Géographie physique et Quaternaire

Late Quaternary Vegetation History of Northern North America Based on Pollen, Macrofossil, and Faunal Remains

Histoire de la végétation de la fin du Quaternaire de la partie nord de l’Amérique du Nord basée sur les pollens, les macrofossiles et les restes d’animaux

Arthur S. Dyke

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Article abstract

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LATE QUATERNARY VEGETATION HISTORY OF NORTHERN NORTH AMERICA BASED ON POLLEN, MACROFOSSIL, AND FAUNAL REMAINS*

Arthur S. DYKE**: Geological Survey of Canada, Natural Resources Canada, 601 Booth Street, Ottawa, Ontario K1A 0E8, Canada.

ABSTRACT: Biome maps spanning the interval from the last glacial maximum to modern times are presented. The biome distributions at 18 ka BP were probably as nearly in equilibrium with climate as are the modern distributions, but deglacial biomes were probably in disequilibrium. Ice sheet configuration was a strong control of climate until 7 ka BP. Regional climate trends can be inferred from changing biome distributions, but during periods of disequilibrium, biome distributions under-represent summer warming. Because of summer cooling by 2-4°C during the Holocene, largely in the last 3-5 ka, middle and certain early Holocene biome distributions and species compositions are reasonable analogues of future equilibrium displacements due to equivalent warming. The configuration of the calotte glaciaire exerted a fort control on the climate as late as 7 ka BP. The tendencies climatiques régionales peuvent être estimées à partir des changements observés dans la répartition des biomes, mais en période de déséquilibre leur distribution soustrait la réchauffement estival. À cause du réchauffement estival de 2 à 4 °C durant l’Holocène, depuis les derniers 3 à 5 ka, la distribution des biomes au cours de l’Holocène moyen et inférieur et la composition des espèces sont similaires aux déplacements de l’équilibre futur lié au réchauffement, du moins pour les régions qui sont déglacées depuis longtemps. Les taux de migration des biomes anciens furent de l’ordre de 100 à 200 m par année. Si ces taux se maintiennent dans le futur, les biomes pourraient se déplacer de 10 à 20 km dans la plupart des régions au cours du prochain siècle. L’obstacle majeur à l’utilisation des conditions qui prévalent durant l’Holocène, pour l’estimation des conditions futures, est que les étés chauds sont accompagnés d’hivers froids tandis que les futurs étés chauds seront accompagnés d’hivers chauds.
INTRODUCTION

In considering the distribution of vegetation during the Late Wisconsin maximum, not only beyond the Laurentide Ice Sheet but in the Cordilleran region as well, we must stress at the outset that paleoecology, whether of plants or of animals, is more complex and its data more obscure than the glacial geology we have been describing. We are dealing here with ecosystems, natural dynamic systems that consist of the entire biotic community and its environment (Flint, 1971: p. 500).

Reconstructions of former vegetation and associated terrestrial mammalian communities of Late Quaternary time have been the focus of much research effort in North America (Wright, 1983; Ritchie, 1984, 1987a; Bryant and Holloway, 1986; Graham et al., 1987; COHMAP members, 1988; Huntley and Webb, 1988; FAUNMAP, 1994; Williams et al., 2004; Strong and Hills, 2005). Early attempts date from the dawn of Quaternary pollen stratigraphy (Sears, 1935; Deevey, 1949; references in Ogden, 1961), which predated the advent of radiocarbon dating, and hence of secure chronologies. For lack of firm chronology and other methodological reasons, these pre-radiocarbon studies have tended to focus on the last glacial maximum (Jackson, 2000) which predated the advent of radiocarbon dating, and hence of secure chronologies. For lack of firm chronology and other methodological reasons, these pre-radiocarbon studies have tended to focus on the last glacial maximum (Jackson, 2000), which predated the advent of radiocarbon dating, and hence of secure chronologies. For lack of firm chronology and other methodological reasons, these pre-radiocarbon studies have tended to focus on the last glacial maximum (Jackson, 2000), which predated the advent of radiocarbon dating, and hence of secure chronologies. For lack of firm chronology and other methodological reasons, these pre-radiocarbon studies have tended to focus on the last glacial maximum (Jackson, 2000), which predated the advent of radiocarbon dating, and hence of secure chronologies. For lack of firm chronology and other methodological reasons, these pre-radiocarbon studies

...
temperature of 7.5 °C; latitudinal treeline — the boundary between forest tundra and shrub tundra — coincides with a July mean temperature of 10 °C, which in turn is fixed by the mean winter temperature of the Arctic Front (Bryson, 1968); the boundary between boreal forest and forest tundra coincides with the 13 °C July isotherm (Edlund, 1988); and the southern boundary of the boreal forest, which approximates the mean winter position of the Arctic Front, roughly follows the 17.5 °C July isotherm (Hare and Thomas, 1974). In the east, this boundary may be more effectively prescribed by the −40 °C minimum winter isotherm, because this threshold evidently determines the northern limit of temperate deciduous trees (Arris and Eagleston, 1989). Shoots are killed by intracellular freezing below that temperature in these trees, but not in boreal species. Where the climate is warm enough to support trees but where moisture is insufficient, grassland and steppe biomes are arranged along a gradient of decreasing moisture and increasing temperature. These biomes occur where the total annual precipitation is <0.5 m and where moisture balance is negative. The boundary between the boreal forest and the aspen parkland on the Canadian Prairies, for example, coincides closely with the zero contour of P-PET (precipitation minus potential evapotranspiration), whereas the boundary between the aspen parkland and the grassland coincides with the −15 cm contour (Hogg, 1994).

Therefore, the former distribution of biomes might be used to infer past climates. However, during times of climate change, biome limits may not have been in equilibrium with the transient climate. Although plant mortality may quickly follow a deleterious climate change at the limit of the geographical range of a species, rates of plant migration and die-off are limited by physiological and edaphic (soil) barriers and by biological processes of seed dispersal, seedling establishment, seedling destruction, and survival of plants through vegetative reproduction. Thus, numerical biome models that assume instantaneous plant migration in response to future climate change predict greatly different biomes than do those that do not, particularly with respect to treeline movements (Lenihan and Neilson, 1995; Solomon and Krilierko, 1997). Similarly, numerical reconstructions of past climates from pollen data assume that former plant species distributions, not just biome boundaries, were in equilibrium with former climates. Multi-proxy data are increasing revealing that plant colonization may have lagged climate warming by millennia and that maximum summer temperatures did not necessarily coincide with the most thermophilous vegetation development. For example, Miller et al. (2005) showed that lacustrine productivity and summer temperature peaked long before the most diverse and apparently most thermophilous plant cover was established on eastern Baffin Island. This is not to say that individual plants do not respond quickly, even seasonally, to climate, but rather that the equilibrium response of plant assemblages may be delayed by centuries to millennia (Williams et al., 2002; Shuman et al., 2004). It follows, therefore, that while climate trends may be inferred from former changes of vegetation cover, a proper assessment of the sensitivity of vegetation change requires an independent reconstruction of climate history. In Canada, such reconstructions are emerging mainly from the study of fossil chironomids, the remains of species of non-biting midges (flies), which are aerooplankton that are abundantly preserved in lake sediments and whose aquatic larval require certain water temperatures for survival (Walker and Pellatt, 2003). Available reconstructions are cited below where appropriate.

Former vegetation cover is here classified into 15 biomes. These are generally familiar to most North American readers and are defined, as used here, in Table I.

DATA SOURCES AND METHOD

The biome reconstructions are based on radiocarbon-dated palaeontological records of three kinds: (1) pollen stratigraphic sequences (1385 sites); (2) plant macrofossils (892 sites); and (3) terrestrial mammal macrofossils (4382 dates <25 ka [tabulated]; 4050 dates <18.5 ka [mapped]). Each data set comprises independent spreadsheets that are interactive with the online GIS-based versions of the paleobiome maps. That is, querying of a site symbol will open the relevant portion of a database. The spatial density of sites is the best measure of the confidence that one might place in a biome interpretation, followed by the internal consistency of the site classifications within a biome (a site classification may differ from the biome interpretation). In places, additional sites will undoubtedly lead to amended interpretations. Additional sites in the modern forest tundra, shrub tundra, and southern herb tundra of central and eastern Canada are those most needed from a biome mapping perspective, along with additional sites dating to 14 ka BP and older.

The online pollen database lists the site name, publication source (author, date), and geographic co-ordinates for each site (only key and representative works are cited below). For each millennium time slice, the following three columns of information are given: Description, Biome, and Association. The entries under “Description” attempt to capture faithfully the published interpretations of the pollen assemblages; e.g., “Alder-birch shrub tundra (Alnus-Betula-Ericaceae zone)” and “White pine forest with spruce, fir, birch, elm, ash, and cedar.” These descriptions were analyzed in a separate spreadsheet by sorting, synonymising (e.g., Picea zone = spruce zone) and generalizing (e.g., White pine forest with spruce, fir, elm, ash, cedar = Mixed Forest) in order to reduce the more than 1500 unique descriptions to the 15 biomes listed in Table I. Only the Biome column is used here for mapping. However, plant assemblages (e.g., White Pine-Spruce-Fir-Birch-Elm-Ash-Cedar, in the mixed forest example just cited) are listed in the database where possible in order to retain more fully the interpretations of the original analysts and to aid in more detailed future mapping. Hence, the database captures most of what is available in the regional palynological literature, which deals mainly with qualitative interpretation. No attempt is made here to treat the vast numerical data sets (pollen counts) such as are available in the North American Pollen Database and are the subject of analyses by others (Williams et al., 2004).

Pollen stratigraphies are subject to a number of chronological uncertainties. Despite increasing use of more precise dating methods (accelerator mass spectrometric dating of small plant macrofossils from lake sediments), most interpretations...
TABLE I

Biomes used in the paleovegetation maps

<table>
<thead>
<tr>
<th>Biome</th>
<th>Characteristics</th>
</tr>
</thead>
<tbody>
<tr>
<td>Herb tundra</td>
<td>A treeless area lacking shrubs other than small, prostrate willows and dominated by bare ground and herbs, typically sedge, grass, and sage with a variety of forbs; includes fellfield.</td>
</tr>
<tr>
<td>Shrub tundra</td>
<td>A treeless area with a nearly continuous cover of sedge, grass, sage, and forbs along with prostrate and semi-erect willows as well as one or more additional shrubs, chiefly dwarf birch, alder, and juniper, in increasing order of required warmth.</td>
</tr>
<tr>
<td>Alpine tundra</td>
<td>Similar to herb or shrub tundra but occurring at high elevations.</td>
</tr>
<tr>
<td>Forest tundra</td>
<td>A zone transitional between shrub tundra and boreal forest. That is, a continuous ground cover of herb and shrub vegetation with open stands of erect trees, typically spruce, larch, and (or) poplar (birch in Iceland).</td>
</tr>
<tr>
<td>Boreal forest</td>
<td>Nearly continuous cover of trees dominated by northern conifers (mainly spruce, jackpine, larch, and fir) and northern hardwoods (mainly birch, aspen, poplar), broken by wetlands.</td>
</tr>
<tr>
<td>Boreal parkland</td>
<td>Open stands of boreal forest trees growing in ground covers dominated by herb and (or) lichen. Includes the modern aspen parkland at the southern fringe of the western boreal forest in the Prairie Provinces and the lichen woodland (open spruce forest) of the eastern boreal forest, which grades to forest tundra.</td>
</tr>
<tr>
<td>Subalpine forest</td>
<td>The conifer-dominated forest in mountainous terrain of the Cordillera. Dominated by subalpine fir, Engelmann spruce, mountain hemlock, lodgepole pine, and whitebark pine in northern ranges; limber pine, bristlecone pine, and juniper farther south.</td>
</tr>
<tr>
<td>Conifer forest</td>
<td>A cover of conifer trees different in composition from modern boreal, subalpine, or interior forests. Typically dominated by lodgepole pine in areas of modern subalpine and interior forests.</td>
</tr>
<tr>
<td>Interior forest</td>
<td>The conifer-dominated forest of the relatively dry interior of the Cordilleran region, which occurs south of the western boreal forest and experiences cold winters; typically dominated by Douglas fir, lodgepole pine, whitebark pine and Ponderosa pine, with western hemlock, Engelmann spruce, Sitka spruce, and cedar.</td>
</tr>
<tr>
<td>Coast forest</td>
<td>The conifer-dominated forest of the wet coastal ranges and lowlands of the Pacific coast, which experience mild winters; typically dominated by western hemlock, western red cedar, and Sitka spruce with Douglas fir, alder, grand fir, and silver fir.</td>
</tr>
<tr>
<td>Mixed forest</td>
<td>Conifer-hardwood assemblages mainly occupying the transition zone between the boreal forest and the deciduous forest of eastern North America. Dominated by boreal elements (conifers and northern hardwoods [birch, beech, alnus]) on the north and temperate elements on the south. Includes a diverse mosaic of associations dominated by white pine, hemlock, white cedar, maple, yellow birch, oak, etc.</td>
</tr>
<tr>
<td>Deciduous forest</td>
<td>The broad-leaf, temperate, deciduous forest of eastern North America; typically dominated by oak with beech, birch, maple, basswood, hickory, chestnut, ironwood, hemlock and white pine.</td>
</tr>
<tr>
<td>Savannah</td>
<td>A zone transitional between grassland and deciduous forest, with oak typically dominating the trees.</td>
</tr>
<tr>
<td>Grassland</td>
<td>Treeless or nearly treeless vegetation dominated by grass, sage, or chenopods, grading to steppe with decreasing moisture; includes long- and short-grass prairie.</td>
</tr>
<tr>
<td>Steppe</td>
<td>Treeless or nearly treeless semi-desert vegetation of western North America dominated by sagebrush, chenopods, shadscale, and grass, with occasional lodgepole pine, Ponderosa pine, and juniper.</td>
</tr>
</tbody>
</table>
series has a 1000-year time step, all dated fossils that are within 500 years of the times portrayed are plotted on the maps. This wide binning of data leads to an occasional site that plots inconsistently within the ice-covered area. Other sites that plot within the ice area are those here judged to have erroneous radiocarbon dates. Plant macrofossils are generally less informative than pollen data for present mapping purposes, because most occurrences indicate only the presence of a single taxon. Thus only biome-level inferences are usually possible. Nevertheless, plant macrofossils are commonly identified to species level, whereas pollen is typically identified only to genus or higher levels. Therefore, plant macrofossils provide welcome supporting evidence particularly at times and places with little or no pollen data. Furthermore, in certain contexts, such as in the fossil packrat (Neotoma spp.) middens in the arid American Southwest, plant macrofossil assemblages are thought to represent rather fully the local vegetation and to allow reconstructions that are not possible with pollen data alone (Betancourt et al., 1980).

The fossil mammal database provides a listing of radiocarbon dates, laboratory codes, co-ordinates, literature sources, material and taxon dated, associated taxa, and biome interpretations. As with plant macrofossils, each map displays sites with dates that fall within 500 years of the time slice. Terrestrial mammal fossils allow only biome-level inferences in most instances. These inferences are based on the modern habitat preferences of extant taxa (Banfield, 1977) and on habitats inferred from dietary habits (e.g. grazers, browsers, carnivores) for extinct taxa (Harigton, 2000). Like plant macrofossils, the mammal fossils help fill in the maps in the absence of pollen data. In addition, particularly in eastern Beringia, the full-glacial to late-glacial mammal fossils provide a view of the regional plant communities that is altogether richer than that indicated solely by the few available pollen records (compare Guthrie, 1985 with Ritchie, 1984).

RESULTS

The biomes familiar to North Americans have existed in nearly modern geographical configurations for only the last 5000-6000 years. Even during that time span, biome boundaries have shifted slightly and their species compositions have changed in response to general late Holocene cooling, particularly during the last 3000 years. For example, boreal elements such as spruce have shown an increase throughout much of the mixed forest biome. Although our present biome-level mapping is too coarse grained and taxonomically too imprecise to recognize association-level changes, we summarize key assemblage changes and distributions below.

Due to the paucity of fossil sites, we assume that the distributions of biomes in North America during the last interglacial period (130 000 to 115 000 years ago) were broadly similar to those of the present day (see discussion below for differences). As the continental ice sheets grew and partially waned, these intervals during the last glaciation (ca. 115 000 to 20 000 years ago), these biomes were necessarily displaced equatorward and changed in species composition. With the possible exception of an extant species of spruce (Picea crichtfield; Jackson et al., 2000), which appears to have been confined to areas south of 39 °N at the last glacial maximum, all plant taxa herein are those found in modern biomes as far as taxonomic resolution can determine. The extreme displacement of biomes during the Late Pleistocene presumably is that shown on the 18 and 14 ka BP maps. The Laurentide Ice Sheet margin was at or approaching its southernmost limit in most places by about 23 ka BP (Dyke et al., 2002). Therefore, the biome distribution at 18 ka BP was probably as well adjusted to its contemporaneous climate as the modern distribution is to modern climate. After 14 ka, the pace of atmospheric warming and deglaciation quickened. It is less safe to assume that biome distributions were in equilibrium with climate from that time until about 6 ka BP. What follows is a brief sketch of the major changes in biome distributions and their plant and faunal compositions from the last glacial maximum to the present day, followed by a comparison of Holocene and Sangamonian conditions.

GLACIAL MAXIMUM

The climate of the last glacial maximum has been elucidated by general circulation model experiments (COHMAP Members, 1988; Bartlein et al., 1998), which have largely confirmed earlier geological interpretations (Barry, 1983). Over North America, the atmospheric circulation was dominated by a large anticyclone above the continental ice sheet, thus generating easterly winds along the southern margin from the Atlantic to the Pacific. This anticyclonic flow split the jet stream in winter, one branch crossing Beringia and the northern flank of the ice sheet, the other crossing the continent from southeastern California to the southeastern ice sheet margin. Mid-latitude storms today track along the jet stream, which separates polar from warmer air masses, and, presumably, that was the case in the past. The anticyclone shrank in radius as the ice sheet retreated and probably dissipated with the deglaciation of Hudson Bay about 7.6 ka BP. The western part of the continent was deglaciated earlier than the east. Hence, the western landfall of the jet stream moved northward to its present position in the Alaska Panhandle (southeastern Alaska) relatively early, by 10-11 ka BP. We shall see that this change of atmospheric circulation from 18 ka BP to about 7 ka BP can explain much of the sequence of biome changes from the last glacial maximum to the middle Holocene.

18 ka BP

The species that comprise the modern forest and grassland biomes of North America necessarily survived the last glaciation south of the ice sheets. However, the paleontological record of the details of species distribution remains sparse, because of the paucity of sites with appropriate depositional records that extend into this time interval. It is generally conceded that boreal forest species – such as black and white spruce (Picea mariana and P. glauca), jackpine (Pinus banksiana), balsam fir (Abies balsamea), larch (Larix laricina), birch (Betula papyrifera) – and mixed forest species – such as eastern white pine (Pinus strobus), eastern hemlock (Tsuga

}
canadensis), eastern white cedar (Thuja occidentalis), the maples (Acer spp.), ashes (Fraxinus spp.), oaks (Quercus spp.), yellow birch (Betula alleghaniensis), ironwood (Ostrya virginiana), beech (Fagus grandifolia), basswood (Tilia americana), and the elms (Ulmus spp.) — were displaced to the American South and Southeast (Delcourt and Delcourt, 1981); that coast forest species — such as Sitka spruce (Picea sitchensis), western red cedar (Thuja plicata), and western hemlock (Tsuga heterophylla) — were displaced to the coastal ranges of California and Oregon (Hedblad and Whitlock, 1997); and that montane-subalpine species — such as subalpine fir (Abies lasiocarpa), whitebark pine (Pinus albicaulis), lodgepole pine (Pinus contorta), and mountain hemlock (Tsuga mertensiana) — were displaced southward in the Cordillera. There has been more debate about the nature of the vegetation cover on the southern Great Plains during the last glacial maximum, but most current interpretations favour a cover dominated by grassland taxa rather than trees (Holliday, 1987).

At 18 ka BP (Fig. 1), herb tundra with willow (Salix reticulata) survived in front of advancing glaciers on the Queen Charlotte Islands of British Columbia (Warner et al., 1982; Blaise et al., 1990), including perhaps areas now below sea level. It has been proposed on DNA evidence that grizzly bears (Ursus arctos) survived the last glaciation in this region, including the adjacent archipelago in Alaska, where they are now more genetically allied with the polar bear (Ursus maritimus) than are the brown bears of the mainland (Heaton et al., 1996). However no full-glacial fossils of this, or other, terrestrial mammal species have yet been recovered there.

The ice sheet in southwestern British Columbia at 18 ka BP was advancing across lowland terrain that supported a forest of fir and spruce (Clague et al., 1980; Hicock and Lian, 1995). Occurrences of Townsend's vole (Microtus townsendii) dated to 18.01 ka BP on southwestern Vancouver Island are in agreement with this interpretation, because this animal occurs today only below alpine treeline (Ward et al., 2003).

Most of the southern margin of the ice sheet abutted water, tundra, or cold grassland. Herb tundra is indicated at pollen sites close to the ice margin in New Jersey (Sirkin et al., 1970), including a site on a mountain nunatak (Cotter et al., 1984). Macrofossils of arctic avens (Dryas integrifolia), arctic blueberry (Vaccinium uliginosum), alpine bistort (Polygonum viviparum), and the dwarf willows (Salix arctica and S. herbacea) — all common in modern herb tundra — are dated at 18.7 ka BP at a site in Minnesota (Baker et al., 1999). A pollen sequence from an ice-marginal site in Ohio indicates forest tundra with spruce at 18 ka BP (Heusser et al., 2002). Forest tundra is also indicated by pollen sequences from Iowa (Szabo, 1980), Maryland (Maxwell and Davis, 1972), Delaware (Russell and Stanford, 2000), and Pennsylvania (Martin, 1958) at this time. The ice evidently pushed into forested areas, shearing off trees and overriding forest soil layers in its great mid-continen- tal lobes. Wood recovered from such sites is typically spruce with occasional larch (Burns, 1958; Ruhe, 1969; Lowell...
et al., 1990). Beetle assemblages of this age recovered from two sites along the Mississippi River in Missouri and Illinois are similar to those living today in the southern boreal forest of Ontario, whereas beetle assemblages from sites closer to the ice sheet indicate forest tundra and tundra conditions (Schwert et al., 1997). A boreal forest, dominated by spruce but with an admixture of limber pine (Pinus flexilis) of Cordilleran origin, evidently extended across the eastern Great Plains as far west as central Kansas, as suggested by both pollen and macrofossil evidence (Gruger, 1973; Wells and Stewart, 1987; May and Holen, 1993). The Cordilleran component is thought to have extended eastward through gallery forests along rivers.

At 18 ka BP, the Great Basin area of the American Southwest was substantially wetter than it is today, as indicated by the large pluvial lakes Bonneville and Lahontan that occupied now-dry basins (Oviatt et al., 1992). Subalpine forest or subalpine parkland with bristlecone pine (Pinus longaeva), limber pine, and Engelmann spruce (Picea engelmannii), which today are limited to isolated mountain blocks within the Great Basin, along with mammals such as the pika (Ochotona princeps) that are adapted to conifer forest or parklands, occupied areas of present-day steppe and desert and adjacent mountains (Betancourt et al., 1990; Madsen et al., 2001). This greater moisture, which persisted until about 13 ka BP, has been explained as the result of the southward-displaced jet stream (COHMAP Members, 1988). However, sagebrush (Artemisia spp.) steppe persisted in the northern part of the Great Basin and vicinity (Barnosky, 1985; Mehringer, 1985), where the anticyclonic easterly winds prevailed. Phytolith evidence from loess sections reveals the presence of altitudinally arranged steppe with sagebrush (Artemisia) and a variety of
grasses (Stipa spp., Poa spp., and Festuca spp.), grassland dominated by Poa spp. and Festuca spp., conifer parkland with fir and spruce, and finally Artemisia steppe, proceeding from the Columbia River valley to the summit of the Blue Mountains in southeastern Washington (Blinnikov et al., 2002). Tree line in the mountains of the Yellowstone region northeast of the Great Basin and in the Front Range of Colorado was about 500-600 m lower than present and alpine tundra was thus much more extensive than it is today (Baker, 1976; Legg and Baker, 1980). Tree line was presumably still lower farther to the north, thus allowing alpine tundra to extend down slope to the level of the northern Great Basin and the Great Plains closer to the ice sheet in Montana.

There is too little paleobotanical information to know with certainty whether the western plains were covered by grassland or by tundra at the last glacial maximum. Jackson et al. (2000) showed tundra in eastern Texas at this time based on pollen data, which presumably would imply tundra farther north on the plains as well. However, grassland beetles of this age occur in Colorado (Elias and Toolin, 1990) and the fairly widespread occurrence of grassland mammals (Table II; Graham et al., 1987) is more suggestive of grassland than of herb tundra. Opal phytolith evidence points to grassland in southwestern South Dakota by 14 ka BP (Fredlund and Tieszen, 1997), when the regional climate was probably similar to that at 18 ka BP if similar ice-marginal positions are indicative of climate.

It is generally recognized that plant assemblages within all of the biomes at 18 ka BP lack close modern analogues. Thus, although spruce and its familiar associates such as larch and fir may have been abundant in the boreal forest at that time, in some places they occurred in association with elements such as elm, ash, and oak, which are more demanding of warmth. The mammal assemblages were also greatly different from those of today, not only by virtue of the fact that they included many extinct species (Tables II-III), but also because animals that now occupy separate ranges then occurred in association. These different-from-present associations, even if we consider only extant taxa, are usually referred to as "disharmonic" (Baker et al., 1986). However, this term is somewhat misleading, because the disharmony amongst the animals or between the animals and their habitats was not necessarily greater than it is today. It is only since the middle Holocene, by which time migration rates had declined, that very close modern analogues can be found for the plant and animal assemblages. This recent marshalling of modern assemblages is believed to be partly a consequence of the fact that many northern biomes now occupy regions that differ fundamentally from those of today.

### TABLE II

<table>
<thead>
<tr>
<th>Mammal</th>
<th>25-20 ka</th>
<th>19.9-19 ka</th>
<th>17.9-16 ka</th>
<th>15.9-13 ka</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. Steppes, Grassland and Savannah</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mammoth* (Mammuthus spp., M. jeffersoni, M. columbi, M. imperator)</td>
<td>15</td>
<td>4</td>
<td>5</td>
<td>8</td>
</tr>
<tr>
<td>Camel* (Camelops hesternus)</td>
<td>9</td>
<td>2</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Bison (Bison spp., B. latifrons*, B. caucasicoms*, B. occidentalis*)</td>
<td>7</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Horse* (Equus spp., E. conversidens)</td>
<td>6</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Prairie dog (Cynomys spp., C. ludovicianus)</td>
<td>5</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Ground squirrel (Spermophilus spp., S. parryii, S. richardsonii)</td>
<td>4</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Pocket gopher (Geomys bursarius)</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>B. Wooded and Tundra areas</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mammoth* (Mammuthus spp., M. primigenius, M. columbi)</td>
<td>3</td>
<td>1</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>Mastodon* (Mammut americanum)</td>
<td>10</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Woodland muskox* (Bunothrium bombifrons)</td>
<td>2</td>
<td>2</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>Elk-moose* (Cervus elaphus ssp)</td>
<td>5</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Caribou (Rangifer tarandus)</td>
<td>1</td>
<td>5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Short-tailed bat* (Uroderus simus)</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Dna wolf (Canis dirus)</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Wolf (Canis lupus)</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ground squirrel (Spermophilus spp., S. parryii, S. richardsonii, S. tridecemlineatus)</td>
<td>5</td>
<td>1</td>
<td>2</td>
<td>9</td>
</tr>
<tr>
<td>Bog lemming (Synaptomys spp., S. borealis, S. cooperi)</td>
<td>2</td>
<td>2</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>Tundra lemming (Zicrostonyx spp., D. torquatus)</td>
<td>6</td>
<td>1</td>
<td>6</td>
<td>3</td>
</tr>
<tr>
<td>Vole (Microtus spp., M. munni, M. montanus, M. pennsylvanicus, M. townsendi, M. xanthognathus)</td>
<td>10</td>
<td>3</td>
<td>18</td>
<td>19</td>
</tr>
</tbody>
</table>
in radiation, seasonality, and daylight regimes from those previously occupied, and partly the result of the differing abilities of individual plant species to shift their ranges in response to climate change. Hence, one may either view sub-recent to ancient biome compositions as differing from "normal" and "harmonious" modern biomes, or one may view modern biome compositions as the rather arbitrary and transient results of displacements during the twenty or so glacial-interglacial cycles of the Quaternary.

From pollen data alone, a plant community dominated by grass (Gramineae), sage (Artemisia spp.), and sedge (Cyperaceae) occupied Beringia at 18 ka BP. Palynologists usually interpret this assemblage as representing herb tundra (Rampaton, 1971; Matthews, 1974a, 1974b; Colvinaux, 1981; Cwynar, 1982; Agar and Brubaker, 1985; P. Anderson, 1985, 1988b; P. Anderson et al., 1988; Esseen and Colvinaux, 1990; Edwards and Baker, 1994; Agar, 2003). Survival of small populations of spruce (probably white spruce), poplar and tree birch in eastern Beringia is possible based on the pollen record (Brubaker et al., 2005). Plant macrofossils of full-glacial age recovered from Beringian sites are typical tundra plants (Goetcheus and Birks, 2001; Zazula, 2003) representing a variety of soil moisture conditions, with willow being the only identifiable wood. Nevertheless, numerous large mammal fossils, especially of woolly mammoth (Mammuthus primigenius), Yukon horse (Equus lambei), and steppe bison (Bison priscus), indicate that this biome was sufficiently productive to support herds of these grazers (Table III; Burke and Cinq-Mars, 1996; Guthrie, 2003, 2006). In contrast, modern tundra can support only caribou (Rangifer tarandus) and muskox (Ovibos moschatus), neither of which relies on grass. For this reason, vertebrate palaeontologists have proposed that eastern Beringia then supported a biome, termed "steppe tundra" or "mammoth steppe," which has no modern biome-level analogue (Guthrie, 2001). Use of the term herb tundra herein is not meant to convey a pervasively wet soil condition nor a biome too unproductive to support the large grazers that evidently lived there. Nevertheless, in much of the High Arctic today, plant cover is more limited by moisture and nutrient availability than by temperature (Edlund, 1992).

The so-called productivity paradox of full glacial Beringia may have been resolved by the analysis of Zimov et al. (1995). They proposed that the change from a more grass-dominated tundra (or steppe) of full-glacial Beringia to the moss-sedge-dominated tundra of postglacial time is the result of megaherbivore extinction, rather than of climate change. Essentially, hoof trampling and grubbing militates against survival of fragile mosses, whereas grasses are not only resistant to trampling because they are deep rooted but also because they transpire much more water and thus reduce soil moisture, further promoting grasses over mosses and wet-ground sedges. Grass survival was also favoured, and moss survival disadvantaged, by widespread loess accumulation, as was characteristic of eastern Beringia (Pévé, 1975). Abundant grasses, being nearly an order of magnitude more nutritious and being less chemically defended from grazing than tundra sedges, ensured the viability of grazing herds. In this view, both Beringian megaherbivore extinction and postglacial tundra evolution resulted from overkill by Paleoindians and Holocene sedge-moss-willow tundra may be seen as a geologically unique anthropogenic biome. Zimov's hypothesis is a reason to apply caution in seeing all Late Wisconsinan botanical changes as being strictly climate forced. On the other hand, only the most general support for it can be drawn presently from the Beringian archaeological record (West, 1996; Dixon, 2001; Yesner, 2001; Guthrie, 2006).

14 ka BP

Although some ice-marginal recession had occurred in the southeast, the ice sheets at 14 ka BP were still in near-maxi

<table>
<thead>
<tr>
<th>Mammal</th>
<th>25-20 ka</th>
<th>19.9-18 ka</th>
<th>17.9-16 ka</th>
<th>15.9-13 ka</th>
</tr>
</thead>
<tbody>
<tr>
<td>Horse* (Equus spp., E. lambei)</td>
<td>33</td>
<td>28</td>
<td>11</td>
<td>24</td>
</tr>
<tr>
<td>Bison* (Bison spp., B. priscus)</td>
<td>29</td>
<td>7</td>
<td>5</td>
<td>12</td>
</tr>
<tr>
<td>Mammoth* (Mammuthus spp., M. primigenius)</td>
<td>32</td>
<td>24</td>
<td>16</td>
<td>50</td>
</tr>
<tr>
<td>Saiga antilope (Saiga tatarica)</td>
<td>1</td>
<td>3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Woodland muskox* (Boscotherium tombul/rons)</td>
<td>3</td>
<td>2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tundra muskox (Ovibos moschatus)</td>
<td>1</td>
<td>2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Caribou (Rangifer spp.)</td>
<td>1</td>
<td>3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dall sheep (Ovis dalli)</td>
<td>4</td>
<td>3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Short-tailed bear* (Arctodus simus)</td>
<td>4</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>American lion* (Panthera atrox)</td>
<td>2</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wolf (Canis lupus)</td>
<td>2</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grizzly bear (Ursus arctos)</td>
<td>2</td>
<td>11</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ground squirrel (Spermophilus spp., S. parryi)</td>
<td>11</td>
<td>2</td>
<td>2</td>
<td>8</td>
</tr>
<tr>
<td>Lemming (Dicrostonyx torquatus)</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
</tbody>
</table>

*Extinct or extirpated taxa are marked with an asterisk.
mal configurations (Fig. 2). Indeed, parts of the southwestern ice margin were at their most advanced positions, specifically in Washington State, South Dakota, and Iowa. The ice lobe in Iowa overrode ground supporting spruce, larch, and hemlock at this time (Ruhe, 1969, 1983; Bettis et al., 1996). The ice lobe in the Puget Sound of Washington displaced Sitka spruce (Porter and Swanson, 1998) and cedar re-invaded quickly after ice recession by 13.6 ka BP (Porter and Carson, 1971). Both these advances are indicated by dated wood and they suggest that the ice contacted a forest similar to the northern part of the present coast forest.

Despite these ice advances in the southwest, warming is indicated in the southeastern periglacial region. The boreal forest, forest tundra, and shrub tundra (Spear and Miller, 1976; Watts, 1979; Gaudreau and Webb, 1985) had advanced northward in the mid-continent to New England region. Newly formed ice-marginal herb tundra was dominated by sedge everywhere from Minnesota eastward. The shrub tundra along the Atlantic seaboard was dominated by shrub birch everywhere except in the south, where alder (Alnus spp.) and juniper (Juniperus spp.) were the most common shrubs. Spruce was the chief tree component of forest tundra, boreal forest, and boreal parkland at all sites known from this time; the main reported associate trees were fir (probably Abies balsamea), jackpines, birch (probably Betula papyrifera), larch, alder, and ash. Warming is also indicated by the development of a mixed forest of blue oak (Quercus douglasii) and digger pine (Pinus sabiniana) with Douglas fir (Pseudotsuga menziesii) in the coastal range of California before 14 ka BP (Adam et al., 1981).

Development of shrub tundra with dwarf birch (Betula glandulosa) in the Bering Strait lowlands of Beringia indicates warming there at 14 ka BP (Ager, 1983; Anderson, 1985; Elias...
et al., 1996). Guthrie (2001) has proposed that this lowest part of eastern Beringia hosted a moister vegetation assemblage throughout the last glaciation, referring to the region as Beringia’s ‘mesic buckle.’ Although it does not appear to have been warm enough to support shrub birch prior to 14 ka BP, it may have supported a more mesic herb tundra community, as opposed to steppe, at that time, as is required by the long-held concept that Beringia served as a major refugium from which mesic tundra plants dispersed during the postglacial (Hultén, 1937). Shrub tundra establishment indicates that warming and moistening occurred at high latitudes, not just at low latitudes, early in the process of global deglaciation. If dwarf birch did not survive the last glacial maximum in Beringia, it probably arrived at this time from Siberia. The three dominant grazers of eastern Beringia, horse, bison and mammoth, remained abundant (Table III; Guthrie, 2006).

EARLY DEGLACIATION (13-11 KA BP)

This period starts with the onset of more rapid recession of southern ice margins and ends with the onset of the Younger Dryas cold interval.

13 ka BP

By this time, herb tundra had been nearly eliminated in the southeast (Fig. 3). As before, the few sites representing herb tundra from Minnesota eastward were dominated by sedge. Sage dominated the newly formed herb tundra in Alberta, thus indicating drier conditions there (Mott and Jackson, 1982 [chronology adjusted]; Hiskiman and Schweger, 1991, 1993; Beaudoin et al., 1996; Mandryk, 1996). The sage could have spread from either the grassland or the alpine tundra to the south, and indeed a distinction of herb tundra from periglacial

FIGURE 3. Biomes at 13 ka BP.
grassland is perhaps meaningless here. Shrub tundra with dwarf birch, juniper, and willow had spread into Atlantic Canada as far as southern Newfoundland (Mott, 1975; Mayle et al., 1993; Anderson and Marchpherson, 1994). Macrofossils of Salix herbacea and Dryas spp. – important plants in the modern tundra – have been directly dated to 13.15 ka BP from a site in Maine (Thompson et al., 1999; Ridge et al., 1999). As earlier, this biome included alder at warmer sites in New York and Massachusetts (Ogden, 1963; Ibe, 1982; Maenza-Gmelch, 1997a, 1997b).

The expansion of forest tundra to the ice margin in central and eastern U.S.A. and southern Ontario left little room for herb tundra. Tundra plants – Salix herbacea, Dryas integrifolia, and Vaccinium uliginosum – and forest tundra assemblages of beetles dating just prior to this time are reported from a site near the ice margin in Michigan (Morgan, 1987). Closeness of spruce to the ice margin in Ontario is demonstrated by the presence in till of wood dated at 13.1 ka BP (Gravenor and Stupavsky, 1976). Similarly, white spruce cones dated at 12.51 ka BP have been recovered from glaciomarine sediment in Maine (R. Anderson et al., 1990) indicating the presence of forest tundra (if not forest) close to the ice margin. Meanwhile the boreal forest expanded into newly deglaciated terrain in the southern Great Lakes region and into tundra farther east (Wem, 1977; Davis and Jacobson, 1985; Schwent et al., 1985; Thorson and Webb, 1991; Morris et al., 1993; Petee et al., 1994; Winkler and Sanford, 1995). This forest expansion brought with it, presumably from areas farther south, the spruce-browsing mastodon (Mammut americanum), whose population appears to have increased markedly north of 39° N after 14 ka BP (Tables II and IV). Spruce was the most abundant tree at most sites in the forest tundra, with jackpine appearing in Pennsylvania, Populus in Maine, and ash in Michigan; black ash extends into the southern boreal forest of eastern Canada today. Similarly, spruce continued to dominate at boreal forest sites, with fir as adjunct at nearby

<table>
<thead>
<tr>
<th>Table IV</th>
<th>The most common fossil mammals south and west of the ice sheets at 12.9-10 ka BP. Extinct or extirpated taxa are marked with an asterisk</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mammal</td>
<td>12.9-12 ka</td>
</tr>
<tr>
<td>A. Steppe, Grassland and Savannah</td>
<td></td>
</tr>
<tr>
<td>Mammoth* (Mammuthus spp., M. columbi, M. jeffersoni, M. primigenius)</td>
<td>11</td>
</tr>
<tr>
<td>Horse* (Equus spp., E. conversidens)</td>
<td>2</td>
</tr>
<tr>
<td>Bison (Bison spp., B. antiquus*, B. occidentalis*)</td>
<td>4</td>
</tr>
<tr>
<td>Camel* (Camelops hesternus)</td>
<td>3</td>
</tr>
<tr>
<td>Pronghorn (Antilocapra americana)</td>
<td>2</td>
</tr>
<tr>
<td>Dire wolf* (Canis dirus)</td>
<td>2</td>
</tr>
<tr>
<td>Short-faced bear* (Arctodus simus)</td>
<td>1</td>
</tr>
<tr>
<td>Ground squirrel (Spermophilus spp., S. lateralis, S. richardsoni, S. tridecemlineatus)</td>
<td>2</td>
</tr>
<tr>
<td>B. Forest tundra, Alpine tundra and Tundra</td>
<td></td>
</tr>
<tr>
<td>Caribou (Rangifer tarandus)</td>
<td>3</td>
</tr>
<tr>
<td>Peccary* (Patiognomus spp., Mylohyus spp.)</td>
<td>3</td>
</tr>
<tr>
<td>Bighorn sheep (Ovis canadensis, O. c. catlowensis*)</td>
<td>1</td>
</tr>
<tr>
<td>Grizzly bear (Ursus arctos)</td>
<td>1</td>
</tr>
<tr>
<td>Lemming (Dicrostonyx spp.)</td>
<td>1</td>
</tr>
<tr>
<td>C. Conifer Forest and Conifer Parkland</td>
<td></td>
</tr>
<tr>
<td>Mastodon* (Mammut americanum)</td>
<td>14</td>
</tr>
<tr>
<td>Mammoth* (Mammuthus spp., M. columbi, M. jeffersoni, M. primigenius)</td>
<td>23</td>
</tr>
<tr>
<td>Elk-moose* (Cervus elaphus)</td>
<td>6</td>
</tr>
<tr>
<td>Woodland muskox* (Bovitherium bombifrons, Symbos spp.)</td>
<td>1</td>
</tr>
<tr>
<td>Bison (Bison spp., B. antiquus*, B. occidentalis*)</td>
<td>2</td>
</tr>
<tr>
<td>Caribou (Rangifer tarandus)</td>
<td>2</td>
</tr>
<tr>
<td>Elk (Cervus spp., C. elaphus)</td>
<td>1</td>
</tr>
<tr>
<td>Deer (Odocoileus spp., O. virginianus)</td>
<td>2</td>
</tr>
<tr>
<td>Giant beaver* (Castoroides cheniensis)</td>
<td>1</td>
</tr>
<tr>
<td>Beaver (Castor canadensis)</td>
<td>7</td>
</tr>
<tr>
<td>Muskox (Ondatra zibethicus)</td>
<td>7</td>
</tr>
<tr>
<td>Bear (Ursus americanus)</td>
<td>6</td>
</tr>
<tr>
<td>Vole (Microtus spp., M. pennsylvanicus, M. xanthognathus)</td>
<td>10</td>
</tr>
</tbody>
</table>
half of sites, but spread throughout the extent of the biome. Larch and ash, as components of the boreal forest, seem to have been concentrated in the mid-continent.

Birch shrub tundra had expanded greatly in Beringia by 13 ka BP (Matthews, 1974b; Ager, 1982; Heusser, 1983; P. Anderson, 1988; Esiner and Collioux, 1992; Oswald et al., 1999), but it was still somewhat less extensive than herb tundra. This shrub expansion at the expense of grass, sedge, and sage does not seem to have led to great reduction in the numbers of the large grazing animals (Tables III and V). It may account for a further reduction in the size of Alaskan horses. However, that process was under way by 25 ka BP, at the beginning of the Late Wisconsinan cold stage and prior to both the last glacial maximum and birch expansion (Guthrie, 2003). Numbers of bison appear to have been increasing at this time, which Guthrie (2006) attributes to an increase in availability of willow forage.

A forest, with lodgepole pine and mountain hemlock as vanguards, advanced northward along the Pacific coast very soon after local deglaciation, reaching the Queen Charlotte Islands by 13 ka BP (Hedba, 1983, 1995, 1997; Brown and Hedba, 2002). Coastal shrub tundra occupied the narrow strip of ice-free land from the Queen Charlottes to Cook Inlet in Alaska (Pryor and Sim, 1980; Sirkim and Tuthill, 1987; Mathewes et al., 1993; Hedba, 1995; Hansen and Engstrom, 1996). Conditions in the American Southwest remained similar to those at 14 ka BP.

12 ka BP

It is possible that by 12 ka BP herb tundra was expanding northward from the easternmost parts of the Beringian refugium on Banks, Prince Patrick, and Melville islands (Fig. 4). A sample containing mainly moss and lichen, but with some willow (Salix arctica), from Ellef Ringnes Island was dated at 13.2-19.6 ka at a site in Pennsylvania (Adovasio, 1977). The most common fossil mammals in Beringia at 12.9-10 ka BP. Extinct or extirpated taxa are marked with an asterisk.

<table>
<thead>
<tr>
<th>Mammal</th>
<th>12.9-12 ka</th>
<th>11.9-11 ka</th>
<th>10.9-10 ka</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. Tundra</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mammoth* (Mammuthus spp.)</td>
<td>17</td>
<td>6</td>
<td></td>
</tr>
<tr>
<td>Bison* (Bison spp., B. priscus)</td>
<td>20</td>
<td>18</td>
<td>8</td>
</tr>
<tr>
<td>Horse* (Equus spp., E. ferus/caballus, E. lambei)</td>
<td>9</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Saiga antelope* (Saiga tatarica)</td>
<td>4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dall sheep (Ovis dalli)</td>
<td>1</td>
<td>9</td>
<td>4</td>
</tr>
<tr>
<td>Grizzly bear (Ursus arctos)</td>
<td>3</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Ground squirrel (Spermophilus spp., S. parryi)</td>
<td>3</td>
<td>11</td>
<td>3</td>
</tr>
<tr>
<td>B. Forest Tundra</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Caribou (Rangifer tarandus)</td>
<td>3</td>
<td>9</td>
<td>3</td>
</tr>
<tr>
<td>Elk (Cervus elaphus)</td>
<td>47</td>
<td>14</td>
<td>11</td>
</tr>
<tr>
<td>Moose (Alces alces)</td>
<td>2</td>
<td>19</td>
<td>9</td>
</tr>
<tr>
<td>Beaver (Castor canadensis)</td>
<td></td>
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<td>1</td>
</tr>
</tbody>
</table>

As the large herbivores continued to expand northward, the last glacial stage ended by 10.9 ka BP (Matthews, 1974b; Ager, 1982; Heusser, 1983; Edwards et al., 1983; Edwards and Brubaker, 1986; Billings, 1987; Lozhkin et al., 2001). However, bison, mammoth, saiga antelope (Saiga tatarica), and possibly horse continued to occupy this area, indicating that grasses and other herbs were still sufficiently abundant to support them (Table V). Of these four extinct Beringian large mammals, however, only bison would continue to occupy the region for long after 12 ka BP, perhaps indicating that self-maintenance of the steppe tundra by herbivores had declined to a critical point (see above and Zimov et al., 1995). Alternatively, herb reduction due to competition, winter snow depth, or icing events due to winter rainfalls were then becoming critical in limiting access to forage. The saiga antelope is particularly intolerant of snow deeper than 20 cm and of wet ground (Harington and Cinq-Mars, 1995). The most remarkable change in Beringian biome composition was the sudden appearance of elk (Cervus elaphus) shortly after 13 ka BP and their great population expansion about 12.5 ka BP, when the first moose (Alces alces) also may have arrived in the region (Guthrie, 2006). Moose are not common in tundra areas today and in Beringia they may have relied on browsing of willow and dwarf birch. Guthrie (2006) suggested that both elk and moose might have arrived in eastern Beringia at this time along with humans from Eurasia. This suggestion is supported by the absence of direct dates on these taxa south of the ice sheets prior to 10 ka BP. Note, however, that Cenius has been associated with radiocarbon dates on charcoal of 13.2-19.6 ka at a site in Pennsylvania (Adovasio, 1977).

By 12 ka BP, an ice-free corridor had opened between the Cordilleran and Laurentide ice sheets, with herb tundra in its place.
northern part (Szeicz et al., 1995), birch shrub tundra in its southern part (White et al., 1985; Mandryk, 1996), and grass-land still farther south (Klassen, 1994). Meanwhile, shrub tun-дра had extended into newly deglaciated parts of New England and Atlantic Canada. Amongst the dwarf trees, this biome was characterized by birch and willow throughout, though juniper occurred as far north as Newfoundland, alder was established in Nova Scotia, and soapberry (Shepherdia canadensis) was present in New Hampshire. Forest tundra extended through parts of that region that were deglaciated earlier, reaching southwestern New Brunswick (Whitehead et al., 1989; Spear et al., 1994; Jetté and Mott, 1996; Miller and Elias, 2000). Plant macrofossils from glacial lake sediments in Vermont dating at 12.35 ka BP reveal the presence of diverse arctic-alpine plants that must have contributed to the forest tundra understory. These include willows (Salix herbacea and S. reticulata), arctic avens, moss campion (Silene acaulis and S. involucrata), mountain sorrel (Oxyria digyna), saxifrages (Saxifraga opposi- tillia and S. aizoides), and arctic blueberry. Several of these survive as relicts today in patches of tundra on the Appalachian Mountains (Miller and Spear, 1999). Amongst the trees, spruce appears to have been the most abundant in the western part of the biome, giving way to poplar and birch in the more oceanic regions of Maine and New Brunswick. By 12 ka BP, maximum lake surface temperatures, as inferred from chironomids, close to the residual ice cap in the shrub tundra of coastal southwestern Nova Scotia, were about 18 °C (Wilson et al., 1993), implying a mean July air temperature of about 14 °C (I. Walker, personal communication, 2004), which is certainly capable of supporting forest. Similarly, July air tem- peratures inferred from fossil beetles at several sites in Nova Scotia and New Brunswick had risen to within 2-4 °C of mod- ern values by 12 ka BP, whereas winter temperatures were 12-13 °C colder than present (Miller and Elias, 2000).
LATE QUATERNARY VEGETATION HISTORY OF NORTHERN NORTH AMERICA

At 12 ka BP, boreal forest and forest tundra fringed most of the southern margin of the ice sheet, with forest forming a great belt extending from south-central Saskatchewan (Pitcher and de Vries, 1964; Terasmae, 1973) and Kansas (Watts, 1983) to the Atlantic Ocean (Newby et al., 2000; Shuman et al., 2001) and occupying vast areas that are today grassland. As before, spruce was the most abundant tree at most sites, though jackpine had come to prominence in parts of New York and Pennsylvania. Larch and ash were common in areas of Minnesota, Iowa, Wisconsin, Illinois and Indiana. Fir was widespread, except perhaps in Minnesota and regions north and west of there. The mastodon evidently continued its expansion in this biome (Table IV), probably most abundant amongst the large mammals (note that the larger number on dates associated with Mammuthus are due to multiple datings at a single site). Elk-moose (Cervus canadensis) and woodland muskoxen (Bootherium bombifrons) also occupied the coniferous forest, while mammoths (Mammuthus jeffersonii, M. columbi, M. primigenius) and bison occupied forest openings and areas of boreal parkland.

Mixed forest had expanded northward nearly to Lake Erie (Shane, 1987, 1989; Shane and Anderson, 1993) and into southern New England (Petet et al., 1994; Maanzu-Gmaci, 1997a, 1997b). At most sites this forest retained substantial amounts of spruce and (or) pine (probably white pine), but ash, ironwood, elm, oak, and – in the east – beech were significant components. Indications of deciduous forest in Ohio and Indiana at this time may suggest very early establishment of more temperate vegetation at favourable sites or, more probably, problems with radiocarbon dating in this hardwood region (Shane, 1987; Shane and Anderson, 1993).

Steppe, still dominated by sagebrush, had expanded in the Great Basin and Death Valley of the American Southwest (Adam, 1967; Mehriinger, 1977) and northward to the Canadian border, where grass and sedge were also significant (Adam, 1967; Mehringer, 1977) and northward to the Great Basin and Death Valley of the American Southwest region (Shane, 1987; Shane and Anderson, 1993). Problems with radiocarbon dating in this hardwater and Indiana at this time may suggest very early establishment of more temperate vegetation at favourable sites or, more probably, problems with radiocarbon dating in this hardwood region (Shane, 1987; Shane and Anderson, 1993).

At 11 ka BP, birch shrub tundra continued to dominate the Alaska to Mackenzie Delta region, which was newly separated from Siberia by submergence of Bering Strait (Fig. 5). The insipient appearance of patches of forest tundra in that region, with the only tree evidently being aspen or poplar (Populus spp.; provided that none of the birch pollen is from true birch), is indicated both by pollen records (Ager, 1983; Brubaker et al., 1983; Spear, 1983; P. Anderson, 1988; Spear, 1993; Hu et al., 1996) and by a few wood macrofossil sites, including one that indicates the presence of beaver (Castor canadensis) (Hicks, 1983, 1984; West, 1981). Being so far from the main continental treelines at that time, these forest patches invite speculation that birds, arriving either from Siberia or North America, dispersed the poplar seeds, though expansion from cryptic refugia within Beringia has also been proposed (Brubaker et al., 2005). Nevertheless, this date places the beaver in an odd environmental context (again provided that none of the birch pollen is from local tree birch), because this animal’s range does not extend beyond latitudinal treeline today (Barfield, 1977). Two of the wood macrofossil sites are north of the present poplar range, which suggests that the climate of Alaska was then warmer than present (Kaufman et al., 2004). Alternatively, both the lake sediment and wood dates may be erroneously old (the oldest poplar date has a large standard error: 11 800 ± 750 (UCLA-1869)) and poplar arrival may date closer to 10 ka BP. As mentioned, mammoth and horse had probably disappeared from Beringia by 11 ka BP, perhaps because of the wetter tundra conditions (Zimov et al., 1995), but mammoths may have succumbed to the newly arrived Paleoindian hunters, who had moved into the area by 11.7 ka BP or earlier (Weiler, 2001), though direct evidence of this cause is lacking. However, Guthrie (2003) argued that horses were extinct in Alaska by 12.5 ka BP before the earliest proven (or currently accepted) arrival of man, and that extinction may have been brought about by the same pressures that caused the body-size reduction of the horses in the preceding millennia. Whatever the cause, this regional extinction left bison, elk, mule, caribou and Dall sheep (Ovis dalli) prominent among the large grazers and browsers along with the omnivorous grizzly bear.
Newfoundland, eight sites reverted from shrub tundra to herb tundra by about 11 ka BP (T. Anderson and Lewis, 1992; T. Anderson and Macpherson, 1994) and remaining shrub tundra was characterized by birch and willow amongst the shrubs. Birch and willow were also the most important shrubs west of the Gulf of St. Lawrence, but alder also survived there. Macrofossil records for this time include arctic avens in herb tundra of western Newfoundland (GSC-1350), willow (Salix herbacea), arctic avens, mountain sorrel, moss campion, and bladder campion (Melandrium affine) in the shrub tundra of Québec (Mott et al., 1981; Govare and Gangloff, 1989), and Salix herbacea in Vermont (Miller and Spear, 1999). Despite that impoverished plant cover prior to the onset of Younger Dryas cooling, the maximum summer surface temperatures of small lakes in Maine, southern New Brunswick, and southwestern Nova Scotia—as indicated by chironomids—had already risen to modern levels (20-25 °C; Wilson et al., 1993; Levesque et al., 1997). Insect remains similarly indicate attainment of modern summer temperatures by 11 ka BP (Miller and Eliaas, 2000). These temperatures are sufficient to support a mixed forest, and they were as high as those experienced during the post-Younger Dryas interval of forest cover. Presumably, therefore, the lack of extensive forest cover at 11 ka BP was due to inadequate migration time in tundra areas and inadequate forest densification time in areas of forest tundra. Farther west in New Hampshire, where lowland sites were already covered with boreal forest at 11 ka BP (sites presently in mixed forest), maximum lake surface temperatures had risen to about 18 °C (Cwynar and Spear, 2001). The boreal forest at 11 ka BP extended from eastern Alberta (Schweger, 1989) and the Dakotas (McAndrews et al., 1967; Watts and Bright, 1968; Radle et al., 1989; Laird et al., 1996) to the Atlantic Ocean, reaching the ice margin from the Ottawa Valley westward (Anderson, 1985). A partial tree...
cover mainly of poplar with spruce and birch extended westward through a boreal parkland to the mountain front in northern Alberta (Lichti-Federovich, 1972; White et al., 1979; Vance et al., 1989; Schweger, 1990; Hickman and Schweger, 1991). West of Minnesota, the boreal forest was characterized by spruce with poplar, juniper, or birch growing where the forest was more open. In Minnesota, Iowa, Wisconsin, Illinois, and Indiana, assemblages were more diverse. Although spruce was prevalent throughout this region, larch, fir, and ash were important along with birch and poplar. Spruce seems to have been the most common tree closest to the ice margin in Ontario and Michigan, while aspden increased southward to characterize some sites in Pennsylvania. Assuming that radiocarbon-dated fossil abundance reflects population size, the mastodon continued its expansion in the boreal forest between 12 and 11 ka BP, as did the elk-moose, the second most commonly dated mammoth fossil (Table IV). Alternatively, human hunting may have increased the numbers of animals dying or being cached at sites of good bone preservation, such as in small ponds and bogs, where finds of these fossils are typically located (Fisher, 1995). Paleoindians using fluted, lanceolate, projectile points had spread throughout most areas south of the ice sheets by 11 ka BP and possibly by 11.5 ka BP (Ellis et al., 1998; Canadian Archaeological Radiocarbon Database, 2005). Many archaeological sites of this period, few of which are radiocarbon dated, are located on the relict shorelines of the glacial Great Lakes (Jackson, 1983). Spruce forests and parkland surrounded these sites; none are known from areas shown here as occupied by tundra.

To the south, mixed forest formed a latitudinal belt from Illinois to the Atlantic (Watts, 1979). It seems to have formed by migration of elm, ironwood, and oak into the fringes of the boreal forest of the mid-continent and by an increase in the abundance of the already established ash there, and by northward migration of white pine and oak into the boreal fringes in Pennsylvania and New York while established birch populations there expanded.

Open ground in the form of grassland and tundra extended from 12 to 11 ka BP across the western plains and through the northern Cordillera to Alaska, interrupted only by the boreal parkland in northern Alberta (Watts and Wright, 1986; Bradbury, 1980; MacDonald, 1986; Martin and Lennson, 1986; Klassen and Vreken, 1987; Barnosky et al., 1987). This interval probably offered the greatest opportunity for postglacial northward dispersal of southern herbs, as invoked by Strong and Hills (2003) to account for northern disjuncts of several species that occur in the region today as far north as Peace River, but whose main distribution extends no farther north than Montana. Mammoths (Mammuthus columbi, M. jeffersonii) and extinct forms of bison (Bison occidentalis, B. antiquus) were widespread on the grasslands along with horse (Equus conversidens), camel (Camelops hesternus), short-faced bear (Arctodus simus), and pronghorn (Antilocapra americana) (Table IV). The distribution of fluted projectile points in western Canada indicates that Paleoindians occupied these recently deglaciated landscapes (Jackson and Duk Rukin, 1996).

The American Southwest remained substantially moister than today, but drier than during full-glacial times (references previously cited). By 11 ka BP, treeline had risen so that subalpine forest replaced alpine tundra at some sites, although alpine tundra remained in some areas. In Colorado, Wyoming, Montana, and Idaho, the subalpine forest was characterized by Engelmann spruce, subalpine fir, white pine, lodgepole pine, and limber pine, with birch and alder in places (Mehring et al., 1977; Carrera, 1995; Fall et al., 1995; Feller et al., 1997). Douglass fir had reached the Rocky Mountains of Montana as a minor component of the subalpine forest (Brant, 1980).

The coast forest seems to have changed little in extent between 12 and 11 ka BP; though lodgepole pine forest reverted to shrub tundra on the northern Queen Charlotte Islands and mountain hemlock was beginning a resurgence at lowland sites in lower British Columbia and Washington at the beginning of Younger Dryas time (Mathewes, 1993). Western hemlock, silver fir (Abies amabilis) and Douglas fir had reached Vancouver Island by 11 ka BP (Heussner, 1983; Hebda, 1987; Brown and Hebda, 2003). The Alaska Panhandle seems to have been mainly covered in shrub tundra with patches of herb tundra (Mann, 1983), although lodgepole pine had reached favourable sites near to 60° N by 10.7 ka BP (Cwynar, 1990; Peteet, 1991) or even by about 12 ka BP (Hansen and Engstrom, 1996). Macrofossils place lodgepole pine at Glacier Bay (58.9°N) and Pleasant Island (58.3°N) by 10.9 ka BP and spruce cones at Glacier Bay date to 11.1 ka BP (Goodwin, 1988). Thus, the true vegetation cover of southeastern Alaska at 11 ka BP may have been a mosaic of forest and tundra irresolvable at small scale. Temperatures were still about 3°C below present in southwestern British Columbia at 11 ka BP (Walker and Pellatt, 2003).

MIDDLE DEGLACIATION (10.9-7.6 KA BP)

The beginning of this interval coincides with the onset of Younger Dryas cooling, which terminated about 10 ka BP. Several pollen stratigraphic studies have identified regional responses of vegetation to this cooling. Cooling was most pronounced in the Canadian Maritimes, where maximum lake-surface temperatures dropped by as much as 20°C from pre-Younger Dryas levels (Levesque et al., 1997) and where forest tundra reverted to shrub tundra and shrub tundra to herb tundra (Mott et al., 1986; Mott and Stiea, 1993). Younger Dryas cooling has also been recognized in the northeastern states (Peteet et al., 1990), and in the mid-continent (Shane, 1987) from resurgences of the pollen of cold-tolerant trees such as spruce. Possible responses in British Columbia and Washington (Mathewes, 1993; Mathewes et al., 1993) include a reversion from forest to tundra on part of the Queen Charlotte Islands and increases in cold-tolerant mountain hemlock in the Fraser Valley and on the Olympic Peninsula. In southeast Alaska the response resembles that on the Queen Charlotte Islands (Engstrom et al., 1990), whereas in southwest Alaska birch shrub tundra reverted to herb tundra (Hu et al., 1995). However, these Pacific region records of Younger Dryas cooling show a much less marked response than those around the North Atlantic. Unfortunately these responses are not fully captured at the coarse time resolution of the present map sets and probably not by some of the pollen records. However, the key ice sheets responded by pausing or...
re-advancing in many places, though without overall increase in area of ice cover (Dyke, 2004). The middle deglaciation interval ends with the deglaciation of Hudson Bay at 7.6 ka BP. It is thus an interval of still-large remnant ice sheets, large enough to strongly affect the continental climate and for the pace and pattern of deglaciation to largely dictate the pattern of plant colonization.

10 ka BP

By 10 ka BP, the herb tundra of the Canadian arctic islands was sufficiently rich to support muskoxen, which had advanced at least as far north as Banks Island by 10.6 ka BP or else had survived there throughout the last glacial maximum (Maher, 1968). Forest tundra, still involving mainly poplar species and possibly some tree birch and including sites north of the present range of poplar, had expanded greatly in the Alaska-Mackenzie region (Fig. 6; Colinvaux, 1981; Ritchie, 1984; Slater, 1985; Edwards and Brubaker, 1986; Anderson et al., 1990; Cwynar and Spear, 1991; Keenan and Cwynar, 1992; Hu et al., 1993; Edwards and Baker, 1994), which was otherwise occupied by birch shrub tundra. The northwestern forest tundra evidently remained unconnected to the continental forest cover. This disjunct distribution may indicate that it is here placed 500-1000 years too early in time due to dating inaccuracies (Kaufman et al., 2004), or alternatively that the first trees (poplar and birch) expanded in eastern Beringia from cryptic refugia (Brubaker et al., 2005) or arrived from Siberia. The birch shrub tundra extended southward through most of the Yukon (Wang and Geurts, 1991; Cwynar and Spear, 1995) and probably into northern British Columbia, where alder was present as well (Miller and Anderson, 1974; Spear and Cwynar, 1997). There are few paleoecological sites in the latter region for this time. Evidence of boreal parkland...
with poplar in the southwestern Yukon at 10 ka BP (Cwynar, 1988; Lacourse and Gajewski, 2000) may indicate inland extensions of the adjacent coastal forest tundra or that poplar forest tundra was more extensive in the Northwest than shown. Alternatively, these outlier sites may indicate anomalously old radiocarbon dates.


In newly deglaciated areas of the Ottawa Valley and westward, the forest biomes shifted northward more quickly, apparently limited only by the rate of ice recession (Terasmae, 1980; T. Anderson, 1987; Bennett, 1987; Richard and Larouche, 1980; T. Anderson and Lewis, 1992). At 10 ka BP, the extent of the eastern boreal forest was being extended by the northward expansion of the mixed forest accompanied by the migration north of 39° of deciduous forest in the mid-continent (King, 1981; Baker et al., 1992) and in the Southeast (Watts, 1979). Nevertheless, in Ohio and vicinity, the spruce forest had expanded southward into what was earlier mixed forest, presumably as the result of Younger Dryas cooling (Shane, 1987, 1989). West of Lake Michigan, spruce- and jackpine-dominated forests were about equally common, with larch and fir important in the former and birch in the latter. The forest was similar in Michigan and Ohio, but jackpine-dominated forests were somewhat less common there. In Ontario, spruce was most abundant with white birch next in appearance.

The western part of the boreal forest was reduced due to northward expansion of the boreal parkland biome, which presumably reflects warming and (or) drying (Mott, 1973). Spruce appears to have been more prominent in the parkland than it is today, though poplar, birch and willow were also present (Lichti-Federovich, 1972; Mott and Christiansen, 1981; Vance, 1986). The western boreal forest at this time was an isolated disjunct that was separated from its eastern counterpart by parkland and by glacial Lake Agassiz. Here again white and black spruces were most abundant with white birch next in importance (Lichti-Federovich, 1970; Hutton et al., 1994; McLeod and MacDonald, 1997).

Warming and drying also characterized the western regions at 10 ka BP. Warming in the American Rockies is indicated by a rise of tline, replacing alpine tundra with subalpine forest of Engelmann spruce, subalpine fir, and white-bark pine on the Yellowstone Plateau of Wyoming and vicinity (Baker, 1983; Gennett and Baker, 1986; Whitlock, 1993; Whitlock and Bartlein, 1993) and in the mountains of northwestern Utah (Mehring et al., 1971). In the Colorado Front Range, tline had been depressed during the Younger Dryas interval (Reasoner and Jodry, 2000) but was recovering by 10 ka BP (Short, 1985). Similarly tline with lodgepole and whitebark pine, spruce, and fir rose to near present elevations in the central and southern Canadian Rockies at this time (Kearey and Luckman, 1983; Hills et al., 1985; Reasoner and Hickman, 1989; Beaudoin and King, 1990; White and Osborn, 1992; Osborn et al., 1995). Drying and warming in the American Southwest is echoed in the expansion of steppe at the expense of subalpine forest in the Great Basin region primarily of Idaho (Baker, 1976; Cotter et al., 1986), by expansion of steppe into the Okanagan region of British Columbia (Hebda, 1982; Heinrichs et al., 1999, 2001) and by the establishment of an interior forest biome characterized by Douglas fir replacing subalpine forest (Heusser, 1985; Hansen and Easterbrook, 1974; Barnosky, 1981; Cwynar, 1987; McLachlan and Brubaker, 1994). Drier and warmer conditions in southwestern British Columbia and Washington – 3-4 °C warmer than present by 10 ka BP according to chironomid assemblages (Walker and Pellatt, 2003) – allowed a forest of more “interior” composition (with more Douglas fir) to expand at the expense of coast forest. Central British Columbia at this time was covered by a conifer forest of mainly lodgepole pine with increasing Slics spruce near the coast (Gottefeld et al., 1991; Hebda, 1995). This pioneer forest was presumably derived from the subalpine forest, which had occupied the Cordillera south of the ice sheet at 11 ka and earlier. Drying and warming from the American Southwest to southwestern British Columbia and continued warming and moistening of Alaska is compatible with the northward shifting of the landfall of the jet stream, which perhaps awaited extensive deglaciation of the Cordillera region. The great width of the tundra zone in the Canadian Maritimes is compatible with the concept of sustained northeasterly winds there caused by the persisting glacial anticyclone, which would have opposed wind dispersal of tree seeds into the region. Temperatures in this region were not to recover fully from Younger Dryas cooling until about 9.6 ka BP (Lovejoy et al., 1997), implying that reduced heat transport in the Gulf Stream also continued to play a role in regional cooling if the thermohaline circulation mechanism for Younger Dryas cooling is correct (Broecker et al., 1989). The lack of a tundra zone west of the Ottawa Valley suggests that direct periglacial cooling was less acute there than farther east and that temperate air masses strongly overrode the ice margin. Intuitively, one expects the development of the large glacial lakes, starting about 11 ka BP, to have strongly affected the mid-continental climate. However, regional circulation model experiments indicate that the lakes essentially functioned as extensions of the ice sheet because of their low surface water temperatures and the expenditure of heat in the water on the melting of glacier ice and ice bergs (Hostetler et al., 2000).

During the millennium ending at 10 ka BP – the interval generally acknowledged to have witnessed the terminal Pleistocene mammal extinction in North America, or at least its culmination – dryland grazers were still dominated by extinct forms of bison and by mammoths and horses (Table IV). There is nothing unusual about the record of faunal remains to suggest that extinction was caused by Younger Dryas cooling at 11 ka BP. Dated fossil specimens are as abundant in the 10.0-10 ka interval as in the preceding...
interval and they are not clustered at the beginning of the interval. There was no apparent shrinkage of available grazing habitat—indeed grassland and steppe expanded between 11 and 10 ka BP—and it is not clear that any cooling event occurred on the grasslands themselves during the Younger Dryas. Similarly, mastodon remained by far the most commonly dated large mammal in the forested region during this interval, along with its familiar associates, the elk-moose and giant beaver (Table IV). Bison and mammoth continued to occupy forest openings and boreal parklands. Hence, unless all of the relatively late radiocarbon dates on the extinct taxa are erroneously young, the extinction event in the southern regions coincides with the end of the Younger Dryas interval; i.e., with the onset of warming. The radiocarbon assays of concern (about 85) are nearly evenly split amongst conventional dates on bone collagen, AMS dates on bone collagen or extracts thereof, and conventional dates on associated wood or charcoal. There is no obvious reason for discarding all of them. It was also at about 10 ka BP that aboriginals in eastern and central North America changed the styling of their stone points from fluted projectile points to non-fluted forms that may have been used more commonly as knives, and shortly thereafter to side- and corner-notched projectile points (Ellis et al., 1998). Possibly such changes reflect the changes of available faunal resources pursuant to extinction.

9 ka BP

By 9 ka BP, willow had spread through the herb tundra of much or all of the then-ice-free High Arctic (Fig. 7). Today it and allied woody shrubs (e.g., Cassiope tetragona, Dryas integrifolia, Vaccinium uliginosum) extend to all but the northwestern fringe of the Canadian Arctic, where July mean temperature remains below 3 °C (Edlund and Alt, 1989). The oldest dated

FIGURE 7. Biomes at 9 ka BP.

Les biomes en 9 ka BP
53.2
far north along the Labrador coast, with alder reaching at least east between 10 and 9 ka BP. Birch shrub tundra extended today, though four other buttercup species do occur.
on Bathurst Island (Blake, 1974). It is apparently absent there on.
Ranunculus trichophyllus
diverse at 9 ka BP than it is today. Seeds of the buttercup, Salix herbacea evidently arrived there at 8.8 and 10.8 ka BP, respectively. There is also an indication that the forb component of the High Arctic tundra may have been more diverse at 9 ka BP than it is today. Seeds of the buttercup, Ranunculus hexaphyllus, are found in peat dated 9.21 ka BP on Bathurst Island (Blake, 1974). It is apparently absent there today, though four other buttercup species do occur.

An orderly northward shifting of biomes occurred in the east between 10 and 9 ka BP. Birch shrub tundra extended far north along the Labrador coast, with alder reaching at least east between 10 and 9 ka BP. Birch shrub tundra extended far north along the Labrador coast, with alder reaching at least east between 10 and 9 ka BP. Birch shrub tundra extended far north along the Labrador coast, with alder reaching at least east between 10 and 9 ka BP.

The western boreal forest had expanded remarkably by 9 ka BP. It advanced northward into forest tundra along the Mackenzie Valley (MacDonald, 1987a), northwestward into forest tundra through northern British Columbia (MacDonald, 1991; Pisarcik et al., 2003) and central Yukon (Cwynar, 1988; Keenan and Cwynar, 1992; Cwynar and Spear, 1995), reaching as far as central Alaska (Hsu et al., 1993). White and black spruce both migrated early and white birch was a significant compo-

net at many sites. Oddly, the forest tundra in the Alaska-
Mackenzie region expanded only modestly between 10 and 9 ka BP. The boreal forest probably also extended southward into parkland reaching near to its modern southern limits in Alberta (Hickman and Klarer, 1981). Hazelnut (Corylus spp.) made a limited appearance in the Alberta parkland about this time, not appearing in pollen records again after 8 ka BP (Lichten-Fedorchich, 1970; note, however, that hazel pollen is difficult to identify and the shrub is common in the southern boreal forest now. A. Beaujot, personal communication, 2005). However, the boreal parkland lost area to grassland in Saskatchewan (Kupsch, 1960; Ritchie and de Vries, 1964; Mott, 1973; Mott and Christansen, 1981) and in Manitoba (Ritchie, 1967, 1969, 1976), where the grassland extended to Lake Agassiz, thus leaving the western boreal forest still dis-

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The western boreal forest had expanded remarkably by 9 ka BP. It advanced northward into forest tundra along the Mackenzie Valley (MacDonald, 1987a), northwestward into forest tundra through northern British Columbia (MacDonald, 1991; Pisarcik et al., 2003) and central Yukon (Cwynar, 1988; Keenan and Cwynar, 1992; Cwynar and Spear, 1995), reaching as far as central Alaska (Hsu et al., 1993). White and black spruce both migrated early and white birch was a significant compo-

net at many sites. Oddly, the forest tundra in the Alaska-
Mackenzie region expanded only modestly between 10 and 9 ka BP. The boreal forest probably also extended southward into parkland reaching near to its modern southern limits in Alberta (Hickman and Klarer, 1981). Hazelnut (Corylus spp.) made a limited appearance in the Alberta parkland about this time, not appearing in pollen records again after 8 ka BP (Lichten-Fedorchich, 1970; note, however, that hazel pollen is difficult to identify and the shrub is common in the southern boreal forest now. A. Beaujot, personal communication, 2005). However, the boreal parkland lost area to grassland in Saskatchewan (Kupsch, 1960; Ritchie and de Vries, 1964; Mott, 1973; Mott and Christansen, 1981) and in Manitoba (Ritchie, 1967, 1969, 1976), where the grassland extended to Lake Agassiz, thus leaving the western boreal forest still dis-

LATE QUATERNARY VEGETATION HISTORY OF NORTHERN NORTH AMERICA
abundant on the plains, bison extended through the boreal parkland and openings in the boreal forest, as wood bison (Bison bison athabascae) do today. Despite some loss of northern grassland and parkland on the Canadian prairies between 10 and 9 ka BP, large areas of grassland remained, making habitat loss seem an improbable cause of the extinction of the large grazers. In fact, the opposite has been argued – that the loss of herds of large grazers allowed the forest to encroach on grassland and parkland that had been maintained in part by grazing and tree destruction. Owen-Smith (1987) noted that the modern African elephant can, by its feeding and other activities, change a closed woodland into open grassy savannah within a decade and that the elimination of such animals could lead to fundamental biome changes. He views megaherbivores as keystone species, partly because their great size renders them immune to non-human predators, virtually ensuring that populations approach habitat carrying capacity. At that point their normal behaviour is an important control of biome dynamics. Hence, caution is again warranted in interpreting all vegetation changes in terms of climatic change, particularly around the time of the widespread large mammal extinctions.

Disappearance of the mastodon, elk-moose, woodland muskox, and giant beaver left the conifer forests to the moose, beaver, and muskrat (Ondatra zibethicus), with elk and woodland caribou (Rangifer tarandus caribou) exploiting open areas. The tundra caribou (Rangifer tarandus tarandus) extended northward through forest tundra and tundra. It is important to note here that these modern survivors amongst the large mammals are not seen as ecological replacements of the extinct taxa (Martin and Klein, 1984). That is, they do not occupy the same ecological niches. Hence, extinction cannot be seen as the result of competition from these modern forms.

Dreimanis (1968) noted that the extinction of the mastodon coincided with a change in composition of the boreal forest in the mid-continent from one characterized by spruce to one more characterized by jackpine. Table VII shows the percentages of spruce- and pine-dominated pollen assemblages in boreal forest and boreal parkland biomes as listed in the current database for 11, 10, and 9 ka BP. The increased abundance of pine, predominantly jackpine, was indeed a strong feature of the changing boreal forest composition in North America during that interval. However, pine never reached widespread dominance and at 10 ka, the approximate time of mastodon extinction, and spruce-dominated assemblages still outnumber pine-dominated assemblages in the available pollen records by more than two to one. If the mastodon became extinct because of loss of its main food source (spruce), something must have prevented it from moving to spruce-rich areas at 10 ka BP and earlier. Alternatively, the reduction of spruce-dominated forests in favour of pine during the interval of maximum regional mastodon populations (assuming that the number of dated specimens reflects population sizes) might be seen as the result of destruction of spruce seedlings and young trees by browsing mastodons.

8 ka BP

Dated macrofossils (GSC-2712) show that shrub willow had spread north at least to central Ellesmere Island by 8 ka BP (Fig. 8). Willow pollen increased at a lake on east-central Ellesmere Island at the same time (Hyvärinen, 1985).

<table>
<thead>
<tr>
<th>Table VI</th>
<th>The most common mammal fossils in various environments at 9.9-7 ka BP. Extinct or extirpated forms are marked with an asterisk</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mammal</td>
<td>A. Steppe, Grassland and Savannah</td>
</tr>
<tr>
<td></td>
<td>Bison (Bison spp., B. bison, B. antiquus*, B. bison occidentalis*, B. priscus*)</td>
</tr>
<tr>
<td></td>
<td>Pronghorn (Antilocapra americana)</td>
</tr>
<tr>
<td></td>
<td>Elk (Cervus spp., C. elaphus)</td>
</tr>
<tr>
<td></td>
<td>Ground squirrel (Spermophilus spp., S. mollis, S. richardsoni, S. townsendi)</td>
</tr>
<tr>
<td></td>
<td>Beaver (Castor canadensis)</td>
</tr>
<tr>
<td></td>
<td>B. Conifer Forest, Parkland and Forest Tundra</td>
</tr>
<tr>
<td></td>
<td>Bison (Bison spp., B. bison antiquus*, B. bison)</td>
</tr>
<tr>
<td></td>
<td>Elk (Cervus elaphus)</td>
</tr>
<tr>
<td></td>
<td>Caribou (Rangifer tarandus)</td>
</tr>
<tr>
<td></td>
<td>Moose (Alces alces)</td>
</tr>
<tr>
<td></td>
<td>Black bear (Ursus americanus)</td>
</tr>
<tr>
<td></td>
<td>Grizzly bear (Ursus arctos)</td>
</tr>
<tr>
<td></td>
<td>Beaver (Castor canadensis)</td>
</tr>
<tr>
<td></td>
<td>Muskrat (Ondatra zibethicus)</td>
</tr>
<tr>
<td></td>
<td>C. Tundra and Alpine Tundra</td>
</tr>
<tr>
<td></td>
<td>Caribou (Rangifer tarandus)</td>
</tr>
<tr>
<td></td>
<td>Bighorn sheep (Ovis spp., O. canadensis)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Year</th>
<th>A. Steppe, Grassland and Savannah</th>
<th>B. Conifer Forest, Parkland and Forest Tundra</th>
<th>C. Tundra and Alpine Tundra</th>
</tr>
</thead>
<tbody>
<tr>
<td>9.9-9 ka</td>
<td>51</td>
<td>15</td>
<td>2</td>
</tr>
<tr>
<td>8.9-8 ka</td>
<td>48</td>
<td>3</td>
<td>25</td>
</tr>
<tr>
<td>7.9-7 ka</td>
<td>48</td>
<td>10</td>
<td>11</td>
</tr>
</tbody>
</table>
Somewhat earlier, shrub willow increased in abundance in the herb tundra of eastern Baffin Island (Short et al., 1985). Willows (Salix arctica, S. herbacea or S. reticulata) appear to have arrived in most of the eastern Canadian Arctic and Greenland between 9 and 8 ka BP, with Salix glauca also appearing in Greenland (Kelly and Funder, 1974; Fredskild, 1983, 1985). By 8 ka BP, shrub willows could have spread to Baffin Island from Labrador, from the north, or from Greenland.

By 8 ka BP, birch shrub tundra had advanced onto Banks Island in the western Canadian Arctic Archipelago (Gajewski et al., 2000a) and east of Bathurst Inlet on the arctic mainland (Seppä et al., 2003). Alder had spread through most of the shrub tundra of Alaska and the Yukon, reaching at least 70°N and 165°W on Seward Peninsula (Shackleton, 1979; Cwynar, 1982; P. Anderson, 1985), but had evidently not quite reached the Mackenzie Delta. Meanwhile alder had spread through the shrub tundra northwards along most of the Labrador coast to at least 58.6°N (Clark et al., 1989), but juniper does not appear to have extended much beyond its 9 ka limit in southern Labrador. Birch shrub tundra was well established in Iceland, where juniper also had become more widespread by 8 ka BP (Vasari, 1972; Hallsdottir, 1996; Wastl et al., 2001). However, the warmest part of Greenland, which

### TABLE VII

<table>
<thead>
<tr>
<th>Pollen assemblage</th>
<th>11 ka</th>
<th>10 ka</th>
<th>9 ka</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spruce-dominated</td>
<td>90</td>
<td>66</td>
<td>51</td>
</tr>
<tr>
<td>Pine-dominated</td>
<td>5</td>
<td>25</td>
<td>37</td>
</tr>
<tr>
<td>Number of sites</td>
<td>258</td>
<td>287</td>
<td>294</td>
</tr>
</tbody>
</table>

FIGURE 8. Biomes at 8 ka BP.

Les biomes en 8 ka BP.
today supports birch, alder, and juniper shrub tundra with occasional tree birch, retained its cover of herb tundra domi-

Nevertheless, summer lake water temperatures and mean annual air temperatures, based on chironomid assemblages and 1° concentrations in chironomid head capsules, respec-
tively, were at postglacial maximum levels by 8 ka BP (2° and 4°C warmer than present, respectively; Woolf et al., 2004).

The southern boreal tree limit moved northward on the Mackenzie Valley, where tundra advanced nearly to the coast and beyond present treeline (Ritchie and Hare, 1971; Hyvärinen and Ritchie, 1975; Ritchie, 1977; Ritchie et al., 1983; Ritchie, 1984a, 1984b, 1985, 1987). The beaver evidently expanded its range in step with treeline, as shown by a lodge dated to 7.8 ka BP in the present tundra on Kondal Island off the Mackenzie Delta (Mackay, 1971). Forest expansion in Alaska was slow in comparison, although forest tundra expanded toward the southwest and farther onto Seward Peninsula (Hopkins et al., 1981; Ager and Brubaker, 1985; Brubaker et al., 2001). The northern part of the western boreal forest was mainly white spruce, black spruce, and white birch; alder spread within the forest to at least 68.5°N (Ritchie, 1987). White and black spruce also characterized the southern part of this forest with white birch; pine, probably jackpine, became more important in northern Alberta, whereas aspen, poplar, and alder were more common in northern British Columbia. The mixed forest had expanded through much of northern New England and the Maritimes by 8 ka BP and it even extended beyond its modern limit in places, such as north of Lake Superior. White pine remained the common tree throughout this biome, as at 9 ka BP West of Lake Huron, the most important associates were oak, elm, and birch. In Ontario and New York, oak and hemlock seem to have been the most common trees, with hemlock reaching greatest abundance – and in places being the most important tree – in New York. In Maine and the Maritimes, oak, fir, hemlock, and birch were the chief associates.

The deciduous forest expanded close to its modern northern limit, and somewhat farther in places, such as in Massachusetts (Ogden, 1963). As at 9 ka BP, the oaks were the most common trees throughout this biome. Hickory and beech were widespread, whereas elm, ash, and ironwood seem to have declined in importance in the east and birch in the west. Hemlock was important in Ontario, Pennsylvania and New England, and maple was most prominent within this biome in Ontario. Meanwhile the southern limit of the deciduous forest moved northeastward leaving oak savannah in its wake in Indiana, Illinois, and Iowa. This change indicates a warming and drying of the eastern Great Plains (Brush, 1967; King, 1981). The same climatic trend is indicated by northward expan-
sion of interior forest and interior parkland in central British Columbia and by the establishment of this forest in presently wet areas of eastern Vancouver Island and the Fraser Lowland (Hebda, 1983). Douglas fir, lodgepole pine, and in places Ponderosa pine were the key trees here, with alder, western hemlock, Sitka spruce, and fir as associates. The adjacent coast forest had almost reached its limit along the south coast of Alaska, having advanced to at least 142°W (Heusser, 1965).

Continued warming and drying in the American Cordillera led to further expansion of steppe from the Great Basin into high ground previously occupied by subalpine forest in Wyoming (Albanese and Frison, 1995), thus fragmenting that forest biome. Meanwhile alpine timberline remained above present elevations in Colorado, Alberta, and southern British Columbia (see above and Elias, 1985; Luckman 1988; Clague and Mathewes, 1989).
virtually the full extent of the continent had been occupied by 8 ka BP. For example, the dwarf Peary caribou (Rangifer tarandus pearyi) had expanded to the north coast of Ellesmere Island by 8.4 ka BP (Stewart and England, 1986) and had reached Greenland by 8 ka BP (Meldgaard, 1986). Thus herb tundra in the highest arctic had achieved a carrying capacity comparable to that of the present shortly after local deglaciation.

LATE DEGLACIATION (7.5-5 KA BP)

This interval starts with the fragmentation of the Laurentide Ice Sheet, caused by deglaciation of Hudson Bay, and ends with the final disappearance of glacier ice in Québec-Labrador. Although the glacial anticyclone probably dissipated as a quasi-permanent feature with the opening of Hudson Bay, the remnant ice masses during this interval were still large enough to affect regional climate in their vicinities, but evidently not far afield.

7 ka BP

Although herb tundra probably prevailed on eastern Baffin Island (Millier et al., 1999), dwarf birch seems to have gained a foothold in places as far north as Clyde Inlet by 7 ka BP (Fig. 9; Short et al., 1985), and as far north as Cumberland Peninsula by 8 ka BP (Fréchet et al., 2003). It is unclear whether the earliest birch on Baffin Island was Betula glandulosa from Labrador or Betula nana from Greenland. The latter has a restricted distribution on southeastern Baffin Island today (Porsild, 1957; Andrews et al., 1980) and it is the less thermophilous of the two.

Shrub tundra also may have made its initial appearance in southwest Greenland by 7 ka BP (Kelly and Funder, 1974). Here green alder (Alnus crispa) and juniper seem to have arrived ahead of dwarf birch, the opposite of the sequence seen in Canada and Alaska. Alternatively, the strong rise in

FIGURE 9. Biomes at 7 ka BP.

Les biomes en 7 ka BP.
alder pollen at sites in Greenland at 7.6 ka BP may reflect enhanced long-distance transport resulting from the spread of alder northward along the Labrador coast after 8 ka BP as discussed above, and an increased easterly wind over the Labrador Sea pursuant to diminution of the glacial anticyclone over eastern North America. Evidently this is the general interpretation accepted by Bennike (1999), who places the arrival of alder in Greenland at 4.4 ka BP. Nevertheless, Bennike accepts the arrival of juniper (Juniperus communis) in Greenland at 7.9 ka BP in agreement with Kelly and Funder (1974). Dwarf birch (Betula nana) had reached Scoresby Sund in East Greenland from Iceland by 7 ka BP as shown by dated macrofossils (Böcher and Bennike, 1996). Plants in Greenland arrived most commonly from Iceland and—at least in the case of alder—from Labrador (Bennike, 1999). The shrub tundra of Labrador at 7 ka BP was characterized by alder and birch, as before, and juniper seems not to have spread northward along the coast between 8 and 7 ka BP. Alder was widespread in Labrador Sea pursuant to diminution of the glacial anticyclone over eastern North America. Evidently this is the general interpretation accepted by Bennike (1999), who places the arrival of alder in Greenland at 4.4 ka BP. Nevertheless, Bennike accepts the arrival of juniper (Juniperus communis) in Greenland at 7.9 ka BP in agreement with Kelly and Funder (1974). Dwarf birch (Betula nana) had reached Scoresby Sund in East Greenland from Iceland by 7 ka BP as shown by dated macrofossils (Böcher and Bennike, 1996). Plants in Greenland arrived most commonly from Iceland and—at least in the case of alder—from Labrador (Bennike, 1999). The shrub tundra of Labrador at 7 ka BP was characterized by alder and birch, as before, and juniper seems not to have spread northward along the coast between 8 and 7 ka BP. Alder was widespread in the shrub tundra of Alaska and eastward to the Mackenzie Delta by 7 ka BP, but failed to spread much to the east of there during postglacial time. In Iceland, a partial cover of forest tundra with tree birch (Betula pubescens) — the only forest tree to reach the island in the Holocene—had been established (Hallsdottir, 1996).

The boreal forest at 7 ka BP was an unbroken biome extending from Alaska to Newfoundland and Labrador. Latitudinal treeline fell somewhat short of its present position across most of Alaska, although forest tundra extended beyond the present limit of trees on Seward Peninsula, where beavers had been present since at least 9.4 ka (McCulloch et al., 1965). Similarly, the boreal forest still extended beyond its present limit in the Mackenzie Delta region. The limit of boreal forest farther east fell somewhat short of its present position (Nichols, 1972a, 1975; Ritchie, 1979). However, forest tundra extended nearly to modern treeline, which probably indicates inadequate in-fill (densification) time since deglaciation for full forest development. The most rapid spread of boreal forest between 8 and 7 ka BP was into southern Labrador from its previous limit in the vicinity of Lac Saint-Jean (Lamb, 1980; Engstrom and Hansen, 1985).

As before, the boreal forest at 7 ka BP can be considered in three sections from a compositional point of view. West of Ontario, spruce was most abundant at almost all sites, with both black and white spruce well represented. Pine was most common at a few sites in Alberta and aspen in British Columbia. White birch was the major associate throughout and alder was important in British Columbia and regions to the north and west. In Ontario and the Ottawa Valley region of Quebec, jackpine was most abundant at about two-thirds of sites in the boreal forest and spruce at others. White birch was the most common associate of jackpine, and jackpine the most common associate of spruce; fir remained unimportant. In Quebec, southeastern Labrador, and Newfoundland, spruce was most common at about half of reported sites in the boreal forest, balsam fir at about a third, and white birch at the rest. Furthermore, fir was a major associate at about half the sites characterized by spruce or birch. Fir seems to have attained its greatest prevalence in southeastern Quebec, where it remains important or dominant today, and it was an aggressive colonizer in southeastern Labrador. Yellow birch, probably the most thermophilous element in the Newfoundland forest today, where it has a restricted distribution, arrived on the Avalon Peninsula about 7 ka BP (Terasmae, 1963), as did black ash (Fraxinus nigra), which survives in the area today as a shrub (Dyer, 1986).

Meanwhile, the mixed forest boundary was well north of its present location in the region from Lake of the Woods to the Ottawa Valley (Vincent, 1973; Bjorck, 1986; Liu, 1990, McIntyre et al., 1991) and this biome had penetrated farther into New England and Quebec (Richard, 1970, 1973, 1975, 1977, 1980). The deciduous forest boundary was north of its present location in the southern Great Lakes region (McMurray et al., 1978; Heide, 1984), the grassland and parkland boundaries remained somewhat north of their present locations on the Canadian prairies, and treeline remained above present elevations in the Colorado and Alberta Rockies and in the British Columbia Coast Range. Conditions were so dry on the prairies by 7.5 ka BP that there was insufficient infiltration of water to the southern basin of Lake Winnipeg to fill the basin to overflow despite the fact that isostatic tilting was tending to raise water levels at the south end of the lake (Lewis et al., 2001). The moisture balance at Winnipeg may have been similar to that at Medicine Hat today. Conditions also may have been sufficiently dry in the Great Lakes region at about the same time to draw water levels in the Huron Basin below overflow levels (Blasco, 2001). But evidently they were not so dry as to desiccate the regional mixed forest. Continued expansion of the mid-continent savannah and grassland biomes into areas formerly occupied by mixed and deciduous forest (Wright et al., 1963; McAndrews, 1986; Cushion, 1967; Durkee, 1971; Grimm, 1982; Brugam et al., 1988; Baker et al. 1992; Baker and Drake, 1994) indicates further warming and drying there, as does replacement of subalpine forest by drier interior forest (Mehring et al., 1977) and by steppe (Albanese and Frison, 1995) in the mountains of Montana. In contrast, a re-expansion of coast forest in the Puget Sound region indicates greater effective moisture in the Pacific Northwest (Heusser, 1985). Summer temperatures there were about 2°C above present values but had declined from the postglacial maximum (Walker and Pellatt, 2003).

The mixed and deciduous forest biomes continued to be characterized by much the same taxa as previously. White pine continued to characterize most regions of the mixed forest, except in New England, where it was somewhat exceeded by hemlock, and in Quebec, where maple and yellow birch were more important. From Minnesota to Michigan, oak was the most important associate followed by birch, elm, and ironwood. In Ontario, hemlock was most common at about 25% of sites and birch, oak, beech, elm, and maple were strongly represented. Hemlock had also become most common in places in Maine and the Maritimes, and oak, birch, and fir remained widespread there. Oak was most common everywhere in the deciduous forest, except for occasional stands of elm, maple, beech or hemlock in Ontario, beech in Michigan, and basswood in Iowa. Elm, ironwood, hickory, and basswood were the prominent associates of the deciduous forest (Michigan eastern); elm, beech, maple, hickory, and ash in the central part (Ohio, Ontario); and hemlock, beech, hickory, and chestnut in the east.
These middle Holocene conditions in the central and eastem part of the continent can be understood as a consequence of the disappearance of the glacial anticlone with deglaciation of Hudson Bay at 7.6 ka BP, combined with a summer radiation receipt that was 6% greater than at present. Although a brief cold event followed deglaciation of Hudson Bay due to oceanographic changes in the North Atlantic caused by proglacial lake drainage (Barber et al., 1999), elimination of the blocking anticlone permitted strengthening and northward shifting of prevailing westerly winds over the prairies and Ontario while in southeastern Quebec-Labrador the westerlies replaced prevailing northeasterly winds, both warming the region during summer and assisting in plant dispersal.

The ascendance of jackpine in the central part of the eastem boreal forest, starting about 10 ka BP and peaking 9-7 ka BP, possibly indicates maximum dryness in that region. Jackpine and white birch, its most common associate at the time, are both early successional trees that are intolerant of shade. Jackpine relies on fire for the release of seeds from its cones, which otherwise remain sealed by resin with a melting point above the range of air temperatures. It is therefore improbable that these two species would have replaced a closed spruce forest in the absence of frequent, major fires. However, lake sediment charcoal records offer only inconsistent support for this hypothesis (Fuller, 1997). The mechanism of replacement of spruce forests by jackpine-birch forests is thus still under discussion. Wright (1968) and Wright et al. (2004) argued that the climate simply became too warm for spruce to regenerate and jackpine took over as the spruce forest opened with the death and windthrow of spruce trees. On the other hand, Critchfield (1985) argued cogently for replacement because of fire disturbance. The case for the warming hypothesis would be strengthened had a more thermophilous pine replaced the spruce. Jackpine has a rather restricted distribution in the mixed forest today, whereas white spruce does quite well there.

6 ka BP

By this time the biomes were in essentially modern positions, except in areas of late deglaciation, of which the most significant were northern Quebec-Labrador and Baffin Island (Fig. 1). Shrub tundra expanded in Labrador and Quebec, where both birch and alder spread quickly after deglaciation (Short and Nichols, 1977; Lamb, 1985a, 1985b; King, 1985, 1986). Shrub tundra also expanded in southwest Greenland, where juniper and birch (Betula nana and B. glandulosa), and possibly green alder (see above) were present (Fredskild, 1973, 1983, 1985). Betula nana, however, is not a strict indicator of Low Arctic conditions; it extends well into the High Arctic tundra of northeast Greenland today, although it has not reached High Arctic Canada during the Holocene (Porsild, 1957; Andrews et al., 1980). Shrub tundra expansion in Greenland indicates either continued warming or continued plant migration under already favourable conditions, because the ice sheet was as small as it is presently by 6 ka BP. The chironomid-inferred temperatures in southwest Greenland were declining by this time but were still about 1 °C warmer than present (Wooller et al., 2004). Shrub tundra failed to expand at this time on Baffin Island from the few putative sites of earlier establishment (Short et al., 1985; Fréchet et al., 2003).

The main change in boreal forest distribution between 7 and 6 ka BP was a large northward advance in Quebec-Labrador (Mott, 1976; Richard, 1979; Richard et al., 1982; King, 1985, 1986), a consequence of deglaciation, preceded by an expansion of forest tundra. Larch was a pioneering tree in the forest tundra of central and western Quebec (Gajewski et al., 1993, 1996), but evidently not in Labrador. The forest limit also advanced nearly to the Hudson Bay coast in Ontario and Manitoba (McAndrews et al., 1982; Dredge and Mott, 2003), advanced slightly in the Great Bear Lake area (Nichols, 1972b) and advanced significantly westward in central Alaska (Edwards and Brubaker, 1986; Brubaker et al., 1983; Hu et al., 1986). Similarly forest tundra expanded into the Thelon River basin (Craig, 1959) and into the mountains west of the Mackenzie River (Szeicz et al., 1995), although treeline was retracted slightly in the vicinity of the Mackenzie Delta. The largest compositional change in the boreal forest involved a reduction of the preponderance of jackpine in Ontario to being most common at less than one-third of sites from two-thirds a millennium earlier, with black and white spruce predominating elsewhere. In Quebec and Labrador, spruce and fir remained the most common trees at nearly equal numbers of sites. Spruce and fir also predominated in Newfoundland, where larch appears to have become more important than previously. White pine, red pine (Pinus resinosa), and ash – all thermophilous and evidently never abundant in Newfoundland – appeared at this time and attained their greatest abundance during the next 2000 years (Macpherson, 1995). White and black spruce remained exceedingly common in the western boreal forest, though jackpine may have increased somewhat in Saskatchewan and Manitoba (Nichols, 1967; Mott, 1973; Ritchie and Hadon, 1979; Ritchie, 1976, 1980; Ritchie and Yarranton, 1978; Wilson, 1981; Dredge and Mott, 2003).

Warmer-than-present conditions in the mid-continent are indicated by the continued more northerly distribution of mixed forest from Lake of the Woods to Ottawa Valley, where white pine pushed well north of its present limit (T. Anderson and Terasmae, 1970), by the somewhat more northerly placement of the boundaries of grassland and boreal parkland on the prairies (Vance et al., 1995), by higher than present treelines in the Rocky Mountains of Alberta and southwestern British Columbia (above and Luckman et al., 1993), and by the greater extent of steps in northeastern Washington and Idaho (Mack et al., 1978, 1979; Baker, 1983). Vance described similar biome departures from present at 6 ka BP for Canadian territory (in Gajewski et al., 2000b).

The faunal record for the middle and late Holocene (Table VIII) is dominated by collections from archaeological sites. Because of the increasing visibility of younger sites and the better preservation of younger bones, there is a general increase in the abundance and diversity of taxa recorded through time that does not necessarily carry any climatic implication. Furthermore, remains at these sites preferentially reflect those animals that were important food, clothing and other resources. Detailed analyses of assemblages of environmentally specialized small mammals reveal some changes
during the middle and late Holocene as well as some still-
disharmonious mammal assemblages (Graham et al., 1987).
However, by 6 ka BP the distribution of larger mammals by
biome groups was unsurprising. Modern bison, elk, mule deer
(Odocoileus hemionus), and pronghorn were prevalent on the
grasslands and ranged into the boreal parklands; white-tailed
deer (Odocoileus virginianus), elk and black bear (Ursus
americanus) are the most abundant remains from the mixed
deciduous forests; moose, caribou, black bear, and snow-
shoe hare (Lepus americanus) are most abundant in the
conifer forests; caribou, moose, and snowshoe hare, in the
forest tundra; and caribou, muskox, arctic fox (Alopex lago-
pus), arctic hare (Lepus arcticus), and polar bear, in the tun-
dra. Beaver and muskrat were exploited in all biomes south of
the continental treeline (Canadian Archaeological Radiocarbon
Database, 2005).

5 ka BP
The major changes between 6 and 5 ka BP were the north-
ward expansion of biomes in the eastern Arctic and Subarctic
(Fig. 11). Alder-birch shrub tundra and forest tundra expanded
in Québec-Labrador (McAndrews and Samson, 1977; Richard,
1979; Stravers, 1981; Gajewski et al., 1993, 1996), and larch
extended to a point somewhat beyond its present range (nee-
dles dated 4.96 ka BP; Richard, 1981). Birch (Betula glandu-
losa) shrub tundra advanced broadly onto southern Baffin
Island (Short et al., 1985; Jacobs et al., 1990; Escamilla, 1994;
Jacobs et al., 1997) and juniper and birch (Betula glandulosa
and B. nana) shrubs continued to expand their range in south-
west Greenland (Fredskild, 1983; Eiserer et al., 1995).
Elsewhere changes were subtler. The limit of forest tundra
and boreal forest advanced in southern Nunavut and south-
eastern Northwest Territories (i.e., the mainland west of
LATE QUATERNARY VEGETATION HISTORY OF NORTHERN NORTH AMERICA

<table>
<thead>
<tr>
<th>Mammal</th>
<th>6.9-5 ka</th>
<th>4.9-3 ka</th>
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</thead>
<tbody>
<tr>
<td><strong>A. Steppe, Grassland and Savannah</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bison (Bison spp., B. bison bison)</td>
<td>113</td>
<td>150</td>
<td>806</td>
</tr>
<tr>
<td>Pronghorn (Antilocapra americana)</td>
<td>36</td>
<td>28</td>
<td>151</td>
</tr>
<tr>
<td>Deer (Odocoileus spp., O. hemionus)</td>
<td>27</td>
<td>22</td>
<td>81</td>
</tr>
<tr>
<td>Elk (Cervus elaphus)</td>
<td>20</td>
<td>14</td>
<td>37</td>
</tr>
<tr>
<td>Wolf (Canis lupus)</td>
<td>10</td>
<td>3</td>
<td>28</td>
</tr>
<tr>
<td>Coyote (Canis latrans)</td>
<td>10</td>
<td>3</td>
<td>21</td>
</tr>
<tr>
<td>Ground squirrel (Spermophilus spp., S. richardsonii, S. tridecemlineatus)</td>
<td>26</td>
<td>22</td>
<td>81</td>
</tr>
<tr>
<td>Pocket gopher (Geomys spp., G. bursarius)</td>
<td>3</td>
<td>1</td>
<td>19</td>
</tr>
<tr>
<td>Gopher (Thomomys spp., T. talpoides)</td>
<td>17</td>
<td>8</td>
<td>36</td>
</tr>
<tr>
<td>Cottontail (Sylvilagus spp.)</td>
<td>23</td>
<td>7</td>
<td>51</td>
</tr>
<tr>
<td>Beaver (Castor canadensis)</td>
<td>4</td>
<td>5</td>
<td>61</td>
</tr>
<tr>
<td>Muskrat (Ondatra zibethicus)</td>
<td>5</td>
<td>1</td>
<td>20</td>
</tr>
<tr>
<td><strong>B. Deciduous and Mixed Forest</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Deer (Odocoileus spp., O. virginianus)</td>
<td>6</td>
<td>32</td>
<td>196</td>
</tr>
<tr>
<td>Elk (Cervus elaphus, C. e. canadensis)</td>
<td>1</td>
<td>5</td>
<td>38</td>
</tr>
<tr>
<td>Bear (Ursus spp., U. americanus)</td>
<td>2</td>
<td>21</td>
<td>81</td>
</tr>
<tr>
<td>Beaver (Castor canadensis)</td>
<td>5</td>
<td>31</td>
<td>120</td>
</tr>
<tr>
<td>Muskrat (Ondatra zibethicus)</td>
<td>5</td>
<td>13</td>
<td>83</td>
</tr>
<tr>
<td>Raccoon (Procyon lotor)</td>
<td>10</td>
<td></td>
<td>73</td>
</tr>
<tr>
<td><strong>C. Conifer Forest and Parkland</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bison (Bison spp., B.b. athabascae)</td>
<td>9</td>
<td>57</td>
<td>106</td>
</tr>
<tr>
<td>Elk (Cervus elaphus)</td>
<td>5</td>
<td>50</td>
<td>84</td>
</tr>
<tr>
<td>Moose (Alces alces)</td>
<td>28</td>
<td>41</td>
<td>113</td>
</tr>
<tr>
<td>Caribou (Rangifer tarandus)</td>
<td>3</td>
<td>2</td>
<td>54</td>
</tr>
<tr>
<td>Deer (Odocoileus spp., O. hemionus)</td>
<td>23</td>
<td>58</td>
<td>129</td>
</tr>
<tr>
<td>Bear (Ursus spp., U. americanus)</td>
<td>11</td>
<td>39</td>
<td>104</td>
</tr>
<tr>
<td>Hare (Lepus spp., L. americanus)</td>
<td>6</td>
<td>37</td>
<td>98</td>
</tr>
<tr>
<td>Beaver (Castor canadensis)</td>
<td>26</td>
<td>71</td>
<td>209</td>
</tr>
<tr>
<td>Muskrat (Ondatra zibethicus)</td>
<td>1</td>
<td>16</td>
<td>74</td>
</tr>
<tr>
<td>Porcupine (Erethizon dorsatum)</td>
<td>5</td>
<td>29</td>
<td>53</td>
</tr>
<tr>
<td><strong>D. Forest Tundra</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Caribou (Rangifer tarandus)</td>
<td>9</td>
<td>14</td>
<td>81</td>
</tr>
<tr>
<td>Moose (Alces alces)</td>
<td></td>
<td></td>
<td>20</td>
</tr>
<tr>
<td>Elk (Cervus elaphus)</td>
<td>2</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>Hare (Lepus spp., L. americanus)</td>
<td>2</td>
<td>1</td>
<td>16</td>
</tr>
<tr>
<td>Beaver (Castor canadensis)</td>
<td>2</td>
<td></td>
<td>16</td>
</tr>
<tr>
<td><strong>E. Tundra</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Caribou (Rangifer tarandus)</td>
<td>13</td>
<td>79</td>
<td>389</td>
</tr>
<tr>
<td>Tundra muskox (Ovibos moschatus)</td>
<td>2</td>
<td>44</td>
<td>173</td>
</tr>
<tr>
<td>Sheep (Ovis canadensis, O. dalli)</td>
<td>5</td>
<td>4</td>
<td>16</td>
</tr>
<tr>
<td>Arctic fox (Alopex lagopus)</td>
<td>19</td>
<td>107</td>
<td></td>
</tr>
<tr>
<td>Arctic hare (Lepus arcticus)</td>
<td>23</td>
<td>60</td>
<td></td>
</tr>
<tr>
<td>Polar bear (Ursus maritimus)</td>
<td>6</td>
<td></td>
<td>73</td>
</tr>
</tbody>
</table>
Hudson Bay; Kay, 1979; Edwards et al., 1996) but apparently changed little between there and the Mackenzie Delta, where treeline remained north of its present location. The boreal forest essentially completed its slow expansion through central and southwestern Alaska between 6 and 5 ka BP (P. Anderson, 1985, 1988), that expansion lagging long after the Holocene thermal maximum (Kaufman et al., 2004). Boreal (aspen) parkland, grassland, mixed forest, and deciduous forest biomes maintained more northerly distributions than present. The deciduous forest boundary retreated and forest was replaced by grassland in Iowa and Wisconsin (Baker et al., 1990; Chumbley et al., 1990) but deciduous forest possibly advanced at the expense of savannah in Ohio and Indiana. These changes indicate a complexly changing effective moisture distribution on the eastern Great Plains, where air masses from the Pacific (dry east of the Cordillera) and from the Gulf of Mexico (moist) are in frequent contact. Alpine treeline was above its present elevation in those areas where it was high a millennium earlier and in the southwestern Yukon (Denton and Karlén, 1977).

POSTGLACIAL (AFTER 5 KA BP)

Significant changes of glacier ice cover after 5 ka BP were limited to Baffin Island (Dyke, 2004).

4 ka BP
The most thermophilous postglacial vegetation development was delayed until 4-3 ka BP in areas of very late deglaciation and in certain areas where plants evidently migrated rather slowly. By 4 ka BP, birch shrub tundra had reached or exceeded its modern limit on Baffin Island (Fig. 12). Neither juniper nor alder extended so far north during the
Holocene. Shrub tundra was nearly at its limit in West Greenland (Fredskild, 1985), where green alder had arrived from Labrador and tree birch (*Betula pubescens*) from Iceland (Bennike, 1999). The latter exists in a small part of southernmost Greenland, which is therefore classified in some schemes as Subarctic, rather than Low Arctic (Funder, 1989). Forest tundra was approaching its modern limit in northeastern Quebec-Labrador (Short and Nichols, 1977; Williams et al., 1995). Forest tundra and boreal forest remained north of their present positions in the Dubawnt Lake-Ennadai Lake region of Nunavut, based on macrofossils dating from 3.54-4.0 ka BP (Bryson et al., 1965; Nichols, 1972b). Treeline was slightly beyond its present position in the Mackenzie Delta and somewhat higher than present in the mountains to the southwest, where spruce macrofossils are dated at 4.4 ka BP (Szeicz and MacDonald, 2001) and in the southwest Yukon, where a spruce log 76 m above treeline was dated to 3.6 ka BP (Denton and Karlén, 1977). Boreal forest continued to expand along the south coast of Alaska, reaching Kodiak Island, as did the northern limit of the coast forest in that state (Heusser, 1985). Forest tundra continued its expansion into shrub tundra in southwest Alaska between 5 and 4 ka BP (Hu et al., 1995).

In other areas, biomes were retracting from more northerly positions at 4 ka BP. The northern grassland boundary retracted to near its modern position and a positive moisture balance inside the adjacent boreal forest allowed the paludi-fi-cation front to advance southward (Zoltai and Vitt, 1990). However, the boundary between deciduous forest and grassland or savannah remained east and north of its present position in most places. The northern boundary of mixed forest continued its slow withdrawal in Ontario although remaining north of its present position (Julig et al., 1990). In the mid-continent, in contrast, deciduous forest was at its most northerly...
postglacial position (Sreenivasa, 1973; Karrow et al., 1975; Webb et al., 1983; Turner et al., 1983; Heide, 1984). However, this was mainly a consequence of the loss of hemlock in the mixed forest, which rendered the resulting forest in its southern part more purely deciduous. Eastern hemlock, a major species in the mixed forest, was greatly reduced in abundance over most of its range at 4.8-4.5 ka BP. It has been argued that the reduction was the result of a pathogen (Davis, 1981) — most likely an infestation by an insect, the hemlock looper (Bhiry and Filion, 1996). However, there is also macrofossil and lake-level evidence that the hemlock decline was driven by severe drought, which might also have stimulated insect outbreaks and left the trees more susceptible to death by defoliation (Haas and McAndrews, 1999; Shuman et al., 2004). Eastern hemlock regained its modern extent mainly in the last 2000-3000 years, but never regained its former prominence, presumably because of competition from trees that occupied its former stand areas. Its partial recovery may have been assisted by moister conditions attending Neoglacial cooling in the mixed forest region (it requires a minimum annual precipitation of 710 mm; Brugam and Johnson, 1997). The interior forest of Douglas fir, lodgepole pine, and Ponderosa pine in northeastern Washington and Idaho expanded at the expense of steppe as a result of cooling and moistening (Mack et al., 1978, 1979), and western red cedar became more prominent in the coast forest of British Columbia for the same reason (Hebda and Mathewes, 1984). Thus, climate trends at 4 ka BP seem to have been spatially complex, with temperature-limited biomes advancing northward toward modern limits in the eastern Arctic and Subarctic and in southern Alaska but retracting southward towards modern limits in central Canada.

3-1 ka BP

The main biome distribution changes during the late Holocene (Figs. 13-15) involved the southward retraction of

![FIGURE 13. Biomes at 3 ka BP](image-url)
the northern limits of biomes and of species ranges and the lowering of alpine treelines. This occurred during a period recognized globally as the Neoglacial, a period generally cooler than the earlier parts of the Holocene (Denton and Karlen, 1973). Although the Neoglacial included intervals that were both warmer and colder than the early part of the 20th century – for example, the so-called Medieval Warm Period and the Little Ice Age – these events are proving to have been spatially complex in terms of temperature patterns and were not always globally or even hemispherically synchronous (Bradley and Jones, 1993). Biome distribution changes in response to these 0.3-1 °C temperature fluctuations were subtle. By 1 ka BP (Fig. 15), all biome limits were close to their present positions on present evidence.

Few changes are documented from the High Arctic, but biotic response to late Holocene cooling probably exceeded what can be presently shown in this poorly studied region. An interesting, but uniquely documented, event is the disappearance of Salix arctica from the Pearyland region of northeast Greenland at 3.9 ka BP (Funder and Abrahamsen, 1988), indicating that the July mean temperature declined below 3 °C. Possibly, it was about this time that woody shrubs disappeared from the ‘barren wedge’ of the Canadian polar margin. Similarly, the moss, Scorpidium scorpioides, which had extended north to Bathurst Island in the central High Arctic until 2.78 ka BP, was thought to have died out there sometime thereafter (Brassard and Steere, 1968; Blake, 1974). It has since been reported living on adjacent Prince of Wales Island (Gajewski and Frappier, 2001), but this occurrence may be a relict of range retraction. On Somerset and Prince of Wales islands, a general reduction of ground cover by plants in the last 3 ka is registered by reduced pollen production particularly by willow (Salix arctica), heather, sedge, and sorrel (Gajewski, 1995; Gajewski and Frappier, 2001). In the herb tundra of Banks Island, grasses expanded at the expense of sedges during the last 3 ka, which is also taken as a sign of cooling (Gajewski et al., 2000a).
Shrub tundra retracted in the eastern Canadian Arctic (Short et al., 1985) and in West Greenland (Fredskild, 1985; Funder, 1989) during the same period.

At 3 ka BP, treelines were still somewhat higher than present in the central Canadian Rockies, in the Mackenzie Mountains, and in the St. Elias Mountains of the Yukon, and in Colorado (references cited above; Carrara et al., 1991). Treelines fell as alpine glaciers advanced shortly thereafter. Similarly, the range of larch was reduced at the forest tundra limit in northwestern Quebec (Gagnon and Payette, 1981). The boreal forest limit retreated slightly in southern Nunavut (Kay, 1979), in the central Northwest Territories (Nichols, 1972a; Moser and MacDonald, 1990), and in the Mackenzie Delta region (Pitchie and Hare, 1971; Spear, 1983). It evidently maintained its position in Alaska, except on Kodiak Island, where boreal forest with tree birch reverted to forest tundra with scattered Sitka spruce by 2 ka BP (Heusser, 1985). The northern limits of the mixed and deciduous forests retreated slightly in the mid continent. This recession was primarily due to retraction of the northern range of white pine in the Lake Superior region (Liu, 1990; Flake, 2003) and the increasing abundance of that tree in Lower Michigan (Bailey and Aher, 1981; Holloway and Bryant, 1985). It was also due to the resurgence of hemlock in the northern fringe of the deciduous forest in southern Ontario and northwestern New York (Sreenivasa, 1973; Spear and Miller, 1976). The grassland boundary in Minnesota and Wisconsin retreated westward between 4 and 3 ka BP but it appears to have been fairly stable thereafter (McAndrews, 1966; Grimm, 1983; Dean et al., 1984; Holloway and Bryant, 1985; Jacobson and Grimm, 1986). Hence, the late Holocene presents widespread evidence of general cooling across the continent, even at this coarse biome level of analysis.

There were also important compositional changes within biomes that more finely reflect cooling and moistening during
the last 3000 years. For example, the northern boreal forest and forest tundra in Québec became less dense and more shrubby (Richard et al., 1982), fire increased in importance in the boreal forest in Newfoundland (Macpherson, 1995), and spruce showed a marked increase as a significant component throughout much of the eastern mixed forest zone, particularly in the last 1000 years (see review by Schauffer and Jacobson, 2002). Thus, not only did the mixed forest retreat somewhat, but also it took on a more boreal character (Table IX). Similarly, western hemlock, a moisture demanding species, expanded into the subalpine zone of southeastern British Columbia starting at about 3.5 ka BP and mountain hemlock appeared about 2.1 ka BP, suggesting an opening of the forest there due to cooling (Rosenberg et al., 2003). A high-resolution pollen analysis of a site in the northern edge of the deciduous forest in Ontario shows a strong decline of beech and concurrent rise of oak and white pine pollen in response to cooling during the Little Ice Age starting 1450 A.D. (Campbell and McAndrews, 1993). That study showed that the vegetation response remained in disequilibrium with climate for more than 650 years as individual species were advantaged or disadvantaged by canopy opening that resulted from the death of beech. Unfortunately there are few studies with such fine temporal resolution.

**SUMMARY OF TREELINE POSITIONS**

Figure 16 draws together all macrofossil dates that indicate when altitudinal and latitudinal treelines, or tree species limits near treeline, were higher than or north of their present positions. In Alaska (Hopkins et al., 1981) and at one alpine site in Alberta at least (Luckman and Kearney, 1986), treelines exceeded present positions just prior to the Younger Dryas. There is no direct macrofossil evidence of higher or more northern treelines during the Younger Dryas cold interval (11-10 ka BP), which is perhaps not surprising. During the millennium after the Younger Dryas interval, treelines exceeded present positions both latitudinally and in elevation in the far Northwest (Northwest Territories, Yukon, and Alaska; Hopkins et al., 1981; Nelson and Carter, 1987), in southwestern British Columbia (van Ryswyk, 1971; Clague and Mathewes, 1989), and in Colorado (Elías, 1985; Carrara et al., 1991). Abundant sites indicate higher than present treelines in the Cordillera and more northern treelines in the Northwest from 9 to about 5 ka BP. As before, these sites are distributed from Alaska to Colorado (Dettmerman, 1970; Eisdale et al., 2001; citations earlier in paragraph). The relative paucity of sites dating between 5 and 3.5 ka BP possibly indicates that treeline was near its present elevation at that time. However, the sites with wood of this age have the same distribution as before 5 ka, except that additional sites from late-deglaciated Keewatin and Québec appear in this interval. The concentration of sites dating 3.6-2.8 ka BP may indicate a new advance of treeline or simply the maintenance of higher and more northern treelines until 2.8 ka BP. These sites are distributed from Québec and Keewatin (mainland Nunavut) to Alaska and Colorado. After 2.8 ka BP, the evidence suggests retreat of the larch limit in northwestern Québec (Gagnon and Payette, 1981) and

### TABLE IX

<table>
<thead>
<tr>
<th>Mixed forest association</th>
<th>3 ka</th>
<th>2 ka</th>
<th>1 ka</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spruce dominated</td>
<td>4</td>
<td>8</td>
<td>20</td>
</tr>
<tr>
<td>Spruce co-dominated (with white pine, hemlock or birch)</td>
<td>9</td>
<td>14</td>
<td>14</td>
</tr>
<tr>
<td>Number of sites classified as mixed forest</td>
<td>196</td>
<td>190</td>
<td>208</td>
</tr>
</tbody>
</table>

**FIGURE 16** Radiocarbon dates on tree remains that grew above (Alpine) or north of (all others) present treeline.

*Dates au radiocarbone de restes d’arbres qui ont poussé au-dessus (Alpina) ou au nord de la limite de pousse des arbres actuelles.*
perhaps brief intervals of treeline advance in Kewatin, in the St. Elias Range and in south-central British Columbia.

Hence, at its simplest, this distribution of radiocarbon dates indicates a warmer than present middle and early Holocene and a cold Neoglacial with brief warm intervals. Magnitudes of minimum treeline displacement indicated by these sites tend to be in the range of 50–300 m for alpine treeline, which implies temperature changes of as much as 3 °C, a value generally in accordance with estimates of Holocene thermal maximum temperature increases (Kaufman et al., 2004). Mid-summer latitudinal temperature gradients in Canada are about 1 °C per 100 km (National Atlas of Canada). Therefore, as a rule of thumb, we might expect a sustained future summer warming of 3 °C to force biome boundaries northward by about 300 km. Temperature gradients are less than that in areas of greater continentality, most conspicuously in the Interior Plains region of Saskatchewan, Alberta, and the Northwest Territories. Larger shifts might be expected there.

**BIOME MIGRATION RATES**

We will consider postglacial biome migration rates along several lines of section drawn in the direction of overall biome expansion during deglaciation. Rates are given in both radiocarbon and calendar time scales using the conversions in Stuiver et al. (1998).

Section A-B of Figure 17 illustrates migration of biome boundaries through time along a line from the American Midwest to the south shore of Hudson Bay, a line essentially normal to the receding ice margin. The northern limit of the boreal forest advanced 1,490 km between 18 and 6 ka BP (16.8 and 6.6 calendar ka BP), at an average rate of 227 m per 14C yr (186 m per calendar year). During two intervals—14 to 12 ka and 8 to 7.6 ka BP—the northern limit of boreal forest advanced more slowly than the ice front retreated and forest tundra or tundra appeared briefly before the forest arrived. Possibly these ecological conditions enhance the rate of ice recession exceeded the ability of forest limits to advance due to edaphic, biotic, or climatic limitations. The average rate of advance of the forest limit by 450 km between 14 and 12 ka BP (16.8 and 14 calendar ka BP) was 225 m per 14C yr (161 m per calendar year). Between 10 and 8 ka BP (11.35–11.55 to 8.85–9.0 calendar ka BP), at the average rate of 124 m per 14C yr (102 m per calendar year). During two intervals—14 to 12 ka and 8 to 7.6 ka BP—the northern limit of boreal forest advanced more slowly than the ice front retreated and forest tundra or tundra appeared briefly before the forest arrived. Possibly these ecological conditions enhance the rate of ice recession exceeded the ability of forest limits to advance due to edaphic, biotic, or climatic limitations. The average rate of advance of the forest limit by 450 km between 14 and 12 ka BP (16.8 and 14 calendar ka BP) was 225 m per 14C yr (161 m per calendar year). Between 10 and 8 ka BP (11.35–11.55 to 8.85–9.0 calendar ka BP), at the average rate of 124 m per 14C yr (102 m per calendar year). During two intervals—14 to 12 ka and 8 to 7.6 ka BP—the northern limit of boreal forest advanced more slowly than the ice front retreated and forest tundra or tundra appeared briefly before the forest arrived. Possibly these ecological conditions enhance the rate of ice recession exceeded the ability of forest limits to advance due to edaphic, biotic, or climatic limitations. The average rate of advance of the forest limit by 450 km between 14 and 12 ka BP (16.8 and 14 calendar ka BP) was 225 m per 14C yr (161 m per calendar year). Between 10 and 8 ka BP (11.35–11.55 to 8.85–9.0 calendar ka BP), at the average rate of 124 m per 14C yr (102 m per calendar year). During two intervals—14 to 12 ka and 8 to 7.6 ka BP—the northern limit of boreal forest advanced more slowly than the ice front retreated and forest tundra or tundra appeared briefly before the forest arrived. Possibly these ecological conditions enhance the rate of ice recession exceed...
FIGURE 17. Biome profiles along four lines of section as shown on the map at lower right.

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as for example where mixed forest replaced boreal forest or where grassland replaced parkland. If these rates are accurate tests of the ability of biome limits to shift in response to rapid climate change, as they appear to be, then over the next century we should expect biome limits in Canada to shift by only 10 to 20 km in most places and 50 km where latitudinal thermal gradients are lowest.

Terrestrial biome shifts of the last 20,000 years were forced primarily by climate's response to changing orbital geometry amplified by the positive feedback from reduction of ice-surface area, both processes operating nearly monotonically over the entire interval. With the possible and important exception of the terminal Pleistocene mammalian extinctions, terrestrial biome responses to shorter, high magnitude events, such as the Younger Dryas cooling and terminal warming, the 8200 calendar year BP cold event, and the Neoglacial coolings, were comparatively small, albeit regionally important. Unfortunately, the resolution and number of paleoecological records from northern North America are inadequate to assess what terrestrial biome responses there may have been to abrupt changes prior to 13 ka BP -- the well-documented Heinrich (or Dansgaard-Oeschger) events seen in the oceans and ice sheets.

Past climate changes were amplified at higher latitudes because of the changing axial tilt of the planet. Because stronger axial tilt leads to both warmer summers and colder winters at middle to high latitudes, intervals of warmer post-glacial summers were also intervals of greater seasonality. Future warming that might be forced by increased greenhouse gas concentrations will also be amplified at higher latitudes of the Northern Hemisphere, as in the past, but because of global land and ocean distributions, land being more readily warmed than water. However, future warming will occur disproportionately in winter months (Houghton et al., 1996), thus further reducing seasonality.

Despite these differences between future and middle Holocene seasonality, and excluding the central and eastern Canadian Arctic and Subarctic areas of late deglaciation, mid-dle Holocene (6-7 ka BP) biome distributions are reasonable guides for long-term biome displacements that might be expected under the initial 2-3 °C of future warming, because natural biome limits seem to be controlled mainly by growing season conditions. Grassland and parkland expansion in Alberta might more closely resemble conditions at 11 ka BP, but with boreal forest rather than tundra to the north if future warming is accompanied by substantial drying. All of these displacements are such that they would be expected to occur over several centuries if the postglacial migration rates discussed above are limiting rates. Future rates of climate change may be quite rapid (Houghton et al., 1996) and more rapid than at most times during the Holocene. However, they will probably not be more rapid than the step-like changes that bounded the Younger Dryas, the pre-Boreal cold period, and the 8.2 ka BP event, when temperature changes of several degrees occurred over decades. Future biomes will probably change in composition because they will have the added benefit of hosting those plants and animals, or the detritus of hosting pests, whose ranges are now and were formerly limited by more extreme winter cold.

**SANGAMONIAN ANALOGUES**

Future warming is expected to exceed that of the Holocene thermal maximum (Houghton et al., 1996), which in most places in northern North America was 3 ± 1 °C (Kaufman et al., 2004). Furthermore, areas of late deglaciation were exposed to the direct biotic effects of the early Holocene summer radiation maximum. Hence, warmer periods of the last (Sangamon) interglaciation are probably better guides to the medium-term impact of future warming.

The available geological information indicates Sangamonian biome adjustments that far exceed those of the Holocene. For example, the patchy shrub tundra of southeastern Baffin Island was much richer in shrub birch than at any time during the Holocene (Miller et al., 1999; Wolfe et al., 2000) and rich shrub tundra extended beyond Clyde River on the central east coast of Baffin Island (Miller et al., 1977). The latter site is 450 km beyond the modern limit of birch and about 1000 km beyond modern birch shrub tundra that is as productive of birch pollen. Similarly, macrofossils of *Betula glandulosa* in fluvial gravel assigned to the Sangamonian on Baffin Island in the central Arctic indicate spread of shrub tundra at least 600 km north of the present birch limit (Dyke and Matthews, 1987). Savé dredge-remains at that site represent a range extension eastward of about 1200 km for this calciphile from its present range limit in the Richardson and Mackenzie mountains of the western Cordillera. This occurrence perhaps illustrates how difficult it might be to estimate future species range extensions. Probable Sangamonian peat on High Arctic Bathurst Island contains macrofossils that are characteristic of lower arctic regions today. There is no indication that the shrub birch limit reached that site (Blake, 1974); hence, the site probably was then in the Mid Arctic floristic zone. It appears that most of what is called the Mid-Arctic in certain Canadian vegetation schemes (Edlund, 1986) was a Low Arctic shrub tundra during the warm parts of the Sangamonian. This degree of shift of biome boundaries was so large that we suggest that most of the higher Arctic herb tundra then had much greater species diversity and that most of the modern shrub tundra was then forest tundra. Even these large Sangamonian biome shifts were not as great as in comparison to those modelled for the next century from certain GCM climate fields (Lenihan and Neilson, 1995).

In unglaciated areas and areas of early deglaciation, Sangamonian environments are better guides than Holocene environments to the long-term impact of future warming should warming exceed that of the Holocene thermal maximum. Chapters in Mott and Matthews (1990), from which some of the examples below are drawn, provide a review of Sangamonian environments in Canada. Unfortunately, few sites seem to capture peak Sangamonian temperature conditions. At present treeline in unglaciated northern Yukon, a Sangamonian pollen profile indicates a closed boreal forest dominated by spruce and birch, and hence a treeline well north of present, possibly reaching the Arctic coast (Matthews et al., 1990). Sangamonian organic beds on Banks Island, a region in the western Arctic that was deglaciated early, are much richer in shrub birch (*Betula glandulosa* and *B. nana*) than is the present environment (Vincent, 1984), probably comparable to the environment just beyond modern treeline. Cape Breton,
Nova Scotia, supported an oak-ironwood-white pine forest during a warm part of the Sangamonian compared to the mixed-boreal transitional forest there today (de Vernal et al., 1986) and a white pine-dominated mixed forest extended to the Magdalen Islands (Mott, 1990). It does not appear to have extended to Newfoundland, where a spruce-fir-birch-pine boreal forest flourished based on the only documented interglacial site (Brookes et al., 1982). Mott (1990) found that Sangamonian pollen spectra in the Maritimes most closely resemble modern pollen rain in Minnesota and Wisconsin, thus indicating warmer and drier – more continental – climate. The Sangamonian Don Formation at Toronto does not necessarily include the warmest part of that interglacial, because its pollen profile shows a long cooling trend. At the beginning, mean annual temperatures about 5 °C warmer than present are indicated by an oak-dominated forest with elm, hickory, basswood, and sweet gum (Liquidambar sp.). (Terasmae, 1960). Macrofossils indicate the presence of Osage orange (Maclura pomifera), black locust (Robinia pseudacacia), southern white cedar (Chamaecyparis thyoides), chestnut oak (Quercus muehlenbergii), iron oak (Quercus stellata), and blue ash (Fraxinus quadrangulata), all of which occur farther south today (Karrow, 1990). Investigations of the Missabi Formation and equivalent interglacial deposits in the Hudson Bay Lowlands indicate conditions at least as warm as present but not greatly warmer (Dredge et al., 1990). The Saskatchewan area, now on the grassland-forest boundary, was occupied by grassland during the Sangamonian; the extant members of its Sangamonian mammalian fauna occur 500 km and more to the south today (Skwara Wolf, 1981). The Sangamonian Muir Point formation of southern Vancouver Island has a pollen profile dominated throughout by Douglas fir indicating conditions at least as dry and warm as present (Hicock, 1990).

CONCLUSION

Biomes are large-scale, climate-controlled, vegetation and animal assemblages. The distribution of Late Quaternary biomes of northern North America and their general assemblages can be reconstructed with reasonable confidence, although the geographical and temporal distribution of data remains uneven. The major remaining source of error in Late Quaternary biome reconstructions (and paleogeography of this interval in general) is poor radiocarbon chronology due to the preponderance of dates on bulk lake organic sediments in currently available data sets. Some of the disjunct patterns seen on the maps herein are probably due to this effect (dates that are too old) but we cannot be confident of this until critical sites are re-dated by modern methods. The ever-growing database will eventually allow more precise and finer grained reconstructions that, along with independently reconstructed climate histories, will allow more significant inferences about biome-climate interactions. There is good evidence that forest compositions responded to climate changes within centuries, but there is also evidence that there were times when temperatures had risen to levels that could have supported much more thermophilous vegetation than actually occurred.

Barring human interference, biomes are in equilibrium with the climate provided that the climate is not changing too rapidly. Because the ice sheets during the last glaciation remained in near maximal configurations for a period of about 10,000 years, the vegetation and animal distributions at that time were probably at least as nearly in equilibrium with the climate as the modern distributions are with the modern climate. Subsequent changes in biome distributions and their compositions during deglaciation and thereafter reflect the complex interplay of climate forcing and the dynamic constraints that limit plant migration rates and individual plant tolerances of climatic conditions. The warming ice sheet configuration was one of the strongest controls of continental climate until about 7 ka BP, particularly early in deglaciation. Late deglaciation of the eastern part of the continent delayed attainment of maximum postglacial warmth there. Despite these complexities, regional climate trends through time can be reliably inferred from changing biome distributions and their assemblage changes. Further analysis of the sensitivity of vegetation to climate change at the biome level would be best facilitated if empirical climate reconstructions were available for the same time interval based on sources other than vegetation history. Data to support such reconstructions are starting to appear from fossil chironomid analyses.

Nevertheless, because there is evidence of general summer cooling during the last 3000-5000 years, and because growing season conditions are more critical than are dormant season conditions in determining plant distributions on the northern part of the continent, middle and early Holocene biome distributions and species compositions are reasonable analogues of future equilibrium displacements and changes due to equivalent warming, at least in areas that were long since deglaciated at these times. Peak postglacial summer warmth, although not synchronous across the continent, has been estimated elsewhere to be mainly in the range of 2-4 °C above mid 20th century values. Some estimates of immediate future warming exceed that range and approximate or exceed the warming reconstructed from deposits of the last interglaciation, the Sangamonian. Sangamonian biome shifts were much larger than those of the Holocene thermal maximum, but information about these biomes is poorly distributed.

Biomes boundaries responded to the large climate forcing of deglaciation by shifting northward and toward ice margins at rates that were mainly in the range of 100-200 m per year, while slowly changing in composition. Although in places, biomes shifted as fast as the rate of ice-marginal recession allowed, there is evidence in several regions that summer climates at times were warm enough to support much more thermophilous vegetation than those that were present. If these rates of biome migration pertain in the future, we might expect biomes to shift by 10-20 km in most regions over the next century. A major impediment to using former Holocene climate conditions as a guide to future conditions is that warmer Holocene summers were accompanied by colder winters, whereas warmer summers of the future will be accompanied by warmer winters. Thus plant and animal pathogens may be less constrained than they were in the past.

The terminal Pleistocene faunal extinction, with its loss of 70% of the North American large mammal community, was the largest compositional change in northern North American
biomes during the deglacial hemicycle. Our failure to satisfactorily resolve its cause is a major outstanding problem of Quaternary science. If the extinctions were primarily climate forced, they happened, as far as can be shown for the northern part of the continent, during a time when plant communities were not changing remarkably enough to – or even in a direct way – lead to the demise of the hemlock. This apparent mismatch between cause and effect might suggest that major components of ecosystems are vulnerable to catastrophic collapse without the starkly conspicuous causes. Alternatively, it favours extinction by over-hunting.

Lack of agreement about the causes of some of the major assemblage-level changes in biomes limits the utility of using past changes to infer vegetation sensitivity to climate change. Prominent examples are the relative roles played by fire versus climate in promoting the dominance of jackpine in the eastern North American boreal forest during the early Holocene and the relative roles of insect infestation versus climate in the hemlock decline in eastern North America during the middle Holocene.

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