

Late Quaternary Palaeoecology of the Yukon: A Review

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Abstract. During the late Wisconsinan glaciation, 28–14 ka B.P., unglaciated Yukon, isolated from the rest of North America by glaciers and joined to Far East Asia via the Bering land bridge, became part of eastern Beringia. The Yukon Pleistocene fauna included mammoth, horse, bison, camel and saiga, a grazing fauna that extended across Eurasia and Siberia. Fossil pollen studies have been interpreted by various researchers to support the presence of both steppe, which best conforms with the fauna, and herbaceous tundra vegetation, supported by multivariate analysis of modern tundra pollen rain. Pollen influx, plant macrofossil and fossil insect remains indicate important topographic and longitudinal moisture gradients, and a mosaic of vegetation types in an arid-climate environment. Climate and ecosystem models have been used to generate research hypotheses such as a climate with warmer than present winters and cooler than present summers, and the presence of productive Rego Brown soils. The late glacial and Holocene were marked by extinction of the Pleistocene fauna and successive appearance of forest species, some of which may still be responding biogeographically to the full-glacial conditions. Quaternary climate changes resulted in many similar forest-tundra oscillations in the past, creating a very dynamic biogeographic and ecological history for the Yukon.

Résumé. *Paléocologie de la fin du Quaternaire au Yukon: un aperçu global.* À la fin des glaciations du Wisconsinien, 28–14 000 ans avant notre ère, la partie non englacée du Yukon, isolée du reste de l'Amérique du Nord par les glaciers et réunie à l'Extrême-Orient par le pont continental de Bering, est devenue une partie de la Beringie orientale. Au Pléistocène, la faune du Yukon incluait le mammoth, le cheval, le bison, le chameau et la saïga, faune de brouteurs répartie partout en Eurasie et en Sibérie. Des études des pollens fossiles ont amené bon nombre de chercheurs à accepter l'hypothèse de la présence simultanée de la steppe, confirmée par la faune, et de la toundra herbacée, confirmée par l'analyse multidimensionnelle des retombées modernes des pollens de la toundra. Les retombées de pollen, les végétaux macrofossiles et les fragments d'insectes fossiles indiquent l'existence d'importants gradients topographiques et longitudinaux d'humidité et mettent en lumière une mosaïque de types de végétation dans un milieu climatique aride. Des modèles de climats et d'écosystèmes ont servi à ébaucher diverses hypothèses de recherche, comme l'existence d'un climat à hivers plus chauds et à étés plus frais que maintenant et la présence de régo-brunisol productifs. La fin de la période glaciaire et l'Holocène ont été marqués par la disparition de la faune du Pléistocène et l'apparition consécutive d'espèces forestières dont certaines sont peut-être encore en train d'ajuster leur répartition en fonction des conditions qui prévalaient au moment des glaciations. Les changements climatiques au Quaternaire ont donné lieu à de telles oscillations forêt-toundra dans le passé, assurant ainsi l'évolution biogéographique et écologique très dynamique du Yukon.

Introduction

Ecologist Henry Gleason (1926) forecast what has become the dictum of present-day Quaternary palaeoecology, that the “biological communities” of any region are the result of fortuitous species dispersal and their individualistic responses to an ever-changing environment. Nowhere is this more true than for the Yukon, where unglaciated portions are among the oldest landscapes of Canada, and Quaternary mountain building and climatic changes have led to dramatic geomorphic and biogeographic changes.

The Quaternary Period is divided into Pleistocene and Holocene Epochs and while the latter arbitrarily began 10 ka ago (Hopkins 1975), the former began either 1.7 or 2.4 ma years ago depending upon the respective criteria, the top of the Olduvai palaeomagnetic reversal or the first evidence of large-scale Northern Hemisphere glaciation (Zagwijn 1992). Subdivisions of the Pleistocene are based on the scale of dated palaeomagnetic reversals and global climatic changes recorded as stages of the marine oxygen isotope record measured by deficit (δ) values in the ^{18}O composition of Foraminifera. As examples, isotope Stage 1

represents the Holocene, Stage 2 the late Wisconsinan glaciation, Stage 5e the last interglacial, and Stages 2 through 5e the late Pleistocene. Pleistocene climatic changes were frequently of a magnitude that produced continental-sized ice sheets resulting in global sea levels lower than at present, about 150 m lower during the last glacial maximum. Lower sea levels exposed the Chukchi and Bering marine shelves, forming the Bering land bridge. During such times, the unglaciated Yukon was cut off by Cordilleran ice from the rest of North America, and joined to unglaciated Far East Russia via Alaska and the Bering land bridge, becoming the easternmost portion of Beringia.

Bluefish Cave III, a small solution feature atop a limestone ridge in the northern Yukon, makes a fine example of just how dramatic the biogeographic and environmental changes were during the late Pleistocene. Excavations here have yielded an in situ vertebrate fauna that includes woolly mammoth, horse, bison, caribou, muskox, mountain sheep and saiga antelope, dated 25–10 ka B.P. (Cinq-Mars 1990). This is a widespread fossil fauna; river erosion and hydraulic mining activities have exposed very similar vertebrate assemblages elsewhere in Beringia. Palynological research has associated late glacial faunas, dated ca. 14–10 ka B.P., with birch-dominated pollen assemblages (the Birch Zone of fossil pollen records) or grass-*Artemisia* (sage)-herb dominated fossil pollen assemblages (Herb Zone) during the full glacial, ca. 28–14 ka B.P. Both pollen assemblages indicate open treeless vegetation (Ritchie et al. 1982; Guthrie 1990). Vertebrate records from full-glacial late Wisconsinan environments are dominated by large grazing mammals, raising the question of how such a fauna could be supported during periods of harsh climate at northerly latitudes unless biological productivity was high (Hopkins et al. 1982). Moreover, the presence of the saiga antelope indicates a significant link to the steppe communities of Central Asia where the saiga is currently found (Harrington and Cinq-Mars 1995). The homogeneity and grassland adaptations of the glacial fauna led Guthrie (1990) to hypothesize the existence of a mammoth-steppe biome that extended from Eurasia eastward across the land bridge to the Yukon during full-glacial times. Dramatic fossil evidence such as that from Bluefish Cave III and the challenge of the mammoth-steppe hypothesis must be included in any discussion of the biota of the Yukon. This chapter reviews the late Quaternary palaeoecology of the Yukon, concentrating on research directed towards reconstructing late Wisconsinan environments and ecology.

Background to a Controversy

The process of palaeoecological reconstruction for ice-age Beringia began a century ago (Hibbert 1982), but accelerated greatly following publication of the classic works by Colinvaux (1964), Hopkins (1967) and Guthrie (1968) that covered fossil pollen, geology and fossil vertebrates, respectively. Pleistocene Beringia was portrayed, largely through fossil pollen assemblages, as an arctic grassland or steppe populated by grazing mammals while subject to full-glacial conditions. Late Pleistocene human populations were supposed to have made their way through this productive game-rich environment from Asia to the New World. The spread of birch in Alaska and the Yukon, evidenced by the rise of birch pollen 13–14 ka B.P., marked the end of this verdant scene (Matthews 1982) and the beginning of the late glacial.

Cwynar and Ritchie (1980) criticized this picture on a number of grounds including reliance on the relative percentage of pollen, an analytical method widely employed in palaeoecology. They advocated the use of pollen influx, the annual rate at which pollen accumulates in lake sediments, as a more useful measure. The very low pollen influx, less

than 100 grains/cm²/yr, they recorded from the herb pollen zone of Yukon lake cores led them to reconstruct full-glacial vegetation as a discontinuous tundra similar to that now found on dry rocky sites above or beyond arctic treeline. To Ritchie and Cwynar (1982) “the ‘arctic steppe biome’ never existed in Beringia during the late Quaternary. [and] The large and diverse ungulate populations probably were present during Pleistocene interstadials...rather than during the time of the herb zone [pollen], 30,000 to 14,000 years ago.” Such a provocative conclusion, which eventually came to be supported by Colinvaux (1980, 1981) and Colinvaux and West (1984), naturally stimulated considerable discussion and debate, especially as it jeopardized the hypothesis of the land bridge as a viable environment for large mammals and humans.

Various views surrounding these issues were published in the *Paleoecology of Beringia* (Hopkins et al. 1982). Two dominant themes emerged from this work: firstly, identification and use of modern analogues in reconstructing Beringia; and secondly, the apparent contradiction offered by the presence of the diverse grazing fauna under full-glacial conditions in an environment that is now boreal forest or sedge-moss tundra and seemingly incapable of supporting such a fauna, creating a “production paradox” (Schweger et al. 1982). Guthrie (1985, 1990) took up this challenge, demonstrating the presence of a dated full-glacial mammal fauna and arguing against the methodological criticisms raised by Ritchie, Cwynar and Colinvaux. Stimulated by the discovery of “Blue Babe”, a frozen Alaskan bison carcass, Guthrie (1990) effectively built a case for an Eurasian mammoth steppe, that has no modern analogue, and was characterized by a continuous and coherent fauna that persisted through the last glacial. Further contributions to the vertebrate record have been made by Harington (1978, 1989), Sher (1986) and Porter (1988). The vegetation history of Beringia, largely emphasizing fossil pollen research, is well covered in research publications by Ritchie (1982, 1984), Ager (1983), Brubaker et al. (1983), Huesser (1983), Ager and Brubaker (1985), Anderson (1985, 1988), Edwards and Brubaker (1985), Edwards et al. (1986), Barnowsky et al. (1987), Anderson et al. (1988, 1990, 1994a, 1994b), Lamb and Edwards (1988), Eisner and Colinvaux (1992), and Anderson and Brubaker (1994). Publication in English of reviews of the Quaternary of Siberia and Beringia (Kontrimavichus 1984; Velichko 1984) has done much to make available research conclusions for Siberian Beringia. Joint research initiatives between Russian and American researchers is furthering our understanding of the vegetation history of Far East Russian and Alaskan Beringia (Lozhkin et al. 1993; Anderson et al. 1994a, 1996; Edwards and Sher in press).

Several trends in Beringian research have emerged: 1) establishment of large pollen data sets and use of multivariate methodologies to search for vegetation analogues, carry out regional studies and extract palaeoclimate measures; 2) use of a wide variety of palaeoecological and ecological methodologies, including recognition of “relict” steppe vegetation; 3) use of climate and other model simulations to generate testable research hypotheses; and 4) documentation of early and middle Pleistocene palaeoecology to provide a temporal context for late Pleistocene ecological changes. Recognition of the need to test hypotheses generated from appropriate dynamic models (Birks 1985), such as ecosystem models (Schweger 1992) or GCM climate simulations (Anderson and Brubaker 1993), has moved research beyond the more intuitive process of “making” history or building scenarios.

Search for Analogues

The search for modern analogues to Pleistocene environments is a fundamental part of palaeoecological research. More than just words, *steppe* versus *tundra*, analogues link the

past to the present facilitating reconstruction of the Pleistocene environment, ecological interactions and quantitative measures of palaeoclimate. This is no less the case for the mammoth steppe, or full-glacial environment of Beringia. The behavioural ecology of the Asian elephant (Olivier 1982), modern grassland ecology (Redmann 1982) and primary production of modern tundra (Bliss and Richards 1982) have been examined, mostly in a qualitative sense, but it is the nature of the full-glacial vegetation, arctic-steppe or herbaceous tundra, as reconstructed from fossil pollen studies that has attracted the greatest attention. It is natural that Beringian vegetation be interpreted as steppe; after all, late Wisconsinan fossil pollen assemblages from Beringia are most similar to modern pollen samples collected from steppes or northern grasslands. However, the low level of taxonomic discrimination for *Artemisia* and Gramineae pollen weakens this interpretation, while similarities between the full-glacial herbaceous pollen component at Hanging Lake in the northern Yukon and the flora of modern fell-field tundra suggest the presence of herbaceous tundra vegetation (Cwynar 1982).

The search for analogues pursued a quantitative approach with the establishment of large data sets of modern pollen spectra (surface samples) from Alaska and Yukon, and adjacent western Canada (Anderson and Brubaker 1986; Ritchie et al. 1987) that represent forest, grassland and tundra communities. Because pollen data are very suitable for multivariate analysis (Birks 1985), researchers used principal components analysis (PCA) (Ritchie et al. 1987) and squared chord-distance measures (Anderson et al. 1989) to compare 303 modern pollen spectra with fossil pollen assemblages from 6 East Beringian lake study sites. PCA results demonstrated that modern and full-glacial pollen assemblages differed in the relative amounts of *Artemisia*, *Oxyria* and Saxifragaceae, while squared chord-distance suggested that modern analogues may exist for some full-glacial lake core records. The closest numerical relationships are found between 18–16 ka B.P. pollen spectra from Hanging, Joe, Squirrel and Kaiyak Lakes and tundra surface samples from northern Alaska, Seward Peninsula and/or Banks Island. Few modern analogues were found for the late glacial (15–10 ka B.P.), a period of rapid climatic and ecological change (Anderson et al. 1989).

These results imply that during part of the late Wisconsinan, vegetation at some East Beringian sites was not arctic steppe but was similar to herb-dominated tundra of north-western North America. This conclusion, however, points out an inherent weakness in the strictly quantitative approach, using only pollen data to reconstruct Beringia's palaeoecology. It remains to be demonstrated that vegetation analogous to modern tundra with its low biological production and slow nutrient turnover could ever have supported a fauna of mammoth, horse, bison, camel or saiga. One must question whether vegetation analogues can ever be reliably established without also considering the Pleistocene fauna. How is the "production paradox" to be factored into the results of multivariate analysis?

A Habitat Mosaic

Pollen influx measures (no. of pollen grains/cm²/yr) from the northern Yukon, at Hanging Lake (Cwynar 1982) and Lateral Pond (Ritchie 1982), were used by Cwynar and Ritchie (1980) and Ritchie and Cwynar (1982) to argue that full-glacial vegetation was discontinuous tundra, not unlike the fell-field tundra currently found in the area. Guthrie (1985, 1990) reviewed the influx method, correctly pointing out that while influx is a measure of pollen production, and therefore a crude measure of biological productivity, it clearly does not measure the amount of production available to a herbivore fauna. He calculated that influx from northwest Alaska, Imuruk, Squirrel, Joe and Kaiyak Lakes at

22–18 ka B.P., is similar to that of modern grasslands in southern Manitoba which supported large grazers such as bison, and domestic horse and cattle. For Hanging Lake, it is possible that old carbon contamination, indicated by presence of pre-Quaternary pollen and spores, led to old ^{14}C dates, slow sedimentation rates and erroneously low full-glacial influx values.

The vegetation history of north-central Alaska is particularly well documented and has yielded results that are surprising in light of the above discussion. Pollen influx values in the Joe Lake herb zone, 28–13.5 ka B.P., are consistently high, reaching a maximum of 7100 grains/cm²/yr (Anderson 1988), and influx values from Squirrel Lake and Kaiyak Lake herb zones consistently exceed 100 grains/cm²/yr. Values from Kaiyak Lake, 120–740 grains/cm²/yr, are similar to values for shrub tundra over the past 4 ka (Anderson 1985). For northwest Alaska, Anderson (1988) suggests a more mesic vegetation of continuous, meadow-like tundra, with shrub birch and *Populus* in sheltered, favourable sites. A mosaic of vegetation types dependent upon surface-water drainage, first proposed by Schweger and Habgood (1976) and Schweger (1982), appears to be supported by these data. Uplands with stony substrates, such as around Hanging Lake or Lateral Pond, may have supported discontinuous tundra vegetation, while lowland or valley bottom sites such as around Kaiyak and Squirrel Lakes had complete, mesic tundra cover. Similar conclusions were reached by Eisner and Colinvax (1992) for lake sites in northern Alaska. Clearly, because the vegetation of Beringia was complex, the use of simple, broad-scale descriptors such as steppe or herbaceous tundra will prove to be inadequate.

Pollen analysis appears to be a somewhat heavy-handed tool for documenting types of open, treeless vegetation, tundra or steppe (Funder and Abrahamsen 1988; Anderson et al. 1994b). Progress in documenting the nature of full-glacial vegetation depends upon application of other palaeoecological methods such as the recovery and identification of phytoliths (silica spicules and cell linings produced by plants), plant macrofossils and insect remains. While it has been demonstrated that phytoliths are abundant in Pleistocene sediments and have potential as a palaeoecological tool (Bombin 1984), there has been little effort to explore this methodology fully. Fossil insects, especially Coleoptera which can be easily recovered and are well preserved, have proven to be of great value because many have very specific habitat requirements (Elias 1994; Matthews and Telka 1997). Matthews pioneered the study of both plant and insect remains for East Beringia (1968, 1974a, 1974b, 1975), proving their usefulness especially when used in tandem. Because both groups of fossils demonstrated that a variety of habitats, from acid-bog to halophytic substrate to aquatic environments existed, Matthews (1982) postulated “a mosaic of communities, some of which were drier and more steppe-like than current treeless areas of East Beringia.” The growing fossil-insect data from Beringian sites have been reviewed by the palaeoentomologist Scott Elias (1994), who concluded, “that this region was not a uniform, coherent steppe-tundra ecosystem during the late Quaternary.” Biogeographic affinities of living insects support these conclusions. Bumble bees and solitary bees common to the interior of Alaska and Far East Russia indicate the existence of both tundra and steppe vegetation at the time of their dispersal across the land bridge (Bishop 1994).

There is, however, still a paucity of Beringian study sites dated to the late Wisconsinan full-glacial period. Sediments of this age often lack obvious fossils, as is the case with upland loess deposits, or—because of colluviation and solifluction—contain mixed assemblages, as in the fossil rich “miners muck” (Guthrie 1990). Greater biological production and occurrence of wood-moss-dominated peats during Pleistocene warm periods has resulted in greater knowledge of Pleistocene interstades and interglacials (Schweger and Matthews 1991). Lake cores most often end in late glacial or early Holocene sediments indicating that

the full glacial was arid and dry lake basins were not accumulating lacustrine sediments. Cores that penetrate or pass through full-glacial sediments frequently display inverted or confusing radiocarbon dates that may be due to slumping, recycling of older organic material or other factors (Gajewski et al. 1995). Much more remains to be accomplished in the identification, collection, analysis and interpretation of palaeoecological materials from full-glacial sediments.

Marine sediment cores, an important new source of palaeoecological information, have been collected from the Chukchi and Bering sea shelves, and analyzed for beetles, pollen, and plant macrofossils (Elias et al. 1996). Core sediments dated 20–14 ka B.P., a time when the land bridge was exposed, are dominated by pollen of *Betula*, Poaceae, Cyperaceae, *Salix*, Ericaceae and *Sphagnum*, while the plant macrofossils include bryophytes (e.g. *Drepanocladus* sp.) and vascular species (e.g. *Hippuris vulgaris* L. and *Potamogeton vaginatus* Turcz.) typical of small ponds. Beetles include *Pterostichus nivalis* F. Sahlberg, *Colymbetes dolobratus* (Paykull), *Olophrum* sp. and *Tachinus brevipennis* (F. Sahlberg), and indicate cold, relatively dry tundra heaths or dry meadows. A mosaic of “moderately dry-mesic environments, with heaths, dry meadows and shrub tundra, interspersed with marshes and small ponds” is reconstructed for the land-bridge environment (Elias et al. 1996). Reviewing these data, Colinvaux (1996) places the tundra-covered Beringian plains on a gradient of lowland mesic tundra to upland tundra sufficiently cold, dry and impoverished for arctic sage (*Artemisia*). This reconstruction is again similar to the vegetation continuum established by Schweger (1982) for East Beringia with unvegetated mountains, a tundra-grassland mosaic at lower elevations and wet meadows and ponds on valley-bottom floodplains. Moisture gradients must have been very important in the very arid environment of full-glacial Beringia.

Beringian Palaeoclimate

Palaeoclimatic reconstructions of East Beringia emphasize the aridity and increased continentality during full-glacial times (Hopkins et al. 1982). The presence of saiga antelope, which have no adaptations for cratering into deep snow for winter grazing and are currently limited in range to areas of Eurasia with a snow cover of only 10–30 cm/yr (Bannikov et al. 1967; Harington and Cinq-Mars 1995), supports this reconstruction. Aridity has enormous repercussions and is seen to have affected all areas of the Beringian ecosystem, especially nutrient cycling, plant community composition, and the development and survival of the unique Pleistocene mammal community (Guthrie 1982, 1990; Schweger 1992). However, one has to be careful not to enter into circular reasoning where mammalian adaptations are interpreted in terms of the aridity they were also used to document. To avoid circularity, independent lines of proxy evidence must be developed. Fossil pollen data have this potential yet the relationship between modern boreal/arctic vegetation, pollen and climate is not always clear, and many caveats must be applied (Anderson et al. 1991). As already noted, full-glacial pollen records do not have clear modern analogues and this greatly weakens the effectiveness of most multivariate palaeoclimatic methods. Although new methodology (Guiot 1990) may overcome this obstacle it has yet to be applied to Beringian fossil pollen sequences.

Output from computer Global or General Circulation Models (GCM) has had a major impact on Quaternary palaeoclimatic research. By changing boundary conditions (e.g. oceans, elevations, ice sheets) or forcing functions (e.g. insolation, CO₂, CH₄), the models can be designed to simulate climate for different time periods of the Quaternary. The

methodology of testing climate simulations for specific time periods through comparisons with palaeoclimatic data sets (COHMAP 1988) marked an important development, the hypothetical-inductive approach to palaeoclimate and palaeoecological research (Birks 1985).

Barnowsky and co-workers (1987) integrated this approach into their reconstruction of vegetation and climate of the northwestern United States. Pollen data from East Beringia suggested an east-to-west gradient with more mesic shrub tundra in the west (Barnosky et al. 1987; Elias et al. 1996) and sparse tundra in the east (Cwynar 1982; Ritchie 1982). The climate must have been more severe in the east which lies closer to the Laurentide and Cordilleran glaciers and within the rainshadows of the Alaska-St. Elias Ranges. Widespread aeolian deposits and stabilized Pleistocene dune fields attest to the aridity of the East Beringian climate. Climate model simulation for 18 ka included anticyclonic and adiabatic circulation for East Beringia, resulting in warmer than present January and colder than present July temperatures, and although July precipitation was less than present, western areas were wetter than in the east. Warmer winters and thinner snow cover may help account for the survival of the Pleistocene mammal fauna (Barnowsky et al. 1987).

Anderson and Brubaker (1993) employed model climate simulations for 12, 9 and 6 ka B.P. in their analysis of late-glacial and Holocene vegetation, and climate histories for Alaska. Fossil pollen records for *Betula*, *Alnus*, Cyperaceae, Gramineae and *Picea* display pronounced fluctuations over these time periods, indicating dramatic changes in vegetation development. While there is agreement between fossil data and model simulations for summer warmth at 9 and 6 ka, the fossil data record indicating increased mean annual or seasonal precipitation is not simulated. For now, climate simulations remain a relatively crude tool. With a grid size of 4.4° latitude by 7.5° longitude and generalized elevations, regions with the size and topographic complexity of East Beringia remain poorly resolved. To provide more detail, meso-scale models driven by the GCM output are being developed and may someday be applied to the area of Beringia.

Variation in the controls of regional climate, particularly insolation, for East Beringia have been reconstructed for the late and middle Pleistocene, a period of 800 ka, and compared to the marine isotope record (Bartlein et al. 1991). This reconstruction shows that the climate has been in a constant state of flux, cooler than the Holocene for nearly all of the past 800 ka and for five time periods similar to full-glacial conditions during the period from 20–14 ka B.P. (oxygen isotope stage 2). For the Yukon, glaciers formed and advanced during some of these cold periods. Late Wisconsinan McConnell Glaciation was preceded in the central Yukon by the Reid Glaciation, dated earlier than 200 ka B.P. (Berger et al. 1996). Even though the climate was cold, prevailing aridity prevented development of glacial ice in the Yukon Cordillera during the second to last glacial cycle, about 185–135 ka B.P. (isotope stage 6), and the early Wisconsinan, about 75–60 ka B.P. (stage 4).

Mesic, shrub-tundra vegetation is documented in the Yukon as early as 2.3 ma B.P. (Westgate et al. 1995) and colder, sedge-grass rich tundra during mid Pleistocene periods (Tarnocai and Schweger 1991; Schweger and Matthews 1991). Uplift of the Alaska/Yukon Cordillera over the past 2 million years had a great effect on the development of early and mid Pleistocene vegetation by cutting off moisture from the north Pacific and Gulf of Alaska (White et al. 1997). Herbaceous tundra or arctic-steppe, presumably expanding from localities in northwestern North America or central Asia, existed in East Beringia several times in the past. Following Guthrie's (1990) mammoth-steppe biome hypothesis, every significant drop in the global sea level, as indicated by the marine isotope record, exposed the land bridge, and the dry, cold climate stimulated an expansion of the mammoth steppe

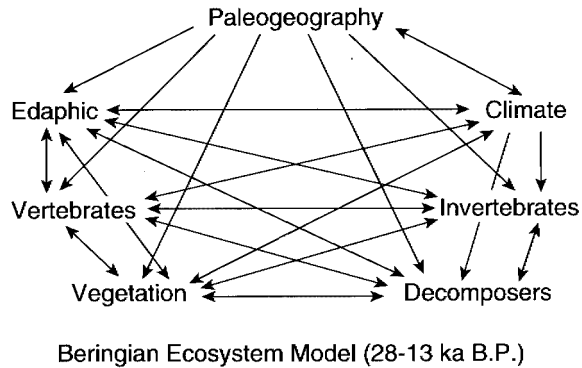


FIG. 1. Diagram of the components and interactions that make up the Beringian ecosystem model (Schweger 1992).

east and west out of central Asia. During the much shorter interglacial periods, sea level rose, flooding the land bridge and spruce woodlands or forests appeared in East Beringia. Under conditions of constantly changing climate, tectonics and palaeogeography, the flora and fauna of the Yukon has probably never been in equilibrium with the environment but has been continually adjusting in range and composition.

Models and Hypotheses

Ecosystem models can also be employed to generate testable hypotheses concerning the palaeoecology of Beringia. A qualitative ecosystem model with seven components and all probable interactions was constructed to facilitate more integrated and dynamic palaeoecological reconstruction (Schweger 1992) (Fig. 1). Special attention was given to the edaphic (substrate) component of the ecosystem because the soil integrates so many physical, chemical, biological and climatic factors, and it is with the soil that one must first approach the issue of biological productivity. Two hypothetical soils were reconstructed (Fig. 2) based on as many palaeoecological observations as possible that separate glacial and interglacial environments. The interglacial Cryosol (Agriculture Canada Expert Committee on Soil Survey 1987), similar to subarctic soils of the Holocene, has low nutrient turnover and organic productivity unsuitable to grazing fauna, which can help account for the "production paradox". In contrast the Rego Brown Soil (Agriculture Canada Expert Committee on Soil Survey 1987) of glacial periods is more deeply thawed, has rapid nutrient turnover and herbaceous-graminoid vegetation suitable for the Pleistocene grazing fauna. It is hypothesized that the incremental deposition of aeolian silt or loess to the Rego Brown Soil surface under full-glacial conditions was a key factor in maintaining this highly productive soil and, ultimately, the Beringian ecosystem. I have advanced arguments to support this hypothesis based on the ecological effects of mineral dust and the chemistry of glacial-derived rock flour (Schweger 1992). However, a study of loessal grassland in the Kluane Lake region, southwest Yukon, comes closer to being a true test (Laxton et al. 1996). Biomass and species diversity of grasslands around the lake increase with the quantity of silt in the soil; so too does total nitrogen, available nitrogen and total carbon. Loess blowing off the Slims River delta is the source of the silt.

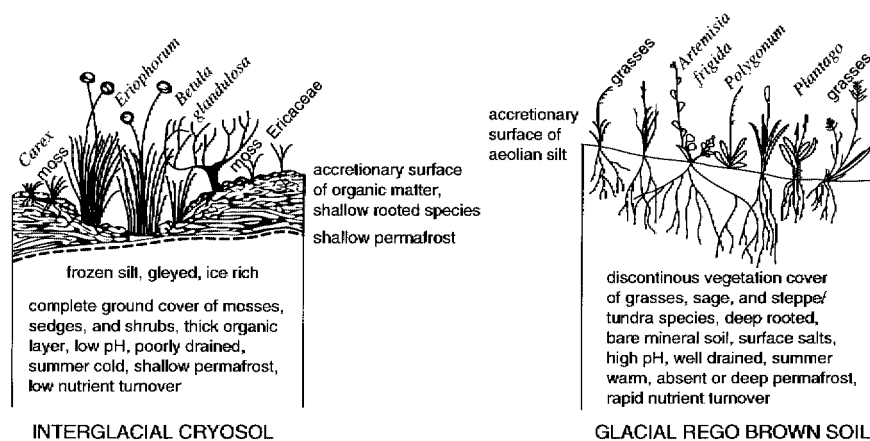


FIG. 2. Hypothetical soil profiles for interglacial and glacial edaphic conditions (Schweger 1992).

Further support for the existence of productive full-glacial soils comes from 17 ka old palaeosols excavated from below a tephra on Seward Peninsula, western Alaska (Hoefle et al. 1994). The silt-loam texture of the soils is characteristic of loess, root distribution suggests syngenetic soil formation, and soil chemistry indicates a dry, vegetated environment and high nutrient availability. Late Wisconsinan aeolian sand-sheet deposits of central and southwestern Alaska contain deformation structures interpreted as mammal hoof- and foot-tracks. Lea (1996) believes the tracks record mammoth and ungulates that were attracted to the sandy, silty lowlands because of the locally important grazing habitat.

Biogeographic studies have long been important in Beringia. In fact, the term *Beringia* was promoted by Swedish plant biogeographer, Eric Hultén (1937), for the Alaskan-Siberian land bridge he hypothesized in order to account for plant distributions in Alaska and Far East Russia. Xerophytic grassland and steppe vegetation of Siberia has been the subject of intense biogeographic interest and even considered relicts of Pleistocene steppes (Yurtsev 1982). Wrangel Island, centrally located on the Chukchi shelf, with numerous steppe plant species and modern pollen assemblages that resemble those of full glacial sediments, is of special interest. Yurtsev (1982) suggests that the landscapes of Wrangel Island "may be the closest living approximations of the northern variants of late Pleistocene tundra-steppe,..." This statement is prophetic in light of the discovery of a dwarf-mammoth population that persisted on the island until 3700 B.P., 6500 years after the full-sized mainland race became extinct (Vartanyan et al. 1993; Yurtsev 1994).

Grasslands with *Artemisia*, *Selaginella* and other steppe species, such as *Carex sabulosa* Turcz., an Asian steppe species found along the Alsek River terraces (Douglas 1974), occur as islands of azonal steppe vegetation in Far East Russia, Alaska and Yukon, mostly on south-facing river-valley slopes. Floristic and soil studies have documented the similarity of these grasslands across Beringia and suggest that a diversity of steppe habitats existed at the time of floristic interchange, presumably during the last full glacial (Roland 1994). Berman et al. (1994) have researched azonal steppes in the Aborigen area, Far East Russia, and Kluane Lake area, southwest Yukon. Low soil moisture due to slope and aspect, and

absence of snow cover, accounts for the presence of steppe vegetation. Floristic comparisons with fossil floras at the species level have not been made, but comparisons of insect faunas, such as the pill-beetle, *Morychus viridis* Kuzmina and Korotyaev, which is rare today yet abundant in the cool steppes of Russia and as a full-glacial fossil (Matthews 1982), suggests that these grassland sites may be good analogues for Pleistocene environments.

Late Glacial and Holocene Environments

Recession of glaciers from their late Wisconsinan moraines and the increase of fossil *Betula* (believed to be shrub birch) pollen in lake cores marks the end of full-glacial conditions in the Yukon. Both events occurred between 14–10 ka B.P. and define the late glacial. The spread of birch shrub tundra in response to increased warmth and precipitation has been implicated in the disappearance of the mammoth steppe and the extinction of the Pleistocene mammal fauna (Guthrie 1984). In the southern Yukon, *Alnus crispa* (Ait.) Pursh and *Betula* increased simultaneously, prior to the Holocene appearance of *Picea*. Elsewhere in the Yukon, the appearance of spruce in pollen records, ca. 8 ka B.P., precedes that of alder, 7–6 ka. B.P. (Cwynar et al. 1987). The mid Holocene saw expansion of *Picea mariana* (Mill.) BSP., black spruce and green alder (*Alnus crispa*) over southern and central Yukon in response to cooler, more mesic climate, and the development of organic terrain and ice-rich permafrost (Cwynar and Spear 1995). *Pinus contorta* Loudon (Lodgepole pine), an important Yukon forest species, first appeared in the southern Yukon about a thousand years ago and reached its present northern limit south of Dawson much more recently (Schweger et al. 1987). The late glacial–Holocene palaeoecology of the Yukon is marked by a series of species expansions (e.g. shrub birch) and migrations (e.g. white spruce) following deglaciation. While all vegetation changes were in response to broad climatic changes, species behaved individualistically: black spruce and alder expanded in response to edaphic changes, while pine may have been responding to fire history. We cannot, in fact, be certain that the biogeographic changes that came about in response to the last glacial/climate cycle are complete. Many plant and animal taxa may not be in equilibrium with the present climate, and range adjustments may continue.

Conclusions

Climate change, mountain building, glaciation and appearance of the Bering land bridge have resulted in dramatic palaeoenvironmental changes for the Yukon. Tundra first appeared over two million years ago and again with each cycle of cold arid climate, while intervening warm periods were characterized by boreal woodland and forests. A great deal more research that makes use of a variety of methods, model building and hypothesis testing must be done before the full glacial palaeoecology of the Yukon is adequately reconstructed. Nevertheless, during the last full glacial, 28–14 ka B.P., the Yukon was geographically part of Far East Asia and supported a flora and fauna that has no modern analogue, although the vegetation shows affinities to both North American herb-dominated tundra and Eurasian steppe. The Yukon appears to have had a harsher, more arid climate than western Alaska and the land bridge where regions of mesic, birch shrub tundra existed. Local differences in elevation, substrate and moisture created a mosaic of vegetation types that supported a diverse Pleistocene mammal community. Climate simulations suggest that winters were warmer and summers cooler than at present, and snow cover was thin or discontinuous.

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