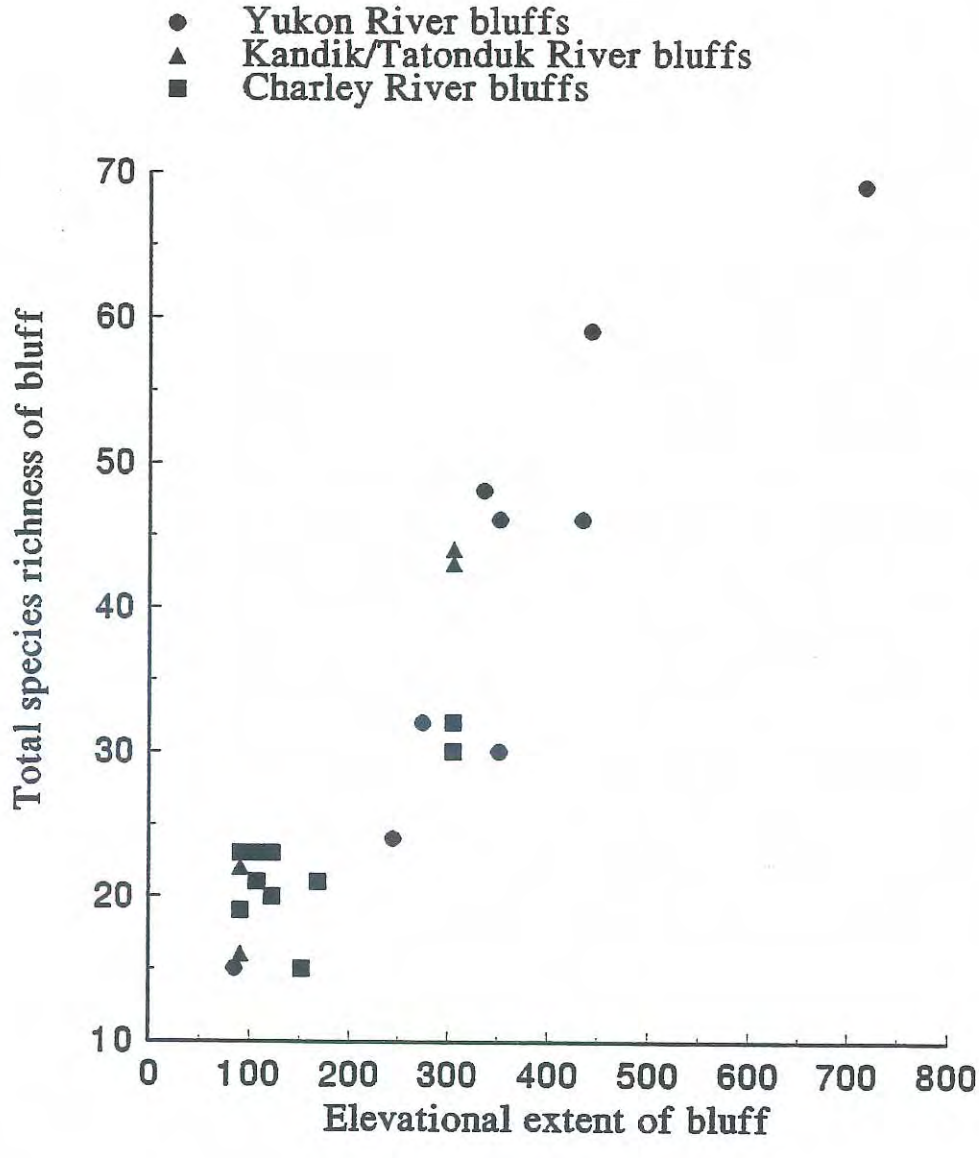


Fig. 52. Total number of species as a function of elevational extent for 24 bluffs in Alaska.

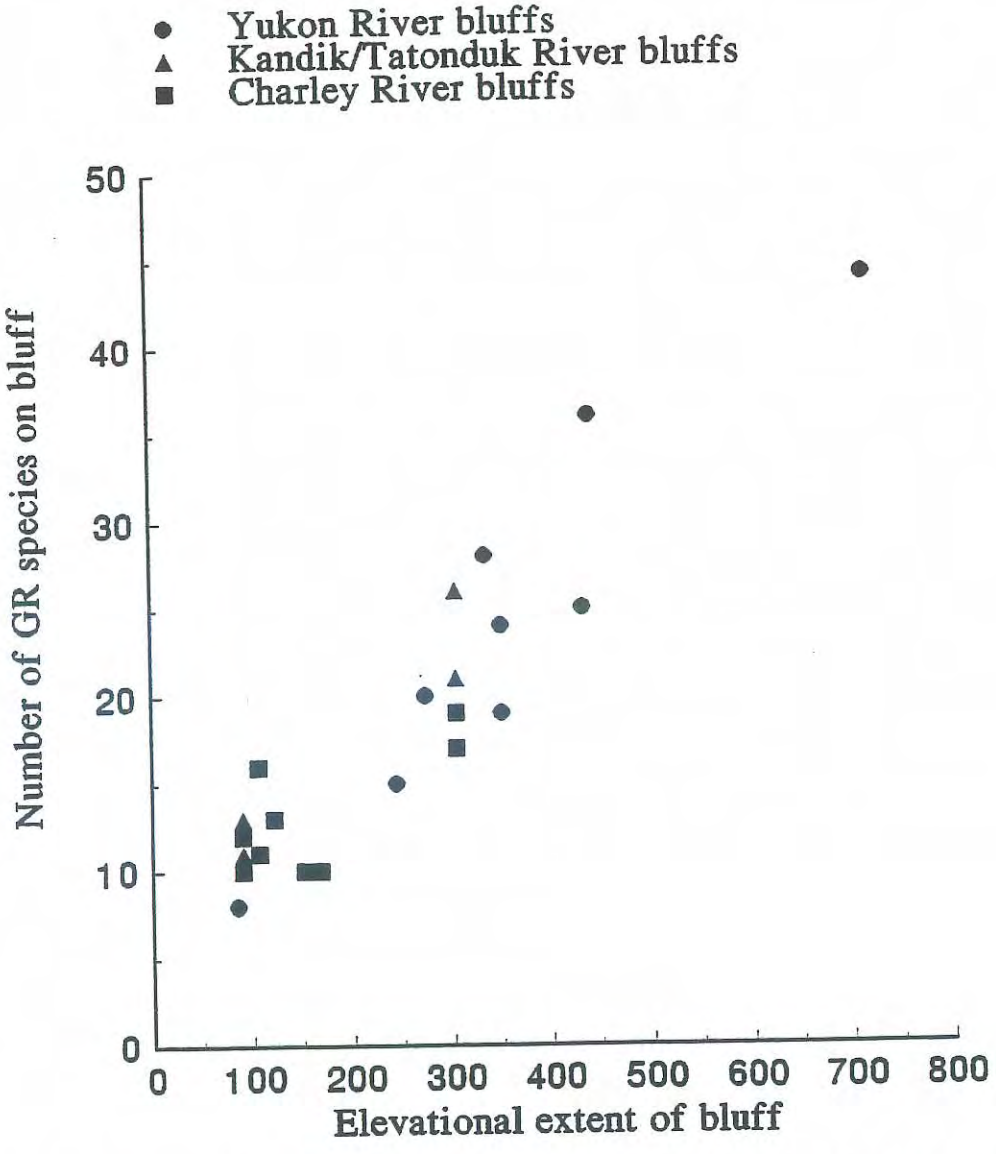


Fig. 53. Number of GR species as a function of elevational extent for 24 bluffs in Alaska.

Analysis of variance of the number of species per bluff among the four study watersheds yields a significant effect of watershed on species richness ($p = 0.037$; Table 30). This relationship disappears when elevational extent is entered as a covariate in the analysis of variance ($p = 0.653$; Table 31). Hence, elevational extent explains the differences in species richness among these watersheds. Furthermore, the absence of a significant interaction effect between drainage and elevational extent means that the slope of the relationship between species richness and elevational extent is essentially the same among these four watersheds.

Six Yukon River bluffs in Canada

The sites surveyed in Canada were not included in the analyses of species richness because digitized topographic data were not available for these bluffs. To assess whether the strong correlation of species richness with elevational extent observed for the Alaskan sites also held for this subset of bluffs, I plotted total and GR species richness against elevational extent (Figs. 54 and 55). There was a highly significant relationship ($p < 0.01$) between elevational extent and both total and GR species richness ($r^2 = 0.95$ and 0.89, respectively).

This data set contains one site (located above Shell Creek) with limited elevational extent, but high mean elevation. Other bluffs of low elevational extent on the Yukon River were limited to generally low elevations. The fact that Shell Creek bluff clusters with these other bluffs of limited elevational extent supports the hypothesis that elevational extent, per se, is the important factor in maintaining high species richness, not just the presence of high elevation facies on a bluff. In this regard, it is worth noting that this high elevation site was the sole bluff where *Agropyron spicatum*, a dominant species over many sites in the area was not encountered.

COMMONNESS AND RARITY OF SPECIES

To assess the distribution of commonness and rarity among the floristic groups in subarctic steppe, I tallied the number of occurrences of each species among all 30 bluffs included in this study. For example, *Astragalus aboriginum* was found at ten bluffs, *Bupleurum triradiatum* at 17, *Pulsatilla patens* at 28, and so on. The number of species from each biogeographic group falling into each of six categories of frequency was then

Table30. Results of an analysis of variance of the number species per bluff for 24 bluffs surveyed in Alaska. Drainage in which the bluff is located was used as a classification variable.

Source	D.F.	Seq. SS	MS	F	p
Drainage	3	1649	1649	3.41	0.037
Error	20	3223	3223		
Total	23	4872			

Table 31. Results of an analysis of variance of the number species per bluff for 24 bluffs surveyed in Alaska with elevational extent of the bluff entered as a covariate. Drainage in which the bluff is located was used as a classification variable.

Source	D.F.	Seq. SS	Adj. SS	Adj. MS	F	p
Elevational Extent	1	2592	1253	1253	39.26	<0.001
Drainage	3	1649	53	18	0.55	0.653
Interaction	3	120	120	40	1.26	0.323
Error	16	511	511	32		
Total	23	4872				

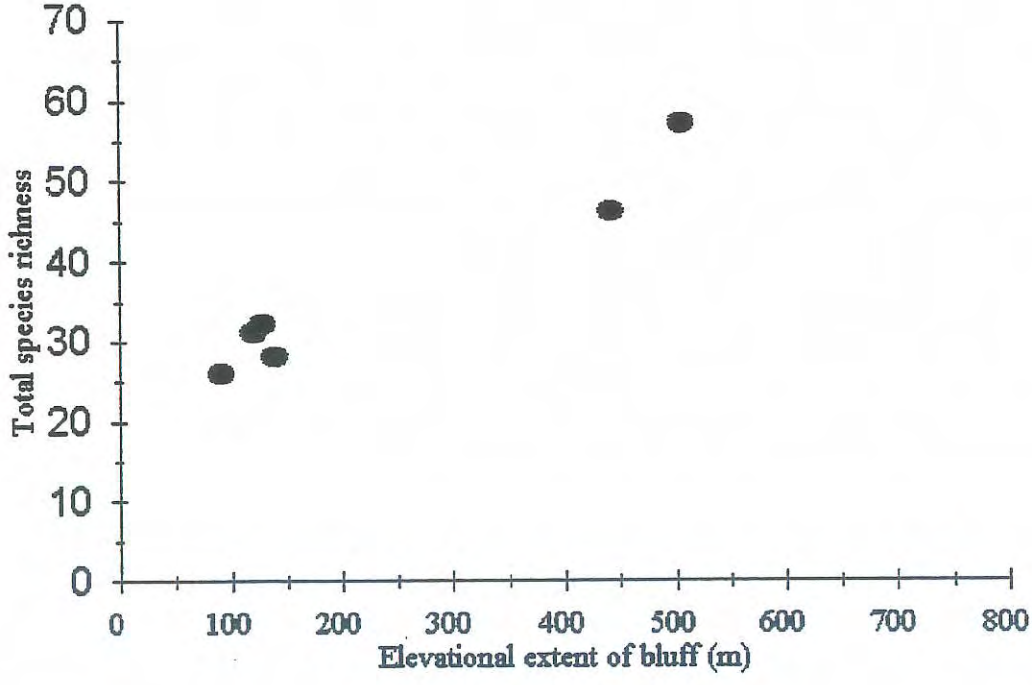


Fig. 54. Total number of species as a function of elevational extent for six Yukon River bluffs in the Yukon Territory, Canada.

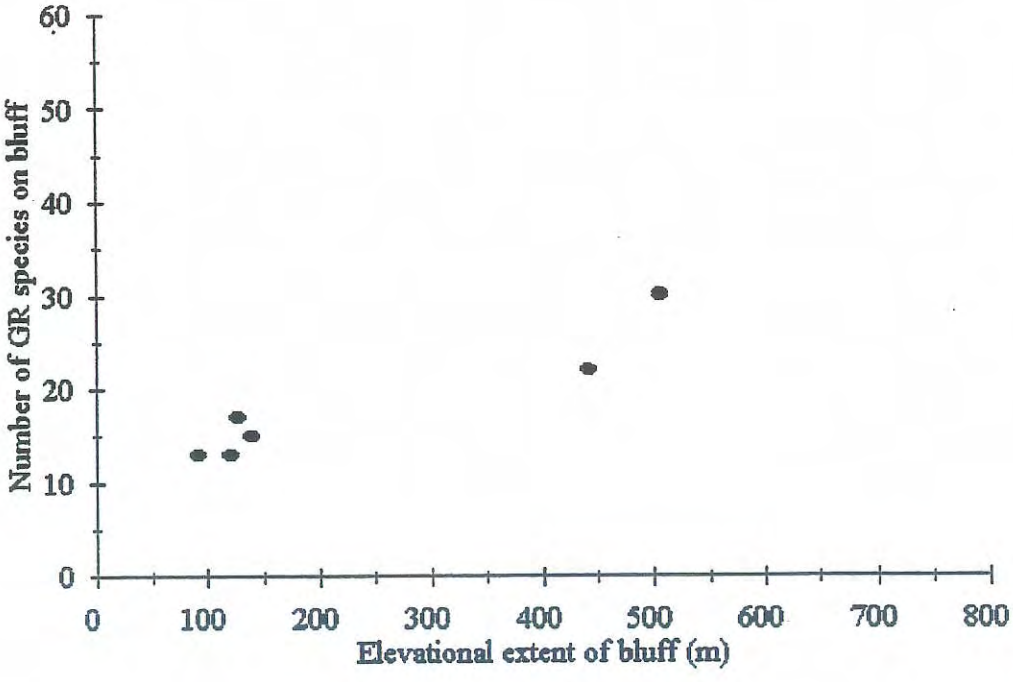


Fig. 55. Number of GR plants as a function of elevational extent on six Yukon River bluffs in the Yukon Territory, Canada.

tallied. The results are presented in four histograms, one for each biogeographic category.

There are marked differences in the frequency of occurrence between the biogeographic groups. Species with widespread distributions (on a global scale) occurred more frequently, on average, than plants from the North American and amphiberingian categories (Table 32). Mean frequency of occurrence was 13.4 sites per species among widespread plants and 7.8 sites per species among amphiberingian plants (Table 17).

Except for widespread plants, each of the biogeographic groups have a unimodal frequency distribution highly skewed towards the left-hand tail (rarest species) (Figs. 56 through 59). This is particularly pronounced for the amphiberingian floristic component. Fifty eight % (11 of 19) of these species occur on only one to five of the bluffs surveyed (Fig. 58). Similarly, plants with North American distributions are concentrated in the two least rarest categories (Fig. 57). None of the endemic taxa occurred on all bluffs surveyed, but the percentage of endemic flora (Fig. 59) in the rarest category was not as high it was for both amphiberingian and North American plants.

IV. DISCUSSION

INDIVIDUAL SPECIES DISTRIBUTION PATTERNS

Many species of generally restricted plants are broadly distributed throughout the open, south-facing sites in interior Alaska. Several species including *Agropyron spicatum*, *Androsace septentrionalis*, *Arabis holboelii*, *Artemisia frigida*, *Carex supina* ssp. *spaniocarpa*, *Potentilla pennsylvannica*, and *Pulsatilla patens* are both common and widespread on bluffs. Some of these plants are absent from a few individual bluffs or certain surfaces on a given bluff; however, they are found at the vast majority of suitable sites and also tend to be abundant within the vegetation of a given site.

Another group of component taxa is less common, even absent from quite a few sites, but occurs in a predictable pattern related to their ecological preferences. An example of a plant in this category is *Artemisia alaskana*, which tends to replace its more widespread congener *Artemisia frigida* in blocky and rubble substrates. Although present on many bluffs, *Artemisia alaskana* does not occur in steppe on deep soils. Similarly, *Erigeron compositus* and *Minuartia yukonensis* are usually found in rocky

Table 32. Mean frequency of occurrence of the species in four biogeographic groups among 30 bluffs in four study drainages in Alaska and Canada . Means of categories with no letters in common (a or b) are significantly different at $p < 0.05$. Standard errors are given in parentheses.

Distribution	Mean number of bluffs occupied per species
Widespread	13.4 (±1.84) (a)
N. American	7.9 (± 1.22) (b)
Amphiberingian	7.8 (± 1.88) (b)
Endemic	10.1 (± 1.85) (ab)

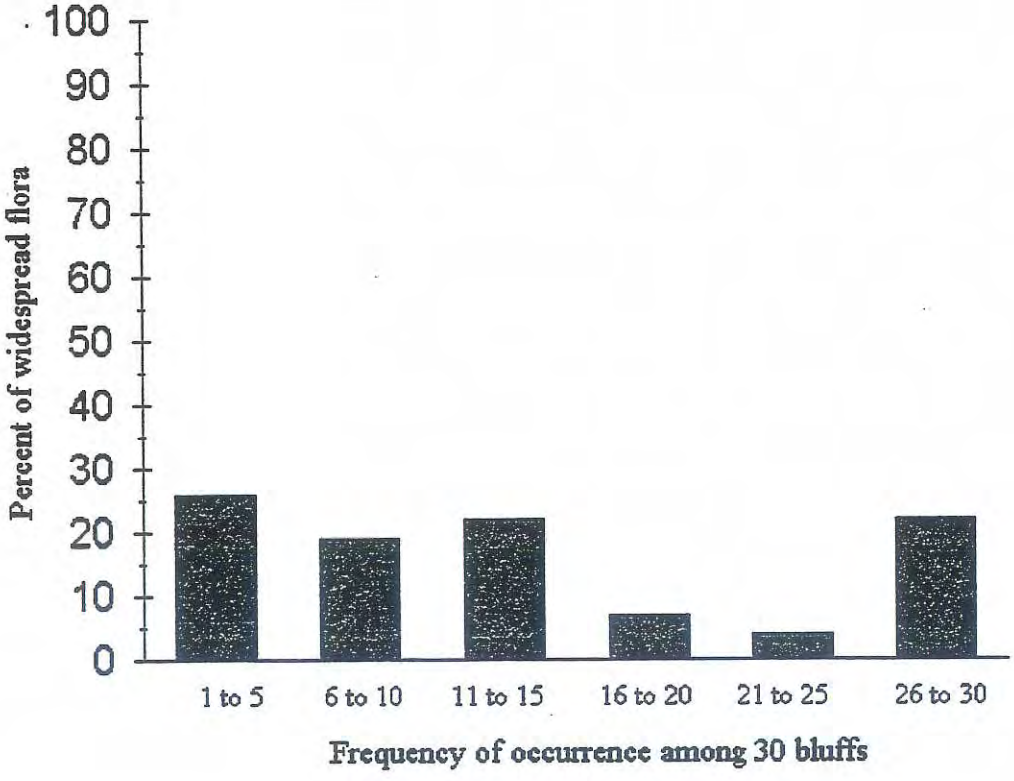


Fig. 56. Histogram showing the percentage of the widespread flora (n = 27) in each of six frequency categories. The categories represent the number of bluffs at which an individual species was observed.

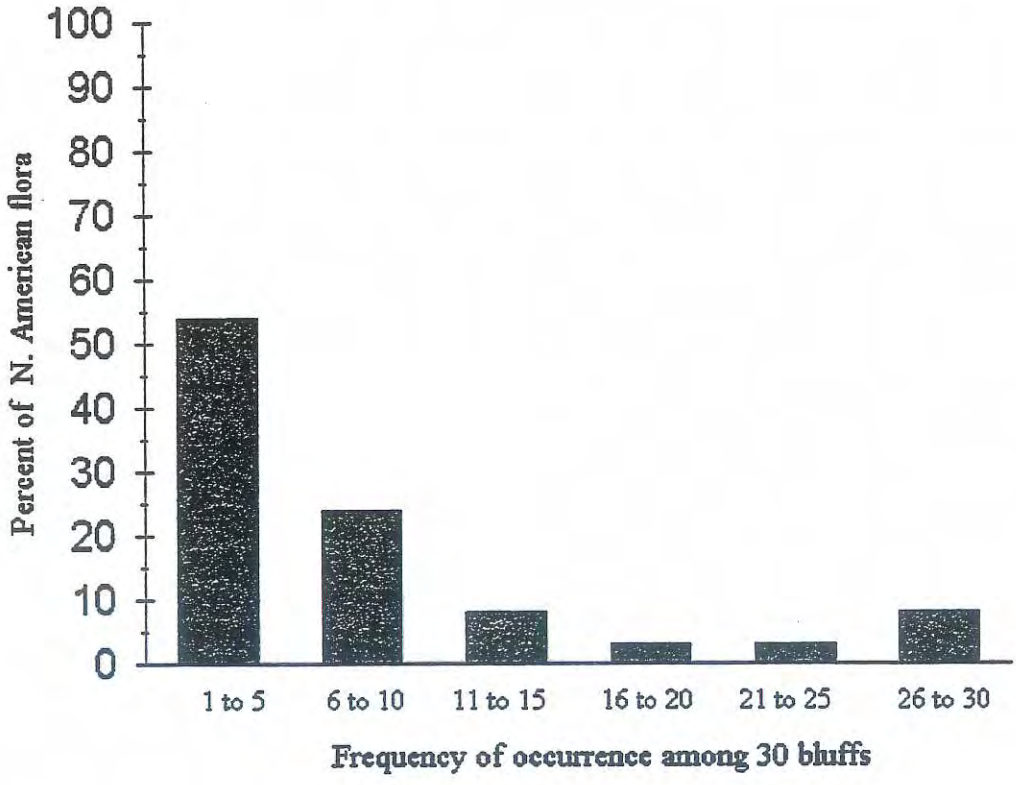


Fig. 57. Histogram showing the percentage of species with North American distributions (n = 37) in each of six frequency categories. The categories represent the number of bluffs at which an individual species was observed.

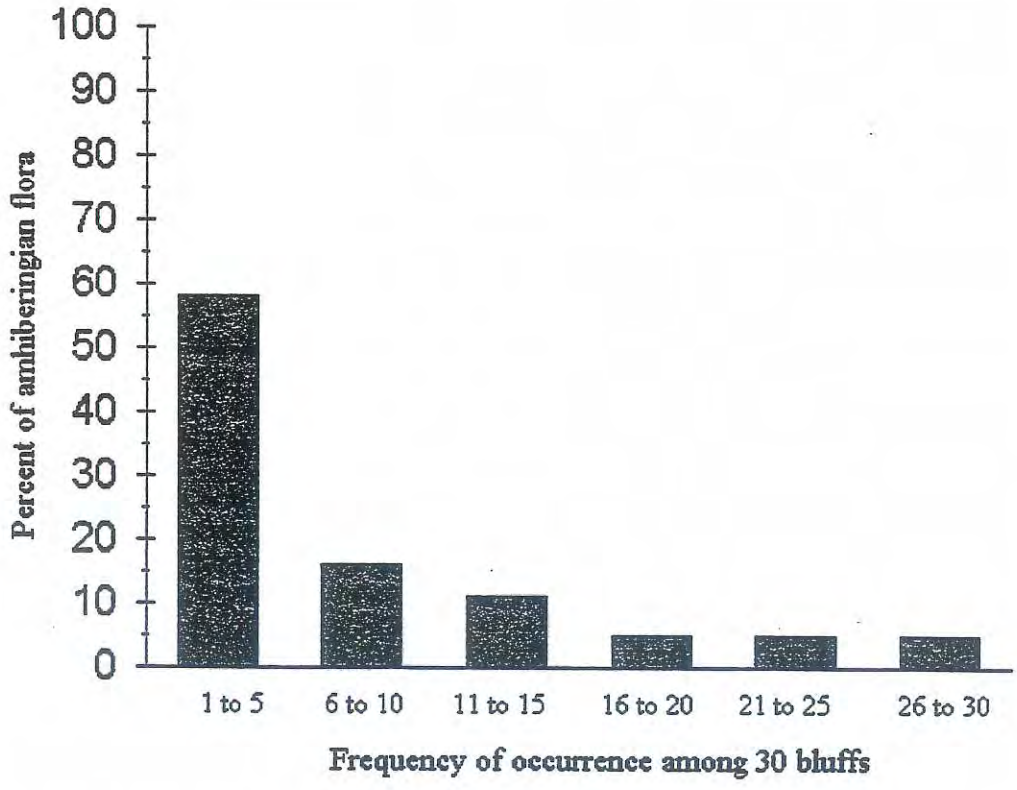


Fig. 58. Histogram showing the percentage of the amphiberingian flora (n = 19) in each of six frequency categories. The categories represent the number of bluffs at which an individual species was observed.

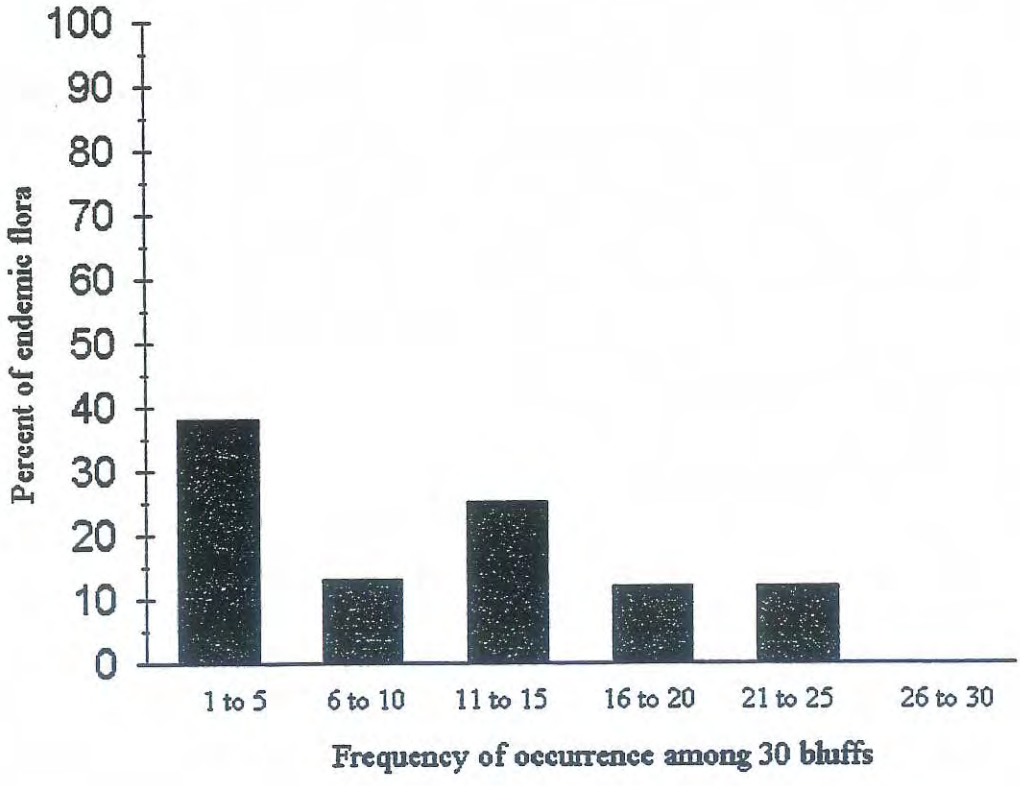


Fig. 59. Histogram showing the percentage of the endemic flora (n = 16) in each of six frequency categories. The categories represent the number of bluffs at which an individual species was observed.

situations on bluffs, at higher than average elevation. Hence, these plants are generally absent from steppe patches on low bluffs of silty terrace deposits. *Penstemon gormanii*, on the other hand, prefers the warmest, most disturbed and xeric conditions within subarctic steppe. This plant is absent from mesic facies and bluffs with low disturbance.

A striking feature of this assemblage, however, is the large number of plants with local disjunctions, range gaps and idiosyncratic distribution patterns in the study area and in Alaska generally. These local patterns mirror larger scale patterns in the biogeography of these plant associations. Plants with peculiar local distribution patterns often show large-scale disjunctions as well. Because unusual distributions patterns are such conspicuous facets of these associations, I will briefly discuss 10 examples in this section. Range information from outside the study area is from Hultén (1968).

1) *Alyssum americanum*

This taxon is closely related to a species whose main range is the dry interior regions of Siberia (*A. obovatum*). Its range is limited to the northeastern interior of Alaska and the extreme northwest Yukon Territory on the Yukon River. In the study area, it is abundant both in grassy steppe and rocky situations on two widely separated bluffs on the Yukon River in the Yukon Territory (at 25 km and 98 km from Dawson City) but is absent from all sites on the Yukon west of the Canadian border. Howenstein (1994) reported it as a codominant component of the vegetation of many Porcupine River bluffs in Alaska.

2) *Chamaerhodos erecta*

The main range of this Asian species is interior Siberia (Hulten, 1968). The distribution of *C. erecta* is farther to the south than *Alyssum* in both Asia and North America, and it has been collected at many localities in interior Canada and the northern Great Basin. This plant was found at three locations on the middle Charley River and four widely spaced bluffs on the Yukon River; the Moosehide Hills bluff downstream from Dawson City, Eagle bluff, Kathul Mountain, and the bluff at the mouth of Eureka Creek. It has not been found on Porcupine or Tanana bluffs; it is more common in steppic associations farther east in the Yukon Territory.

3) *Cryptantha shackletteana*

Only two locations have been reported for this species; at Eagle and Calico bluffs on the Yukon River (Batten et al. 1979). There is some taxonomic uncertainty whether these specimens represent a unique species or should be included under *C. spiculifera*

(Batten et al. 1979). Regardless, these populations represent the only perennial *Cryptantha* species found in Alaska to date. It grows with healthy populations of both *Erysimum asperum* and *Eriogonum flavum* at both Eagle and Calico. These associated taxa are more widespread in interior Alaska, although their habitat requirements, as we understand them, overlap substantially with those of this species.

4) *Erigeron caespitosus*

The range of this species is centered in the Great Basin of the interior in temperate North America in . Its disjunct subarctic range includes the steppe bluffs on the Porcupine , Tanana and Yukon rivers. In both the Yukon and Tanana drainages it is primarily restricted to the easternmost upstream sites, except for a population at Kathul Mountain. It reaches the northwestern tip of its range on the dry slopes along the Porcupine River.

5) *Eriogonum flavum* var. *aquilinum*

This is an endemic variety of a species with a wide distribution in the dry intermountain west of continental North America. It has been found in both grassy steppe, rubble slopes, and cliffs on five widely separated bluffs on the Yukon River. Howenstein (1994) reported it as abundant at several stations on the Porcupine River. Nevertheless it is absent from seemingly appropriate habitats on many bluffs on the Yukon and Porcupine rivers and is absent from the Tanana River bluffs and the tributaries the Yukon River visited in this study.

6) *Halimolobus mollis*

This primarily arctic plant species has a peculiar distribution that includes interior Alaska and Yukon Territory, the arctic coast of Canada and populations on the west coast of Greenland. *Halimolobus* was found on very dry, disturbed surfaces on the two largest bluff features of the upper Charley River. It has not been found on Yukon River bluffs in Alaska or those of the south-flowing tributary rivers studied here. I collected it at two sites on the Yukon River bluffs in Canada, and Howenstein (1994) reported it from the Porcupine River.

7) *Phacelia mollis*

This plant is a narrow endemic to unglaciated parts of east-central Alaska and the western Yukon Territory (Hulten 1968). It is relatively common in dry and open alpine plant communities in the Mentasta and Nutzotin mountains, and in the upper White River area (C. Roland and M.B. Cook, unpublished data). It has also been found at Chicken,

Alaska (Batten et al, 1979). The populations found on the Kandik River in this study are northern outliers of its known range. It has not been found on Yukon, Porcupine, or Tanana River bluffs. Remarkably, the closest Yukon River bluffs to the Kandik River sites (Kathul Mountain and Biederman bluff), support large populations of the North American disjunct *Phacelia sericea*, but *Phacelia mollis* does not occur there.

8) *Phacelia sericea*

The range of this plant is centered in the Rocky Mountains and reaches its northwestern limit at Biederman bluff on the Yukon River. It was found at three new widely separated localities in Yukon Territory in this study whereas previously, it was known from Eagle, Kathul and Biederman bluffs in Alaska. It has not been found on the Porcupine or Tanana Rivers.

9) *Plantago canescens*

This amphiberingian plant has a relatively a broad distribution on dry, disturbed slopes in the eastern half of Alaska (Hulten 1968). It is not common in the upper Yukon River bluff communities. It was found at one site on the Charley River and on the bluff at Funnel Creek on the Tatonduk River. Howenstein (1994)reported it from near Eagle village and Biederman bluff on the Yukon River. It is otherwise absent from the sites on the Yukon River in Alaska and the Yukon Territory. It has also been collected on the Porcupine and Tanana rivers.

10) *Smilacina stellata*

This plant is very widespread in North America, reaching across the continental United States to the Atlantic coast (Hulten 1968). Populations at Montauk, Nation, Kathul, and Woodchopper bluffs on the Yukon River represent the north-western limit of its range in North America. It is one of the few plants of limited range that grows on Nation or Montauk bluffs.

These 10 examples illustrate the degree to which these assemblages contain species with very discontinuous distributions in the subarctic. This basic facet of the biogeography of the bluff flora is the result of two possibilities: 1) these plants are prone to frequent long distance dispersal and/or 2) extant populations represent fragments of once more continuous ranges. Because few of the rare elements of this flora appear to be particularly dispersal-adapted, the second explanation is more parsimonious. In fact, other lines of evidence I will present concerning the control of species richness among

bluffs provide the context for understanding how these unusual distributions have come about.

COMMONNESS AND RARITY OF SPECIES IN BIOGEOGRAPHIC GROUPS

The mean number of bluffs occupied by widespread species is greater than that of both North American and amphiberingian species groups. Mean frequency of endemic plants is intermediate and statistically indistinguishable from any of the other groups. In addition to these differences in mean frequency, there appear to be differences in the frequency distributions among floristic groups. Widespread plants are more evenly distributed among the frequency categories while North American and Amphiberingean plants have unimodal distributions, strongly skewed towards the rarest category.

Why are species with North American and amphiberingian distributions prone to rarity? Disjunct members of these floras are largely responsible for the low mean frequency of occurrence shown by these groups. Almost all of the amphiberingian plants are infrequent members of bluff communities in the area. This group is dominated by plants with disjunct distributions. In contrast, two types of rare species account for the low mean frequency of occurrence of species with North American distributions: disjunct species and species for whom steppe habitats are generally unsuitable ecologically. North American disjuncts such as *Erigeron caespitosus*, *Phacelia sericea*, *Phlox hoodii*, and *Smilacina stellata* are all uncommon on bluffs in the study area.

Some North American plants that are common in subarctic taiga and tundra are very uncommon on steppe bluffs for ecological reasons. Species such as *Arnica alpina*, *Delphinium glaucum*, *Lupinus arcticus*, and *Mertensia paniculata* are found only in unusual ecological circumstances in marginal steppe habitat on south-facing bluffs. *Arnica* and *Lupinus* are associated with tundra habitats and *Delphinium*, *Lupinus*, and *Mertensia* are meadow species. The low frequency of these North American taxa on south-facing bluffs is a function of the lack of suitable habitat there.

In addition to having wider distributions globally, then, species in the widespread category tend to have more numerous populations regionally than members of the other groups; and few of them are rare on bluffs in the study area. This is unsurprising, but it is instructive when considering the biogeographic reasons for the strong differences in floristic composition among bluffs and study watersheds, which I will address in a subsequent section.

DISTRIBUTION OF SPECIES RICHNESS AMONG BLUFFS

There are strong patterns in the distribution of species richness at several spatial scales within the areas encompassed by this study. Large bluffs, particularly those with considerable elevational extent, harbor significantly more species than bluffs of limited elevational or areal extent. Furthermore, the Yukon River flora is generally richer, on both a per bluff and total flora basis than its tributaries. Bluffs on tributaries of the Yukon River support subsets of its flora, although the character of these subsets is different for different tributaries.

The species richness data do not support the null hypothesis that passive sampling effects result in the patterns of floristic diversity observed in this system. I base this conclusion on the greater predictive power of elevational extent than potential habitat area or any other single geographic variable. I interpret elevational extent as principally signifying the habitat heterogeneity of a bluff. South-facing bluffs with large elevational extents present a greater variety of microclimatic conditions with regard to growing season length and soil temperature than do bluffs of limited elevational extent. High bluffs also tend to present a greater variety of geomorphic situations (stable slopes, active slopes) and greater variation in surface ages than do low bluffs. As a result, high bluffs support a greater number of species.

These data support the habitat diversity hypothesis as a driving force of species richness patterns in this system. Nonetheless, I cannot reject the area per se hypothesis due to the nature of bluffs. A true test of this hypothesis requires the comparison of areas of different size but truly homogeneous habitat characteristics (Connor and McCoy 1979). The strong effect of both elevation and EQ on local species richness demonstrated in the previous chapter shows the distinctly non-homogeneous nature of the habitats on these bluffs.

In fact, there are several clues that the processes associated with the area per se hypothesis are important in creating the patterns in species richness, particularly with regard to the amphiberingian and endemic components of the flora. There are three reasons:

1) Species richness was found to be consistently and significantly positively correlated with the amount of potential habitat on a bluff in simple linear regression analyses. Furthermore, area had a significantly positive influence on

amphiberingian species richness in the model that included both elevational extent and the distance-1 measure for the nine Yukon River bluffs.

2) Local extinction of populations of component species from individual bluffs are likely to have occurred and even may have been fairly common during the late Holocene.

3) Certain classes of species richness are negatively influenced by increased isolation of a bluff.

I will address each of these points in turn.

1. Effect of area

The measure of area I used has both a temporal and a spatial component with regard to these plant communities. The area polygons identified by the G.I.S. analysis outline the potential habitat area for these plants on a bluff, not the actual amount of habitat available. Since the nature of the vegetation on a bluff is dynamic, the amount of open, treeless habitat available at any given point in time is variable. The amount of habitat is principally dependent on topographic factors (slope and aspect) but is also affected by factors such as the time since the last fire, short term climatic fluctuations and geomorphic disturbance. Nevertheless, there is certainly a strong correlation between actual and potential habitat area for a bluff, particularly if one integrates these variables over time. The potential area measure correlates better with amount of habitat over time because the effect of stochastic differences manifest on the current landscape is minimized.

Potential habitat area is consistently significantly correlated with all aspects of species richness among Yukon River bluffs in simple linear regression analyses. This suggests that area per se could be a contributing factor in creating the species richness patterns. The fact that this variable is included in the best model for amphiberingian species richness at Yukon River bluffs also supports this conclusion for this class of species.

The heterogeneous nature of the habitat characteristics of south-facing bluffs in the study area makes impossible firm conclusions concerning the role of area per se in creating species richness patterns. However, while habitat diversity is clearly the stronger factor in determining species richness in this system, certain components of the flora do appear to have higher species richness in larger habitat islands.

2. The importance of extinction within this system in the late Holocene

On balance, local extinction likely has predominated over immigration as a causative agent of species richness patterns on subarctic bluffs over the course of the late Holocene. This is particularly true with regard to the disjunct and endemic components of this flora. Under present climatic conditions, it is difficult to believe that the ranges of a majority of the rarer elements of this flora are expanding, hence resulting in numerous immigration events between habitat islands. Instead, it is probable that small population size and contracting habitat have resulted in local extinction events without replacement and the contraction of ranges for many of these plants. Brown (1971) inferred a similar nonequilibrium condition for the fauna of boreal islands in the Great Basin. I have three reasons for this inference:

1) Ecological conditions on south-facing bluffs are dynamic and likely to produce local extinction events.

2) Relatively large distances between habitat islands reduce the likelihood of repeated immigration between them.

3) Distribution patterns of a variety of component species show numerous gaps and local disjunctions of range. Local extinction is the parsimonious explanation for these patterns.

The data presented in Chapter One suggest that ecological conditions on these bluffs are highly dynamic and are likely to cause localized extinction. The warmest and driest surfaces of these bluffs are very species-poor. An increased frequency of drought coupled with high soil temperatures winnows all but the most stress-tolerant taxa from these surfaces. On the other hand, in the absence of disturbance, boreal forest encroaches upon more mesic surfaces, displacing members of this flora. These two processes increase the probability of local extinction for many component species of the bluff flora.

The second reason for the primacy of extinction in forming these species richness patterns is that the probability of immigration between bluffs is low. There are two reasons for this. First, the relative isolation of many bluffs decreases the likelihood of repeated exchanges between them; for example, the mean distance-1 value for the bluffs studied on the Yukon River is over 13 kilometers. Secondly, the population size of many of the component species is relatively small. Given the low number of propagules

produced by these restricted populations, the probability of enough landing at a bluff many kilometers distant to establish a viable population is remote.

Most species present at almost all of the sites are either graminoids (which produce many small seeds) or plants with specific adaptations for seed dispersal. Examples of the former are *Agropyron spicatum* and *Carex supina* ssp. *spaniocarpa*; examples of common steppe taxa with obvious adaptations for seed dispersal are *Artemisia frigida* (pappus), *Juniperus communis* (edible fruits), and *Pulsatilla patens* (plumose styles).

The large number of disjunct taxa in the bluff flora also supports the idea that local extinction has been an important process affecting these patterns. The numerous continental-scale disjunctions in the distribution of Asian and temperate North American steppe plants on these bluffs are best explained by contracting ranges rather than by repeated long-distance dispersal events (Murray et al. 1983). These large-scale discontinuities in range are presumably the net result of numerous localized extinction events. In fact, the prevalence of local disjunctions and idiosyncratic distribution patterns in this flora mirrors these larger scale patterns. The inadequate perfusion of many bluff plants of the available sites also argues against the idea that active expansion of ranges of many of these plants is occurring.

I do not argue that local extinction of populations is the most influential factor structuring the distributions of all members of this flora, only that it is more important than dispersal in creating the species richness patterns. There are certainly exceptions; some plants are becoming more common and widely distributed components of these sites. An example of an endemic plant species that may be increasing its range is *Draba murrayi*. It is evenly distributed throughout the bluffs on the upper Yukon and its northern tributaries in Alaska (i.e. does not show the spotty distribution of so many rare species in this flora). It is very abundant in the Ogilvie Mountain sites (Funnel Creek and Johnson Gorge). The lack of disjunctions and consistent appearance on the available sites within its known range suggests that the species may be a neo-endemic formed in the Ogilvie Mountains that is in the process of dispersing outward and filling an available niche on these bluffs.

3. Effect of bluff isolation

Bluff isolation (as reflected by the distance-1 measure) did not influence widespread or North American species richness among the nine Yukon River bluffs. This

measure, however, did have a significant negative influence on both amphiberingian and endemic species richness in this data set.

That isolation differentially affects the floristic elements in this system is instructive. Fragmented ranges are common in the amphiberingian and endemic biogeographic categories. This pattern may thus reflect the fact that once a species is lost from an isolated bluff, there is a low probability that it will recolonize it. The reason that the cumulative effect of isolation on these particular classes of species richness is more pronounced may be because local extinctions are more common among plants in these two classes.

Ecological gradient analyses (presented in the first chapter) suggest that plants from the amphiberingian and endemic floristic groups are more likely to increase in cool and high elevation facies of steppe than members of the other groups. With the encroachment of forest into all but the driest, hottest sites during the Holocene, these relatively cryophytic plants may be disproportionately prone to local extinction and hence particularly affected by bluff isolation.

Differences in the response of floristic groups to geographic variables

Widespread Species

Elevational extent was the only significant path in the causal model predicting widespread species richness in every data set analyzed. Similarly, it was the only variable included in the stepwise regression models in each case. This strongly suggests that a bluff accrues additional widespread species as it accrues additional habitat types. While there may be an area effect contributing to this pattern, it is likely that habitat heterogeneity is the principal driving force for increased richness of widespread species .

North American Species

North American species richness is also primarily related to habitat heterogeneity as determined by elevational extent. Elevational extent is the only significant path for this group of species in the Yukon River data set.

Amphiberingian Species

The predictive power of the geographic factors in the causal model predicting amphiberingian species richness is higher than for any other floristic component (r^2 of

0.95). Elevational extent, habitat area and isolation are all significant paths in this model. Larger (both elevationally and areally) and less isolated bluffs maintain higher levels of amphiberingian species richness in these data sets.

The hypothesis that populations of amphiberingian species have experienced numerous localized extinction events over the course of recent history was based on the fragmented distribution patterns of many of these plants. These analyses provide a measure of independent support for this hypothesis. It suggests that factors associated with the theory of island biogeography (extinction and immigration) help structure the species richness patterns of this floristic component on the current landscape.

The best geographic predictor of amphiberingian species richness in this system might be the amount of potential habitat area above a certain elevation contour (perhaps 550 or 600 meters). Low elevation surfaces, particularly those that are directly south-facing, tend to be notably species-poor, particularly with regard to the Amphiberingean component. As a result, these surfaces may not enlarge the habitat area for many of the members of this restricted flora.

Endemic Species

Elevational extent and isolation of a bluff are both significant paths in the model predicting endemic species richness for the Yukon River data set. Bluffs spanning large elevational extent support larger numbers of endemic species while isolated bluffs have fewer endemic species.

DISTRIBUTION OF SPECIES RICHNESS AMONG WATERSHEDS

Earlier studies have noted inequalities in the richness of south-facing bluff floras among the watersheds that support them in interior Alaska (Murray et al. 1983, Howenstein 1994). This study shows the landscape factors responsible for these inequalities. Elevational extent is a strong predictor of species richness at both spatial scales considered in this study (within and among watersheds). This suggests that the amount of relief encompassed by south-facing terrain in a drainage is largely responsible for the level of species richness found there. For example, the low mean richness of Charley River bluffs is a function of the low relief of the bluffs there. Similarly, the Tanana River bluffs surveyed by Howenstein (1994) have both comparatively limited elevational extent and low species richness (20.7 species per site).

An additional factor embedded in the contribution of elevational extent to species richness is the fact that high elevation treeless surfaces are, on average, more species-rich than similar low elevation surfaces in this study area. Aside from habitat diversity per se, then, tall bluffs contain surfaces that hold more species than bluffs limited to low elevation. Interestingly, ordination analysis associated many of the amphiberingian and endemic taxa with cooler habitats associated with high elevation surfaces within the Yukon River study area (see Chapter One). The high species richness of the Yukon River watershed, then, is due to the coincidence of high and low elevation south-facing surfaces on large individual bluffs.

DIFFERENCES IN FLORISTIC COMPOSITION AMONG WATERSHEDS

In addition to differences in species richness, there are differences in floristic composition among the watersheds that support the south-facing bluff flora. These differences in the importance of the biogeographic groups among the floras of these watersheds is most striking with regard to the widespread and endemic biogeographic groups. The response of the floristic components to geographic variables help explain the reason for these differences.

Widespread species

Widespread species contribute a larger fraction to the total bluff flora of all watersheds examined in comparison to the Yukon River flora (but the small difference in the percentage of widespread species between the floras of the Porcupine and Yukon Rivers suggests that this is not true for this pair of watersheds). The flora of the Charley and Tanana River bluffs are particularly enriched in widespread species in comparison with the Yukon River flora.

How can we account for the increased importance of species with widespread distributions in these floras? I propose that it reflects differences in the degree to which bluffs in these drainages represent refuges to groups of species whose ranges are fragmenting on the current landscape. High landscape diversity and large areal extent of bluffs on the Yukon River results in a greater degree of retention of rarer species by providing more continuous open habitat over time and more "kinds" of such open habitats.

The co-occurrence of isolated populations North American disjuncts, narrow endemics and amphiberingian taxa on a single bluff (such as we find on several Yukon River bluffs) suggest that these bluffs have contained open habitats over a considerable span due both to their large elevational extent (thus providing a range of habitats) and large area (thus diminishing the likelihood of chance extinction of a population, once established).

The probability that the small, relatively low bluffs inventoried on the Charley and Tanana Rivers have experienced a severe limitation of habitat in recent history (due to forest encroachment for example, or a large mass wasting event) is much higher. Such an event would result in the local extinction of all or most of the restricted flora resident there. If substantial areas of open habitat on such a bluff were to become available once again, its flora would necessarily be derived from recent immigrants to the bluff. I would argue that these immigrants would be disproportionately from the widespread group because: 1) these species tend to have more populations regionally (as demonstrated in greater mean frequencies of occurrence of widespread species) and 2) the traits that make these species widespread globally (e.g. their disperability or broad ecological tolerance) could favor their colonization as compared to species from the other groups.

The flora of smaller bluffs in areas of low landscape diversity may thus reflect recent immigration events to a greater degree than the flora of bluffs with prolonged residence of open habitats. The probability of immigration of widespread plants such as *Androsace septentrionalis*, *Arctostaphylos uva-ursi*, *Calamagrostis purpurascens* and *Pulsatilla patens* is high relative to the restricted floristic groups. An increased frequency of extinction events on small bluffs would therefore result in the gradual replacement of the rarer (or relictual) elements of the flora by more widespread taxa. Thus the floristic composition of the sites in a drainage is strongly affected by the amount of relief and areal extent of steep south-facing terrain there.

Endemic species

The relative importance of endemic plants in the bluff flora of the Yukon River and its tributaries (particularly the ones flowing out of the Ogilvie Mountains) distinguishes them from other interior Alaska bluff floras. For example, the Tanana River bluff flora contains only four endemics (7.5 % of the total) and bluffs on the Porcupine River contain only six (or 7.8 % of the total) in contrast to the 15 endemic taxa (16.1

percent) found on Yukon River bluffs. Furthermore, the bluffs of the Charley, Tanana and Porcupine Rivers are particularly depauperate in narrowly endemic plants. Bluffs in these drainages contain only one narrow endemic each (*Papaver nudicaule* ssp. *americanum* and *Eriogonum flavum* var. *aquilinum,* respectively) whereas the Yukon River bluffs support six narrow endemics. What accounts for these differences in floristic composition?

There are (at least) two principal geographic reasons for the increased importance of endemic plants within the floras of the Yukon River and its north-flowing tributaries as compared to the floras of other drainages. These are:

1) The high relief and large areal extent of bluffs in this area.
2) The unique position of the upper Yukon River area on the landscape in relation to past dispersal corridors.

Several members of the endemic flora of Yukon river bluffs are associated with arctic and/or alpine plant communities. Examples of such species are *Eritrichium splendens*, *Douglasia arctica* and *Podistera yukonensis*. The fact that these plants coexist on bluffs with endemic plants such as *Penstemon gormanii*, which is associated with particularly warm and dry microhabitats of steppe and rubble slope habitats, is a function of the diversity of habitats available on bluffs of large elevational extent.

Several of the narrowly distributed endemic taxa are close vicariants of temperate North American steppe species. Plants such as *Erysimum asperum* var. *angustatum* and *Cryptantha shackletteana* are close relatives of plants with wide distribution in the Rocky Mountains and Great Basin. The Tintina trench, a major geological feature of this area connects with the more southerly Rocky Mountain trench (Roddick 1967). This proximity may have facilitated the dispersal of xerophytic plants along the escarpments along these fault zones during particularly warm and xeric intervals. It has been suggested that these plants migrated northward during the Holocene hypsithermal event (Murray et al. 1983).

Differences in the size and character of the distribution patterns exhibited by endemic vicariants of North American species and Asian disjuncts suggests that there are differences in the timing of the arrival of these different groups plants in this area. Many disjunct temperate North American species and endemic vicariants of North American taxa of the bluffs are very geographically limited in Alaska. For instance, the North American plants *Cryptantha shackletteana*, *Eriogonum flavum, Erysimum asperum,*

Phacelia sericea, and *Phlox hoodii* all have relatively limited ranges in Alaska. In contrast, the principal rare amphiberingian species on these bluffs such as *Artemisia furcata*, *Arenaria capillaris*, *Chamaerhodos erecta*, *Festuca lenensis*, *Plantago canescens*, and *Phlox sibirica* have distributions that encompass sites across several of the major drainages in interior Alaska and the Yukon Territory.

Although there are certainly exceptions, this pattern is general support for the hypothesis that many disjunct North American plants arrived in the subarctic during a warm period in the Holocene (Murray et al. 1983). The warmest period was probably 9,000-6,000 years before present. However, palynological data suggest that barriers to the dispersal of steppe plants (i.e. areas occupied by taiga ecosystems) existed in subarctic Alaska during the Holocene hypsithermal event (Edwards and Barker 1993). Hence the potential for the dispersal of these plants within Alaska would have been limited by the presence of a partially forested landscape throughout the Holocene.

In comparison, the essentially treeless landscape that existed during glacial maxima, when the Bering platform was exposed, would have facilitated a more complete penetration of Alaska by Asian xerophytes from across the land bridge. Repeated influxes of Asian taxa correlated with successive glacial advances (and concomitant exposure of the land bridge) and longer residence time of these plants in eastern Beringia would also result in the more complete diffusion exhibited by amphiberingian species as compared to many North American disjuncts.

SUMMARY

These results show that there are strong differences in both the number and kinds of species found among bluffs and among watersheds in the study area. This study helps clarify some of the ecological and biogeographic causes of these patterns. The most species-rich bluffs are those spanning a large elevational gradient. The strong prediction of species richness by elevational extent suggests that landscape diversity is a primary reason that the floras of certain bluffs within a drainage and the floras of certain drainages are particularly rich.

Watersheds where the landscape is characterized by relatively low and small bluffs (such as the Charley River) tend to contain very few rare taxa and proportionally more species with widespread distributions. Rare and endemic elements of the flora generally reside on bluffs with large elevational or areal extent. This fact, along with the

observation that many bluff plants have unusual and spotty distributions, suggests that the ranges of many of these plants have fragmented during the Holocene. This process probably occurred as populations of bluff plants were extirpated from bluffs but were not replaced due to isolation from other source populations.

Conditions within an individual bluff are very dynamic (due to the geomorphic and ecological conditions there). Local immigration and extinction of populations of component species between surfaces on a bluff likely occur with high frequency. The relative isolation of these bluffs from one another, on the other hand, suggests that immigration events between bluffs may be infrequent in comparison with extinction from a bluff. Widespread plants that have a greater number of populations in a region and/or plants with specific adaptations for dispersal are more likely to move from one bluff to another. Large bluffs with significant elevational extent represent foci for plant diversity on the landscape. On one hand, they offer a greater variety of habitats than small and low bluffs. On the other hand, they represent refugia over a longer period of time than small bluffs because the amount open habitat available is never severely constricted.

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