Modern analogues of late-Quaternary pollen spectra from the western interior of North America

P. M. Anderson,1 P. J. Bartlein,2 L. B. Brubaker,3 K. Gajewski4 and J. C. Ritchie4 1Quaternary Research Center AK-60, University of Washington, Seattle, WA 98195, U.S.A., 2Department of Geography, University of Oregon, Eugene, OR 97403-1218, U.S.A., 3College of Forest Resources AR-10, University of Washington, Seattle, WA 98195, U.S.A., 4Division of Life Sciences, Scarborough College, 1265 Military Trail, Scarborough, ON M1C 1A4, Canada

Abstract. The western interior of Canada and adjacent north-central Alaska is a well-defined phytogeographic region, centred on the boreal forest, and including marginal grassland, parkland, forest-tundra and tundra zones. Late Quaternary fossil pollen spectra from twelve lake sites across this area are compared with each of 303 modern pollen sites by a chord-distance similarity measure. The resulting analysis, presented in mapped and downcore form, provides an objective assessment of the range of similarity between fossil and modern pollen spectra in space and time. In general, full-glacial (18,000–15,000 yr BP) spectra have analogues with modern arctic and mid-arctic sites. Late-glacial (14,000–9000 yr BP) spectra have no or very few analogues, but modern analogues are found among the modern spectra for most Holocene spectra, with regional variation in the patterns.

Key words. Alaska, western Canada, boreal forest, pollen analogues, late-Quaternary, pollen diagrams.

INTRODUCTION

The reconstruction of Pleistocene and Holocene biogeography requires a knowledge of the pollen spectra deposited by a variety of modern vegetation types. Quantitative estimation of the similarity between modern and fossil pollen assemblages permits an objective assessment of the past vegetation, its similarity with modern types, and the origin and development of the modern forests.

The distribution of sites of modern pollen samples in northern Alaska and in the adjacent western interior of Canada is now sufficiently dense to permit numerical comparisons of modern and fossil assemblages in lake sediments (Anderson & Brubaker, 1986; MacDonald & Ritchie, 1986; Ritchie, Hadden & Gajewski, 1987; Lichti-Federovich & Ritchie, 1965, 1968; Ritchie, 1974). We present such a comparison of pollen spectra from twelve fossil lacustrine sites to 303 modern pollen spectra within the combined Alaska-Canadian area, referred to as western interior North America (Fig. 1).

Overpeck, Prentice & Webb (1985) and Prentice (1980) discuss various means of estimating the similarity between modern and fossil pollen data. Following their suggestion, we use a squared chord-distance measure in our analyses. The results of this analysis provide an objective assessment of the location within our study area of modern spectra that are similar to fossil spectra.

The geographical extent of a search for modern analogues can be important in distinguishing analogous and non-analogous spectra (Birks & Gordon, 1985; Overpeck et al., 1985). Modern pollen spectra should come from a range of vegetation with potential similarity to past conditions. Our choice of area has been determined in part by its phytogeographic coherency and in part by what is known of its late-Quaternary pollen record (Barnosky, Anderson & Bartlein, 1987; Ritchie, 1987). The region encompasses the intermontane region and North Slope of north-central Alaska and the western interior of adjacent Canada, extending to the western limit of the Great Lakes-St Lawrence forest zone. It is bounded to the west by the Cordilleran-Pacific montane axis, a vegetational-floristic complex of significantly different modern composition and postglacial history to preclude possible analogues (Ritchie, 1987). The modern pollen sites represent the full range of Interior vegetation from southern grasslands through boreal forest to high arctic tundra zones. The plant communities and pollen spectra are dominated by a restricted number of arctic, boreal and nemoral species, including both complete and partial transcontinental taxa (Picea, Pinus banksiana Lamb., Abies, Betula) and regionally restricted elements (Fraxinus, Quercus and others).

The following is the usage of geographical terms: northern Alaska includes the Brooks Range and the North Slope; central Alaska is the intermontane region between the Brooks and Alaska Ranges; in Canada we use the primary political subdivisions (provinces, territories, districts).

METHODS

Fossil pollen spectra were compared with modern using squared chord-distance, a dissimilarity measure whose
properties have been described by Prentice (1980) and Overpeck et al. (1985). Squared chord-distance has several desirable properties when applied to pollen data (Overpeck et al., 1985): (1) it is sensitive enough to differentiate pollen samples from different vegetation types at the scale of the formation and even the forest type; (2) its critical values are robust with respect to the choice of the number of pollen types in the pollen sum; and (3) at the large geographic scale considered here, it suppresses local variability, or noise, emphasizing the large-scale patterns in the data. The value of squared chord-distance can vary between zero and 2, with larger values indicating more dissimilar pollen spectra.

The critical values of the squared chord-distance were chosen by comparing modern pollen spectra, both between and within vegetation types as defined and mapped by Rowe (1972) and Vierreck & Little (1975). Histograms of the 12,676 within-type, and the 33,127 between-type comparisons are shown in Fig. 2. In the display and discussion of the results, we use squared chord-distance values of less than 0.095, 0.096–0.185 and 0.186–0.400 to identify ‘good analogues’, ‘analogues’ and ‘possible or weak analogues’ in the modern data set for individual fossil spectra. Values of greater than 0.400 are considered ‘no-analogues’. 25% of the within-type comparisons but only 2.5% of the between-type comparisons in the modern data resulted in squared chord-distance values smaller than 0.095. Only rarely does a smaller value occur when comparing pollen spectra from different vegetation types, and it is therefore taken as an indicator of a ‘good’ or ‘strong’ analogue. Squared chord-distance values less than 0.185 occur in 50% of the within-type comparisons, but less than 10% of the time in between-type comparisons. The 0.185 value is therefore taken as an indicator of clear similarities among spectra, and is probably a conservative threshold for separating ‘analogue’ from ‘no-analogue’ spectra. Whereas 75% of the within-type comparisons result in squared chord-distances less than 0.400, 75% of the between-type comparisons remain greater than this value; 0.400 thus is taken as an indicator of broad similarity between pollen spectra, and is probably a liberal threshold dividing ‘analogue’ from ‘no-analogue’ spectra.

The squared chord-distance values between a particular fossil spectrum and an individual modern one are displayed by means of shading on the accompanying maps (Figs. 5–8). It would be impractical to illustrate all the mapped fossil spectra from the twelve sites, so for each site we have chosen the maps with interpolated ages that lie closest to 1000 yr intervals. This series of maps provides a graphical summary of the spatial location of good and poor modern analogues for Holocene vegetation at these twelve sites. In addition, the temporal variation of the minimal values of the squared chord-distance are plotted for each fossil site (Fig. 9), to illustrate times in the past when good analogues can be found in the modern data.
The pollen sum consists of twenty-five types, which comprise the most abundant pollen types in the region (Picea, Betula, Pinus, Alnus, Gramineae, Cyperaceae), taxa of low or intermediate abundance found throughout all or most of the study area (Larix, Populus, Salix, Juniperus, Myrica, Rosaceae, Compositae (excluding Artemisia and Ambrosia), Artemisia), and geographically restricted taxa (Ulmus, Fraxinus, Quercus, Abies, Ostrya, Thalictrum, Ericaceae, Saxifragaceae, Cruciferae, Oxyria/Rumex, Chenopodiaceae). Some modern samples were omitted in areas where the number was particularly abundant to provide a more uniform spatial field of modern data. In addition, the pollen data from Banks Island and the Melville Horton region of coastal Northwest Territories were adjusted following Ritchie et al. (1987), thereby removing the influence of long distance transport of exotic pollen.

**DATA**

The study area is occupied by tundra, boreal forest, aspen parkland, grassland and minor areas of other vegetation.
FIG. 4. Summary pollen diagrams for twelve lakes from western Canada and northern and central Alaska.
associations (Fig. 1). Gramineae spp., Salix spp., Betula glandulosa Michx. and locally, Alnus crispa (Ait.) Pursh are important tundra plants in most areas, although Betula and Alnus are lacking in northern Banks Island and some areas of coastal Alaska. Boreal forest, the most common vegetation type, is dominated by Picea, Pinus and Betula papyrifera Marsh, with Pinus more common in the south-east and B. papyrifera more abundant in the northwest. Although we have neither mapped the vegetation nor grouped modern pollen sites into subdivisions within the Boreal Forest Region, it is important to note two sub-zones that differ in the proportions of the dominant taxa, the presence/absence of Pinus, and in several geological and edaphic characteristics that undoubtedly play a controlling role (Ritchie, 1987; Timoney, 1988). The boreal region to the east of Great Bear Lake, referred to here as southern boreal forest, is underlain by Precambrian Shield bedrock geology and has been completely glaciated in the late-Pleistocene. Soils are acidic regosolic or dyric brunisols. Picea mariana (Mill.) B.S.P. is more common than Picea glauca (Moench) Voss, particularly near treeline, and Pinus banksiana is abundant in younger, post-fire stands. Westward from Great Bear Lake and the Mackenzie River Valley and throughout central Alaska, the terrain was either unglaciated or deglaciated early and the sedimentary bedrock produces deeper, eutric brunisols. In this northern boreal forest, Pinus is absent, B. papyrifera is the dominant associate of Picea, and treeline stands are dominated by P. glauca. Parkland and grassland occupy relatively small areas. The former is characterized by Populus and other eastern deciduous trees (e.g. Quercus, Fraxinus, Ulmus) and the latter by Gramineae and prairie herbs (e.g. Chenopodiaceae).

The modern pollen registers these main patterns of vegetation (Fig. 3) (Anderson & Brubaker, 1986; Lichit-Federovich & Ritchie, 1965, 1968; MacDonald & Ritchie, 1986; Ritchie, 1974; Ritchie et al., 1987). Grassland spectra are characterized by >10% Gramineae, Artemisia (20%), Chenopodiaceae (5–15%), and low Picea (<20%). Pinus (<20%) and Cyperaceae (<10%) pollen. Spectra from the aspen parkland exhibit moderate amounts of Pinus (20–30%), Picea (<10%), Gramineae (10%), Artemisia (5%), with deciduous tree pollen in low but constant frequencies (Quercus, Ulmus, Fraxinus, Populus).

The boreal forest is characterized by 10–20% Picea, Pinus frequencies that decrease from >20% at southern Canadian sites to <10% near its northern limit at Great Bear Lake and trace amounts in northwest Canada and central Alaska. Betula is more common in eastern and central Alaska (>40%) than in Canadian sites (10–20%). Tundra spectra have increasing frequencies of Gramineae and herb (e.g. Oxyria/Rumex) pollen from south to north, and decreasing percentages of Ericaceae, Betula and Alnus.

Pollen diagrams from twelve sites summarize the full-glacial, late-glacial and postglacial vegetational history of the study area (Figs. 1 and 4). Riding Mountain and Lofty Lake (Ritchie, 1964, 1969; Lichit-Federovich, 1970) show the development of the southern boreal forest and the expansion of grassland and aspen parkland during the mid-Holocene. Wild Spear Lake, Lac Demain and Lac Mélèze (MacDonald, 1987) are in the Mackenzie River watershed in the transition from southern to northern boreal forest. Their pollen records trace the history of the boreal forest and show the late Holocene migration of Pinus banksiana. Twin Tamarack (Ritchie, 1985) and Tiinkdhul Lakes (Anderson, Reanier & Brubaker, 1988) show the early Holocene development of northern boreal forest following the late-glacial dominance of shrub tundra. Hanging Lake (Cwynar, 1982) lies in open tundra 10 km beyond the northern limit of Alnus and roughly 25 km north of treeline. Full- and late-glacial pollen spectra indicate an herbaceous tundra with varying importance of Salix and Betula shrubs; the Holocene spectra record Betula-shrub tundra, but with significant components of exotic pollen from nearby northern boreal forests. Ruppert, Joe and Squirrel Lakes (Brubaker, Garfinkel & Edwards, 1983; Anderson, 1985, 1988), located in the lowland northern boreal forests of the southern Brooks Range, record full- and late-glacial vegetation of herb and Betula-shrub tundra. Along with other Alaskan sites, their records document the expansion of Alnus from the west in the early Holocene followed by the spread of Picea from the east in the mid-Holocene. Kaiyak Lake (Anderson, 1985), a lowland lake in shrub tundra of the western Brooks Range, lies 35 km northeast of treeline. Full- and late-glacial pollen spectra were generally similar to other Brooks Range sites, but Holocene spectra indicate shrub tundra rather than forest.

RESULTS AND DISCUSSION

A transect of sites are illustrated (Figs. 5–8) to show regional trends in the analogue results. Four sites had full-glacial records (18,000–15,000 yr BP) (Fig. 5) and nine sites were chosen to illustrate late-glacial (14,000–10,000 yr BP) and Holocene (9000–0 yr BP) analogues (Figs. 6 and 7). An additional example (Fig. 8) illustrates problems in applying our analogue analysis to sites with important components of exotic pollen.

Full-glacial spectra (18,000–15,000 yr BP)

Hanging and Joe Lake pollen spectra have analogues to modern spectra from northern Alaska, and, to a lesser extent, Banks Island and Seward Peninsula (Fig. 5). Fossil spectra at Squirrel and Kaiyak Lakes show no or weak analogues at 18,000 yr BP. However, at 17,000 and 16,000 yr BP all four sites show possible analogues with northern Alaska and/or Banks Island samples. A general decrease in the numbers of analogues occurs at 15,000 yr BP.

In all four lakes the pollen spectra consist of high percentages of Cyperaceae, Gramineae and Salix. However, Hanging Lake also has relatively high percentages of Betula, resulting in a broad geographical range of modern analogues from arctic tundra to boreal forest. By contrast, possible modern analogues for Joe, Squirrel and Kaiyak Lakes consistently delimit herb-dominated tundra.

That full-glacial pollen spectra are predominantly associated with modern shrub or herbaceous tundra sites is noteworthy, as there has been a long debate about the character of full-glacial vegetation in Alaska and the Yukon (see
FIG. 5. Modern analogues for full glacial pollen assemblages from five lakes in Alaska and Yukon Territories. Note: the maps in Figs. 5–8 are at a scale of roughly 1:60,000,000.
FIG. 5 (continued)
FIG. 6. Modern analogues for late glacial pollen assemblages from nine lakes in western Canada and Alaska.
FIG. 6 (continued)
Late-glacial spectra (14,000–10,000 yr BP)

Pollen spectra from the late-glacial period generally have few modern analogues, but the reasons for this poor correspondence differ across the study area (Fig. 6). Sites in central Alaska (Tiinkdhul and Ruppert Lakes), far northwestern Canada (Hanging and Twin Tamarack Lakes), and the Mackenzie watershed (Lac Demain, Lac Méleze, Wild Spear Lake) lack analogues during some or all of the late-glacial because of high Betula, Populus, Salix and non-arboreal pollen in fossil samples. Weak late-glacial analogues for the southern sites of Riding Mountain and Lofty Lake are due to the combined abundance of fossil Picea, Populus and/or non-arboreal pollen.

Squirrel and Kaiyak Lakes in westcentral Alaska are unusual in having relatively common possible analogues, predominantly in tundra of the North Slope and occasionally in the Alaskan boreal forest. These similarities reflect the relatively high percentages of Cyperaceae, Gramineae and Betula pollen as well as the absence of Populus in these fossil records. The late-glacial period was a time of rapid environmental change from glacial to interglacial conditions. The general lack of analogues during this period may indicate that environmental shifts were too rapid for plant populations to follow or that environmental conditions were substantially different from the present causing plant associations not found on the modern landscape. The relative importance of these alternatives is difficult to resolve.

Holocene spectra (9000–0 yr BP)

The modern boreal forest developed during this period, as shown in the maps by a trend toward the modern analogue patterns illustrated in the 0 yr BP maps (Fig. 7), and a general reduction in squared chord distance, illustrated also by the downcore plots of minimum squared chord distance (Fig. 9). Between 9000 and 4000 yr BP, analogues for Riding Mountain fossil spectra are found in the modern grassland/parkland. Modern conditions at Riding Mountain with analogues to modern spectra throughout the southern boreal forest appeared by 2000 yr BP.

The early Holocene analogues of Lofty Lake are located mostly in Alaska, but also in the Prairie Provinces. This is due to the presence of Picea, lack of Pinus and relatively high values of Betula in the fossil assemblages at Lofty Lake and in the modern assemblages of Alaska. There are few good analogues, however. By 7000 yr BP, analogues are mostly found in the southern boreal forest, due to an increase in Picea and Gramineae and a decrease in Betula pollen. Between 5000 yr BP and the present, numerous analogues are found throughout the Canadian, and, at certain times, the Alaskan regions. The overall analogue pattern becomes evident by 5000 yr BP, but is not well developed until 3000 yr BP, indicating a continued but lesser variation among the above-named pollen taxa. This sequence indicates that relatively brief temporal changes in a pollen diagram can find large-scale spatial differences in analogues.

Sites in the Mackenzie River watershed show an early Holocene concentration of central Alaska and northwest Canada analogues, reflecting high Betula and Picea frequencies. In the mid-Holocene, these sites are clearly differentiated between southern boreal forest analogues showing relatively high Pinus (Wild Spear and Lac Demain) and northern boreal forest analogues in Alaska and northwest Canada (Lac Méleze), with no Pinus and high Picea pollen. Analogue patterns similar to 0 yr BP are established at all three sites between 6000 and 5000 yr BP. The separation of these sites after the mid-Holocene indicates that this method can detect differences between closely spaced sites but such differences may be driven primarily by one taxon.

Analogues are rarely found in the early Holocene at Twin Tamarack, Tiinkdhul and Ruppert Lakes, but Squirrel Lake shows strong analogues by 8000 yr BP. The lack of analogues at the first three sites is due to the continued high percentages of Betula and Populus pollen, whereas the early analogues for Squirrel reflect the early arrival of Alnus in westcentral Alaska. By 7000–5000 yr BP, Twin Tamarack, Tiinkdhul and Ruppert spectra are similar to modern samples from central Alaska reflecting an increase in Picea and/or Alnus pollen and the establishment of modern vegetation patterns.

Comparisons between Hanging and Kaiyak Lake (Fig. 8), both currently in shrub tundra close to northern boreal forest and presumably in shrub tundra throughout the Holocene, illustrate the need for caution in interpreting analogue patterns. Despite their broadly similar present and historical settings, these lakes show different analogue patterns. The proximity of Hanging Lake to woodlands of Picea, Betula and Alnus accounts for the good analogues to Alaskan and northwestern Canadian boreal forest. By contrast, Kaiyak Lake registers less pollen of these types and shows greater similarity to modern tundra. This example points to the importance of long-distance pollen dispersal and the possible ambiguity of interpreting pollen spectra close to vegetation boundaries. In these situations pollen accumulation rates and indicator species may modify interpretations based solely on numerical comparisons.

In summary, analogue patterns during the Holocene clearly show the development of the southern and northern boreal forest of northwest Canada and central Alaska due to the early presence of Picea, Alnus and/or Betula across the region. Analogues to the southern boreal forest are found only after the mid-Holocene due to the later expansion of Pinus banksiana in central Canada.

A summary of the temporal changes of the value of the minimum squared chord distance (best analogue) shows the presence of good analogues at each site (Fig. 9). The five sites in Canada all find analogues by 8000 yr BP, indicating vegetation similar to today was present by the early Holocene. By contrast, the northern Canadian and eastern Alas-
FIG. 7. Modern analogues for Holocene pollen assemblages from nine lakes from western Canada and Alaska.
FIG. 7 (continued)
FIG. 7 (continued)
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Modern analogues of late-Quaternary pollen spectra
FIG. 7 (continued)
FIG. 8. Modern analogues for late-glacial and Holocene pollen assemblages from Kayak Lake, Alaska, and Hanging Lake, YT.
kan sites show a peak in the value of squared chord-distance centred at 9000 yr BP, separating periods where analogues can be found before and after that time. Further to the west in Alaska (Kaiyak Lake) this peak disappears.

CONCLUSION

Our results identify tundra affinities for full-glacial vegetation of western interior North America, but corroborate previous subjective views that late-glacial vegetation lacks similarity in the present landscape. Boreal forests originated during the Holocene, with the southern boreal forest developing more recently than the northern boreal forest. Overall, this study has shown that mapping the distribution of modern analogues of fossil pollen spectra is an efficient method to summarize the spatial and temporal aspects of the vegetation history of the region. The ability of this method to synthesize the pollen data of a large coherent phytogeographic region is thus clearly demonstrated.
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