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Analysis of Surface Pollen from Alberta, Canada, by Polar Ordination

Abstract

Surface pollen assemblages from 29 vegetational stands located throughout the Province of Alberta were analyzed using polar ordination and were then compared to vegetational data analyzed using the same techniques. The results revealed that a correlation between these sets of data does exist. By using the techniques of polar ordination, the surface pollen assemblages of the 29 stands clustered into five groups which were representative not of the vegetational composition of the stand, but of the dominant vegetational association in that area. These results suggest that polar ordination is a promising analytical technique that may be particularly useful in delimiting fossil pollen assemblages.

Introduction

Pollen analysts have long been interested in the relationships that exist between the vegetational composition of a plant community and its constituent pollen rain. Previous investigators approached this problem by a variety of methodological procedures, including the analyses of surface moss polsters (Hansen 1946, King and Kapp 1963, McAndrews and Wright 1969, Mack and Bryant 1974, Heusser 1977) and pollen traps (Rowley 1955). More recently, Webb and McAndrews (1976) have used trend surface analysis to map the distribution of the pollen rain across broad vegetational zones in Canada. These data have proven invaluable as an aid in the interpretation of fossil pollen chronologies, but, unfortunately, the basis for many of these studies are geographically restricted.

The palynological record from Alberta is only poorly known from a few selected sites located principally in the central part of the province (Hansen 1949a, 1949b; Lichti-Federovich 1970, 1972; Jackson 1979; Kroker 1979; Holloway *et al.* 1981). However, in order to precisely interpret these palynological records, it is necessary to first understand the existing relationships between the vegetation and the surface pollen rain from this region.

Janssen (1970) has correctly observed that the pollen rain of any particular plant community is comprised not only of the pollen rain produced locally, but in addition, contains pollen deposited as a result of long distance transport from adjacent communities in the paths of prevailing winds. Thus, in attempting to interpret the distribution of the major pollen rain, it is necessary to view the spatial distribution of major plant associations throughout the region. Since vegetational patterns and the distribution of extant plant communities can be easily investigated by using the gradient analysis approach (Whittaker 1967), I decided to apply this methodology to analyses of surface pollen data collected from communities located throughout the Province of Alberta (Fig. 1).

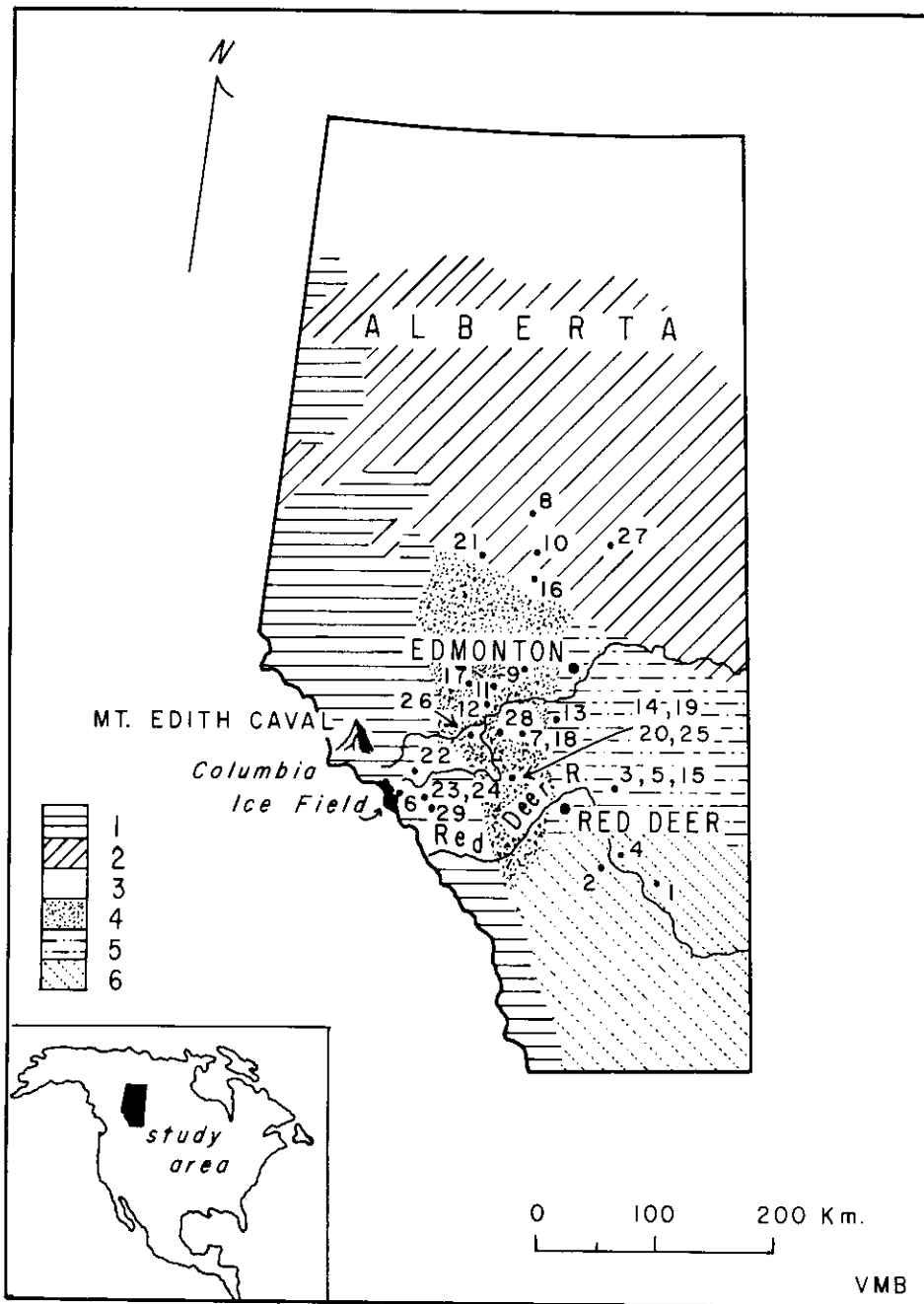


Figure 1. Map of Alberta, Canada, showing sampling locations and major vegetational associations. 1=Montane and Foothills region; 2=Mixedwood Forest Region; 3=Northern Mixedwood Forest Region; 4=Spruce-Aspen Ecotone; 5=Aspen Parkland; 6=Grasslands. Vegetational associations are generalized after Rowe (1972) and North (1976).

Methods and Materials

The vegetational composition of 29 plant communities, which represent the major plant associations of Alberta (North 1976), were studied using the releve method of Muller-Dombois and Ellenberg (1974). This method allowed for the statistical analysis of data recovered from several stands of each plant association. A 10 X 10 m plot from each stand was used throughout, irrespective of the vegetational composition of the stand, in order to provide a more nearly accurate comparison between stands (Muller-Dombois and Ellenberg 1974). The vegetation of each plot was described by vertical stratification levels consisting of canopy, secondary canopy, tall shrub, low shrub, herb and grass. Space limitations prevent the inclusion of the raw vegetational data. These data may be obtained by corresponding with the author. The relative abundance of each species was determined separately for each stratigraphic level by Daubenmire's (1974) percent cover estimates, and all species identifications were based on Moss (1974). Modern surface pollen samples were collected from each stand using the "pinch" method of Adams and Mehringer (1975). Each composite pollen sample consisted of 25 sub-samples.

The pollen samples were prepared for microscopic analysis following the method of Faegri and Iversen (1975). Small sub-samples of the surface "pinch" samples collected from each stand were first treated with 10 percent NaOH and screened through 200 μ m screen. The residue was acetylated (Erdtman 1960). After dehydration, the concentrated pollen residues were transferred to a mounting medium of 1000 cs silicon oil prior to routine examination at 430X magnification. Horizontal transects of 1 mm intervals were used throughout, and the entire slide was scanned to avoid non-random distribution of pollen on the slide (Brooks and Thomas 1967). A minimum sum of 200 grains per sample was used throughout (Barkley 1934).

Both pollen and vegetational data were then analyzed using polar ordination. Polar ordination is defined as an arrangement of units in a uni- or multi-dimensional order (Goodall 1953 in Bray and Curtis 1957). Ordination, as further developed by Bray and Curtis (1957), is based on the selection of two samples as poles (endpoints) with all other samples positioned along an axis with reference to these endpoints. Three different measures of community similarity are available: percentage distance (PD), Euclidian distance (ED), and coefficient of community (CD). The ordination for this study used percentage distance as the measure of the computations. The endpoints were automatically selected by the Ordiflex Program (Gauch 1977) and provide for a spatial arrangement of the communities along one or more axes based on the degree of similarity between pairs of communities.

Relative pollen frequencies of the 19 most commonly occurring taxa from these samples were used (Table 1). Because of the morphological similarity of palynomorphs, identification and assignment of pollen morphological types to taxonomic categories (except in rare instances) require the use of more inclusive taxa, such as genus or family. On the other hand, identification of the vegetational composition of such stands is usually to the species or sub-species taxonomic level. In the past, studies such as these have computed the vegetational composition and pollen directly, regardless of the level of distinction of the taxonomic level (Cross *et al.* 1980, Fine 1980, Margraf *et al.* 1981). These comparisons using different taxonomic levels in the data base, have led to confusion and lack of agreement of the statistical analyses. In order to compare

TABLE 1. Pollen percentages from surface samples of 29 plant communities.

Pollen taxa	1	2	3*	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29				
<i>Pinus</i>	8	11	13	19	24	30	33	38	37	35	47	46	55	60	66	54	63	62	62	58	74	70	77	78	77	73	78	86	94				
<i>Picea</i>	3	+	4	6	7	8	6	18	5	25	11	30	23	7	10	31	10	20	16	9	15	17	14	15	5	11	18	7	2				
<i>Abies</i>						2			+	+	+	+	+	+	+	+	+	+	+	3		3											
<i>Larix</i>							3																										
<i>Populus</i>	3			+	3		+		+	+	+	+	+	+	3		4								+	2							
<i>Betula</i>			+	2	+	12	30	19	7	2	13	12	8		3	8	11	4	9	15	2	3	2	1	7	6	4	1					
<i>Alnus</i>			4	3	1	21	9	10	2	4	2	6	3	12	4	2	4	2	7	6	4	4	2	2	6	6	+	2	+				
<i>Salix</i>	3	12	12	5	3	10	5	3	7	+	3	2	3	+	+	+	+	3	2	1	1	+	+	2	2	+	+						
GRAMINEAE	20	35	20	13	51	3	2	3	2	3	7	2	3	5	6	4	4	1	1	+	3	+	+	+	1	+	+						
Checo-am	13	7	2	7	12	+	+	+	+	+	+	+	+	1																			
ROSACEAE						11	4											4	+	+	+				2								
ERICACEAE						+	2								3						4												
CRUCIFERAE			+	+	+	+	1		3	+	+	+																					
COMPOSITAE	+		7	1	1	+	1	+	2	+	2				1						+												
LIGULIFLORAE	+		1	+	+				2		17																						
<i>Artemisia</i>	45	12	27	25	1	+	+	+	+																								
CYPERACEAE			+	+	2	+																											
<i>Typha</i>																																	
<i>Opuntia</i>																																	
<i>Selaginella</i>																																	
OTHER			6	8	10																												
Total grains	208	101	214	207	213	229	210	235	258	248	326	248	213	208	208	215	277	213	234	258	239	226	259	385	290	217	328	278	268				

*Pollen sum=101 grains, not statistically valid.

NOTE percentages calculated to nearest whole percentage.

+ = Less than 1%.

data from similar taxonomic levels, I collapsed the precision of the vegetational data in favor of the most precise level of identification that is available from the pollen record.

Results

Ordination of the surface pollen samples from 29 releve plots provided a single dimensional ordering of these stands (Table 2). Pollen percentages of five dominant taxa (*Pinus*, *Picea*, *Betula*, *Alnus* and Gramineae) were then plotted in relation to the axis position of these stands as delineated by the ordination (Fig. 2). The stands were divided into five groups (G1 through G5) based on the observed distribution of these

TABLE 2. X-axis co-ordinates and group placement of stands by ordination.

Stand no.	Pollen data	Group	Vegetational data	Group
1.	0.00000	1	0.00000	A
2.	14.07146	1	3.44531	A
3.	14.97954	1	2.04519	A
4.	20.45224	1	1.43805	A
5.	40.99825	1	14.09084	B
6.	63.01531	2	62.61801	C
7.	67.86011	2	90.42969	D
8.	68.45145	2	51.05864	C
9.	69.41211	2	23.78120	B
10.	70.06535	2	44.67065	C
11.	71.74953	3	45.80246	C
12.	79.39542	3	45.21080	C
13.	80.02547	3	51.04027	C
14.	82.41209	3	38.29805	C
15.	84.05510	3	40.32820	C
16.	84.76803	3	86.06071	D
17.	85.16086	3	33.84874	C
18.	86.87184	3	60.92207	C
19.	87.17326	3	47.42842	C
20.	87.74373	3	76.25789	D
21.	89.88901	4	59.69341	C
22.	91.30963	4	20.34209	B
23.	92.39781	4	23.74863	B
24.	92.54359	4	18.25023	B
25.	92.71649	4	90.09758	D
26.	94.12788	4	51.23453	C
27.	95.00801	4	85.17970	D
28.	96.70612	5	75.71429	D
29.	99.99998	5	99.99998	D

five pollen taxa and natural breaks in the axis position. These group designations are delimited in Fig. 2 by vertical dashed lines.

As a test for the statistical significance of these groups, the mean frequency and ranges of pollen percentages were computed for each of the five dominant pollen taxa by group. A Chi-square test for the strength of this relationship was performed and yielded a Chi-square value of 222.86 with 24 degrees of freedom. This value revealed that the distribution of pollen taxa was statistically significant at least at the 0.001 level.

A second polar ordination was then performed on the vegetational data. The resulting axis positions of these stands are also presented in Table 2. Based on the natural breaks in the ordination, four groups were identified (denoted alphabetically in Table 2). In an attempt to statistically compare the degree of similarity between the vegeta-

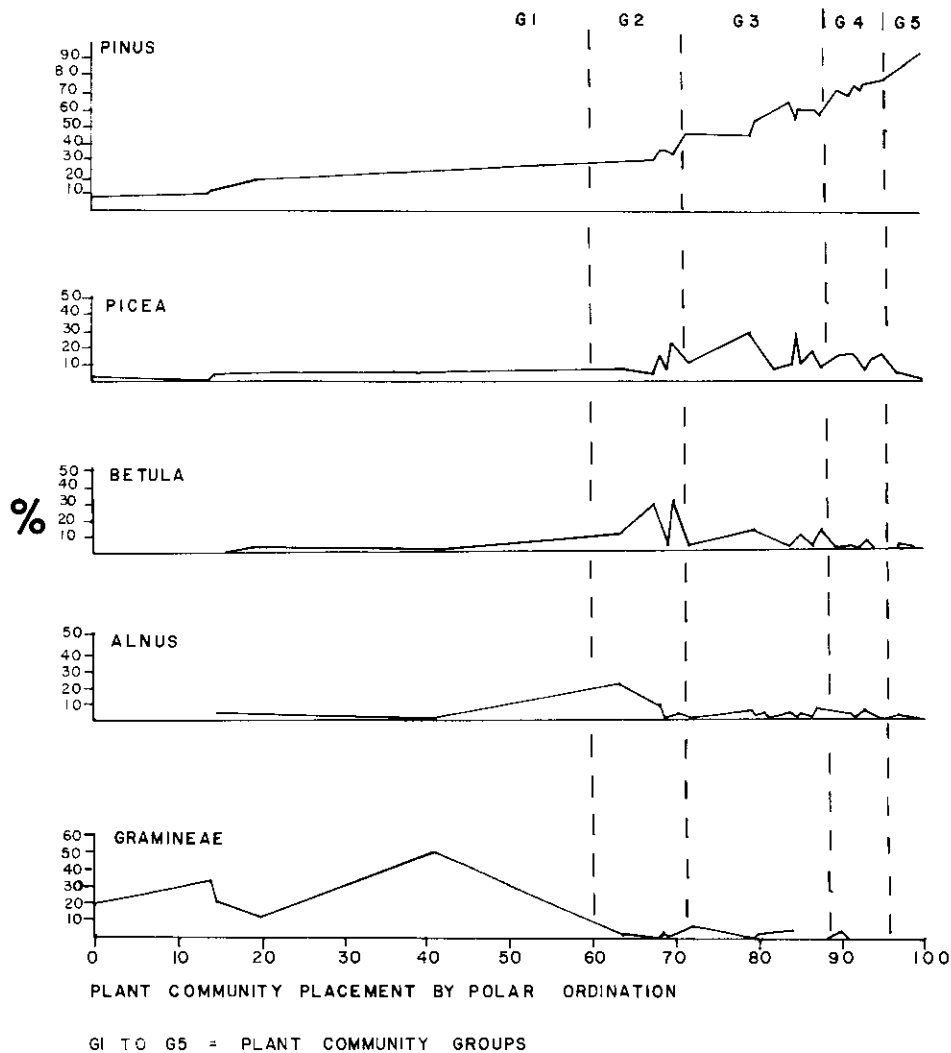


Figure 2. Relationship of selected pollen taxa to community placement by Polar Ordination.

tional and the pollen data, I used a correlation analysis available through the SAS package (Hedwig and Council 1979). The results are presented in Table 3.

The correspondence between the surface pollen spectra and the vegetational composition is close. Using the groups of stands delimited by the ordination of the palynological data, the types of vegetational stands included within each group can be examined.

Group 1. These five stands (no. 1-5) were all located in the southeastern portion of the province, and vegetationally were all described as grassland communities. Gramineae, as expected, dominated the vegetational record. *Artemisia* sp. was also present in large quantities. *Pinus* pollen was present in the surface samples in frequencies ranging from 7-24 percent, although it was absent in the vegetation. Gramineae pollen was high (13-50 percent) as was that of *Artemisia* (1-45 percent). Cheno-am (pollen

TABLE 3. Correlation coefficients of vegetational and pollen data.

		Pearson Correlation Coefficient	
		Pollen	Plant
Pollen		1.00000	0.66938
Plant		0.66938	1.00000
		Spearman Correlation Coefficient	
		Pollen	Plant
Pollen		1.00000	0.53135
Plant		0.53135	1.00000
		Kendall Tau B Correlation Coefficient	
		Pollen	Plant
Pollen		1.00000	0.37238
Plant		0.37238	1.00000
		Pollen	Plant

of the family Chenopodiaceae and the genus *Amaranthus*) pollen was also present (2-12 percent), but again, no specimens of this taxon were observed in the stand.

Group 2. The five stands in this group (no. 6-10) varied in their vegetational composition. Pine pollen ranges from 30-37 percent, *Picea* from 5-25 percent, and *Betula* from 7-31 percent. While the vegetational composition was varied, some correlations were present. Four of the five communities did not have a well developed canopy. Most of the stands in this group were located in the transitional area between the parkland and the boreal forest (no. 7, 9), or were located in the southern boreal forest region identified by Rowe (1972) as the Mixedwood forest region (no. 8, 10). Stand no. 6 was an alpine tundra located near Mt. Edith Cavel in the Jasper National Park. This stand probably clustered with this group because of the reduced pine frequencies.

Group 3. Ten stands (no. 11-20) were included within this group. These stands were principally dominated by aspen (*Populus tremuloides*) and varying percentages of birch (*Betula papyrifera*). Stand no. 11, 12, 16, 18, and 20 (all small and isolated) were not dominated by *Populus* but were located within the area described as the aspen parkland. Pine pollen was intermediate in frequency (45-66 percent), and *Picea* pollen increased to its highest mean frequency (16 percent). *Populus* pollen ranged from 0-4 percent, but this is not unusual because this taxon is normally underrepresented in pollen assemblages (Sangster and Dale 1961, 1964; Holloway 1981) due to poor preservation. *Betula* and *Alnus* pollen are present in moderate amounts (3-14 percent and 2-12 percent, respectively). Rosaceae and Fricaceae pollen are relatively high (4 percent), given their dispersion mechanism and low pollen production, and both indicate the well developed understory component of these stands.

Group 4. This group consisted of stand no. 21-27, and most were dominated by black spruce (*Picea mariana*), larch (*Larix laricina*), or pine (*Pinus contorta*). In addition, most sites contained an understory dominated by *Ledum* and other herbaceous taxa. This understory was not as well developed as those in Group 3 stands. Pine pollen percentages were quite high, ranging from 70-78 percent. *Picea* pollen is also high (5-18 percent) with *Betula* and *Alnus* present but in lower frequencies. One stand (no. 26) was dominated solely by *Populus tremuloides*.

Group 5. This group consisted of the final two stands (no. 28, 29), both dominated by *Pinus contorta*. The surface pollen assemblage reflects this vegetational dominance as *Pinus* pollen is present in excess of 85 percent.

Discussion

The degree of correspondence between the surface pollen rain and the vegetational composition is significant, as shown by the correlation coefficient of 0.66 (Table 3). However, other factors may also be responsible for the observed distribution of the pollen.

Pinus produces larger quantities of pollen that are easily dispersed by the wind. Over one million grains of pollen are produced by each male strobilus (Erdtman 1969); thus, it is not surprising that pine pollen was recovered from several communities in which the taxon was not physically present.

Many of the understory plants of these communities are insect pollinated and therefore produce only small numbers of pollen grains per anther. The presence of any of these entomophilous pollen types in the pollen spectra, even in very low frequencies, usually indicates a well developed herbaceous component. Other pollen grains, such as *Larix* and *Populus*, are thin-walled and do not preserve easily even under ideal conditions (Sangster and Dale 1961, 1964; Holloway 1981). Thus, the pollen spectra would not be expected to reflect accurately the precise vegetation composition of the dominant tree species in a community composed of taxa whose pollen preserved poorly (Mack and Bryant 1974, Mack *et al.* 1978).

The results of the ordination have revealed that the percentages of pine pollen is an important factor in the ordering of the stands. Pine pollen is easily dispersed and is usually over-represented, especially in communities in which pine was not present. Thus, the proximity and density of pine stands to other vegetational communities is largely responsible for the distribution of pine pollen in the local and regional pollen rain. Pines are primarily dominant in the foothills region of Alberta (Rowe 1972), located east of the front range along the western boundary of the province. Since winds are primarily westerlies, *Pinus* pollen is easily dispersed to adjacent, more easterly plant communities.

Muskeg communities (Group 4) are more typically present in the western portion of the province, or scattered within blocked drainage depressions irregularly distributed throughout the southern areas of the Boreal Forest (Rowe 1972). These are wetter sites where spruce dominates the canopy. Local stands of pine may be found on drier, well-drained uplands, but only rarely are other arboreal elements in close proximity to these stands. The large pollen production of nearby pine stands often masks the lower production of *Picea* pollen distribution in these muskegs. As indicated in Table 1, however, this community-type can still be recognized by slight increases in the percentage of spruce pollen. Even though the muskeg community-type is often discontinuous, small pine stands are sometimes in close proximity to them. The presence of these pine stands often effectively obscures the local production of spruce pollen, and this over-representation of pine pollen virtually eliminates the presence of other pollen taxa from inclusion within the pollen record.

Aspen stands (*Populus tremuloides*) are common in both the Aspen Grove and Mixedwood forest regions (Rowe 1972). According to the data recovered from the surface pollen spectra, communities located within each of these forest areas can be identified even though the presence of *Populus* pollen is small. The Aspen Grove region is primarily an ecotone between the forest and the grasslands (Moss 1932, Rowe 1972). Dominant species include *Populus tremuloides*, with sub-dominants of

balsam poplar (*P. balsamea*), *Betula* sp., and *Alnus* sp. In the western portion of this area, representatives of this sub-alpine forest are present, commonly forming a spruce-aspen ecotone. Since *Populus* pollen preserves poorly, larger percentages of *Picea* pollen are often present. Pine is also farther removed from these stands and contributes less pollen to the surface assemblage, and therefore the local pollen production is masked more by *Picea* pollen than by the pine pollen. The presence of other arboreal species in the Aspen Grove is indicated by smaller percentages of *Betula* and *Alnus* pollen. Finally, since these stands are generally open with a well developed herbaceous level, minor increases in Gramineae pollen are recorded in stands from this region.

The Mixedwood (Rowe 1972) is composed of a variety of arboreal species. The dominance of *Betula* and *Alnus* pollen in these Mixedwood assemblages is interpreted as a result of their high pollen productivity and their more successful preservation. While pine and spruce are present within this forest region, their distribution is somewhat restricted. The restrictive occurrence of both *Pinus* and *Picea* in this community-type act to increase the relative pollen frequencies of *Betula* and *Alnus* pollen, which in turn is responsible for clustering of these stands.

The grassland communities are far enough removed from the pine sources so as to contribute little to the surface pollen rain. These stands are clearly dominated, palynologically, by taxa that are present in the vegetational composition, Gramineae and *Artemisia*. This increase in Gramineae, Chen-Am, and *Artemisia* pollen effectively characterizes these grassland communities.

As stated earlier, the one stand recovered from an alpine tundra was an anomaly. This stand clustered with the Mixedwood stands (Group 2). Its high altitude location effectively removed it from distant *Pinus* pollen sources. The vegetation of this stand was dominated either by relatively low pollen producing plants (such as Rosaceae and shrub forms of *Picea* and *Salix*) or by plants whose pollen production had been curtailed by local conditions.

Conclusions

Polar ordination is an effective and simple method for differentiating regional plant community associations based on their surface pollen rain. By reducing the recovered vegetational data base to its lowest common denominator, a more nearly precise analysis of the relationships can be obtained. Using modern surface pollen frequencies, the stands were clustered by ordination into groups that corresponded not to the vegetational composition of the stand but rather to the vegetational component of the major plant associations located within the province.

The inferred gradient obtained by ordination appears to mirror the latitudinal distribution of these plant associations. These associations follow the decreasing pine pollen percentages from areas with high pine pollen (the western montane forests) to those where pine pollen is low (grasslands).

Since polar ordination has been effective in delimiting plant associations based on surface pollen assemblages, it should likewise be useful in grouping fossil pollen assemblages that contain similar component taxa. While small, local vegetational differences will normally not be identified, the results of this study show that major plant associational differences, as reflected by the regional pollen rain, can be identified. The differentiation of major plant associations as revealed through use of pollen or-

dination may, perhaps, also be a beneficial technique for use with fossil pollen records. If fossil pollen samples within a continuum (such as those recovered from lake or bog cores) are treated as discrete community samples, much like the surface pollen spectra discussed in this study, then those levels with similar pollen rain will probably cluster together. The application of polar ordination techniques to the fossil pollen record may reveal additional, quantifiable data concerning changes in major plant associations and successional patterns than are apparent only by use of other standard techniques.

To test this hypothesis, fossil pollen data already available from Central Alberta (Holloway *et al.* 1981) will be analyzed using this technique. The results of this on-going research should elaborate the successional and migration patterns of major plant associations throughout this region of central Alberta during the past 16,000 years and should demonstrate the utility of the polar ordination technique in fossil pollen studies.

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