earities, some deliberately introduced for enhancement and some unknown. A better understanding of oceanic backscatter models (*1*, *4*) is also a prerequisite for further progress here.

An overall comparison of all available measures of wave frequency (by wavelength and bathymetry) and direction for 28 September yields a variance between measurements of the same order as the confidence in a particular measurement. For the data set presented here, the SAR measured ocean wavelength and direction as well as any of the alternate techniques available. It is possible that, for separating swell systems in a mixed ocean, its accuracy may exceed that of any other existing technique.

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Arctic Steppe-Tundra: A Yukon Perspective

Abstract. *The first reliable, securely dated full- and late-glacial pollen stratigraphy from Eastern Beringia forces the rejection of the widely held hypothesis of a steppe-tundra or grassland associated with extinct vertebrates and early humans. The arctic-alpine fossil flora and low pollen influx suggest a sparse tundra similar to modern herb fell-field vegetation.*

Beringia was a land bridge for plants, animals, and people between Siberia and North America (*1*). The northern Yukon and adjacent Alaska, commonly referred to as Eastern Beringia, were isolated from the rest of North America by the maximum extensions of Late Quaternary ice sheets (*2*), and recent discoveries suggest that the area was a full-glacial refugium for a varied fauna, now mostly extinct, and for humans (*3*, *4*). The assumption is widely held that the apparently rich, largely herbivorous fauna of extinct horse, bison, mammoth, camel, and saiga antelope was supported by an arctic steppe or grassland. Since the work of Livingstone (*5*), pollen data from the few sites in Alaska that have been investigated show an herb assemblage dominated by grass, sage, and sedge, widely regarded as registering this "extinct biome." Our results do not support a steppe or grassland interpretation for the period between 30,000 and 14,000 years before present (B.P.).

We report here late Pleistocene pollen records from two lake sites (*6*). Both lie just outside the western limit of Wisconsinan glaciation (*7*) and are 275 km apart. Hanging Lake is in the tundra on rolling plains, and Lateral Pond is within forested mountains, so they are representative of easternmost Beringia.

Hanging Lake (informal name) is 500 m above sea level in shale and sandstone on an undulating tundra surface 35 km northeast of the edge of the Old Crow Flats (Fig. 1). It has a surface area of about 60 ha and a maximum water depth of 9.5 m. There is no inlet stream, and a single small outlet occurs at the northeastern end. White spruce (*Picea glauca*) occurs in an outlying stand 30 km west-northwest of the lake. There are four main types of vegetation: (i) extensive cotton grass (*Eriophorum vaginatum*) tussock tundra on flat and gently sloping surfaces; (ii) local sedge (*Carex*) meadow on poorly drained sites; (iii) heath tundra with *Empetrum*, *Vaccinium vitis-idaea*, *Arctostaphylos alpina*, *Betula glandulosa*, and lichens on upland granular soils; and (iv) species-rich discontinuous tundra or fell-field vegetation on widespread rocky surfaces of exposed upland sites.

The percentages (Fig. 2) show that the pollen stratigraphy conforms to the pattern typical for Eastern Beringia. The basal herb zone (30,000 to 14,000 years B.P.), dominated by *Artemisia*, Gramineae, and Cyperaceae, is replaced by a rapid increase in birch, then spruce, and finally alder. The high percentages of *Artemisia* and Gramineae are usually cited as the main evidence for the steppe or grassland interpretation. The influxes of these herb pollen types (Fig. 2), however, as calculated from close-interval radiocarbon dates (*8*), are equal to their Holocene values; this result suggests that these herb types were no more abundant in the past than they are today. Furthermore, the herb and total pollen influxes are lower during the herb zone than at any subsequent time. Of the major herb types, only Cruciferae, Chenopodiaceae/Amaranthaceae, *Plantago canescens*, and Tubuliflorae (the latter two not shown in Fig. 2) have maximum influxes in the herb zone, but at very low values of less than 5 grain cm^{-2} $year^{-1}$. The influx of birch within the herb zone is negligible despite percentages of up to 30. The influx data thus show that the vegetation must have been sparser and herbs less abundant in arctic steppe-tundra than at present.

The floristic affinities of the herb zone are clearly arctic-alpine and not cold-temperate grassland. These include *Aconitum*, *Bupleurum triradiatum*, Caryophyllaceae, *Dryas*, *Astragalus*, *Oxytropis*, *Hedysarum*, *Androsace*, *Lesquerella arctica*, *Pedicularis*, *Phlox*, *Polemonium*, *Polygonum alaskanum*, *P. viviparum*, *Oxyria*, *Rumex*, *Saxifraga hi-*

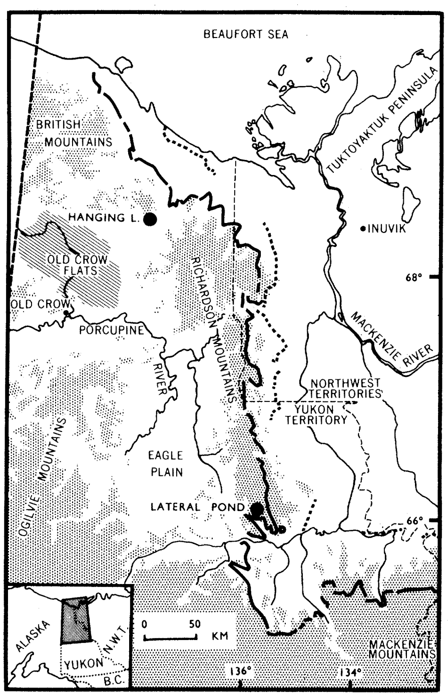

Fig. 1. A sketch map of the northern Yukon and adjacent Northwest Territories, showing the locations of Hanging Lake and Lateral Pond. The heavy dotted line indicates the maximum westernmost extent of Wisconsinan glaciers. The heavy dashed line marks the maximum westernmost extent of the penultimate glaciation.

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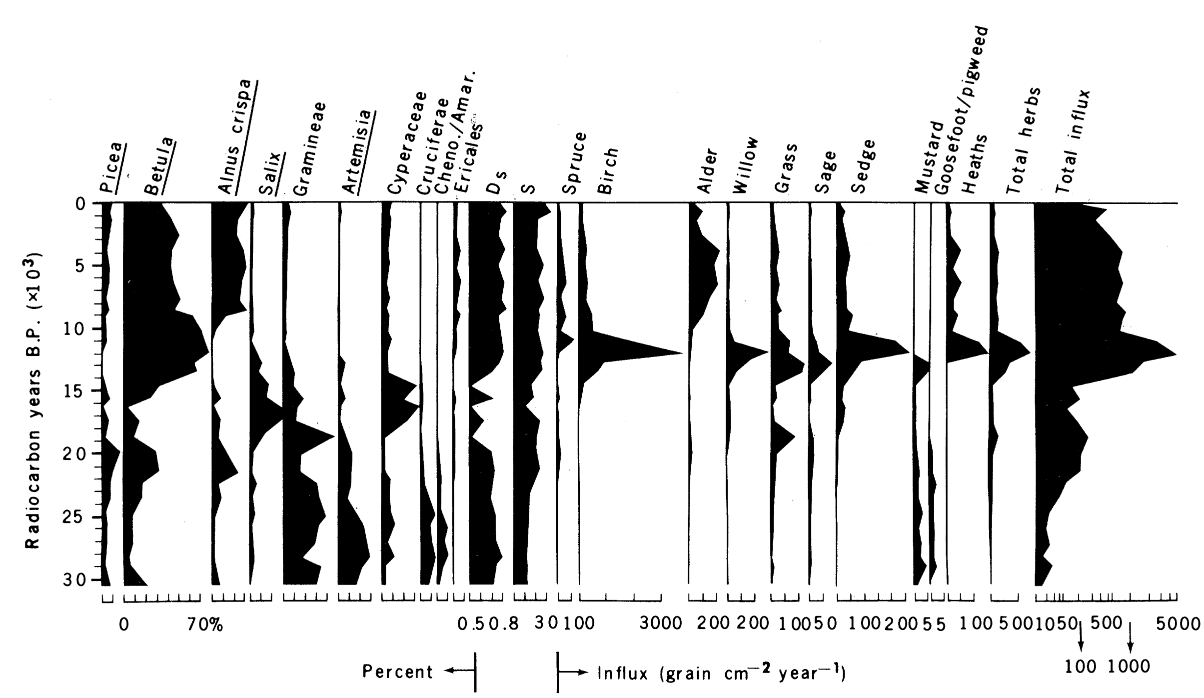
eracifolia, *S. tricuspidata*, *Saussurea*, *Selaginella sibirica*, *Thalictrum*, and *Lagotis glauca*. Taxa typical of mesic habitats in boreal-subarctic climates, such as *Linnaea borealis* and *Valeriana*, appear after the decline of the herb zone. Despite the apparent variety of herb pollen types in the herb zone, their number (S) and diversity (D_s) are generally lower prior to 14,000 years B.P. than after, an indication that the steppe-tundra flora was less diverse than in Holocene times.

Lateral Pond (informal name) is at 500 m above sea level (Fig. 1), lying between two lateral moraines in the valley of Doll Creek, South Richardson Mountains. The surrounding mountains are 800 to 1400 m above sea level and are composed of limestone, sandstone, and shale (*9*). Spruce forests occupy the lower valleys, and tundra varies according to bedrock type.

Lateral Pond has a surface of 3.25 ha and a maximum depth of 3.4 m. The



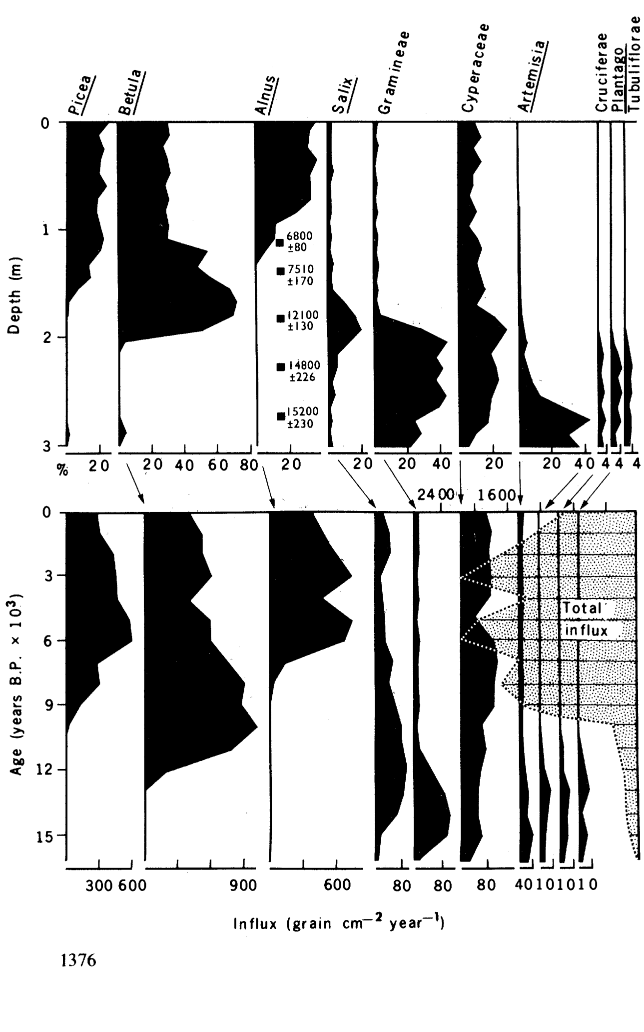


Fig. 2 (above). A summary percentage (left) and influx pollen (right) diagram for Hanging Lake. Values are plotted against radiocarbon age. Total influx is plotted on a logarithmic scale; D_s, Simpson's diversity index; S, number of herb pollen taxa included in the pollen sum. Fig. 3 (left). A summary percentage and influx pollen diagram for Lateral Pond. Percentages (top) are plotted against depth in sediment, and influx (bottom) is plotted against radiocarbon age. The total influx is plotted on a linear scale from 0 to 2400 grain cm^{-2} year^{-1} (shown on the upper axis of the lower half of the figure).

lower part of the section (Fig. 3), from 15,500 to 12,500 years B.P., is dominated by herb pollen with a single peak of willow (*Salix*), and the upper part has a predominance of tree and shrub pollen. The boundary at 12,500 years B.P. is abrupt, with an increase in pollen influx from 50 to 400 grain cm^{-2} $year^{-1}$, due mainly to the increase in dwarf birch. The lower levels are dominated by small birch pollen ascribed to *Betula glandulosa*. The herb assemblage has low total influx made up chiefly of Gramineae, Cyperaceae, *Artemisia*, Cruciferae, *Plantago canescens*, and Tubuliflorae. However, the presence of the following taxa in many samples, usually at very low influx, is significant: *Aconitum*, *Epilobium*, *Bupleurum triradiatum*, *Astragalus*, *Oxytropis*, *Hedysarum*, *Lupinus arcticus*, *Pedicularis*, *Phlox* (*sibirica*), *Polemonium*, *Polygonum alaskanum*, *P. viviparum*, *Dryas*, *Oxyria*, *Saxifraga hieracifolia*, *S. tricuspidata*, *Saussurea*, and *Thalictrum*. Most are arctic-alpine types, common in tundras of the modern northern Yukon. Total herb influx remains more or less constant throughout Fig. 3, although some types (grass, *Artemisia*, Cruciferae, *Plantago*, and Tubuliflorae) decrease after 12,500 years B.P. and the proportion of sedge increases, a reflection of local sources from the marginal sedge mat that probably developed around the pond. The pond margins today have thick peat accumulations with abundant sedge and *Sphagnum*.

The resemblance of the herb pollen zone to modern grassland assemblages, reinforced by the apparent requirement for a productive landscape to support a rich herbivore fauna, has generally been accepted as adequate documentation of the arctic steppe concept, and the apparent absence of a modern analog in surface samples seemed to confirm that the vegetation, as well as the animals, had become extinct. However, we reject the steppe or grassland concept for three reasons: the influx values are too low, by at least an order of magnitude; the floristic affinities are arctic and tundra rather than cold-temperate and grassland; and there are local analogs.

A modern analog for the low influx values is not available for lake-sediment samples. The end of the postglacial prairie zone recorded at Riding Mountain, southern Manitoba (*10*), provides the closest comparison, but the influx values there are ten times those of the Beringian herb zone. Air samples from the Canadian arctic (*11*) give influx values similar to those of the herb zone, but the arctic survey was for only one season and the open dish traps used inside weather screen are likely to differ significantly from lake basins as pollen repositories. In any case, it is unlikely that influxes less than 1000 grain cm^{-2} $year^{-1}$ would be expected from a productive, continuous grassland ecosystem, and values less than 100 grain cm^{-2} $year^{-1}$ suggest a very sparse vegetation cover. Furthermore, the sediments bearing the herb zone contain little organic matter, unlikely if the vegetation had been a closed productive grassland.

The modern pollen spectra from the fell-field tundras surrounding the Old Crow Flats resemble the herb zone in percentage composition (*12*). However, in many modern samples from lakes the herb zone pollen types are swamped by birch, alder, and spruce. But it is clear that today at Hanging Lake, for example, in the absence of pollen of birch, alder, and spruce and with a reduction in the area of cotton grass tundra, one might expect regional pollen spectra very similar to those of the full- and lateglacial herb zones.

We conclude that the Beringian herb zone represents a sparse, discontinuous vegetation of herbaceous tundra on upland sites and local sedge-grass meadows on lowlands.

The rapid increase of birch pollen between 14,000 and 12,000 years B.P. marks the top of the herb zone. It has been interpreted (*1*) as a shift from herb to shrub tundra, resulting in a reduction of suitable grazing habitat and contributing to the extinction of the herbivorous fauna. The Hanging Lake influx data show that grass and sage were most abundant during this shift, indicating no loss of grazing habitat. Because of its high pollen productivity, shrub birch is overrepresented (*13*) and the physiognomic change is exaggerated. We suggest that after 14,000 years B.P. heaths, absent from the herb zone, increased markedly, forming closed birch-heath shrub tundra on mesic sites, but that the open herb tundra persisted to the present day on xeric sites. The increase in heaths, dwarf birch, and total pollen influx suggests a change to warmer and moister conditions favorable for the development of peaty terrain with cotton grass tundra. Such a change should be considered as one of the factors that might have contributed to the demise of some of the large vertebrates. The concept of an environmentally harsh ecosystem capable of supporting small populations of both vertebrates and people may be tested by study of the modern musk-oxen/Inuit analog rather than of elephants in the African savanna (*4*).

Ager's (*14*) results from central Alaska are similar to those reported here, and it seems probable that further work in Alaska will show that the herb zone has very low influx values. If large pollen sums are counted in the herb zone and if primary sediment with secure ^{14}C stratigraphy is sampled, various hypotheses about the nature of these important communities can be further tested, including the arctic steppe idea. Equally important, little progress will be possible until the stratigraphic context of animal fossils and archeological evidence is placed on a firm basis.

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