Pollen deposition in the boreal forest of west-central Canada

Eun Ju Lee, Norm C. Kenkel, and Thomas Booth

Abstract: Deposition of tree and tall shrub pollen was examined along a 5.5-km transect in mixed boreal forest in west-central Manitoba, Canada. Annual pollen deposition averaged ca. 6850 grains/cm^2 in 1992, with jack pine contributing 67.3% and spruce 24.5% of the total. In general, flowering plant species released their pollen in early to late May, while conifer (spruce and pine) pollen release occurred in early to mid-June. Pollen deposition was poorly correlated with relative species abundance in the community, with some species (e.g., jack pine) being over-represented in the pollen rain and others (e.g., aspen poplar) being under-represented. In 1993, spruce pollen deposition was 63% of that in 1992. By contrast, total pollen deposition by jack pine showed little variation from 1991 to 1993. However, pollen release dates varied between years, occurring earlier in years with warmer spring temperatures. Jack pine pollen release exhibited diurnal variation, with the majority of pollen being released during daylight hours on warm, sunny days.

Key words: Manitoba, jack pine, black spruce, boreal forest, pollen rain, palynology.

Résumé : Les auteurs ont examiné la déposition des pollens d'arbres et d'arbustes le long d'un transect de 5,5 km dans la forêt boréale mixte du centre-ouest du Manitoba. En 1992, la déposition annuelle totale de pollen a atteint en moyenne environ 6850 grains/cm^2, la contribution du pin gris étant de 67,3% et celle de l'épinette de 24,5% du total. En général, les plantes à fleurs relâchent leur pollen du début à la fin de mai, alors que les conifères (épinette et pin) le font au début de juin. La déposition du pollen montre une faible corrélation avec l'abondance relative des espèces dans la communauté, certaines espèces étant (e.g., pin gris) sur-représentées dans la pluie pollinique et d'autres (e.g., le peuplier faux-tremble) sous-représentés. En 1993, la déposition pollinique de l'épinette atteint 63% de celle de 1992. Au contraire, la déposition pollinique du pin gris montre peu de variation de 1991 à 1993. Cependant, les dates de relâchement du pollen varient entre les années, survenant plus tôt au cours des années aux températures printanières les plus chaudes. Le relâchement du pollen du pin gris suit une variation diurne, la majorité du pollen étant relâché pendant les heures du jour, au cours des journées chaudes et ensoleillées.

Mots clés : Manitoba, pin gris, épinette noire, forêt boréale, pluie pollinique, palynologie.
[Traduit par la rédaction]

Introduction

In many temperate forest ecosystems, large quantities of tree pollen are deposited over a short period in early summer (Doskey and Ugoagwu 1989). Because pollen grains decompose rapidly and have high macronutrient concentrations, the pollen rain may be an important component of nutrient dynamics in natural terrestrial and aquatic ecosystems (Stark 1972; Doskey and Ugoagwu 1989). Despite this, pollen has been overlooked in studies of boreal forest nutrient cycling (e.g., Foster and Morrison 1976).

A number of pollen deposition studies in anthropogenically altered regions of continental North America have been undertaken to quantify human allergens (e.g., Walton and Dudley 1947; Durham 1933; Bassett 1964). Lichti-Federovich and Ritchie (1964) examined contemporary atmospheric and sediment pollen rain along the forest–grassland transition in southern Manitoba. However, little information is available on the phenology of pollen deposition in the natural boreal forests of continental North America.

A number of studies have described late-Wisconsinan pollen stratigraphy in the western interior of Canada (summarized in Ritchie 1976, 1987; Ritchie and Yarranton 1978; MacDonald and Ritchie 1986). In these studies, pollen assemblages preserved in lake sediments and peat were used to reconstruct past vegetation. However, interspecific differences in pollen production, dispersion, deposition, and preservation limit the resolving power of paleo-vegetation reconstructions (Erdtman 1943; Prentice 1985). Information on pollen deposition in natural boreal forest stands would be useful in helping refine interpretations of the fossil pollen record.

This study was designed to examine early summer (1991–1993) pollen deposition in boreal mixed-forest stands in west-central Manitoba, Canada. The objectives were to determine pollen deposition and temporal profiles for dominant tree and tall shrub species, to examine interannual variation in spruce and jack pine pollen deposition, and to quantify diurnal variation in the deposition of jack pine pollen.

Study area

Location

The study area is located in west-central Manitoba (54°40′N, 101°30′W), approximately 10 km northwest of Cranberry Portage (Fig. 1). Mean elevation is approximately 300 m asl. The climate

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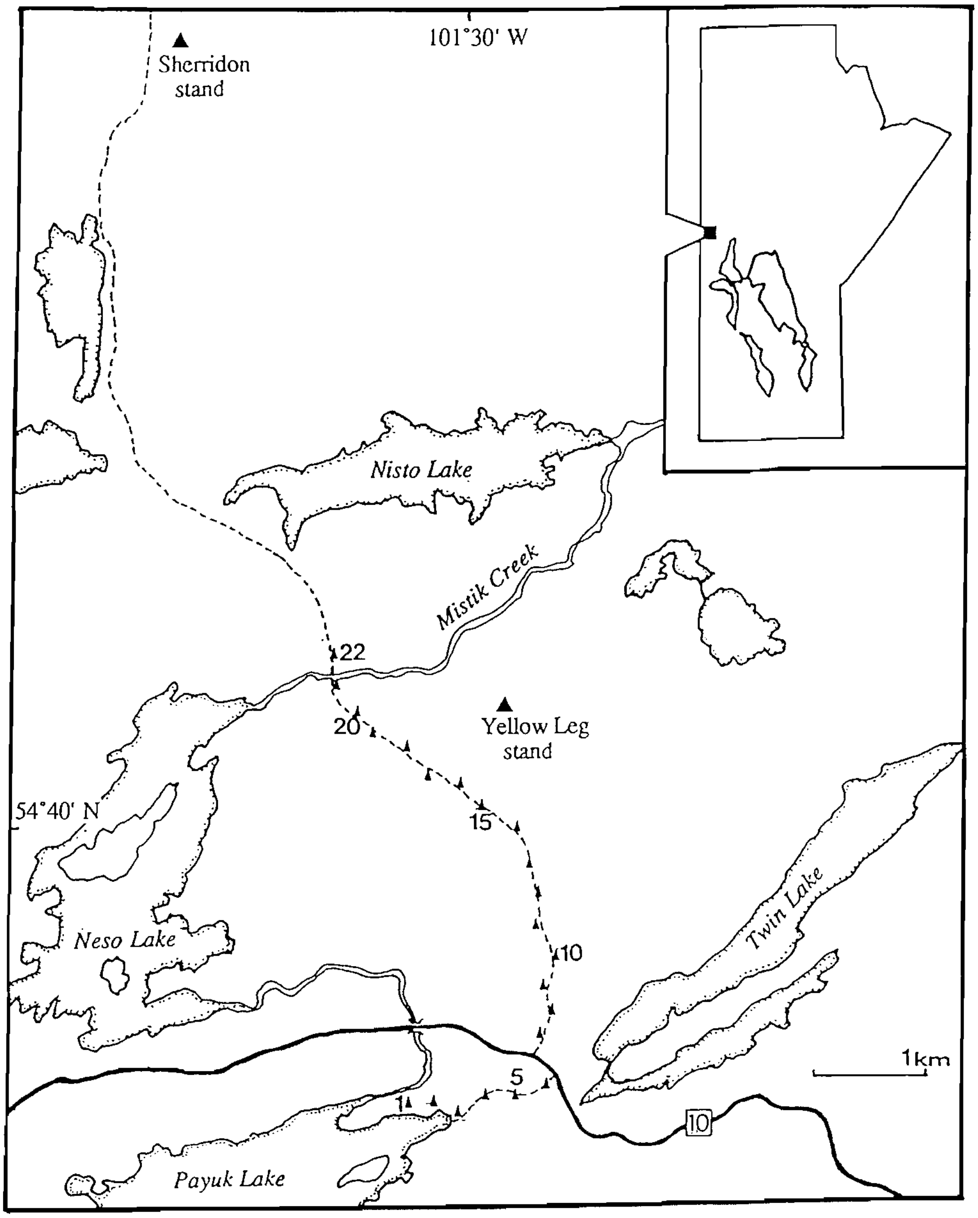
Fig. 1. Location of the study area in west-central Manitoba, Canada. The 5.5-km transect is located along the Sherridon Road (dotted line). The 22 sampling station locations are indicated by triangles.



is subhumid continental, with mean annual precipitation of 484 mm and a mean annual temperature of −0.5°C. Prevailing winds are from the northwest. Climate data is based on 27 year normals (1964−1990) at Flin Flon airport weather station, approximately 11 km northwest of the study area.

Geology and Vegetation

The study area lies on the Canadian Precambrian Shield. Intense glaciation has resulted in irregular relief characterized by granitic rocky ridges separating poorly drained depressions and narrow lakes. Exposed rock barrens are common, and soils are generally thin and of low fertility with a weakly developed podzolic profile (Rowe 1972).

The region lies within the northern coniferous section of the boreal forest (Rowe 1972). Black spruce (*Picea mariana* (Mill.) BSP.) is the dominant tree of poorly drained lowlands. Jack pine (*Pinus banksiana* Lamb.) is common on well-drained sands and on the thin soils of upland rock outcrops. Under more favourable soil conditions, white spruce (*Picea glauca* (Moench) Voss), balsam fir (*Abies balsamea* (L.) Mill.), aspen poplar (*Populus tremuloides* Michx.), and balsam poplar (*Populus balsamifera* L.) form mixed stands. The study transect is located in a mixed boreal forest stand of density ca. 3200 trees/ha. Trees are 8−30 m high with a mean diameter of 11.2 cm at breast height. The mean age of jack pine trees in the area is 65 years (n = 49).

Methods

Study site

A 5.5-km transect through mature boreal mixed forest was established along the Sherridon road between Payuk Lake and Mistik Creek (Fig. 1). This region is readily accessible, and is representa-

Table 1. Composition of mixed boreal forest near Cranberry Portage, Manitoba (based on n = 1760 trees).

Species	Proportion of individuals (%)	Total basal area (cm^2/ha)	Relative basal area (%)
Alnus crispa	12.2	4 407	1.5
Alnus rugosa	4.2	2 064	0.7
Betula papyrifera	3.9	6 138	2.1
Abies balsamea	2.0	3 155	1.1
Populus balsamifera	2.6	9 570	3.3
Populus tremuloides	10.0	50 688	17.4
Larix laricina	2.0	3 610	1.2
Salix spp.	5.4	1 972	0.7
Picea mariana	45.3	90 707	31.2
Picea glauca	4.1	67 570	23.2
Pinus banksiana	8.4	51 245	17.5

tive of the boreal forests of west-central Canada. Twenty-two sampling stations (regularly spaced, approximately 250 m apart) were established along the transect for sampling in 1992 and 1993. At each sampling station, two pairs of pollen collectors were established, one pair on each side of the road (88 pollen collectors in total). Collector pairs were located at least 10 m apart. To minimize forest–road edge effects, collectors were randomly located between 12 and 44 m from the road. In 1991, 26 pollen collectors at 13 sampling stations were sampled.

Vegetation sampling

Forest stand information along the transect was determined using the point-centered quarter method (Mueller-Dombois and Ellenberg 1974). At each sampling station, two transects (one on each side of the road) were located from the roadside into the forest. Ten points were located at 10-m intervals along each transect, and at each point the distance to and basal area of the nearest tree (>2.5 cm in diameter and >2 m in height) in each of four quadrants were measured. A total of 1760 trees and tall shrubs were enumerated.

Phenology of pollen deposition

In 1991, pollen sampling was undertaken from May 31 to June 17 to determine jack pine pollen deposition. The sampling period was extended in 1992 (May 3 – June 22) to allow for determination of pollen deposition by all tree and tall shrub species in the region. In 1993, sampling occurred from May 20 to June 18 to determine jack pine and spruce pollen deposition. In 1992, direct daily observation of collected catkins and male cones were made to determine timing of pollen release. Flowering periods for each species were subjectively determined to include the time during which at least 10% of cones or flowers were undergoing anthesis. A similar approach was used by Ritchie (1977).

Durham (1946) gravity pollen collectors were used in this study. These collectors were selected in preference to mechanical samplers for reasons of (*i*) cost; (*ii*) inaccessibility to power for mechanical samplers; (*iii*) the likelihood of animal damage; and (*iv*) the need for uninterrupted data collection. A Durham pollen collector consists of two horizontal disks (23 cm in diameter, 15 cm apart), with the lower disk 9 cm from ground level. A standard 2 × 8 cm glass slide covered with a thin film of petroleum jelly was placed on the lower disk to collect pollen. Slides were exposed for 24 h (1991) or 48 h (1992, 1993). Slides were kept in a tightly sealed slide box before and following exposure to prevent contamination, and were examined within 24 h under a stereomicroscope (100× magnification) to identify pollen and estimate pollen amounts. Reference slides were used to aid in pollen identification: spruce, alder, and willow pollen could be identified only to genus. Pollen deposition was determined by counting all grains within a randomly selected 0.18 cm^2 area. Amounts of pollen rain were expressed as the number of pollen grains per square centimetre. Raw data and voucher slides from the 1992 field station are available from Dr. T. Booth, Department of Botany, University of Manitoba.

Table 2. Total tree and tall shrub pollen deposition near Cranberry Portage, Manitoba in 1992 (based on n = 88 pollen collectors).

Tree species	Total pollen deposition (grains/cm^2)	Percent of total	CV (%)*
Pinus banksiana	4604±1316 (2595–7599)	67.3	25.58
Picea mariana, Picea glauca	1673±375 (1064–3031)	24.5	22.41
Alnus crispa, Alnus rugosa	295±506 (12–2666)	4.3	171.53
Populus tremuloides, Populus balsamifera	128±71 (7–414)	1.9	55.47
Betula papyrifera	71±25 (23–146)	1.0	35.21
Larix laricina	58±43 (0–203)	0.8	74.14
Salix spp.	14±18 (0–91)	0.2	128.57

Note: Pollen deposition values are mean ± SD, with the range indicated in brackets.
*Coefficient of variation.

Diurnal variation in pollen deposition

Diurnal variation in jack pine pollen deposition was examined over a 48-h period from June 7 to 8, 1993. The experiment, which was carried out at sampling station 3 near Payuk Lake (Fig. 1), consisted of exposing slides (n = 4) to catch pollen. Slides were changed every 3 h, and stored and analyzed as described above. Microclimatic data were also measured every 3 h during the sampling period. Wind speed was measured with an anemometer, relative humidity using a sling psychrometer, and temperature using an alcohol thermometer.

Results

Tree frequencies and basal area values along the 5.5-km transect are summarized in Table 1. The most common tree species are black spruce, trembling aspen and jack pine. *Alnus crispa* is the most common tall shrub.

Total pollen deposition at the 88 pollen trap sites ranged between 4314 and 11 575 grains/cm^2 during May–June 1992. Seven tree and tall shrub pollen 'types' were identified (see Table 2). Jack pine accounted for over two-thirds and spruce (mainly black spruce) an additional one-quarter of the total. The remaining tree and tall shrub species accounted for only minimal amounts of pollen. Pollen or spores from other species (e.g., members of the Rosaceae family, the genus *Equisetum*) were collected in very small amounts and are not summarized.

In 1992, pollen deposition began in early May. Overall deposition rates were relatively low prior to June 7 and

Fig. 2. Pollen grain deposition in 1992. Values are totals for each 48-h period. Lines above the histograms indicate observed times of pollen release.

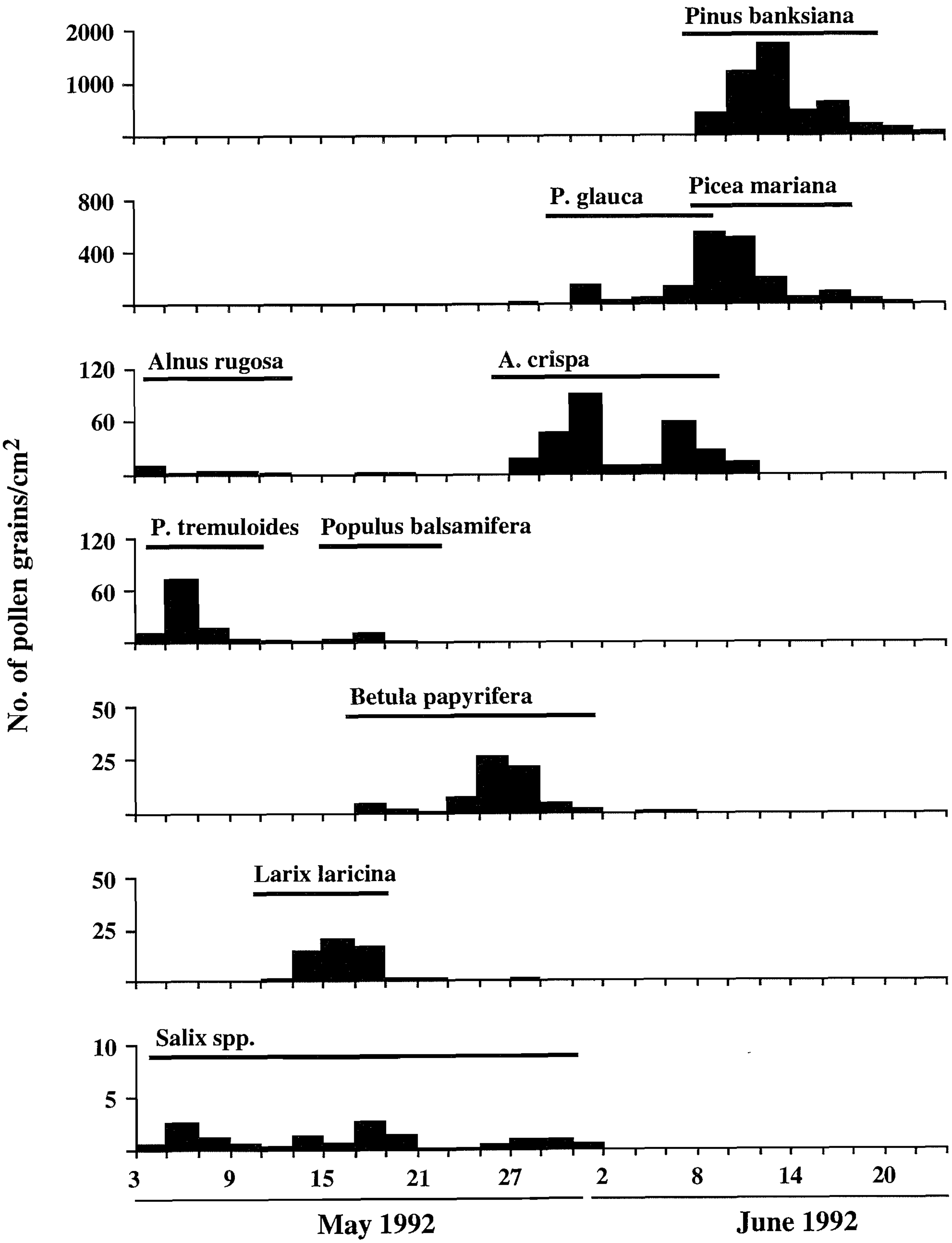
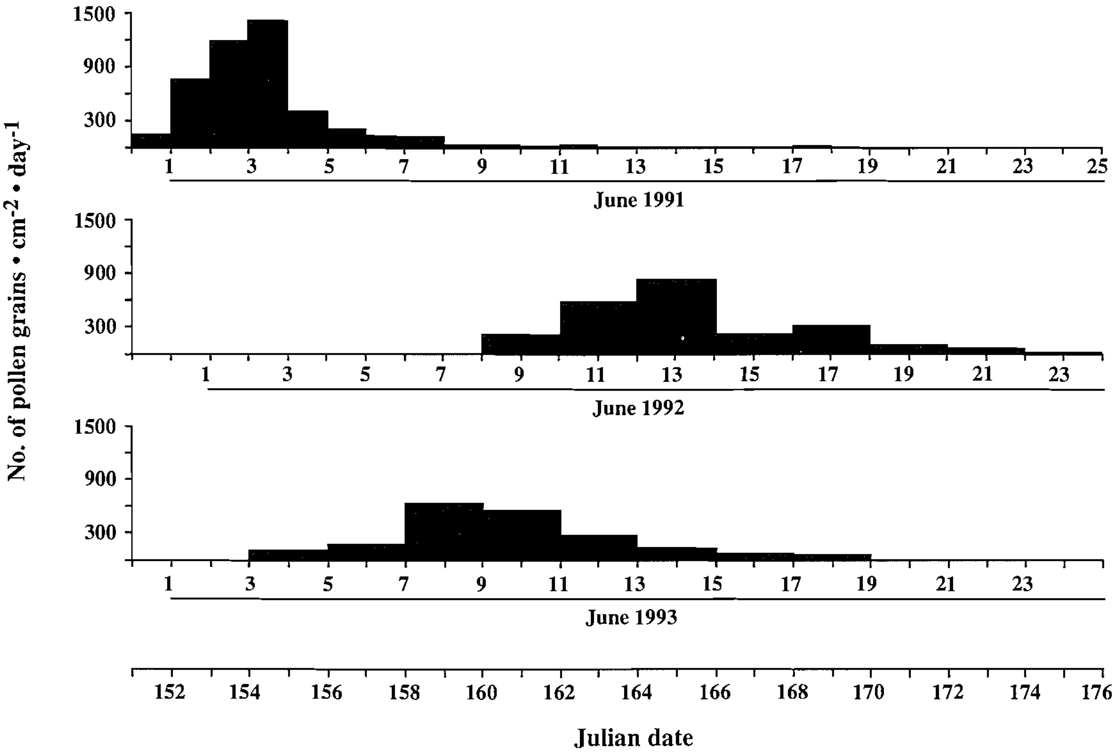


Fig. 3. Jack pine pollen deposition (grains · cm^{-2} · day^{-1}) in 1991, 1992, and 1993, standardized by Julian date. Note that collections were made every 24 h in 1991, and every 48 h in 1992 and 1993.



ceased after June 20. Pollen deposition of flowering plants (poplar, willow, birch, and alder) generally occurred between late April and early June (Fig. 2). *Alnus rugosa* released pollen in early May, and *Alnus crispa* in late May to early June. Alder pollen was unevenly distributed among sites. The pollen of birch (*Betula papyrifera* Marsh.) was fairly evenly deposited at all sites, but never in large amounts. Birch pollen rain lasted for about 2 weeks (May 18–30). Willow (*Salix* spp.) pollen was collected in small amounts throughout the sampling period, though variation among the 88 sites was high. Between May 5 and May 30, there were two or three indistinct peaks in willow pollen deposition, probably reflecting different willow species. *Populus tremuloides* released pollen in early May, and *Populus balsamifera* in mid-May. Poplar pollen was relatively evenly distributed among the sites.

Conifer pollen was generally released later than that of flowering plants. The exception was larch (*Larix laricina* (Du Roi) K. Koch), which showed peak deposition in mid-May. Larch pollen was deposited in small amounts at most sites. The two species of spruce (white and black) differed in the timing of pollen release, with white spruce beginning pollen release in early June, a week earlier than black spruce. Spruce pollen was fairly evenly deposited over all sites, with black spruce pollen accounting for >80% of the total. Jack pine was the last species to release pollen, the first collection being made on June 7.

Total jack pine pollen deposition was similar over the 3 sampling years: 4476 grains/cm^2 in 1991, 4604 grains/cm^2 in 1992, and 3980 grains/cm^2 in 1993. Peak periods of deposition occurred on June 3, June 12–13, and June 7–8, respectively (Fig. 3). Warmer than normal spring temperatures in 1991 resulted in early deposition, whereas below-seasonal temperatures in 1992 delayed deposition (Table 3). Jack pine pollen release in 1992 did not occur until June 6–10, during which time the maximum daily temperature rose from 11 to 31°C. Spruce pollen deposition varied between years, with mean annual deposition in 1992 of 1673 grains/cm^2 but only 1060 grains/cm^2 in 1993 (Fig. 4). Peak periods were June 8–9, 1992 and June 3–4, 1993.

Table 3. Mean monthly temperature, precipitation, and growing degree-days (temperature >5°C) for May and June 1991–1993 at Flin Flon Airport, and corresponding normals for the 27-year period 1964–1990.

Month	Variable	1991	1992	1993	Normals
May	Temperature (°C)	9.8	7.3	8.7	8.9
	Precipitation (mm)	39.0	43.0	16.2	41.0
	Growing degree-days	170.4	101.7	122.1	140.2
June	Temperature (°C)	16.4	12.3	13.3	14.7
	Precipitation (mm)	51.6	48.8	109.2	70.2
	Growing degree-days	341.3	222.4	246.9	291.0

Large quantities of jack pine pollen were liberated over about 10–14 days, with peak diurnal deposition occurring during daylight hours (Fig. 5). Deposition was positively correlated with air temperature (r = 0.95) and windspeed (r = 0.86), and negatively correlated with relative humidity (r = −0.93). Very little pollen was deposited in the early morning (03:00–06:00). We also noted that pollen deposition was low during cool, wet weather. These results suggest

Fig. 4. Spruce pollen deposition (grains · cm^{-2} · day^{-1}) in 1992 and 1993, standardized by Julian date.

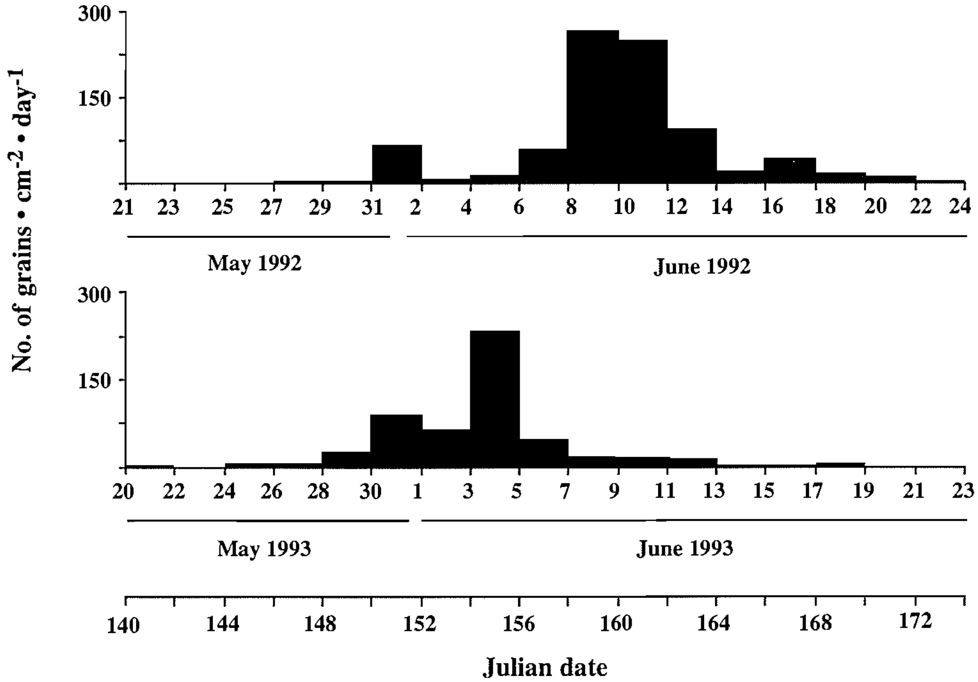
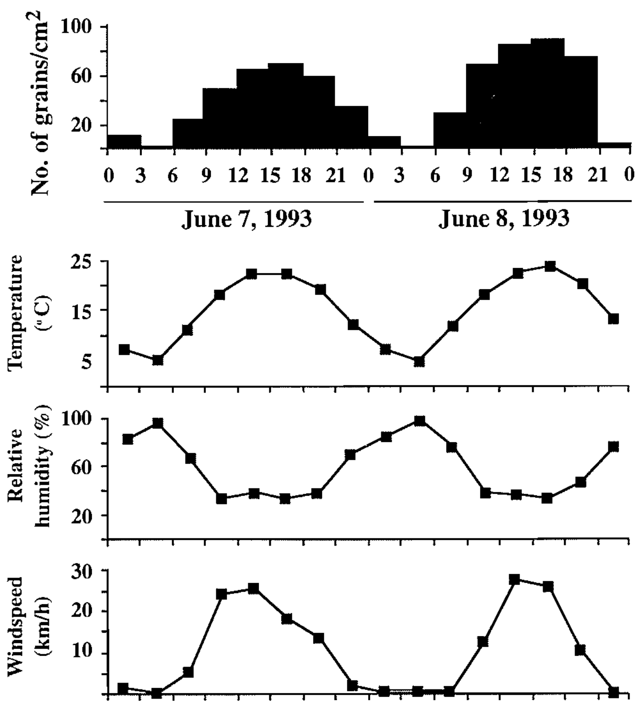


Fig. 5. Diurnal deposition of jack pine pollen, June 7–8, 1993 at sampling station 3. Values are totals for each 3-h period. Temperature, relative humidity, and wind speed profiles are also shown.



that jack pine anthesis occurs during daylight hours, though climatic conditions also play a role.

Discussion

Mean annual tree and tall shrub pollen deposition in the study area was ca. 6850 grains/cm^2 in 1992. This is somewhat higher than the ca. 5000 grains/cm^2 obtained by McLennan and Mathewes (1984) in coastal British Columbia.

Jack pine was disproportionately represented in our samples, accounting for 67.3% of pollen rain despite it being a relatively minor component of the forest (relative basal area was 17.5%). This result indicates that jack pine produces pollen in great quantity. Previous studies have shown that pines (genus *Pinus*) produce large amounts of pollen compared with other tree species (Stark 1972; Bradshaw and Webb 1985; Doskey and Ugoagwu 1989).

Spruce pollen was also well represented in the pollen spectra, accounting for 24.5% of total deposition. However, this value is low relative to the abundance of white and black spruce in these forests (relative basal area was 54.4%).

Pollen of flowering plant species (alders, poplars, willows, and birch) was poorly represented. Although aspen poplar was as common as jack pine, it accounted for <2% of total pollen deposition. Studies based on pollen deposition in lake sediments (e.g., Davis and Goodlett 1960; Webb 1974) have also revealed that aspen poplar is poorly represented in the pollen spectrum.

Interspecific differences in deposition variability along the transect are apparent (coefficient of variation (CV) values; Table 2). Variability in jack pine and spruce were comparatively low, reflecting the relatively even spatial distribution of these species along the transect. In addition, these species generally produce microstrobili in the upper canopy branches, thus promoting long-distance wind dispersal (Bradshaw and Webb 1985). Scots pine (*Pinus sylvestris*) pollen is normally deposited within 700 m of source (Stanley and Linskens 1974), while Buell (1947) found that pine pollen deposition at 400 m was 10% of that at source. For common species, pollen dispersal may be sufficient to mask patchiness in the spatial distribution of source trees (Li and Yao 1991). Spatial variability in pollen deposition was somewhat higher in birch, poplar, and larch, which probably reflects the much smaller amounts of pollen produced by these species. Variability in deposition was highest for tall shrubs (willows and alders). This likely reflects the smaller stature of these species, their patchy distribution in the field, and the low dispersablity of alder pollen (Bradshaw 1981).

Tree and tall shrub pollen deposition occurred between early May and late June of 1992. In general, pollen deposition of a given species lasted for about 2 weeks, with pollen release occurring earlier in flowering plants than in spruce or jack pine. Pollen release in jack pine varied between years, reflecting differences in ambient air temperatures in May and early June. Previous studies have found that the timing and extent of pollen release is strongly dependent on ambient air temperature (e.g., Bringfelt et al. 1982). In longleaf pine (*Pinus palustris*), low temperatures delay and extend the period of pollen release (Boyer 1973). Temperature and precipitation in early summer were found to affect jack pine reproductive success at the northern limit of its distribution (Houle and Filion 1993).

High tree pollen yields often occur in years following a warm, dry summer (Hyde 1952; Ritchie 1977). Our observation of higher amounts of spruce pollen in 1992 than 1993 is consistent with this finding. Total growing degree-days (temperature >5°C) from May to July 1991 were ca. 940, compared with only 660 for the same period in 1992 (the 27-year mean is ca. 850). The cool 1992 summer may have affected staminate bud production in spruce, resulting in low pollen production in 1993.

Jack pine pollen deposition occurs mainly in the daylight hours, when temperature and windspeed are highest and relative humidity is lowest. Such diurnal periodicity has also been observed in both temperate (Hyde and Williams 1944; Ogden et al. 1969) and European boreal species (Käpylä 1981; Janzon et al. 1977). Rempe (1937) demonstrated that pollen trapped in the early morning mainly represents sedimentation of grains released during daylight hours.

Ritchie (1976) used pollen diagrams to summarize the post-glacial vegetation history of the Flin Flon, Manitoba area. Spruce species were the dominant trees between 10 500 and 8200 years ago, with pine pollen abruptly increasing about 7000 years ago. The pollen diagram for the period 6400 years ago to present indicates 30–40% pine, 20% each for spruce, alder, and birch, and <10% for other species. These values differ somewhat from those obtained in the present study. In particular, the proportion of jack pine pollen recorded in this study is much higher than the 30–40% determined by Ritchie (1976). This difference may reflect a trend toward a drier climate in the late Quaternary, favouring jack pine because of increased forest fire frequencies. Recent logging practices may also have increased jack pine abundance. However, results obtained from gravity collectors are not directly comparable to lake sedimentation data because of interspecific differences in pollen dispersability and preservation (Sangster and Dale 1961, 1964; Prentice 1985). Pollen source area must also be considered, since sediments in large lake basins receive pollen from much larger areas than do pollen collectors in forests (Jacobson and Bradshaw 1982; Bradshaw 1981; Prentice 1985).

Our results reveal some limitations inherent in reconstructing long-term vegetation dynamics of northern boreal forests from preserved pollen records. We found that aspen poplar produced small amounts of pollen relative to its abundance, whereas jack pine is over-represented in the pollen rain. Erdtman (1943) obtained similar results in Alberta boreal forest: aspen poplar was common in the flora but poorly represented in the pollen record, whereas pines were uncommon but well represented. Thus, the absence of aspen poplar from the Flin Flon pollen record does not prove that the species was not present historically. We conclude that paleovegetational reconstructions of boreal forest based on the pollen record must be interpreted with caution, since pollen abundance is not indicative of relative species importance in plant communities (cf. Davis and Goodlett 1960; Bradshaw and Webb 1985).

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