CANADA GEESE DISPERSED CULTIGEN POLLEN GRAINS FROM PREHISTORIC IROQUOIAN FIELDS TO CRAWFORD LAKE, ONTARIO, CANADA

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Abstract

Crawford Lake, Ontario, Canada (43°28.1' N, 79°56.9' W, 278 masl) has varved and AMS dated sediments containing fossil pollen that record native Iroquoian farming ca. AD 1268 to 1520. From before AD 1000 to 1268, bioturbating organisms caused poor varve preservation but since then, well-preserved varves and dung pellets reflect anoxic bottom water due to meromixis. The onset of varve preservation coincides with the occurrences of pollen grains of *Zea* (maize), *Helianthus* (sunflower), *Phaseolus* (bean), *Cucurbita* (squash) and *Portulaca* (purslane), and spores of *Ustilago* cf. *maydis* (maize smut). These pollen grains and spores are more abundant in pellets between varve laminae than in the surrounding sediment matrix. Analyses of DNA from five pellets demonstrate that they are dung from wild Canada geese (*Branta canadensis*). In the autumn, as geese foraged in Iroquoian fields, they inadvertently ingested pollen and spores before flying to the lake. There they roosted and cast the pollen-rich dung pellets, which became part of the sediment. This study demonstrates that birds, wild geese and perhaps ducks, can be important vectors of pollen to lake sediments located near agricultural settlements.

Key words: pollen dispersal; Canada geese; Iroquois farming; Holocene; lakes; paleoecology.

INTRODUCTION

Pollen and spores of upland plants disperse to lake sediment by wind (Faegri and Iversen, 1989), by streams of water (McAndrews and Power, 1973; Birks and Birks, 1980; Chmura and Liu, 1990), and by birds that defecate remains of pollen-laden insects (Binka, 2003). It is shown here that prehistoric Canada geese also dispersed pollen grains by ingesting them while foraging, then flying to Crawford Lake where they roosted and cast pollen-laden dung pellets that persisted in the lake sediment.

Crawford Lake is 50 km southwest of Toronto (Text-Figure 1). It is believed that the 33 m deep basin was hydraulically excavated in dolostone bedrock 15,000 years ago when subglacial meltwater flowed over the site (Karrow, 1987). In the deepest part of the lake, 22.5 m of water overlie 4.5 m of postglacial sediments. Water enters the lake by seepage from a catchment of ca. 80 ha (Yu et al., 1997). The lake water is meromictic (partly mixing) owing to its great depth (22.5 m), and small surface area of 2.4 ha. Protection from wind by forested slopes, and cliffs up to 6 m high inhibits complete circulation. In the epilimnion to 9
m depth, temperature (Dickman, 1985) and dissolved oxygen (Prepas and Rigler, 1978) vary with the season. By contrast, in the hypolimnion below 15 m, the perennially anoxic water is constantly at 6°C. In the summer, a metalimnion between 14 to 12 m depth supports a plate of anaerobic photosynthetic sulfur bacteria (Moenig et al., 1970). In the autumn, when cold water circulates downward, these bacteria die to produce a dark organic lamina (Dickman, 1979). White laminae of summer-deposited calcite crystals separate dark laminae. Sediment laminae are distinct to 59 cm depth, but there are lamina remnants to at least 70 cm. These laminae appear as yearly couplets or varves (Boyko-Diakonow, 1979). A core taken in the summer has a white calcite layer on top, whereas a winter-collected core has an overlying dark lamina of organic matter. Dickman (1979) stated that black pyrite framboïds colored the dark laminae, but the present authors have never seen such crystals; it is possible that Dickman (1979) misidentified charcoal particles (Byrne and Finlayson, 1998; Clark and Royall, 1993) for pyrite. White laminae are likely to be missing from intervals where there are unusually wide dark laminae, which may account for the 10% of missing varves demonstrated by the AMS 14C chronology (Ekdahl et al., 2004). Because meromixis and anoxia of the bottom water prevent bottom-feeding detritivores from disrupting varves, the varve remnants below 60 cm record a time when sediment-disturbing fauna such as ostracodes inhabited oxic water of a dimictic but varving lake. It is proposed that anoxia and meromixis began with goose dung-driven eutrophication, which produced blooms of diatoms (Ekdahl et al., 2004) and rotifers (Turton and McAndrews, 2006).

The regional climate is humid cool-temperate-continen-
tal with precipitation that averages 910 mm, spread evenly through the year. The mean July temperature is 20.3°C and the mean January temperature is -6°C (Environment Canada, Millgrove Climate Station, 1993). On the cliffs around the lake grow Thuja occidentalis (eastern white cedar), which may be centuries old (Larson and Kelly, 1991), which colonized the cliffs throughout the Holocene (Yu, 1997). On the upland is mixed forest (Scott, 1995), dominated by the deciduous Acer saccharum (sugar maple), Fagus grandifolia (beech), Ostrya virginiana (ironwood), Fraxinus americana (white ash), Tilia americana (basswood),
Populus grandidentata (large-toothed aspen), and Betula papyrifera (white birch); common evergreens are Pinus strobus (white pine), Tsuga canadensis (hemlock), and Thuja occidentalis. Ulmus americana (white elm) trees were common until the 1960s, when disease killed them. Most of the forest trees post-date logging of the late 1800s; cut white pine stumps persist in the forest, and their size indicates that most of the oldest started to grow in the early 1700s (Kevin Kavanagh, personal communication). In the late 20th century on deep soils north of the lake (Text-Figure 1), maize was grown where Iroquoians probably grew it during prehistoric times.

In the first half of the second millennium AD, prehistoric Iroquoian people lived in agricultural villages. Within 3 km of the lake, there were seven Middle Iroquoian villages, each occupied for up to 30 years, with estimated populations ranging from 200 to 3000 people (Finlayson, 1998). These villages date to AD 1200–1500 (Dodd et al., 1990). Village excavations uncovered charred seeds of the cultigens Zea (maize), Helianthus (sunflower), Cucurbita (squash), Phaseolus (bean), and Nicotiana (tobacco). The Crawford Iroquoian Village, located 300 m north of the lake, had 200 to 250 inhabitants. Around 1520, Iroquoian villages disappeared from the area and the area was unoccupied until between 1822 and 1864, when Canadian farmers acquired land within 2 km of the lake (McAndrews and Boyko-Diakonow, 1989). The land was deforested, and the deeper soils were tilled while the shallow soil on the rocky land surrounding the lake (Text-Figure 1) returned to forest. Until 1972, a house and barn stood on the site of Crawford Iroquoian Village; the excavated and reconstructed village now hosts public visitors.

PREVIOUS POLLEN STUDIES

Pollen analysis of the lake sediment delimits two zones of human impact on the landscape, Iroquoian and Canadian (Byrne and McAndrews, 1975; McAndrews and Boyko-Diakonow, 1989; Byrne and Finlayson, 1998; Turton et al., 1998; Ekdahl et al., 2004; Turton and McAndrews, 2006). The prehistoric Iroquoian Zone has pollen of Zea, Helianthus, and Cucurbita together with pollen of the weed Portulaca, and Poaceae (grass), while the historical Canadian Zone has Zea together with the herbs/weeds Ambrosia (ragweed), Poaceae, Rumex acetosella (sheep sorrel), and Plantago (plantain). Macrofossils include leaves of Quercus rubra (red oak), Fagus grandifolia, Ulmus sp., Populus grandidentata, Populus tremuloides (trembling aspen), Thuja occidentalis, and Pinus strobes; the latter two species are sometimes green due to chlorophyll (Boyko, 1973).

In this paper, it is demonstrated that wild Canada geese (Mowbray et al., 2002) transported cultigen and weed pollen to the lake. Analyses of DNA from pellets found in sediment indicate they are goose dung pellets. Other indications of contemporary geese include fossil bone at two 15th century Iroquoian village sites located near the lake (Sadler and Savage, 2003), and two possible goose feathers in the lake sediment (McAndrews et al., 1971; Boyko, 1973).

METHODS

In 2001, the upper 70 cm of unconsolidated sediment was collected with a hollow-wedge freezing sampler (Ekdahl et al., 2004). In the laboratory, the sediment crust was photographed, and contiguous samples collected and freeze-dried for chemical and microfossil analyses. A sedimentation chronology for the last millennium links AD 1867 to 2000 varve counts with 23 AMS dates spanning AD 910 to 1867 (Ekdahl et al., 2004). Polynormorphs were concentrated from 136 contiguous levels with dilute HCl and KOH, followed by sieving to remove particles greater than 150 µm, staining with safranin, and mounting in glycerin. Pollen and spore identifications, supported by reference material, generally follow McAndrews et al. (1973). Percentages of pollen and spores were calculated on a sum of 200 or 100 tree pollen grains. To ensure the pollen diagram is compact, the herb pollen counts were individually added to the tree pollen sum before their values were calculated.

During 2005 at the same location, the upper 70 cm of sediment was collected and easily correlated with the dated image of the 2001 core. For comparative pollen analysis, pellets and sediment matrix surrounding the pellets was collected. For DNA analysis, nine pellet samples and one non-pellet control sample were scraped from the frozen sediment crust and stored in 95% ethanol. Extraction of DNA followed the PCR method for species-specific genes of Cytochrome b (Branicki et al., 2003).

RESULTS

The pollen diagram from the 2001 core (Text-Figure 2) shows two zones of human farming around the lake. The Iroquoian Zone spanning ca. AD 1268 to 1520 comprises Ustilago cf. maydis (maize smut) spores and Zea, Helianthus, Portulaca, Cucurbita, Phaseolus, and Poaceae pollen grains. In the Canadian Zone, which began in 1810, Poaceae appear first followed by the introduced Rumex acetosella and Plantago (plantain) and later by the native Ambrosia together with Zea and Ustilago. Byrne and Finlayson (1998) reported pollen of Mollugo (carpetweed); in the present study this pollen was not found, but a seed was recovered.
Tree pollen reflects forest succession. In the Pre-Iroquoian Zone to ca. AD 1300, the assemblage indicates deciduous forest dominated by *Fagus* and *Acer saccharum*. *Pinus* trees were rare and the likely source of the *Thuja* pollen was from trees growing on the lakeside cliff. In the Iroquoian Zone, there is succession to *Quercus* followed by mixed forest with *Pinus strobus*. In the Post Iroquoian Zone, *Pinus* peaks but declines in the Canadian Zone due to historical

Text-Figure 2. Pollen diagram from the 2001 core of Crawford Lake spanning the second millennium AD (expanded from Ekdahl et al., 2004). **A** the main tree pollen types; **B** the main shrub and herb pollen types. The identifications follow McAndrews et al. (1973) and Kapp et al. (2000). Analyses were by C.L. Turton. To increase visibility of the diagram, the *Zea, Helianthus, Cucurbita*, and *Portulaca* counts were multiplied by 10. The pollen sum is 200-tree pollen; to reduce extreme values, shrub and herb pollen, and spores were individually added to the pollen sum before their values were calculated. Rare types with little stratigraphic significance are not shown. These are *Picea, Abies, Larix, Castanea, Juglans nigra, Salix, Alnus, Corylus, Sarcobatus, Thalictrum, Artemisia, Urtica, Impatiens, Typha latifolia, Sparganium* type, *Tubuliflorae, Cyperaceae, Onagraceae, Caryophyllaceae, Apiaceae, Rosaceae, Brassicaceae, Lamiaceae, Dryopteris* type, *Pteridium, Equisetum*, and *Lycopodium*. The pollen and spore counts are in the North American Pollen Database (Grimm, 2006).
logging of white pine to be succeeded by the pioneer trees *Betula* and *Ulmus*. The *Ulmus* pollen decline since 1960 reflects the death of trees due to disease, whereas the pre-1810 record shows forest succession responding to climate change.

Plate 1 shows a section of mostly varved sediment from 66 to 35 cm in the 2001 core, which spans AD 1150–1600. Before AD 1300, bioturbating disrupted most white carbonate laminae leaving only a few intact varves, whereas after AD 1300 the varves are well preserved. Between 1331 and 1520, 34 prominent pellets are attributed to Canada geese. Similar pellets from the 2005 core (Text-Figure 3b) contain relatively abundant pollen of *Zea, Helianthus, Portulaca*, and Poaceae and spores of *Ustilago*, together with rare pollen of *Phaseolus, Cucurbita*, and *Solanum cf. americanum* (American nightshade). They also contain seeds and seed fragments of *Helianthus, Portulaca*, and *Solanum*, leaf epidermis, charcoal particles, and silt-sized mineral clasts; these indicators of cultivation are sparse or absent in the matrix around the pellets (Text-Figure 3a).

Tree pollen percentages and trends are similar, i.e., *Quercus* and then *Pinus* succeed *Fagus*. However, the cultigen and weed pollen percentage and density (Table 1) are an order of magnitude higher in the pellets than in the adjacent

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Text-Figure 3. Pollen diagrams of the 2005 core featuring the Iroquoian Zone. **A)** results from non-pellet sediment; **B)** results from pellets. The percentages are based on 100 tree pollen grains; non-tree pollen and spores were individually added to the sum before their values were calculated. Analyses were by C.L. Turton.
sediment. Note that in the pellets the herb pollen spectra vary greatly from level to level.

Pellets are mostly confined to the Iroquoian Zone (Plate 1). They are yellow, black or brown and, in section, they appear linear, lenticular, or circular, depending on their orientation and content. The mass of overlying sediment flattened most pellets, but the brown circular pellets resist flattening because they contain fragmented *Helianthus* seeds. In general, black pellets are richer in mineral clasts and charcoal fragments than adjacent sediment; this is attributed to geese foraging on plants growing at the surface of previously burned fields. Yellow pellets are full of pollen and epidermis of Poaceae and *Portulaca*. Of the nine pellet samples that were examined for species DNA, five were positive for *Branta canadensis* (Canada goose); two for an indeterminate mammal, one for an invertebrate and one had a mixture of undeterminable DNA. A sediment control sample was negative for DNA.

**DISCUSSION**

In the prehistoric sediment of eastern North America, fossil maize pollen is rare (Crawford et al., 1997). Maize is a wind-pollinated annual grass, cultivated by Iroquoians and Canadians. However, because of its large pollen (> 60 µm diameter; McAndrews et al., 1973), and short stature (< 2 m high), it was not readily dispersed by wind. Conversely, *Ustilago maydis*, an obligate parasite of *Zea* kernels, has tiny (8 µm diameter) wind-dispersed spores. Consequently *Ustilago maydis* spores were expected to be more abundant than *Zea* pollen and thus good indicators of regional *Zea* cultivation. Although there are other species of *Ustilago*, the fact that the stratigraphic range of the spores and pollen coincide, indicates that maize is the host plant.

Iroquoians cultivated *Helianthus annuus*, an insect-pollinated annual; its tricolporate pollen with distinctively long echinae (McAndrews et al., 1973) is especially abundant in pellets containing fragmented *Helianthus* seeds. From 58–50 cm depth (AD 1310–1375), two whole *Helianthus annuus* seeds were found, presumably from pellets, which measure 8 x 4 mm and 7 x 5 mm. These specimens are larger than wild and weed varieties, but similar to seeds from Iroquoian archaeological sites (Fecteau, 1985). Three *Cucurbita* (squash) pollen grains were identified; these large, 100–150 µm in diameter, periporate–echinate pollen grains (Kapp et al., 2000) are adapted to insect dispersal.

<table>
<thead>
<tr>
<th>Depth</th>
<th>Sediment type</th>
<th>Tree</th>
<th>Poaceae</th>
<th><em>Helianthus</em></th>
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<tr>
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<td>Black dung pellet</td>
<td>6</td>
<td>&lt; 1</td>
<td>52</td>
</tr>
<tr>
<td></td>
<td>Matrix</td>
<td>51</td>
<td>&lt; 1</td>
<td>0</td>
</tr>
<tr>
<td>51 cm</td>
<td>Yellow dung pellet</td>
<td>6</td>
<td>73</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Matrix</td>
<td>43</td>
<td>2</td>
<td>0</td>
</tr>
</tbody>
</table>

**PLATE 1**

1. Varved sediment (2001 collection) of Crawford Lake dated as AD 1150–1600 by AMS. The depth scale is centimeters below the surface of the sediment. The dung pellets of Canada geese are marked with white arrows. In varved sediment after 1510, pellets are absent; before 1400, pellets are rare and the varves are mostly bioturbated. The original digital image made by Jane Teranes has been scaled, labeled, and color-enhanced.

2. Enlargement of the varved section showing goose pellets: a) yellow pellet colored by plant epidermis, b) black pellet colored by charcoal, and c) brown pellet with fragments of *Helianthus* seeds.

3. Monoporate pollen grain of *Zea mays* from 54 cm depth; diameter is 75 µm.

4. Pericolpate pollen grain of *Portulaca oleracea* from 39 cm depth; diameter is 55 µm.

5. Tricolporate, echinate pollen grain of *Helianthus annuus* from 44 cm depth; diameter is 21 µm.

6. Tricolporate pollen grain of *Phaseolus vulgaris* from pellet at 39.5 cm depth; diameter is 40 µm.

7. Periporate pollen grain of *Cucurbita pepo* from 50 cm depth; diameter is 115 µm.

8. Tricolporate pollen grain of *Solanum cf. americanum* from 39 cm depth; diameter is 19 µm.

9. Spore of *Ustilago cf. maydis* (surface and amb) from 55 cm depth; diameter is 8 µm.
Portulaca oleracea is a self-pollinated annual weed common in gardens and maize fields across southern Canada. It has no obvious seed dispersal mechanism, but bird dung may contain its seeds (Miyanishi and Cavers, 1980) and presumably pollen grains. Formerly, we attributed the abundance of Portulaca to Iroquoians who, after collecting plants growing in maize fields, supposedly took plants to the lake where washing led to the pollen and seeds entering the lake sediment (Byrne and McAndrews, 1975; Turton et al., 1998). Pollen and seeds of Portulaca, together with Zea pollen, also occur in the massive sediment of nearby Miller Lake (Turton et al., 1998). In both lakes, introduction by geese is the most plausible explanation, as shown by the elevated densities of these pollen types in fecal pellets (Text-Figure 3). Solanum americanum, like Portulaca, is an annual weed of waste ground and cultivated fields in southern Ontario (Alex and Switzer, 1976), and has edible berries. In addition to pollen, seeds in the Iroquoian Zone were found, and Yu (2003) reported seeds from the Pre-Iroquoian Zone.

The size, shape, color, DNA (derived from cells lining the intestinal tract), and fossils including pollen and spores, herb epidermis, seeds of Portulaca, Solanum, and Helianthus, and herb charcoal indicate that the pellets are fossil goose dung. In contrast with the sediment matrix, pellets have sparse fossil limnic organisms such as diatoms and rotifers. Pellets are present in the sediment deposited during the Iroquoian occupation, but absent before and after when there were no fields in the landscape.

The most likely cause for eutrophication and accompanying meromixis was the pellets of Canada geese, which today eutrophy small lakes with their dung (Manny et al., 1994). The evidence presented here indicates that in Middle Iroquoian time geese fed in maize fields and not only ate Zea and Helianthus seeds, but also grazed on Poaceae, Portulaca, and other herbs. Burned fields rather than forests accounted for the ingested herb charcoal. After feeding, the geese flew to the lake, roosted and defecated pellets, many of which dispersed in shallow water above the chemocline to provide nutrients for the eutrophication that led to meromixis. However, some pellets preserved in the varved sediment located below the epilimnion. Pellet deposition ceased when the Iroquoians moved away, and geese ceased to roost but meromixis persisted. The lack of pellets during the Canadian Zone indicates that, despite cultivated fields, few if any geese roosted on the lake. It is possible that they did not feed in historic fields or, if they did, they failed to roost on Crawford Lake due to hunting with firearms. In recent years, a few geese land on the lake, which is in a Conservation Area where hunting is prohibited.

Crawford Lake may not be unique in having pollen delivered to lake sediment via the dung of grazing birds. For example, in prehistoric sediment of lakes in the rain forests of Ecuador and Panama, maize pollen accounted for up to 2% of the pollen sum (Bush et al., 1989; Bush and Colinvaux, 1994). The explanation these authors offered for this high value was that native people grew maize on the seasonally dry lakebeds. Neotropical ducks could have transported maize pollen. For example, black-bellied whistling duck may have flocked together to forage in cultivated fields and roost on lakes and the Muscovy duck, although less gregarious, was a prehistoric domesticate and therefore would be associated with people, their fields, and nearby lakes. Because the surface mud of these lakes is bioturbated, dung pellets are unlikely to have fossilized.

CONCLUSIONS

During the 14th and 15th centuries, Canada geese roosted on, and defecated in, Crawford Lake. Their dung, confirmed by DNA analysis, supplied nutrients that eutrophied the lake. This led to diatom blooms, an oxygen-poor hypolimnion, meromixis, and the preservation of varves and goose dung pellets. Preserved dung pellets contain, relative to the adjacent sediment, abundant pollen of Zea, Helianthus, and Portulaca, together with rare Phaseolus and Cucurbita. Poaceae pollen from weed species is also abundant. When fossil field crop and weed pollen is abundant, water bird delivery should be considered.

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