Vegetation–pollen–climate relationships for the arcto-boreal region of North America and Greenland

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Abstract. We examine modern pollen, vegetation and climate relationships for the arcto-boreal region of North America using isopollen maps, scatter diagrams and response surfaces. These analyses are based on an array of 119 modern pollen sites extending from Alaska to Greenland (excluding the Pacific-Cordillera region of western North America) and north of 42°N latitude. The pollen sum consists of thirty-one taxa selected for their abundance on the modern landscape or significance as indicators of particular vegetation types. Response surfaces were calculated using a locally weighted-average procedure in order to display the percentages of the various taxa as a function of one to three climate variables.

The isopoll maps accurately reflect taxa abundance and range limits, although the actual percentage at these limits may vary. Pollen of the major boreal taxa have optima at 10–20°C and dry (Pinus), moist (Abies) and intermediate (Picea) values of precipitation. Monospecific pollen taxa and those where the species have similar ecologies show a simple climate optimum, whereas pollen taxa with several species, such as Betula, show multiple optima. Each boreal taxon, even those with similar ranges, has a unique surface, suggesting that community level responses to climatic change, whether past or future, are likely to be complex and variable throughout North America.

Key words. Climate–pollen response surfaces, isopollen maps, modern pollen assemblages, boreal forest, Alaska, Canada, Greenland.

INTRODUCTION

The North American boreal forest is a transcontinental biome of vast areal extent. The forest is relatively young, as nearly the entire land surface that it presently occupies was covered by ice during the Wisconsinan. Except for activity associated with recent resource exploitation, there has been little anthropogenic impact on the region. The boreal forest thus provides excellent opportunities to investigate the relationships between modern climate, vegetation, and pollen spectra. Such studies are of considerable scientific interest, due to the possible impact on the boreal forest in affecting concentrations of atmospheric CO2 (D’Arrigo, Jacoby & Fung, 1987), and the suggestion that future climatic changes may significantly affect the extent of this biome (Emanuel, Shugart & Stevenson, 1985).

Recent paleontological work in the boreal forest and tundra (summarized in Barnosky, Anderson & Bartlein, 1987; Lamb & Edwards, 1988; Richard, 1981; Ritchie, 1987) now makes possible a closer examination of vegetational response to climate changes in high latitudes of North America. Interpreting these fossil data requires an understanding of relationships between modern pollen, vegetation and climate. In this paper we examine relationships in these modern data using isopoll maps, scatter diagrams and response surfaces. Because we are primarily interested in high latitudes, our analyses centre on the arcto-boreal region of North America; however, we also include data from the bordering prairie and eastern mixed forest to illustrate the transition to more temperate regions (Fig. 1). With the isopoll maps we characterize the spatial pattern of modern pollen percentages of major taxa, qualitatively compare the isopolls to known plant ranges, and specify continent-wide pollen–vegetation relationships. We then define the relationships between pollen assemblages and one to three climate variables through scatter diagrams and climate response surfaces, using a modification of the method applied to eastern North America by Bartlein, Pretice & Webb (1986). In our analysis, we include a network of 119 modern pollen spectra, extending from western Alaska to Newfoundland and Greenland and from the northern tier of the conterminous United States to the northernmost arctic areas of Canada and Greenland (Fig. 2). We have omitted data from the western Canadian mountains because of the uneven, inadequate coverage of sites and the extreme elevational gradients that result in complex vegetation patterns and indistinct pollen signals (Ritchie, 1987).

The present paper follows our analysis of pollen analogues in the region of continental western Canada and northern Alaska (Anderson et al., 1989) and is a continuation of our research into the climatic and vegetational history of the boreal region (COHMAP, 1988). The

* Order of the authors is alphabetical.
FIG. 1. Maps showing (a) localities discussed in the text and (b) major vegetation types of northern North America.
analogue and response surface analyses will provide the basis for quantitative estimates of late-Quaternary paleoclimates for northern North America.

DATA
The pollen spectra used in this study were deprived from 1119 sites (Fig. 2) where the uppermost few centimetres of sediment were sampled and analysed by standard laboratory methods (Faegri & Iversen, 1975). Our data are primarily from lakes larger than 10 ha and well represent vegetational composition at regional scales (Bartlein et al., 1986). However, in the Great Plains region of the United States, where lakes are rare, samples were also obtained from cattle watering tanks and soil surface layers. There is some uneveness of coverage in the spatial array of sites. For example, in parts of Alaska, the northern Northwest Territories, and the Great Lakes and eastern North American sectors the network is dense, whereas the central High Arctic is virtually unsampled. In setting the spatial array of sites we have extended the coverage well beyond both the northern and southern boundaries of the boreal zone in order to completely encompass the ranges of the major taxa.

The pollen data used herein were derived from a large number of sources. Data from eastern North America are described and referenced in Webb (1985) and Delcourt, Delcourt & Webb (1984); sources for the western Canadian and Alaskan data are listed in Anderson et al. (1989). Data from Greenland were obtained from Bick (1978), Bjorck & Persson (1981), Fredskild (1967, 1969, 1973, 1983, 1985), Funder (1978) and Funder & Abrahamsen (1988). In addition, unpublished data from southwestern Alaska (Anderson and Brubaker) and northwestern Quebec (Gajewski) were included.

Pollen percentages of the following thirty-one taxa were assembled for each site. These taxa were selected because they are either important components of the pollen rain, and/or taxa of significant indicator value: *Picea, Betula, Populus, Thuja*/*Juniperus, Pinus, Abies, Larix*, all trees of transcontinental or regional importance in the boreal forest; *Salix, Alnus, Myrica* and Ericaceae, shrubs of widespread occurrence in boreal and subarctic vegetation; *Gramineae, Cyperaceae, Chenopodiaceae/Amaranthaceae, Artemisia, Compositae, Thalictrum, Oxyria, Rosaceae, Saxifragaceae* and *Cruciferae*, herbaceous taxa of widespread distribution, or in certain instances, important indicator taxa of arctic tundra; and *Tsuga, Fagus, Quercus, Fraxinus, Ostrya*/*Carpinus, Ulmus, Acer, Juglans, Carya* and *Tilia*, deciduous and coniferous trees important in the eastern temperate forest that borders the boreal forest in eastern Canada.

Climatic data were abstracted from published long-term climate normals from stations adjacent to pollen sites. Climatic data for eastern North America were obtained from T. Webb, III (Bartlein & Webb, 1985; Bartlein et al., 1986), and for Alaska from NOAA (1951–80). Climate normals for the Prairie Provinces, Yukon and Northwest Territories, and northern Quebec, were obtained from Environment Canada (1981a, b, 1982), and those for Greenland from NOAA (1981). In regions with few climatological sta-
tions (Yukon and Northwest Territories, Northern Québec and Labrador, and Alaska), trend surfaces were fitted to the available climate normals to estimate climatic values for the pollen sites. We selected three climate variables – July and January temperatures and annual precipitation – to represent the macroclimatic controls of plant distribution and abundance. At the continental scale, these controls include summer warmth, winter cold and moisture availability.

Nomenclature follows Scoggan (1978).

METHODS

Maps of the percentages of modern pollen were prepared by interpolating the data onto a 100 km equal area grid and contouring by hand. Labelled scatter diagrams were produced to depict the relationships between climate and pollen variables, and to identify potentially anomalous data points. Isopoll maps were restricted to continental North America because data from Banks Island and Greenland were too few to reasonably contour. Nonetheless, all data were included in the scatter diagrams and response surfaces.

The response surfaces were generated by a three-step procedure that applied a locally weighted averaging technique (Huntley, Bartlein & Prentice, 1989). First, a grid was generated for the climate space defined by the three climate variables (July temperature, January temperature, annual precipitation), with twenty nodes along each axis. Second, a robust locally weighted average of the pollen percentages was calculated for each grid point. Third, the response surface was displayed by interpolating among these fitted values. The climate grid therefore contains either a total of 20 points (for the response functions that show the relationship between pollen abundance and a single climate variable), 400 points (for the response surface defined by two climate variables), or 8000 points (for the hypersurfaces defined by three climate variables). Only a portion of the potential climate space contains data, so the actual number of fitted values in each instance was less than the total number of grid points.

The locally weighted average at each grid point was constructed using the data that fell within a window centred on the grid point. The window width was one-fifth of the length of the climate variable axis. Within the window, the tricube weight function was used to generate weights for each data value, so that values closer to the centre of the window contributed more to the resulting mean than did values near the edge of the window. The shape of the tricube function is such that the data points that contribute most heavily to each fitted value are those that fall within one-twentieth of the axis length either side of the grid point. This method of determining the fitted values approximates the smoothing of scatter diagrams by the robust locally-weighted regression method (Cleveland & Devlin, 1988). After the fitted values are determined for the grid in climate space, contour diagrams of the surface were obtained by interpolating among the fitted values.

Two important boreal forest pollen taxa are not further discussed – *Populus* and *Larix*. Both are important regional components of the forest and form treeline in certain areas (Payette, 1983). Both are significantly under-represented in the pollen rain (Richard, 1981), and estimation of the response surfaces is not possible using these methods. These could be further studied using presence-absence probability surfaces.

MODERN VEGETATION AND CLIMATE

The boreal forest extends from western Alaska throughout the western Canadian interior (continental Northwest Territories and the Prairie Provinces), across Ontario and Québec to Newfoundland (Fig. 1b). It is dominated by conifers and a few associated deciduous trees and exhibits little variation in floristic composition. The western region, from Alaska to the geographical mid-point of the continent, is dominated by *Picea glauca* (Moench) Voss and *Picea mariana* (Mill.) BSP (white and black spruce respectively). The western limit of *Pinus banksiana* Lamb. (jack-pine) lies near Great Slave Lake with its eastern limit near the estuary of the St Lawrence River. *Abies balsamea* (L.) Mill. (balsam-fir) is most abundant in the eastern region (Québec and New Brunswick), becoming increasingly rare west of Ontario. The deciduous trees, *Betula papyrifera* Marsh. (white birch), *Populus tremuloides* Michx. (quaking aspen) and *Populus balsamifera* L. (balsam-poplar), have transcontinental ranges and assume local dominance on sites recently affected by fire or other disturbance.

In the shrub and herb tundra (Fig. 1b), the proportion of anemophilous taxa is significantly smaller than in the boreal forest with the result that modern pollen spectra are dominated by very few taxa: Gramineae (grasses), Cyperaceae (sedges), *Betula glandulosa* Michx. (dwarf birch) and *Alnus crispa* (Ait.) Pursh (green alder).

In the western interior of Canada, the southern boreal forest borders a narrow zone of aspen parkland, a region extensively modified by agriculture. Remnant communities consist of small groves of *Populus tremuloides* with local populations of *Quercus macrocarpa* Michx. (bur oak) surrounded by prairies or agricultural fields. Farther south, trees disappear and prairies prevail, although only fragments of natural prairie remain in the predominantly agricultural landscape.

In eastern Canada and the adjacent United States, a broad transitional tract, from southeastern Manitoba eastward along the northern shore of Lake Superior across Ontario and Québec to the upper reaches of the Gulf of St Lawrence, marks the southern boundary of the boreal forest with the eastern temperate, mixed forest zone (Fig. 1b). The boundary coincides roughly with the northern range limits of the dominant tree taxa that characterize the eastern temperate forests: *Tsuga canadensis* (L.) Carr (eastern hemlock), *Pinus strobus* L. (white pine), *Acer saccharum* Marsh. (sugar-maple), *Betula lutea* Michx. f. (yellow birch) and *Fagus grandifolia* Ehrh. (beech).

Climatic descriptions for northern North America are available in several major publications (e.g. Bryson & Hare, 1974; Hare & Hay, 1974; Hare & Thomas, 1979). The central feature of the boreal forest climate is the
dynamic effect of the Cordilleran axis on the westerlies producing a standing wave over eastern and central North America. This wave displaces northward the important summer boundary between Arctic and Pacific air masses in the western interior of the continent. To the west of Hudson Bay, boreal climates are characterized by relatively low total annual precipitation (300–450 mm), growing seasons of 4–5 months, and mean July temperatures between 12 and 17.5°C (Fig. 3). By contrast, eastern boreal regions have up to twice the annual precipitation, longer growing seasons, and similar mean summer temperatures. The same west-to-east gradient of total annual precipitation prevails at higher latitudes, with values ranging from 200 mm in northwest Canada and Alaska to 800 mm in northern Labrador and western Greenland. Arctic summers shorten northward to growing seasons of 6 weeks at 80°N in Canada and mean July temperatures of less than 5°C. To the south of the boreal core, higher

<table>
<thead>
<tr>
<th>Pollen Type</th>
<th>January Temperature</th>
<th>July Temperature</th>
<th>Annual Precipitation</th>
<th>July Temperature and January Temperature</th>
<th>July Temperature and Annual Precipitation</th>
</tr>
</thead>
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<tr>
<td>Picea</td>
<td>0.35</td>
<td>0.51</td>
<td>0.09</td>
<td>0.58</td>
<td>0.61</td>
</tr>
<tr>
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<td>0.10</td>
<td>0.37</td>
<td>0.17</td>
<td>0.45</td>
<td>0.57</td>
</tr>
<tr>
<td>Abies</td>
<td>0.13</td>
<td>0.26</td>
<td>0.34</td>
<td>0.43</td>
<td>0.56</td>
</tr>
<tr>
<td>Betula</td>
<td>0.05</td>
<td>0.20</td>
<td>0.11</td>
<td>0.31</td>
<td>0.50</td>
</tr>
<tr>
<td>Alnus</td>
<td>0.34</td>
<td>0.52</td>
<td>0.20</td>
<td>0.57</td>
<td>0.61</td>
</tr>
<tr>
<td>Salix</td>
<td>0.08</td>
<td>0.26</td>
<td>0.14</td>
<td>0.37</td>
<td>0.40</td>
</tr>
<tr>
<td>Cyperaceae</td>
<td>0.21</td>
<td>0.52</td>
<td>0.34</td>
<td>0.57</td>
<td>0.59</td>
</tr>
<tr>
<td>Cruciferae</td>
<td>0.00</td>
<td>0.06</td>
<td>0.00</td>
<td>0.40</td>
<td>0.30</td>
</tr>
<tr>
<td>Gramineae</td>
<td>0.11</td>
<td>0.26</td>
<td>0.05</td>
<td>0.37</td>
<td>0.34</td>
</tr>
<tr>
<td>Artemisia</td>
<td>0.05</td>
<td>0.04</td>
<td>0.14</td>
<td>0.20</td>
<td>0.66</td>
</tr>
<tr>
<td>Tsuga</td>
<td>0.34</td>
<td>0.37</td>
<td>0.35</td>
<td>0.59</td>
<td>0.61</td>
</tr>
</tbody>
</table>
mean summer temperatures and dry continental climates are associated with the aspen parkland and prairies of the western interior of Canada. Similar mild summers, but with humid conditions, are associated in the eastern Great Lakes–St Lawrence regions with mixed deciduous–coniferous forests.

RESULTS
We prepared and examined scatter diagrams and response surfaces for a number of different climatic variables, including mean annual, mean January and mean July temperatures and total annual precipitation for all pollen types in the pollen sum. We present and comment upon only a portion of these analyses to illustrate the scope of our results. For each selected taxon we illustrate and discuss: (1) isopoll maps, (2) scatter diagrams and response surfaces that show the relationship between pollen percentages of a single taxon and one climate variable, and (3) scatter diagrams and response surfaces of pollen percentages and two climate variables. For Picea, we also present response surfaces depicting pollen percentages as a function of three climate variables. Primary vegetational literature is not cited in the following section as the pertinent
information has been abstracted from a recent compilation by Ritchie (1987).

The $R^2$ of the response surface of pollen percentage and one climate variable ranges between 0.52 and 0.00 (Table 1). These values measure the goodness-of-fit of the response surfaces. The values in Table 1 show how well each of the individual climate variables predict the abundance of pollen percentages and how well two combinations of a pair of climate variables predict the abundance of pollen percentages. Values tend to be greater for boreal forest pollen types than for tundra taxa and greater for July temperature than for the other climate variables. The $R^2$ of response surfaces of two climate variables are larger than with one climate variable (0.66–0.20), and in some cases (e.g. Cruciferae) much larger. The July temperature–annual precipitation values are nearly always greater those of July–January temperatures.

**Picea**

The central axis of the Canadian boreal forest generally is characterized by greater than 40% *Picea* pollen, with values exceeding 50% near Great Bear Lake and south-central Labrador (Fig. 4a). Although areas of closed boreal forest exist within central Canada and interior Alaska, *Picea* frequencies remain below 40% in these regions. The *Picea* isopoll map, however, is affected by the regional presence of *Pinus* (Fig. 4b; see Discussion), a prolific pollen producer. The tree’s southern range limit is approximated by the 10% isopoll but the northern limit is not so easily defined. The northern edge of the Alaskan forest closely follows the 10% contour, whereas in Canada tree-line falls between the 20–30% isopoll.

Scatter diagrams of *Picea* versus mean July temperature, mean January temperature and total annual precipitation (Fig. 6) show unimodal patterns, although the distribution is less clear for the latter two plots. The *Picea* response surface (Fig. 6) shows a well-defined optimum centred on mean July temperatures of 12–15°C and annual precipitation values of 750–1050 mm. Highest *Picea* percentages also occur in areas with cool (–17 to –24°C) January temperatures, corresponding to the main core of the boreal forest. The surfaces show generally steeper gradients along the July temperature axis than either January temperature or annual precipitation axes, reflecting a somewhat stronger correlation between the abundance of *Picea* and July temperatures.

*Picea* relationships with January and July temperatures at four stepped values of total annual precipitation (Fig. 7) indicate that maximum pollen percentages occur at higher precipitation values. This portion of the response surface corresponds to the boreal forests of Labrador and
Newfoundland, areas with warm January and moderate July temperatures. The highest *Picea* percentages on the low precipitation (<280 mm) surface are associated with relatively cool January and moderate July temperatures of interior Alaska where closed *Picea*-dominated forest occurs.

**Pinus**

A single species of *Pinus*, *P. banksiana*, grows in the central region of the boreal forest, as outlined by the 40% isopoll (Fig. 4b). The northwestern limit of *P. banksiana* is marked by a rapid decrease in *Pinus* from 30% to 10% between Great Slave and Great Bear Lakes. The northeastern limit coincides with the 10% isopoll. Relatively low *Pinus* pollen in the eastern United States corresponds to low tree abundance in the southeastern portion of its range. In southwestern Canada, the general east–west pattern of the isopolls changes to north–south. This steep gradient reflects the presence of such Pacific–Cordilleran types as *P. contorta* Dougla. (lodgepole pine) and *P. ponderosa* Dougla. (ponderosa pine).

The scatter diagrams of *Pinus* pollen and either annual precipitation or July temperature (Fig. 8) show unimodal patterns for the individual climatic variables, with some skewing of the temperature diagram towards higher values.

The response surface shows an optimum centred on July temperatures of 15–20°C and mean precipitation values of 480–800 mm (Fig. 8). These high values represent the high *Pinus* percentages of western Interior Canada and adjacent western Ontario. There is little relationship with January temperature.

**Abies**

*Abies balsamea* is restricted to the eastern region of the boreal forest (Fig. 4c). It is an under-represented taxon with values of approximately 6% corresponding to areas of maximum tree abundance. The 0% isopoll lies within the tree’s range. A group of low frequencies in the western interior probably records the pollen from *A. lasiocarpa* (Hook.) Nutt (alpine fir), a common Rocky Mountain species.

Maximum *Abies* values are associated with high precipitation and mild January or July temperatures (Fig. 9). Pollen abundances decrease abruptly to minimal values at July temperatures of 11°C, January temperatures of ~24°C, and annual precipitation of 500 mm. The response surface suggests a more important effect of annual precipitation on the value of the pollen percentages than was evident for either *Picea* or *Pinus*. Of the three conifer species so far discussed, *Abies* pollen is centred on the warmest January

![Diagram showing scatter plots and response surfaces of Picea and Pinus pollen percentages](image-url)
temperatures (>−12°C), but as for the other conifers, a strong relationship with July temperature is evident.

**Betula**

The primary boreal species in this genus is *B. papyrifera* (Fig. 4d). The genus is also common at higher latitudes where shrub or dwarf birch (*B. glandulosa, B. nana L.*) grows on southern Banks Island, western Victoria Island, southern Baffin Island, and the southwestern coasts of Greenland (Fig. 4d). In eastern Canada and the adjacent United States, the range of *B. papyrifera* overlaps with that of *B. lutea*, an important tree of the mixed deciduous–coniferous forests. Although our pollen data recognizes none of these taxonomic separations, the *Betula* isopoll map displays the above distributional complexity. For example, the abundance of shrub *Betula* in subarctic tundra and forest-tundra in southern Greenland, northern Quebec and Labrador, and northwestern Canada and coastal Alaska correlates directly with a transcontinental belt of *Betula* frequencies c. 20–30% with values of greater than 30% in northwestern Labrador. A core of high frequencies (>30%) corresponds with the concentration of *B. papyrifera* and *B. lutea* in the eastern maritime and northern Great Lakes forest region. The highest percentages (>30%) of *Betula* pollen corresponds to abundant *B. papyrifera* in interior Alaska.

The scatter diagram of *Betula* pollen percentages versus mean July temperature shows an irregular, roughly bimodal pattern, probably derived from the two major *Betula* species (Fig. 10) whereas the diagram of total annual precipitation and pollen shows a wide relationship across a precipitation range from 150 to 1500 mm. The response surface for July temperature and annual precipitation (Fig. 10) shows an optimum (>30%) centred on 13–20°C, and 1120–1600 mm, with a secondary centre (20–30%) at 5–15°C and less than 650 mm. Values of greater than 10% at 5°C and 1000 mm probably corresponds to the populations of shrub *Betula* on southwest Greenland. The July and January temperature surface (Fig. 10) indicates the strong control summer temperature exerts over the abundance of *Betula* in the southern and northern portions of its range. Within its range, however, greater frequencies of *Betula* pollen occur with both the warmest (>7°C) and coolest (<−17°C) January temperatures. The first region corresponds to tree *Betula* of the eastern temperate forests whereas the second maximum
FIG. 8. As in Fig. 6, for Pinus pollen.

FIG. 9. As in Fig. 6, for Abies pollen.
FIG. 10. As in Fig. 6, for Betula pollen.

FIG. 11. As in Fig. 6, for Alnus pollen.
FIG. 12. As in Fig. 6, for *Salix* pollen.

FIG. 13. As in Fig. 6, for Cyperaceae pollen.
FIG. 14. As in Fig. 6, for Gramineae pollen.

FIG. 15. As in Fig. 6, for Cruciferae pollen.
FIG. 16. As in Fig. 6, for *Artemisia* pollen.

FIG. 17. As in Fig. 6, for *Tsuga* pollen.
reflects *B. papyrifera* of the western forests and shrub *Betula* of the tundra.

**Alnus**

*Alnus* is represented in our region by two major taxa: *A. crispa*, a transcontinental shrub with a boreal range, extending short distances beyond tree-line into both the western and eastern subarctic zones, and *A. rugosa* (Du Roi) Spreng. (speckled alder), a less common species with a similar boreal range. Although some authors distinguish the species palynologically, most of the analyses used in our data set do not include separate frequencies for the two taxa. The isopoll map for *Alnus* (Fig. 4e) shows highest values in the forest–tundra and northern boreal regions, with consistently lower frequencies throughout the southern boreal and adjacent eastern temperate forest. In Alaska there is a broad maximum on the southern slopes of the Brooks Range (Anderson & Brubaker, 1986), and in Greenland *Alnus* is found only in the south (Bocher, Holmen & Jakobsen, 1968).

The scatter diagram of *Alnus* pollen and July temperature shows a well-defined peak centred on 12–13°C, whereas the precipitation diagram shows a skewed distribution towards the lower values (Fig. 11). The highest pollen frequencies are associated with moderate July temperatures (12.5°C) and low precipitation (100–450 mm). As with other boreal species, *Alnus* pollen abundance is strongly affected by mean July temperature, but the response surface (Fig. 11) indicates that January temperatures are also important, with the greatest frequencies occurring between 10 and 12°C July and −24 to −30°C January temperatures.

**Salix**

Although the genus *Salix* contains between fifty and sixty species, occurring in a wide range of communities throughout our study region it is a low pollen producer and thus is underrepresented in the modern pollen spectra (Fig. 4f). *Salix* species are most abundant in arctic landscapes where pollen frequencies can exceed 10%. The scatter diagrams of pollen percentages versus July temperature or annual precipitation reflect this distributional pattern, with low frequencies across the full climatic range and high percentages clustered at low precipitation and temperatures (Fig. 12). The response surface (Fig. 12) shows maximum values at July temperatures less than 8°C, across a range of precipitation from the lowest values to 1100 mm, and probably reflects the abundance of *Salix arctica* Pallas (arctic willow) throughout the North American and Greenland mid- and high-arctic regions. A second minor increase in *Salix* pollen associated with high July temperatures and low precipitation results from the regional abundance of willow species in the interior prairie of southern Canada and adjacent United States.

**Cyperaceae**

Pollen from different genera and species of this large family are indistinguishable and the many taxa occur in a wide range of upland, lowland, and aquatic plant communities. However, we have included the collective taxon in our pollen sum because, as the isopoll map shows, its highest pollen frequencies are consistently associated with subarctic and arctic regions (Fig. 5a). The scatter diagrams show a clear tendency for high pollen values to be concentrated at the lower precipitation and cooler temperature values (Fig. 13). The response surface also registers maxima where July temperatures are less than 10°C, with a secondary concentration of high Cyperaceae percentages at dry, cold conditions (Banks Island).

**Gramineae**

Like Cyperaceae, the Gramineae family is very large. Many of the species are widespread, often dominants, across a wide range of climatic and geographical regions and the pollen is not identified below the family level. This family also shows consistent regional pollen patterns (Fig. 5b). The central forested axis of our area has low frequencies (0–1%). Higher percentages are found in areas corresponding closely to the prairie and tundra, especially the coastal tundras of Alaska. The scatter diagrams (Fig. 14) of pollen percentages versus either July or January temperature or annual precipitation show little relationship between climate and Gramineae pollen. The response surface has a marked trough of less than 10% Gramineae pollen at temperatures between 10 and 17.5°C July temperature across the full span of precipitation or January temperature values. The surface rises steeply at higher July temperatures with a discrete optimum at 24°C and 480 mm of annual precipitation, corresponding to prairie samples.

**Cruciferae**

Several minor herb pollen taxa characteristic of arctic areas occur in many of our modern samples, and as their isopoll maps, scatter diagrams and response surfaces are similar, we have selected Cruciferae to illustrate the group. The other taxa are Saxifragaceae, *Oxyria*, Rosaceae, *Thalictrum*, Chenopodiaceae/Amaranthaceae and Compositae (not including *Artemisia*). Although none of these taxa is confined to the arctic region, all four groups show their maximum pollen frequencies there.

The isopoll map (not illustrated) shows highest values in the western arctic, but scattered percentages elsewhere. The scatter diagrams (Fig. 15) show maximum pollen percentages at low temperatures and low precipitation values. The response surfaces are confined to a small sector of climate space centred on July temperatures of 4°C, January temperatures of −30°C, and precipitation of 150 mm indicative of high arctic conditions.

**Artemisia**

This genus is represented in our area by roughly twenty-five species and several varieties and sub-species. Several taxa are abundant in temperate prairies, while others are widespread in the arctic region from western Alaska to Greenland. The isopoll map (Fig. 5c) registers this distributional pattern, with the maximum values centred on the prairie region. The scatter diagram of *Artemisia* pollen and mean July temperature is roughly bivmodal, with a pronounced peak centred on 17.5°C, and a minor one at 5°C.
(Fig. 16). The annual precipitation scatter diagram shows maximum values at the low end of the scale, centred on 450 mm. The response surface shows a concentration of highest values at 22°C and 200 mm (Fig. 16) reflecting the abundance of *Artemisia* in the prairies. A minor cluster of values less than 2% but greater than 1% centred on 5°C July temperature and 150 mm precipitation (i.e. arctic climate) is registered in our tabular output of data but does not appear on the response surface where values less than 2% are smoothed to zero. A maximum of *Artemisia* pollen which occurs at 20°C July and −16°C January temperatures again reflects prairie samples.

*Tsuga*

A relatively large number of arboreal pollen taxa occur in the eastern temperate region of North America and several types reach their northern limit in the boreal region of eastern Canada. These types show significant pollen frequencies in both modern and fossil pollen assemblages. For these reasons, we include them in our pollen sum. We have selected one, *Tsuga*, to illustrate the range, isopoll pattern, and climatic relationships of the group. Other important taxa are *Fagus* (beech), *Acer* (maple), *Carya* (hickory), *Juglans* (walnut), *Fraxinus* (ash), *Ostrya* (ironwood), *Carpinus* (hornbeam) and *Ulmus* (elm). It should be noted that some of their geographical and climatic ranges and their pollen values differ from those of *Tsuga* in particular details (see also Delcourt *et al*., 1984, and Bartlein *et al*., 1986).

*Tsuga canadensis*, the eastern hemlock, is a dominant tree in the mature forests of the Great Lakes–St Lawrence River region. Like *Abies*, it is an under-represented pollen taxon. The range of *T. canadensis* coincides closely with the 2% isopoll (Fig. 5d). The scatter diagrams (Fig. 17) show roughly unimodal patterns of July temperature centred on 20°C, January temperatures of −7°C and precipitation of 1000 mm. The response surface (Fig. 17) is restricted to higher July temperatures (>15°C) and precipitation (>800 mm) with an optimum at 20°C and 1300 mm. The highest percentages of *Tsuga* pollen are associated with January temperatures warmer than −11°C. At warmer July temperatures, January temperatures seem to have more influence over the shape of the surface.

**DISCUSSION**

The most immediate and striking aspect of our analyses is the presence of large-scale transcontinental patterns in both the isopoll maps and response surfaces. Such coherence underscores the potential of these data for use in paleo-vegetational and paleoclimatic interpretations.

The boreal forest is characterized by high percentages of *Picea* and *Pinus*, whereas tundra is delimited by high frequencies of graminoid pollen (Anderson & Brubaker, 1986; Ritchie, 1987). Variations within the boreal forest (e.g. LaRoi, 1967; Ritchie, 1987) are also evident in the abundance of the major taxa expressed as isopoll maps and response surfaces, as well as in pollen spectra (Ritchie, 1987). For example, the dominance of *Picea* and lack of *Pinus* in Alaska, *Picea–Pinus* predominance in central Canada and *Picea–Abies* in easternmost Canada is clearly reflected in the maps (Fig. 4). High percentages of Gramineae pollen accurately delimit areas of predominately wet tundra. Even the complex map of *Betula* is interpretable in terms of the relative abundance and distribution of its tree and shrub taxa. Pollen data correctly represent the major arcto-boreal vegetation types – within the boreal forest as well as between the biome and adjoining tundra and conifer–hardwood forest.

The spatial consistency and relatively detailed resolution represented in the isopoll maps are necessary if modern pollen data are to be used for either qualitative or quantitative interpretations of past climates. This spatial consistency and resolution are evident in the modern pollen–climate relationships as illustrated with response surfaces.

Certain broad-scale generalizations can be made. The major boreal taxa show maximum values at July temperatures between 10 and 20°C and moderate (*Picea*), drier (*Pinus*) or moister (*Abies*) annual precipitation values. Arctic taxa show their maxima under cool, dry conditions, although some types common in both prairies and arctic tundra (e.g. *Artemisia*) show a maximum only in the warm, dry prairie. Although consistently present, the percentage of *Artemisia* is too low in the arctic to cause an increase in the response surface.

The response surfaces are particularly helpful in depicting those taxa which are affected by a complex, and not always readily apparent interaction of several climate variables. For example, the northwestern limit of *Pinus* does not correlate with any particular isopleth, yet the response surface shows an interaction of July temperature and annual precipitation in affecting pollen abundance. Further, the isopoll map indicates two areas of high *Pinus* pollen (one associated with *P. banksiana* and one with *P. contorta*) but only one maximum occurs in the response surface. Thus, in spite of the presence of at least two species, there exists a ‘*Pinus* climate’ in the boreal region. The converse is also seen; two species with similar geographic ranges can have different climate response surfaces (*Tsuga* and *Fagus*; Bartlein *et al*., 1986).

Certain pollen taxa have strong regional mapped patterns, but the relationship of modern vegetation and climate is poorly understood. For example, the precise regional climate control over such ecologically diverse pollen types as Gramineae and Cyperaceae is not well known, even though the fossil assemblages are interpreted broadly to indicate cold-dry conditions (i.e. a tundra climate). There is little relationship between either Gramineae or Cyperaceae pollen and any climate variable individually, but a better relationship when two variables are considered (Table 1). The interaction of two climate variables can suggest a stronger climate–pollen relationship than is evident with one variable alone. On the one hand, the results presented here show that there is a climate signal in these data, at least on a large scale. However, because cold conditions are always dry, there is a limit to the resolution that can be obtained at the scale of our analysis. Thus suggests that plants in the arctic must be able to tolerate cold and dry conditions simultaneously, or the
discrimination in the arctic is of a different scale, or our samples are too limited.

A consequence of the uniqueness of the response surfaces is that each taxon should exhibit a differential response to a particular climate change (Webb, 1986). The response of a pollen taxon depends not only on the direction of climate change, but also on the climate at the beginning of the change, as both determine the slope of the trajectory on a response surface. For example, a climate that is becoming warmer and moister can cause several different responses in the vegetation depending on the initial conditions. In a region originally at 15°C (July temperature) and 900 mm annual precipitation, the response would be a decrease in *Picea* and no change in *Pinus*, but if originally at 16°C and 400 mm, the response would be no change in *Picea* and an increase in *Pinus* (see Figs. 6 and 8). The most direct implication for this problem is the likelihood that vegetational changes will be complex and vary regionally, even if ultimately caused by the same change in climate (Webb, 1986; Gajewski, 1987).

The isopoll maps and response surfaces are excellent reminders of the dangers of oversimplifying paleoclimatic interpretations. For example, the 10% contour of *Picea* coincides with treeline in Alaska (Anderson, Reanier & Brubaker, 1988), whereas the 20% contour coincides with treeline in eastern Canada. On the response surface, the 20% *Picea* isopoll coincides with a 10°C July temperature in Canada, whereas the 10% isopoll coincides with the same isotherm in Alaska. Such differences in the modern patterns are explicable as a function of topography and wind patterns. Latitudinal treeline of Alaska occurs along the southern flanks of the Brooks Range where the gradient from forested to treeless vegetation is steeper than elsewhere. There and in western Alaska, the prevailing winds during the pollinating season of spruce are westerly, thus minimizing dispersal of *Picea* pollen to tundra landscapes. By contrast, the prevailing winds during the same season in central and eastern Canada flow from the southwest, thus carrying abundant conifer pollen from the forests across the low-lying landscapes to the tundra. This demonstrates that a simple percentage index of treeline may provide inaccurate interpretation of past vegetation or climate. Criteria used in paleovegetation interpretation in one region may not be applicable to another (e.g. using 10% *Picea* as indicating a transcontinental treeline). This problem has been recognized, but these isopoll maps clearly indicate these regional differences, and re-emphasize the need to account for such large variance when interpreting the fossil record.

Another example is the observation, depicted on the response surface, of the importance of temperature in determining the continental distribution of *Alnus* on a biogeographical scale. On a local scale, *Alnus* distribution seems affected more by available moisture, as it is most abundant in lowlands and bogs, and only this latter is typically invoked in interpreting changes in the fossil record. These relationships can be interpreted by comparing isopoll and isotherm maps, but the response surfaces more clearly demonstrate the nature and importance of multiple climatic variables in affecting plant distribution and abundance.

The response surfaces presented above are derived using a geographically broader data-set than the surfaces previously for eastern North America (with some overlap) and a statistical method modified from Bartlein *et al.* (1986). Despite these differences, our results are generally consistent with the earlier results. Any disagreement between the two sets of results are due to inclusion of arctic and boreal sites having lower temperatures and higher precipitation than found in the temperate region. Consequently, trends seen in the eastern North American surfaces are further specified by using the additional northern data. For example, the *Picea* surfaces are similar, except that the maximum at lower temperatures and higher precipitation depicted by Bartlein *et al.* (1986) appears as a peak in our analysis, with lower pollen percentages as temperatures continue to decrease. Although these qualitative comparisons are limited, the general agreement of trends depicted by both sets of results lends confidence that the different methods used in estimating the surfaces do not seriously distort the results. Both studies, however, indicate the need to use large numbers of sites from a geographically extensive array.

We have here presented two views of the same data – isopoll maps and climate response surfaces – which together present complementary approaches to understanding vegetation–pollen–climate relationships. These results can be used to interpret past climates in two ways. Firstly, fossil pollen can be transformed to ‘fossil climate’ by using the climate response surface as a transfer function (cf. Bartlein & Webb, 1985). Alternatively, fossil pollen can be compared to modern pollen, and the appropriate modern climate assigned to the fossil pollen (cf. Webb, Bartlein & Kutzbach, 1987). Although both are related methods of analysis, they together can increase our understanding of past vegetation and climate by providing quantitative estimates of past conditions.

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