Identifying fossil wild rice (Zizania) pollen from Cootes Paradise, Ontario: a new approach using scanning electron microscopy

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Abstract

Although prehistoric native peoples probably used wild rice for food and ceremony, evidence is sparse. Macrofossil remains of wild rice are uncommon on archaeological sites even where the plant is still common nearby. The association between documented human habitation and wild rice is explored with pollen records from associated wild rice wetlands. For this, reliable identification of wild rice pollen is essential. Three approaches are examined: (1) the pollen spectral signature (percentage and density of grass pollen), (2) coeval community pollen types, and (3) the pollen morphology (size and sculpturing) of wild rice versus other stand-forming wetland grasses. We report pollen spectra from a contemporary wild rice marsh and compare it with fossil pollen from Cootes Paradise, a wetland at the western end of Lake Ontario. The pollen signature from the modern wild rice wetlands was similar to that of the fossil site, but this correspondence does not confirm that the fossil grass pollen is wild rice. Wild rice pollen is separable by size from that of all the stand-forming wetland grasses examined, but the fossil pollen from Bull’s Point is not the same size as that of modern wild rice. Scanning electron microscopy (SEM), however, indicates that wild rice pollen is identifiable by its sculpturing and that the fossil pollen has an identical micromorphology.

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Keywords: Wild rice; Pollen signature; Pollen micromorphology; Great Lakes region; Princess Point complex; Plant foraging

1. Introduction

Wild rice (Zizania sp.) is a stand-forming aquatic grass of eastern North American rivers and lakes. It is well documented as an important food for historic and contemporary native people in the Great Lakes region, such as the Menominee and Ojibway [13,38]. Although the ethnobotany of wild rice indicates long-standing exploitation by humans, macrofossil remains are seldom found in archaeological contexts. Crawford and Smith identify 37 sites in eastern North America that have yielded wild rice remains [8]. A few sites have also revealed scorched soil and jig pits where wild rice may have been parched or hulled [3,15]. Except in these sites, the relationship between prehistoric peoples and wild rice is unclear, and usually depends on two often temporally unconnected distributions: that of wild rice, documented only after European contact, and a prehistoric settlement pattern that spans the Holocene. Most of the material evidence for the use of wild rice spans the transition to crop cultivation, between 1000 and 2000 years ago.

Reconstructing the spatial and temporal distributions of wild rice requires reliable identification of its pollen. Fossil grass pollen from numerous contemporary and historic wild rice stands has been recognized as wild rice from abundance, size and surface appearance [12,20–22]. Here we establish a firmer palynological identity for wild rice. First, we examine the representation of grass pollen and the presence of indicator taxa that covary with wild rice and then we describe and distinguish the pollen
morphologies of wild rice and several stand-forming grasses with similar ecologies.

Our research focuses on the pollen record from Cootes Paradise, a 250 hectares wetland at the western end of Lake Ontario (Fig. 1). Archaeological research shows that native people inhabited the margins and islands of the marsh from ca. 5000 to 350 years BP [29,31,33]. The most intensive occupation was ca. 1000–1500 years BP by people of the Princess Point Complex. Princess Point is an archaeological culture found in south central Ontario (Fig. 1). The culture features the earliest maize yet documented in southern Ontario (AMS radiocarbon dated to ca. AD 500), suggesting that this society was the first to cultivate the grain in the region [7,30,32,33]. Their subsistence economy was not, however, fully horticultural; hunting, fishing, and gathering of wild plants remained important. Princess Point people did not build substantial longhouse communities as did later Iroquoian societies, although their settlements were more substantial than those of the preceding Middle Woodland period. Princess Point sites orient toward river floodplains, wetlands and lakeshores, especially at Long Point, several locales in the Lower Grand River Valley and the marsh at Cootes Paradise (Fig. 1).

There are ten Princess Point sites around Cootes Paradise: two on promontories, two on terraces, two on islands and at least four sites in dry ravines. The latter are very small sites situated on the wetland margins, an unusual site situation in southern Ontario. Our working hypothesis is that they were seasonal special-purpose stations for exploiting a specific resource, such as acorns, wetland fauna or wild rice. However, we found no wild rice macrofossils from archaeological contexts at Cootes Paradise. Thus, to argue for exploitation of wild rice by the Princess Point inhabitants depends upon documentation that wild rice grew in the marsh between 1500 and 1000 years ago.

2. People and wild rice

Wild rice grows throughout eastern and north-central North America; two annual species dominate, *Zizania aquatica* L. (southern wild rice) and *Z. palustris* L.
(northern wild rice). The former ranges from the Gulf of Mexico to the southern Great Lakes, but among several varieties, only Z. aquatica var. aquatica L. is common [1]. Northern wild rice Z. palustris var. palustris L., the only commercially important variety, is patchily distributed from the Maritime Provinces and northern New England though the Upper Great Lakes and across the Prairies.

The Ojibway harvested wild rice in August [38]. Sometimes there were as many as three sweeps of the rice beds where the grain-laden stalks were beaten over a boat, although some rice may have been cut, sheaved and separated on shore. The grain was dried in the sun on racks over slow fires, then parched (roasted) to further reduce water content and loosen the hulls; threshing and winnowing completed the process. The technology was simple and required no robust or specialized equipment that might be preserved in archaeological sites other than jig pits used for threshing. Thus, the connection between prehistoric native people and wild rice is mostly inferential. Because of the historical importance of wild rice, we assume that prehistoric people had a similar dependence on the grain. The proximity of archaeological sites to wetlands that presently and historically supported wild rice suggests that the grass was important since Archaic times [21,22]. The coincidence is particularly striking for Middle and Late Woodland sites; for example, Rajnovich notes the juxtaposition of nearly 200 native campsites and modern wild rice localities around Lake of the Woods in northern Ontario [26]. A similar coincidence occurs with Princess Point sites in south central Ontario (Fig. 1), but at only one site, Grand Banks, has carbonized wild rice been identified [28]. The fragility of charred grains may determine their rarity, but they can be abundant locally [2,23]. Perhaps wetland resources other than wild rice were the primary reason for waterside settlement.

Archaeological wild rice increases after AD 300, perhaps reflecting a greater dependence on the grain [8]. Johnson and Salzer conclude that a shift from riverine to lacustrine settlement by some Late Woodland cultures in the Upper Midwest reflected increased importance of wild rice to subsistence economies [14,27]. Alternatively, Lovis et al. suggest an increasing preference for lowland sites, particularly floodplains, may reflect increasing dependence on maize [19]. The persistence of Princess Point people around Cootes Paradise suggests that wetland resources remained important despite their cultivation of maize.

Based on its size and abundance, wild rice pollen appears in many lakes across the Great Lakes region. Huber summarizes pollen records from 16 pollen diagrams in Minnesota [12]. Across southern Ontario, about a dozen diagrams have wild rice zones. Most of these records are from embayments of Lakes Erie and Ontario. Terasmae et al. report abundant grass pollen from six wetlands in the Hamilton-St Catharines area [36]. In three of these, Dundas Marsh (Cootes Paradise), Fifteen Mile Creek and Sixteen Mile Creek, the abundant Poaceae extended to the Ambrosia (ragweed) zone, implying the persistence of wild rice at least until the time of European settlement in the early 19th century.

Wild rice still grows behind Long Point and has been there for at least 200 years [4]. Several Poaceae peaks in a pollen diagram from Redhead Pond at Point Pelee probably reflect variations in abundance of wild rice in response to changing lake levels [16]. There are still extensive wild rice stands at Rondeau Provincial Park. They have survived there since the development of the Point aux Pins spit from about 4500 BP [5, S. Finkelstein, pers. com.]. Wild rice macrofossils and pollen also occur at Gates Creek [25] where there is a contemporaneous archaeological site [F. McCarthy, pers. com.]. All of these Lake Erie locales have associated archaeological sites.

3. Field and laboratory techniques

A 4.6 m core was lifted from the north side of the wetland some 80 m east of Bull’s Point and within 200 m of several archaeological sites. Samples for analysis were at 10 to 30 cm intervals. Sample preparation followed the standard procedure of Ref. [11]. Before treatment, a tablet containing approximately 13,000 Lycopodium spores was added to each sample. Samples were stained with safranin and mounted in silicone oil. Percentages were calculated on a sum that included all trees and shrubs, but not herbs and wetland taxa. Pollen concentrations were calculated using the Lycopodium count. Two bulk radiocarbon dates from the Princess Point zone provide chronological control (Fig. 2): 840 ± 70 BP (Beta-106245) and 1170 ± 70 BP (Beta-106246).

A preliminary diagram for the complete sequence is in Ref. [34]. Here we focus on the section between 170 and 270 cm, which spans the Princess Point period. To provide a modern pollen analog, we analyzed surface sediments from a wild rice stand at the southern end of Lake Scugog, 50-km northeast of Toronto. Sample preparation was identical to that used for the Bull’s Point core, as was the calculation of percentages and concentrations.

Fifty pollen grains from each of nine samples of wild rice were measured (Table 1). Two hundred pollen grains from each of six other wetland grasses were measured: Calamagrostis canadensis, Phragmites australis, Leersia oryzoides, Glyceria borealis, G. canadensis, and Phalaris arundinacea. Calamagrostis canadensis (Canada bluejoint) is a common perennial grass of wetlands across Canada and with sedges a major component of beaver hay [24]. Phragmites australis (common reed) is also broadly distributed with a wide ecological tolerance. It colonizes ditches and will grow in
Fig. 2. Pollen percentage (A) and concentration (B) diagrams for Bull’s Point core, Cootes Paradise (ml × 1000). Pollen sum indicates all upland plants. Note scale changes for Poaceae in A. Shaded area represents 5 × exaggeration.
Leersia oryzoides (rice cutgrass), another rhizomatous perennial, prefers lake margins and tolerates prolonged immersion [10]. In addition, *G. canadensis* (rattlesnake manna grass) was examined because the size range of its pollen grains measured was not statistically different from that of the fossil grass pollen grains from Cootes Paradise (Table 2). This perennial grows in shallow water, on shores and is often abundant in beaver meadows [24].

Wild rice and all other grasses were derived from the reference collection of the Royal Ontario Museum (ROM). Two hundred pollen grains from levels of the mid-section of the Bull’s Point core were also measured. Four species, *Z. aquatica*, *P. arundinacea*, *G. borealis* and *G. canadensis* and samples of grass pollen from the Bull’s Point core had the micromorphologies of their exines examined first under a light microscope with fluid immersion at 1300× magnification, and then under a scanning electron microscope (SEM). For the latter, the pollen grains were acetolysed and dehydrated with 70%, 80% and 100% alcohol. After two days, the suspensions were mounted on stubs coated with argon and examined with a Hitachi 2000 model SEM. Acceleration voltage was 20 kV.

### 4. Results and discussion

#### 4.1. The pollen spectra

The Bull’s Point core provides a pollen record of nearly 2000 years [34]. There were three zones based on wetland taxa. Zone 1, from 460 to 220 cm, has large percentages and concentrations of Poaceae. In Zone 2, between 220 and 60 cm, pollen from *Typha latifolia* (cattail), *Sparganium* sp. (burreed) and *Thelypteris* sp. (marsh fern) replaced that of Poaceae pollen. Zone 3, from 60 cm to the surface, shows a major increase in the weedy taxa associated with European settlement, notably *Ambrosia* sp. (ragweed). We interpret the sequence to indicate a wetland succession from wild rice marsh (Zone 1) to modern wetland (Zone 3).

In this discussion, we focus only on the section between 170 and 270 cm, the upper part of the wild rice phase and the transition to cattail marsh (Fig. 2). This section spans the Princess Point occupation and the Early Ontario Iroquoian that replaced it. The percentage values of tree and shrub pollen (upland plants) show little variation through the 170 to 270-cm section of the Bull’s Point core.

<table>
<thead>
<tr>
<th>Bull’s Point</th>
<th><em>Z. aquatica</em></th>
<th><em>C. canadensis</em></th>
<th><em>L. oryzoides</em></th>
<th><em>P. australis</em></th>
<th><em>G. borealis</em></th>
<th><em>G. canadensis</em></th>
<th><em>P. arundinacea</em></th>
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<tbody>
<tr>
<td>Number</td>
<td>200</td>
<td>450</td>
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<tr>
<td>Mean</td>
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<td>26.60</td>
<td>23.34</td>
<td>29.48</td>
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<td>Standard deviation</td>
<td>2.30</td>
<td>2.83</td>
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<td>t value</td>
<td>5.70</td>
<td>12.91</td>
<td>16.27</td>
<td>40.07</td>
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\( a=0.05, \text{ df}=648, \text{ for } *Z. aquatica*=648, \text{ other grasses}=398. \)

### Table 1

Student’s t-test comparison of modern pollen grain sizes of *Z. aquatica* and six other wetland grasses

<table>
<thead>
<tr>
<th></th>
<th><em>Z. aquatica</em></th>
<th><em>C. canadensis</em></th>
<th><em>L. oryzoides</em></th>
<th><em>P. australis</em></th>
<th><em>G. borealis</em></th>
<th><em>G. canadensis</em></th>
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<td>23.68</td>
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\( a=0.05, \text{ df}=648. \)
The wetland taxa, the emergents and the aquatics, change most. Excluding them from the pollen sum enhances the fluctuations in the percentages of the wetland taxa, especially Poaceae. Values for Poaceae exceed 600% or six times the total tree contribution below 250 cm. This relative domination of Poaceae pollen parallels density values that exceed 120,000 grains per ml. These values imply dense stands of wetland grasses. Although this domination does not preclude the other species, wild rice is the most likely candidate. Its remarkable tillering ability allows it to produce stem densities of over 300/m² and large numbers of florets [1].

The other wetland taxa, although less strongly represented, are indicators of water depth and may help identify the grass. The section of the diagram dominated by Poaceae pollen has low Typha and Sparganium, but these increase up the core as Poaceae declines. Wild rice does not coexist with these taxa, because it is an annual of deeper water.

Pollens from the water lilies, Nuphar and Nymphaea, in the grass-dominated section of the core suggests deep water. Growth and persistence of wild rice depends on its ability to compete with other emergents [1]. Deep water favors it over Typha (cattail) and Sparganium (burreed). Although wild rice may be restricted by floating-leaved plants, particularly Nuphar and Nymphaea, their presence in modest amounts may encourage its growth by eliminating other perennials [9]. Contemporary wild rice stands in Lake Scugog flourish in water with Nymphaea odorata.

Few emergents are strict competitors of wild rice because they occupy different niches within the wetland environment. For example, the replacement of wild rice by Typha and Sparganium higher in the core section suggests succession due to decreasing water depth. Abundant fern spores identical to the spores of Thelypteris palustris support this interpretation; this fern of shallow water is common in Typha latifolia stands but not in Zizania stands [6].

The pollen spectra from the Poaceae-dominated section of the Bull’s Point core are like those from a contemporary wild rice marsh in Lake Scugog (Fig. 3). The percentages and density values of Poaceae pollen are high in both locations and there is an association with Nymphaea. Some sequential changes with water depth are noticeable, but they are much less pronounced than at Cootes Paradise. The differences between the pollen spectra of the two sites may be due to both geography and differences in human impact. Lake Scugog lies in the Great Lakes–St Lawrence mixed forest region, while Cootes Paradise is in the transition with the Carolinian deciduous forest. The pollen spectra from Lake Scugog reflect European settlement and modern disturbance. The lower concentrations at Lake Scugog probably reflect the low density of the surface sediment.

4.2. Size characteristics

Histograms of the size distributions of Z. aquatica, P. arundinacea, G. borealis, G. canadensis and the Poaceae pollen from the Bull’s Point core overlap (Fig. 4). The smaller grains of C. canadensis, L. ozyoides and P. australis have little overlap. The mean grain size of each of the candidate Poaceae was compared to that of Z. aquatica using the Student’s t-test. The same technique was then used to compare Poaceae pollen data from the Bull’s Point core with Z. aquatica and other Poaceae. These analyses show statistically significant differences in size between Z. aquatica and all of the other wetland Poaceae, although the differences between Z. aquatica and G. borealis, G. canadensis and P. arundinacea are small. When the size characteristics of Z. aquatica and the latter three species are compared with those grass pollen from the Bull’s Point core, the fossil pollen was statistically similar only to that of G. canadensis.

Thus, the grass pollen in the Bull’s Point core cannot be identified as wild rice by size alone. This failure is unlikely to be the result of tearing and other distortions although the process of fossilization might be a factor. Poaceae pollen grains in the Bull’s Point core were sufficiently abundant to allow selection of well-preserved individuals. The size distribution histogram for the Bull’s Point Poaceae pollen is like that of wild rice and shows no obvious skewness or kurtosis. The similarities in size indicate a single Poaceae species. If more than one species was represented, the distribution would likely exhibit multimodality, be positively or negatively skewed and have high or low kurtosis [35].

It is also unlikely that the differences in grain size are functions of differences in the ages and treatments of the reference materials. Although the ROM collection dates range from 1929 to 1994, there were no systematic differences in size attributable to length of storage. The most likely explanation for the size mismatch is the between site variability in wild rice. Because the distribution of wild rice is naturally patchy, peripheral and isolated populations display genetic divergence [18]. In wild rice, isolation is probably reflected in morphological variation and behavior [9], and by genetic variations [39]. Like many annuals, wild rice can self-pollinate, a habit that facilitates genetic isolation. The effects are demonstrated in the size differences of the ROM reference samples. Although these are collectively different from the Bull’s Point wild rice, three of the samples are statistically identical to the fossil pollen.

4.3. Sculpturing

Because the size comparisons between modern wild rice pollen and the Poaceae pollen from the Bull’s Point core gave ambiguous results, we investigated the
Fig. 3. Pollen percentage (A) and concentration (B) diagrams for Lake Scugog, Ontario (ml × 1000). Pollen sum indicates all upland plants. Note scale changes for Poaceae in A. Shaded area represents 5 × exaggeration.
potential of surface micromorphology for identification. We selected *G. canadensis* and *P. arundinacea*, the two species with similar sizes to wild rice, and *G. borealis* to compare with wild rice, and pollen grains from the 270-cm level of the core. *G. borealis* was included because, although size precluded it, its ecology is like that of wild rice for which it is sometimes mistaken [24].

The exines of Poaceae pollen are microscabrate with individual protuberances called spinulae that may be grouped to form insulae. The shape and size of insulae and the numbers of spinulae that form them can be used to identify some grasses at least to the generic level [17].

Initially, the specimens were examined by light microscope at 1300× magnification under fluid immersion. At these low magnifications, the major surface elements were recognizable, but the details were not. The two candidate grasses and *Z. aquatica* were classified as having coarse or smooth sculpturing. *Z. aquatica* and *P. arundinacea* were smooth with microscabrae indistinct and fused. *G. borealis* pollen was coarse textured with distinct microscabrae. Thus, the two taxa with similar size statistics have indistinguishable surface morphologies at this magnification. Poaceae pollen from the wild rice zone in the core is smooth, like *Z. aquatica* and *P. arundinacea*.

Scanning electron microscopy distinguished all of the candidate species by their surface micromorphologies. The differences are clear at magnifications above 5000× magnification (Fig. 5). The photographs show that *G. borealis* has single, isolated spinulae, while *P. arundinacea* has densely spaced insulae composed of two to seven spinulae. *G. canadensis* has insulae that are less densely spaced, but without isolated spinulae. In *Z. aquatica*, the surface morphology consists of both isolated spinulae and large, widely spaced insulae. Each has the densest sculpturing on its annulus, the collar around the single pore. Poaceae pollen from the wild rice zone of the Bull’s Point core has sculpturing like *Z. aquatica*.

5. Conclusion

Each of the approaches used here contributes to wild rice pollen identification, but only the SEM provides incontrovertible evidence. The technique is time-consuming, however, and may not be accessible to everyone. The traditional interpretation of pollen spectra is still both easy and useful for wetland community reconstruction and for local paleoenvironment interpretation. It offers a reliable and expedient approach to recognizing a wild rice signature. At Cootes Paradise, the huge contribution of Poaceae pollen implies production by a local grass growing in dense, monospecific stands. Floating-leaved aquatics suggest deep water as does the slight representation of shallow water dominants, *Typha* and *Sparganium*. The spectra from the contemporary wild rice stand at Lake Scugog are similar to those from Cootes Paradise, although the wild rice signature is weaker.

Size measurements are useful to eliminate *Phragmites australis*, and *L. oryzoides*, and *C. canadensis* that have pollen too small to match the fossil Poaceae pollen. A limitation with the use of size criteria is in the large variability in pollen size across the range of *Zizania*. This probably results from the isolation of sub-populations of the species.

With this research, we have documented the pollen signature for wild rice at Cootes Paradise. Further, the pollen spectra recovered from cores indicates at least a 3000 year history of dense wild rice stands. Such evidence does not confirm the hypothesis that native communities exploited the wild rice stands at Cootes

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Fig. 4. Histograms for pollen diameters of *Z. aquatica*, six wetland grasses, and grass from levels 250 and 270 cm at Bull’s Point.
Paradise. Such confirmation depends on other lines of archaeological evidence, particularly the recovery of wild rice pollen and/or phytoliths from residues on pottery as documented in Minnesota [37]. Preliminary investigation of plant silica from the Bull’s Point core indicates wild rice phytoliths through the wild rice pollen zone [28]. Another important line of evidence would be plant macrofossil remains in direct association with artifacts in features, with the wild rice directly dated by AMS radiocarbon assay.

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References

[34] D.G. Smith, T.L. Ormerod, A.M. Davis, M. Peros, Prehistoric native ecology at Cootes Paradise, Royal Botanical Gardens,


