The late Holocene history of prairie, brush-prairie, and jack pine (Pinus banksiana) forest on outwash plains, north-central Minnesota, USA

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Abstract: Pollen diagrams from six sites on outwash plains of north-central Minnesota are interpreted as records of similar extralocal vegetation changes since c. 5000 BP. All of the study sites have undergone a shift from prairie to an aspen-oak community, followed by the jack pine-dominated vegetation that now occupies the sites. All of the species capable of directly invading prairie (aspen, bur oak, willow and some entomophilous shrubs) were probably established on the surrounding moraines prior to their invasion of the adjacent prairie-occupied outwash plains. Only short distances (<20 km) were involved in these local invasions, and the chronology of their establishment does not indicate a regional westward migration of these taxa in the late Holocene. Because climate varies little over the short distances separating the study sites, the asynchronocity of the dates for the establishment of aspen brush (Zone 3/Zone 4 boundary) and the following establishment of jack pine (Zone 2/Zone 3 boundary) indicates that locally varying conditions determined where and when these vegetational shifts occurred. Sloughs and wet swales are apparently prerequisite for aspen to invade prairie, and they probably appeared on the outwash plains at different times because locally varying hydrologic conditions determined the absolute increase in precipitation required for the water table to rise and flood depressions. The rate at which afforestation proceeded, culminating with the establishment of jack pine, appears to be related to local variability in the distribution of wet depressions as they serve as fire breaks. Where peat-filled channels and chains of lakes occur, afforestation occurred first and was relatively rapid. Where lakes and peatlands are scattered, afforestation occurred later and required more time. Where wet depressions are rare, some patches of prairie have persisted since the mid-Holocene.

Key words: vegetation history, pollen analysis, prairie, brush-prairie, jack pine forest, outwash plains, local variation, plant migration, Minnesota.

Introduction

The former presence of prairie on now-forested outwash plains in north-central Minnesota has long been inferred from the vegetation and soils. Many historical descriptions of presettlement forests on outwash refer to occasional prairie openings within the forest matrix (Public Land Survey records, c. AD 1850–1880). Where pristforest stands of bur oak (Quercus macrocarpa) or aspen (Populus tremuloides) occurred, the soils are characteristically dark-coloured and clearly of prairie origin despite the present tree cover (McMillan et al., 1930; Elwell et al., 1926). Mixed stands of jack pine (Pinus banksiana) and oak, described physiognomically as barrens by the early surveyors, also occurred on relic prairie soils. On the large areas of outwash occupied by jack pine forest on light-coloured, highly leached forest soils, however, the only indication of a former prairie stage is the occurrence of ground-layer species that are typical of modern tallgrass prairies.

This study documents the vegetational sequence and chronology of afforestation of outwash plains where jack pine eventually replaced prairie. The pollen stratigraphy was radiocarbon-dated for six lakes, selectively located along a gradient from organic relic-prairie soils to highly leached forest-soils (Figure 1), so that the successional and chronolo-
gic variability of afforestation could be related to the modern vegetation and soils (see Almendinger, 1985). Much of the interpretation is based upon the ordination of the fossil pollen spectra together with presettlement samples that might serve as analogues.

Site descriptions

Peterson Slough
Location: 95°19’ W, 46°58’ N, SW 1/4 Sec. 2, T.140 N, R.37 W, Becker County, 4.8 km W and 5.0 km N of the town of Osage. The slough is presently an elongate Typha marsh (800 × 250 m, 14 ha, 460 m OD) with about one hectare of open water in its eastern end, where the core was taken through 3.9 m of water. The slough occupies a steep-walled E-W-trending channel 4-6 m lower than the surrounding level outwash.

The portion of the Park Rapids outwash plain (Figure 2) that surrounds Peterson Slough is exceptionally flat (local relief <2 m). The soils are dark-colored relict-prairie soils (Udic Haploborolls) and have a loamy epipedon (Minnesota Soil Atlas, 1969). Peterson Slough is the only permanent lake on the plain.

The present upland vegetation consists mostly of woodlots of jack pine and oak isolated among fields. Most of these woodlots are characterized by a sparse canopy of jack pine, a continuous subcanopy of Quercus macrocarpa, Q. borealis (northern red oak), and Corylus americana (hazel) and a sparse groundcover. The channel in which Peterson Slough lies is occupied by several taxa that do not occur outside the catchment, such as Picea glauca (white spruce), Larix laricina (tamarack), Abies balsamea (balsam fir), and Betula papyrifera (paper birch). Surveyors described the pre-settlement vegetation as jack pine barrens with openings of brush prairie (Quercus macrocarpa and Populus tremuloides thickets) and small patches of grassland (the Shell and Fishhook prairies, Figure 2).

Wentzel’s Pond
Location: 94°57’ W, 46°57’ N, NE 1/4 of SW 1/4 of Sec. 11, T.140 N, R.34 W, Hubbard County. 0.5 km E of the town of Dorset. The oval pond (270 × 130 m, 435 m OD) is the largest and deepest (1.6 m) of a chain of small ponds in a steep-sided discontinuous channel that is 10-20 m lower than the surrounding outwash. It is the only site having sediments that show no signs of recent drying and humification.

The portion of the Park Rapids outwash plain (Figure 2) that surrounds Wentzel’s Pond is strongly rolling (local relief 5-10 m), with dark-colored relict-prairie soils (Boralfic Udic Argiorthols, Minnesota Soil Atlas, 1969) on sandy loams to coarse sands with gravel (McMillen et al., 1930).

The present upland vegetation consists of scattered woodlots similar to those described for Peterson Slough, and patches of jack pine, aspen, and Quercus macrocarpa also cover the catchment slopes to the lake margin. The understory is a dense thicket of Quercus macrocarpa grubs, Corylus americana, Prunus virginiana (chokecherry), P. pensylvanica (pincherry) and Amelanchier humilis-complex (juneberry). As inferred from surveyor’s notes, the presettlement vegetation consisted of scattered patches of jack pine, thickets of Quercus macrocarpa and Populus tremuloides, scattered individuals of Pinus resinosa (red pine), and some grassland (the Hubbard prairie, Figure 2).

Hostage Lake
Location: 94°58’ W, 46°33’ N, SW 1/4 NW 1/4 Sec. 31, T.136 N, R.27 W, Crow Wing County, 11 km N and 3 km E of the

Figure 1 Map of Minnesota showing the distribution of sandplains occupied by prairie soils (black) or by forest soils (grey). The prairie/forest border at the time of settlement (100 BP) was displaced to the east at 6000 BP to the position estimated by the 20% isopoll for prairie herbs (Webb et al., 1983). The western limit for jack pine today is shown by the dashed line. Soil distributions redrawn from Arnesson (1963).

Figure 2 Location of pollen sites in north-central Minnesota. Prairie openings with prairie soils are shown as grey (S = Shell, F = Fishhook, H = Hubbard) on outwash plains (white). The rest of the area is largely till on moraines or drumlin fields. The locations of Stevens Pond (Jansen, 1967) and Onond Pond (Jacobson, 1979) are also shown. Each pollen site is located at the centre of a hexagonal clockface that runs counterclockwise from 6000 BP to the present, showing the duration of prairie occupation, reforestation of aspen oak, and jack pine occupation.
town of Merrifield. The teardrop-shaped lake (380 × 190 m, 368 m OD). It is one of the smaller (4.6 ha) and shallower (maximum depth 1.5 m) lakes in a district of many ice-block depressions. The surrounding portion of the Crow Wing outwash plain is level (local relief 2-5 m) and generally less than 5 m higher than the lakes. The soils are light-colored forest soils on well-sorted sands (Typic Udipluderts, Minnesota Soil Atlas, 1969).

The present vegetation is largely jack pine forest with a discontinuous subcanopy of Quercus borealis, Q. macrocarpa, Corylus cornuta, C. americana, Prunus virginiana, P. pensylvanica and Amelanchier intermedia-complex. Where gaps occur in the subcanopy, the ground is carpeted with Pleurozium schreberi (feathermoss), Vaccinium angustifolium (blueberry), broadleaf evergreens, herbs, and grasses. Stands of Populus tremuloides are common around lake margins and where jack pine has been logged. Stands of Quercus borealis and Betula papyrifera are common on small outcrops of till, which are scattered across the outwash plain (Armman et al., 1965).

**Big John Pond**

Location: 94°58′ W, 47°33′30″ N, SE 1/4 SE 1/4 Sec. 10, T. 147 N, R. 34 W, Beltrami County, approximately 10 km W and 8 km N of Bemidji. The small (1.8 ha) oval lake (240 × 110 m, 421 m OD) lies in a closed depression 2-5 m lower than the surrounding level outwash. It has a maximum depth of 0.6 m.

The surrounding Bemidji sand plain (Figure 2) is characterized by patches of flat, well-sorted outwash with few lakes, alternating with patches of gently rolling, moderately sorted outwash with several shallow lakes or peatlands. The soils are sandy light-colored forest soils (Psammic Eutruborals, Minnesota Soil Atlas, 1980).

Jack pine occurs in nearly pure stands on the flat outwash around Big John Pond. The understory is similar in both composition and structure to that described for Hostage Lake.

**Mud Lake**

Location: 94°45′ W, 46°52′ N, NE 1/4 Sec. 17, T. 139 N. R. 32 W, Hubbard County, 2.4 km W of the Badoura State Nursery. The lake consists of two basins partially separated by a point on the northwest side of the lake. The southwest basin is shallow (<2 m), whereas the northeast basin, where the core was taken, has a maximum depth of 11 m. Mud Lake lies in a channel trending NE-SW with a four-lake chain. It has an area of 20.5 ha, and with an elevation of 424 m it is 3-10 m lower than the surface of the surrounding undulating outwash.

The outwash around Mud Lake is a thin veneer of well-sorted sand that blankets a drumlin field (Wright, 1962) with NE-SW-trending crests and swales. Most swales are filled with peat (McIver et al., 1930) or chains of lakes like the Mud Lake chain.

The sand-capped drumlins are presently occupied by jack pine forest, with a sparse understory of Corylus cornuta, C. americana, Salix humilis, Viburnum rafinesquianum, and lesser amounts of Quercus macrocarpa, Q. borealis, and Populus tremuloides. Near the margins of the peat-filled swales the subcanopy coverage is greater and the canopy of jack pine is locally mixed with Populus tremuloides and some Betula papyrifera. Typically Pleurozium schreberi provides a continuous moss carpet that is interrupted by clones of Vaccinium angustifolium, Arctostaphylos uva-ursi (bearberry), and Ceanothus ovatus (redroot).

**Lake Minnie**

Location: 95°00′30″ W, 47°14′40″ N, SE 1/4 Sec. 32, T. 144 N. R. 34 W, Hubbard County, 1.5 km W and 5.3 km N of Lake George. The oval lake (900 × 410 m, 429 m OD) has an area of 28.5 ha and a maximum depth of 8.5 m at the point where the core was taken by J.H. McAndrews.

Moraine occupies the northwest quadrant of a circle of 6 km radius with Lake Minnie at its centre. The remaining quadrants are outwash (Lake George outwash plain, Figure 2), which is interrupted by several peat-filled channels and steep-sided, widely spaced, elongate hills that are 25-40 m higher than the intervening flat outwash. Both the peat-filled channels and the elongate hills trend N-S and are probably galio-fluvial features. The sandy soils of the flat outwash are light-colored forest soils (Typic Udipluderts, Minnesota Soil Atlas, 1980).

Jack pine, common on the moraine northwest of Lake Minnie, forms nearly pure stands on the outwash. On the well-drained portions of the outwash plain, *Pinus resinosa* is the only other taxon to share the canopy with jack pine. *Populus tremuloides, Betula papyrifera, Quercus macrocarpa,* and *Q. borealis* occur as seedlings 2 m high. The sparse shrub layer contains scattered individuals of *Corylus cornuta,* *Prunus virginiana,* P. pensylvanica, *P. pumila* (sand cherry), and *Amelanchier intermedia-complex.* The ground has a continuous mat of *Pleurozium schreberi* and other mosses, with small patches of *Cladonia rangiferina* and *C. alpestris* (reindeer lichens) on drier spots. Large clones of *Vaccinium angustifolium* are common, as are several broadleaf evergreens, including *Arctostaphylos uva-ursi,* *Pyrus secunda,* *P. repens* and *Chamaedaphne umbellata*.

**Methods**

Short cores of the upper soft sediment were collected from the ice surface at the deepest part of each lake with a clear plastic tube 5 cm in diameter fitted with a piston (Wright, 1980). Deeper sediment was obtained with a square-rodd piston corer of the same diameter (Wright, 1967) and were extruded in the field and then wrapped in plastic and aluminium foil. The sediment lithology was described in the Troels-Smith (1955) system, and the total dry matter and proportions of organic matter, carbonate, and mineral matter were determined by weight loss on heating to 110°, 500°, and 900°C (Dean, 1974).

Samples were prepared for pollen analysis by standard methods (Faegri and Iversen, 1975). In the pollen diagrams the basic sum includes all upland taxa. Obligate aquatic and wetland taxa as well as Cyperaceaeae are excluded from the basic sum (see Lichti-Federovich and Ritchie, 1965). Indeterminable grains were also excluded.

The zonation of the diagrams is based entirely upon the curves for *Pinus banksiana/resinosa,* culturally influenced taxa (cf. *Avena,* undifferentiated Cerealia, *Zea* mays, *Medicago sativa,* *Melilotus* type, *Trifolium repens* type, and *Salvia kalh*) and the sum of prairie types (*Poaceae,* *Artemisia,* *Chenopodium* type, *Tubuliflorae,* *Iva xanthifolia* type, *Iva ciliata* type, *Liguliflorae,* *Petalogetium candidum* type, and *P. purpureum*). These restrictive zoning criteria were used for all six study sites to provide matching zones that are consistent with the inferred history jack pine invading prairie, which is the focus of the paper. The zone boundary based upon the culturally influenced taxa (Zone 1/2 boundary) was determined so that a radiocarbon date could be obtained for a core segment of known age (c. AD 1880) and the difference
Figure 3: Pollen diagrams for the six sites. The loss-on-ignition curves show (from left to right) the proportions of organic matter, carbonate, and inorganic matter. The shaded curves show 10x exaggeration of the percentage scale.
Table 1 Radiocarbon dates. The corrections are based on the difference between the reported dates and AD 1880, which is the approximate date for the inception of logging and agriculture in the area.

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<th>Sample depth (cm)</th>
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<th>Lab. number</th>
<th>Reported date (BP)</th>
<th>Correction (yr)</th>
<th>Corrected date (BP)</th>
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used for correcting down-core dates. The assumption that the carbonate errors were uniform throughout the time under consideration may not be valid, but the corrected dates may be closer to the truth than the uncorrected dates. The date from Lake Minnie was not corrected, because no date was available for the settlement horizon.

Local taxa are defined as representing those plants growing in the lake (aquatic) or in the lake-margin wetland (wetland and Cyperaceae). Extralocal taxa refer to types that grow on the surrounding outwash plains, on the uplands, or in peatlands. Regional taxa are those that are generally restricted to moraines or occur outside the area.

To compare visually the prairie-to-jack pine transitions among the six study sites and to compare the fossil pollen spectra with pre-settlement pollen spectra (c. 100 BP), 109 fossil spectra were ordinated with 105 pre-settlement samples collected in the Minnesota area from different vegetation types to represent the time just before agricultural disturbance and logging (unpublished data made available by E.J. Cushing). Detrended Correspondence Analysis (Hill, 1979) was used to ordinate the samples.

### Results and discussion

#### Zone 4, Prairie Occupation

This zone, at the base of the diagrams, is characterized by high percentages of prairie herbs, ranging from 47% at Peterson Slough to nearly 70% at Wentzel's Pond (Figure 3). The upper boundary is placed where the sum of prairie herbs begins a decline to values generally less than 20%. Indeterminable pollen grains (not shown) are common (2-12%) in this zone at some sites and consist mostly of crumpled grains or grain fragments that are apparently inaperturate (probably Cyperaceae, Populus, or broken Poaceae).

In the ordinations (Figure 4) the high percentages of prairie herbs cause the fossil-pollen samples in Zone 4 to have high first-axis scores and low second-axis scores. These samples generally fall close to, but not within, the cluster of pre-settlement samples that constitute the Poaceae-Artemisia assemblage (Figure 4A) from sites in the tallgrass-prairie regions of western Minnesota and eastern South Dakota. The prairie surrounding the pre-settlement sites there was essentially continuous, interrupted only by riparian forests along rivers and by brush that rimmed prairie sloughs. Most of the pre-settlement sites were more than 40 km west of the nearest woodlands, so the source of arboreal pollen is presumed to have been distant.

Moderate percentages of pine (8-18%) in the Zone 4 samples of Wentzel's Pond, Big John Pond, Mud Lake, and Lake Minnie cause some samples from these sites to be ordinated outside the Poaceae-Artemisia assemblage and to differ from Peterson Slough and Hostage Lake, which have slightly lower percentages of pine (6-12%) and much higher percentages of Quercus (16-27%) than the other sites (5-17%). The Zone 4 samples from these two sites therefore fall in the upper part of the Poaceae-Artemisia assemblage or at the edge of the Poaceae-Quercus assemblage, respectively.

The Zone 4 samples for Hostage Lake are ordinated within the Poaceae-Quercus assemblage, which comprises sites along the prairie/forest border in southern Minnesota. Most of these pre-settlement sites occurred in prairie, but close to patches of bur oak. These oak-dominated patches have been variously described as savanna, oak openings, and scrub (Dauenhower, 1956; McAndrews, 1968; Grimm, 1983), indicating the physiognomic variability of oak communities as they intergrade with prairie. Apparently the oaks can flower under all of these physiognomic circumstances (Grimm, 1983) and deliver moderate amounts of oak pollen to sites in nearby prairie.
Figure 4 Ordination by detrended correspondence analysis (Hill, 1979) for 105 pre-settlement samples (A) and 21 pollen taxa (B). The pollen assemblages are outlined and named in A. Where two assemblages overlap, the border of the assemblage with generally lower third-axis scores is broken and the sites indicated by open circles. The analysis does not include any of the 109 fossil samples from the six sites. The remaining diagrams (C–H) show the ordination for fossil samples from the six sites (see A for abbreviations of pollen assemblages). Stratigraphically adjacent samples are connected. Dates for pollen-zone boundaries are taken from Figure 5. Pollen zones are shown by characteristic symbols.
Zone 4 represents a period during which prairie occupied the outwash surrounding all six study sites. Unlike their closest presettlement analogues, the study sites were possibly occupied by relatively small prairies (10–100 km²) limited to the surrounding outwash. The moraine that encompasses the outwash plains has been forested since about 4000 BP (McAndrews, 1966; 1969; Jacobson, 1979) and has served as a nearby source of arboresal pollen during the period represented by Zone 4. The moderate percentages of total pine and oak, which cause some of the Zone 4 samples to be ordinated outside the presettlement assemblages (Figure 4) may be attributed to oak and white pine (Jacobson, 1979) growing on the adjacent moraines.

High percentages of locally derived Poaceae (27–45%) and Tubuliflorae (4–12%) in the Zone 4 samples at Wentzel's Pond and Big John Pond cause their exceptionally low second-axis scores (Figure 5). Similarly high percentages of Poaceae pollen have been attributed to wild rice, Zizania aquatica, at sites within the study area (McAndrews, 1969), but this is probably not the case for these two sites. Apparently both of these sites were wet meadows at the time (Zone 4), as indicated by exceptionally high percentages of Poaceae and Cyperaceae pollen (43–47%, outside the sum). Humified silty sediments with sand lenses at and below the pollen samples characterize the Zone 4 sediments of these sites. These sedimentological features indicate periodic drying. The sand could have been wind-deposited, as Holocene dunes do occur on these outwash plains (Norton, 1982), but a large sand lens at Wentzel's Pond at 215–225 cm appears to be a mud-crack filling, as it is wedge-shaped in vertical section. Thus it is unlikely that these sites were sufficiently wet to support wild rice. Local populations of Calamagrostis, Glyceria, and other wetland grasses present at these sites today may have caused the high percentages of Poaceae. The high percentages of undifferentiated Tubuliflorae (some of which is Bidens-type) is consistent with the interpretation that these sites were wet swales and not wild rice beds. Because of its high percentages in Zone 4 at these two sites, Cyperaceae was removed from pollen sums for all study sites and was not included in the ordination (Figure 4).

Chronology

The duration of prairie occupation at the study sites is undocumented except at Lake Minnie (McAndrews, unpublished data), where prairie replaced a woodland of jack pine or red pine at about 8140 BP (WAT-1032) and prevailed for roughly 3600 radiocarbon years. Because prairie persisted still longer at the other study sites than at Lake Minnie, it was probably established earlier as well. Thus 3600 radiocarbon years may be a minimal estimate of the duration of prairie occupation at the other study sites.

The historical records (Public Land Survey records c. AD 1850–1880; Upham, 1888; Todd, 1899; West, 1907) indicate that some patches of outwash were so prone to repeated fire (or were otherwise so suited to the persistence of prairie) that they remained prairie until settlement. This includes the Hubbard, Fishhook, and Shell prairies of the Park Rapids outwash plain (Figure 2), which were located well within the conifer-hardwood forests, some 40–80 km east of the prairie/forest border. These prairies persisted in spite of the fact that the nearby pollen sites, Peterson Slough and Wentzel's Pond, indicate that afforestation began prior to 2000 BP (see below). Thus prairie has probably occupied some small
patches of outwash within regions of Minnesota that have been mostly forested since about 8000 BP, leaving little evidence of their existence in the pollen record.

**Subzone 3b. Afforestation of the outwash-plain prairies**

Subzone 3b represents a transitional period in which the pollen of prairie herbs decreased by 20% (Figure 3). The *Quercus* curves show slight to moderate maxima. *Pinus strobus*, *Betula*, and *Ostrya* percentages increase and contribute most to the consistent 10-20% increases in the sum of tree and shrub types that are restricted to moraine (regional taxa). This is in contrast to the slight changes in the sum of tree and shrub taxa that can grow on outwash. The upper boundary of the subzone is placed where the *Pinus banksiana* *resinosa* curves begin a consistent rise to >30%.

In the ordination for Subzone 3b, samples have the most between-site variability (Figure 4). Peterson Slough and Hostage Lake are the only sites having fossil samples that clearly track through the presettlement assemblages, with scores similar to those of the *Quercus-Betula assemblage*, because they have percentages of *Quercus* that range from 7-30% and because their *Betula* curves rise prior to increases in *Pinus strobus*. For Wentzel's Pond, Big John Pond, and Mud Lake, the low percentages of *Quercus* (<12%) and roughly coincident rises in *Betula* and *Pinus strobus* cause the samples to have lower second-axis scores. For the numerous Lake Minnie samples the ordination scores span the range of variability exhibited by all of the other study-site samples in Subzone 3b.

An analogue-based interpretation of Subzone 3b suggests that Hostage Lake and Peterson Slough have presettlement analogues in the *Quercus-Betula assemblage*, which is found at sites that generally occur in regions mapped as oak-dominated brushland by Marschner (1974). For the other sites, the closest presettlement analogues are two sites that have the lowest second-axis scores of the *Quercus-Ostrya* assemblage, viz: Horse and Faith Ponds (McAndrews, 1966), which occurred in prairie with oak savanna or oak scrub nearby (<5 km). Thus by analogy prairie occurred near Wentzel's Pond, Big John Pond, Mud Lake, and Lake Minnie, and the differences among their Subzone 3b samples may result from distances to the nearest oak-dominated community.

Horse Pond and Faith Pond (McAndrews, 1966) are not only the closest presettlement analogues for many of the Subzone 3b samples, but they also occur close to the study area in a region where woody species were actively invading prairie prior to widespread agriculture. Fortunately these two sites fall within the area where Ewing (1924) described in detail the vegetation, succession, and mechanics of afforestation. Ewing's observations are consistent with sedimentological features and with fluctuations of minor taxa that have little or no influence on the ordination scores and therefore on the interpretation by analogy.

Ewing (1924) observed that the initial invaders of northern Minnesota prairies are willows (*Salix interior* and *S. discolor*) and aspen (*Populus tremuloides*), especially along the margins of sloughs or in swales that are wet at least in the spring. Waterlogged soils are critical for these taxa for three reasons. First, the woody seedlings compete poorly for water at sites with an established prairie sod. This is particularly important in prairie regions, where precipitation is seasonal and variable from year to year (Transeau, 1935). Second, the sloughs and wet soils may serve as firebreaks and protect woody seedlings from the nearly annual prairie fires (Grimm, 1981, 1983).
Once willow and aspen seedlings have been spared for several years, their rootstocks are sufficiently developed to produce vigorous post-fire sprouts, even if they burn nearly every fall (Ewing, 1924). Third, prairie sloughs typically dry down in the early summer, leaving exposed mud flats where spring-fruiting taxa like willow and aspen can germinate on mineral soil.

An unfortunate but characteristic property of pollen diagrams from sites where aspen and associated shrubs actively invade prairie is the lack of positive evidence for tree and shrub establishment. Many of the invading shrubs, such as Salix, Symphoricarpos, Rhus, and Amorpha, are predominantly insect-pollinated and thus poorly represented in the pollen record. Aspen pollen is produced in abundance, but it is poorly preserved in some lake sediments (Lichti-Federovich and Ritchie, 1965, 1968; Janssen, 1966). Also, aspen may not flower at all if the sprouts are burned at intervals of less than 10 years (Grimm, 1983). Ewing’s observations suggest that it is unlikely that the aspen brush-prairie region just west of the study area escaped fire for more than 10 years. Under these circumstances clones of aspen and its associated entomophilous shrubs would create palynological “blind spots” (Davis, 1963) in the landscape. Such a circumstance, which could cause a decrease in the influx of extralocal pollen (prairie types) and a corresponding percentage increase in regional types (sum of regional tree and shrub taxa), is observed at all of the sites, along with some direct evidence of tree and shrub establishment. At Peterson Slough, Big John Pond, Mud Lake, and Lake Minnie, the values of Populus in Subzone 3b samples range from 1 to 4% but are higher than in Zone 4. Although differential preservation of Populus pollen may be a problem, these percentages are slightly higher than those recorded at sites in Manitoba’s aspen parkland, where aspen is actively invading prairie (Lichti-Federovich and Ritchie, 1965, 1968). The percentages of Salix are highest in Subzone 3b at Lake Minnie, Mud Lake, and Big John Pond, but the percentages are low (<5%) and variable. As described by Ewing (1924), the initial stage of Salix domination is shortlived, and any peaks of Salix pollen could be missed by the wide sampling intervals used in this study.

On flat terrain such as outwash plains, aspen can rapidly expand into grassland by suckering (Bird, 1961; Buell and Buell, 1959; Buell and Facey, 1960; Grimm, 1983). On more rolling terrain, where aspen roots cannot reach the water table, the advance of aspen into prairie is slower, and the margins of the expanding clones are often invaded by Corylus americana. For all the study sites, the percentages of Corylus are higher in Subzone 3b than in Zone 4. Ewing (1924) observed that Corylus reduced the number of aspen sprouts (by shading), and Quercus macrocarpa, Prunus virginiana, and P. serotina became established. Because the seeds of these species are not wind-dispersed, Ewing concluded that their establishment resulted in part from chance and the proximity to a seed source. Thus the proximity of a study site to moraine (where oak was established) and the ruggedness of the local topography may have determined the degree to which oak became established relative to aspen in the extralocal vegetation around that site. This could explain the high percentages of oak at Lake Minnie, which lies adjacent to moraine. Hostage Lake and Peterson Slough also have high percentages of oak, and they lie close to areas of rolling ice-contact moraine that presently support oak-dominated forests.

In summary, Subzone 3b is interpreted as representing a period during which an aspen-dominated brush prairie as described by Ewing (1924) became established around the margins of the study sites. Aspen brush probably also became established around other sloughs and wet swales on the surrounding outwash. While the drier portions of the outwash remained prairie. Differences among ordination scores of the Subzone 3b samples caused by the decline in prairie taxa and by the apparent increase in taxa restricted to moraine are attributed to aspen replacing prairie and to the resultant relative increase in the proportion of regional versus extralocal pollen. Increases in taxa associated with aspen brush (Salix, Corylus and perhaps Quercus) and sedimentological evidence of rising water tables during deposition of Subzone 3b are consistent with Ewing’s observations concerning the afforestation of prairie just west of the area.

**Subzone 3a. Expansion of pine**

Subzone 3a is characterized by increases in Pinus banksiana/ resinosa pollen from less than 10% to 30-60% (Figure 3). The upper boundary is placed where the percentages of Pinus banksiana resinosus decrease to zero and begin to fluctuate about a mean (Zone 2). Quercus (15% at the top of the subzone) and prairie herbs decline. The sum of regional tree and shrub pollen is essentially constant or rises slightly above Subzone 3b levels. The percentages of Pinus strobus and Betula tend to be inversely correlated. At Peterson Slough, Wentzel’s Pond, Big John Pond, and Lake Minnie, the percentages of Picea increase in this zone. At Big John Pond and to some extent at Lake Minnie, the pollen of other lowland conifers such as Larix, Abies and Thuja-type also rises.

Higher percentages of total pine cause the first-axis scores of the Subzone 3a samples to be much lower than for the Subzone 3b samples (Figure 4). At the base of Subzone 3a, Pinus strobus is the major contributor to total pine, whereas at the top of the zone Pinus banksiana resinosus is the predominant taxon. The samples for Lake Minnie have much higher percentages of pine than the other study sites and span a narrow range of first-axis scores within the Pinus assemblage. Samples from the other sites have higher first-axis scores, comparable to those of the Pinus-Quercus and the Pinus-Betula assemblages. In two dimensions, the samples from Peterson Slough, Hostage Lake, and Mud Lake fall within the Pinus-Quercus assemblage, but these fossil samples and the pre-settlement samples that constitute the Pinus-Betula assemblage have considerably higher third-axis scores than does the Pinus-Quercus assemblage. Thus when three ordination axes are considered the Subzone 3a samples do not fall within any pre-settlement assemblage and are equally close to the Pinus-Quercus and the Pinus-Betula assemblages. Higher third-axis scores are caused by higher percentages of lowland conifers such as Picea, Abies and Larix. Conifer swamps are presently a common feature of the outwash plains so their pollen was included as extralocal taxa. There are no pre-settlement analogues because of the odd combination of prairie, Quercus, Pinus banksiana resinosus, and lowland conifer pollen types.

Subzone 3a represents a period during which jack pine invaded the extralocal vegetation to a limited extent by intraspecific competition in a closed-canopy forest. At Peterson Slough and Wentzel’s Pond, where jack pine became established most recently (300-500 radiocarbon years ago), historical descriptions of the vegetation indicate that by the end of Subzone 3a the coverage of jack pine was sparse and not closed. Surveyor records indicate that bearing trees of jack pine occurred at roughly 70% of the survey corners on the outwash surrounding Peterson Slough and Wentzel’s Pond, with the remaining corners falling in regions of aspen-oak scrub or open grassland. The average distance from the
survey corner to a jack pine bearing tree was 35 m, indicating that the pines were scattered.

The surveyors of the region around Peterson Slough and Wentzel's Pond described the understorey of jack pine stands as tall, dense, and composed of oak, aspen, hazel, and willow (Salix humilis?), like the oak-aspen scrub of Ewing (1924). Apparently the jack pine invaded patches of oak-aspen scrub rather than open grassland. No historical evidence was found to indicate that jack pine directly invaded prairie. Jack pine stands containing prairie grasses and forbs have an open understorey and occur on forest soils where jack pine has been established for more than 1200 radiocarbon years (see below). Because the so-called 'prairie' plants do not occur in recently established (< c. 500 BP) stands of jack pine on prairie soils, they do not indicate former prairie occupation (i.e., relics) nor the direct invasion of prairie by jack pine. Rather they are simply heliophytes that can apparently grow equally well in prairie and in jack pine stands with an open understorey.

The rise of Pinus pollen in Subzone 3a is believed to represent establishment of extralocal populations of white spruce (Picea glauca) near Peterson Slough, Wentzel's Pond, Big John Pond, and Lake Minnie. White spruce presently occurs along the margins of the shallow peatlands that are common on the outwash plains. These peatlands (Badoura and Riffe peats, Elwell et al., 1926) are characteristically open sedge fens where the peat is deep (> c. 1.5 m), or are forested with Larix laricina where the peat is shallow. Abies balsamea, Thuja occidentalis, and rare individuals of Picea mariana also occur along the peatland margins. Big John Pond and Lake Minnie are the only sites that show risks of lowland conifers other than spruce in Subzone 3a. Wood fragments and stumps occur in the upper horizons of the Riffe peats (Elwell et al., 1926). The former tree cover of these relatively deep peats may have been black spruce (Picea mariana), and the spruce pollen present in the Subzone 3A sediments may be a mixture of both white and black spruce pollen, which were not distinguished.

**Chronology of afforestation**

The decline of prairie and the establishment of aspen-dominated brush was asynchronous among the sites (Figure 5). The estimated uncorrected date for this event (Subzone 3b/Zone 4 boundary) is about 4500 BP at Lake Minnie, and the estimated corrected dates are 3600 BP at Big John Pond, 3500 BP at Hostage Lake, 3200 BP at Mud Lake, 2900 BP at Peterson Slough, and 2600 BP at Wentzel's Pond (Figure 3). If the corrected dates are accurate, the establishment of woody plants on the outwash plains was a continuous process resulting from increasingly moister and perhaps cooler climatic conditions between about 4500 and 2500 BP (Webb et al., 1983). The lack of a clear relation between geography and chronology (Figure 2) suggests that the differences in timing among the study sites are caused by local factors rather than regional climate. The initial rise in Pinus banksianae resinosa, which determine the position of the boundary between the subzones, could be the result of either the establishment of a few jack pines within the lake catchment or the large stands of jack and red pine on distant moraines.

Zone 3 as a whole is consistent among the sites. It begins with the establishment of woody species on the outwash plains and culminates with the establishment of jack pine woodlands or bogs -- i.e., the zone represents the period of afforestation. For four of the sites, the duration of afforestation is similar: 2580 years at Peterson Slough, 2235 years at Big John Pond, 2175 years at Hostage Lake, and 2060 years at Wentzel's Pond. But it was just 1620 years at Lake Minnie and 1135 years at Mud Lake, which are the two sites where a jack pine community was first established (Zone 2/Zone 3 boundary at Lake Minnie and Mud Lake are 2545 BP and 2120 BP, respectively). Both of these sites occur on the Menafla soil series (McMuller et al., 1930), which is characterizedly associated with sinuous interconnected peat-filled channels that break the outwash plain surface into small isolated patches of upland (Figure 6). In contrast, where jack pine has been established since 1300-1400 BP, the outwash plain surface is pitted with isolated lakes (Hostage Lake area) or wetlands (Big John Pond area), and where jack pine was most recently established (300-500 BP) the outwash plains have few permanently wet depressions (Figure 6).

The asynchrony (Figure 5) of similar vegetation changes among closely spaced study sites indicates that locally varying factors largely determined the timing and rate of vegetation change, although the increasingly moist and cool climate (Webb et al., 1983) was probably the ultimate cause of the regional afforestation (see Grimm, 1983).

According to Ewing (1924), the presence of perennially or seasonally wet swales was required for brush to invade established prairie in northwestern Minnesota. Thus the establishment and persistence of brush in Subzone 3b and the eventual development of jack pine forest in Zone 2 may have been the result of the formation of sloughs and wet swales in depressions that had been dry during Zone 4 time. In this study, the patches of outwash that were never afforested (Hubbard, Fishhook, and Shell prairies) are characterized by shallow sloughs that contain no limnic sediment, suggesting that they have been only recently flooded. In contrast, the patches of outwash within uplands that are now occupied by jack pine forest generally have 10 to 50% of their surface occupied by lakes with sediments or shallow peatlands.

Sloughs and wet swales formed during Subzone 3b time may have formed as a result of a rising water table, permitting the establishment of brush at various times throughout the late Holocene -- i.e., the asynchrony of the Subzone 3b/Zone 4 boundaries (Figure 5). The development of the Glacial Lake Agassiz peatlands just north of the study area was almost certainly the result of a regional rise in water table over the same period (4000-2000 BP) (Glaser et al., 1981).

The sedimentary sequence at three of the sites is consistent with a rising water table. At Wentzel's Pond the transition from compact, highly humified sediments with sand lenses to looser, slightly humified sediments with no sand lenses is exactly coincident with the decline of prairie taxa at 2600 BP. At Big John Pond the transition from silty, slightly humified sediments with sand lenses to marly sediments occurs within Subzone 3b, slightly after the decline in prairie taxa at about 3400 BP. At Stevens Pond (Figure 2), a small peat-filled depression on outwash, Janssen (1967) describes a transition from 'completely decomposed black amorphous peat' to well-preserved woody peat that is exactly coincident with the decline in prairie taxa. Although the Stevens Pond core is undated, a comparison of the Betula, Pinus strobus, and Ostrya curves with those of the dated record at nearby Bog D (McAndrews, 1966) indicates that conditions favourable for peat preservation, i.e., probably a water table rise, prevailed at Stevens Pond at about 4000 BP. The other sites had deeper water so had not dried out during the mid-Holocene time of low lake levels.

An alternative hypothesis for the afforestation is that increased precipitation as snow could favour the establishment of brush in depressions about the water table, for persistence of snow in such depressions throughout much of the spring fire season could protect woody seedlings from spring fire. Freeze-and-thaw cycles in the depressions could
favour the establishment of wetland graminoids and woody plants such as Salix and Populus. This mechanism may have been important on the outwash at Peterson Slough and Wentzel’s Pond, where most of the depressions are well above the water table or have just recently been flooded. This mechanism, however, does not easily explain the asynchrony of brush invasion among all the study sites, because it is a regional climatic event, and all the depressions are deep enough to trap snow.

The inundation of depressions either seasonally or permanently may explain the establishment and persistence of aspen-dominated brush, but it does not explain the eventual spread of aspen onto the uplands. It also does not explain the spread of taxa like oak and jack pine, which require fire return-intervals greater than their minimum age of seed production, about 30 and 10 years respectively (Fowells, 1965), in order to spread by sexual means. The most likely explanation is that the clones of aspen, which are less flammable than prairie, provided the firebreaks that allowed some upland patches of outwash to escape fire for several years (Grimm, 1981, 1983). Therefore the abundance of brush-filled depressions and the degree to which they are interconnected may have determined how well they could insulate a particular patch of outwash from prairie fires – and thus determine the probability that woody species could invade that patch. This would explain why afforestation was most rapid (see above) at sites where depressions occur as channels (1100-1700 years) versus sites where depressions are scattered or rare (2000-2600 years, Figure 6).

Zone 2. Full occupation by jack pine

This zone is characterized (Figure 3) by the highest percentages of Pinus banksiana/resinosa (30-60%) and the lowest percentages of Quercus (2-15%). The percentages of Pinus strobus, Betula and Ostrya generally decline throughout the zone. The summed percentages of regional trees and shrubs are 5-20% lower than in Zone 3. The lowest percentages of prairie taxa are recorded in this zone, from about 10% at most sites to 15-20% at Peterson Slough and Wentzel’s Pond. The upper boundary of Zone 2 is placed where total pine percentages decline and Ambrosia percentages increase as a result of logging and land clearance.

In the ordinations (Figure 4), the Zone 2 examples for Peterson Slough, Wentzel’s Pond, Hostage Lake, and Mud Lake are ordinated near the contact between the Pinus assemblage and the Pinus-Quercus assemblage. The samples for Lake Minnie and Big John Pond have lower first-axis scores than the above sites and are ordinated near the Pinus assemblage. The differences in first-axis scores among the Zone 2 samples is the result of different percentages of pine, which range from 35% at Peterson Slough to 65% at Lake Minnie. The Lake Minnie samples with near-zero first-axis scores have the highest percentages of total pine recorded in Minnesota sediments. With the exception of a single sample for Peterson Slough, the second-axis scores vary little among the sites, and these differences cannot be attributed to a particular taxon. The study sites themselves constitute the bulk of presettlement samples from outwash plains dominated by jack pine in Minnesota and therefore serve as their own analogues.

The vegetation represented by the Zone 2 samples is presumed to be analogous to the presettlement vegetation around the study sites as described by the early land surveyors and mapped as jack pine barrens and openings by Marschner (1974). Outwash plains with light-coloured forest soils were occupied by an essentially continuous forest of jack pine that was not extensively mixed with deciduous trees. Hostage Lake, Big John Pond, Mud Lake, and Lake Minnie occur in such areas. Outwash plains with dark-coloured relic prairie soils were occupied by jack pine barrens, described by the surveyors as a mosaic of jack pine, oak and aspen thickets, and some open grassland. Peterson Slough and Wentzel’s Pond occur in these regions. The only palynological distinction between these two types is slightly higher first-axis scores (Figure 4) and somewhat higher percentages of prairie types for the barrens sites. The overwhelming abundance of pine pollen in these samples influences the percentages of minor taxa and ordination scores in such a way that it is difficult to differentiate palynologically the pine-dominated communities that have considerable compositional and physiognomic differences.

The variable lengths of time of jack pine occupation represent the historical factor most correlated with the present vegetation and levels of soil organic matter (SOM). SOM declines from c. 4% to less than 2% during the first 1000 years of jack pine occupation, along with a decrease in both the height and cover of deciduous trees and shrubs growing as associates of jack pine (Aimenderg, 1990). On sandy soils with little silt and clay, SOM is probably the most important soil component governing cation-exchange capacity and soil-moisture retention (Brady, 1974). Thus this is a clear case of a shift from the deciduous habit on sandy soils with c. 4% SOM to the evergreen habit (conifers, broadleaf evergreens, and mosses), because sandy soils with less than 2% SOM are impoverished in both nutrients and water. The percent SOM is correlated with the duration of jack pine occupation (Zone 2/Zone 3 boundary) rather than the time since the establishment of deciduous taxa (Zone 3/Zone 4 boundary) so the establishment of jack pine and its associated litter and microflora probably caused the decline of SOM and the gradual loss of deciduous elements.

Post-settlement. Zone 1

This zone is characterized (Figure 3) by rising percentages of Ambrosia, declining percentages of total pine, and the occurrence of introduced or agricultural pollen types (cf. Avena, undifferentiated Cerealia, Zea mays, Medicago sativa, Melilotus-type, Trifolium repens-type, and Salsola kali). Ambrosia percentages are typically 5% higher than in Zone 2. The peak values of Ambrosia are between 5 and 10%, which is low in comparison with sites in agricultural regions of southern Minnesota. The declines in pine pollen range between 10 and 30% and result from logging. Quercus and Populus percentages rise at all sites, and Betula increases at Lake Minnie, Hostage Lake, and Mud Lake, presumably as these taxa expanded into regions logged for pine. The Zone 1 percentages of Chenopodium-type are 1-4% higher than those recorded in Zone 2 and are probably the result of timber harvest or land clearance for farming. The increased percentages of Quercus, Populus, Betula, Ambrosia and Chenopodium-type cause the Zone 1 samples to have higher first-axis scores than Zone 2 samples in the ordination (Figure 4).

The accounts of Alvin Wilcox, the surveyor of several townships in the western portion of the study area, indicate that settlement was sparse in the early 1870s, and many townships had no settlers (West. 1907). Agriculture at this time consisted largely of sustenance farming and providing for livestock. Some of the first cash-crop farms in the study area were located on the dark-soil outwash in Wadena and Hubbard counties. In Hubbard county, these initial farms were established in 1879 on the Hubbard and Fishhook prairies, which are within 10 km of Wentzel’s Pond and Peterson Slough respectively. By 1880 Hubbard County had
Conclusions

Outwash plains in north-central Minnesota, occupied by prairie during most of the mid-Holocene, have been succeeding to jack pine forest since c. 5000 BP. The inferred vegetational shift from prairie to an aspen-oak community to jack pine forest has been similar among all sites investigated thus far and would probably continue today were it not for the fact that available habitat for jack pine invasion (aspen-oak woodland) has been cleared for agricultural use and the wetlands drained. A coarse scale, this same vegetational sequence occurs spatially in northern Minnesota as the ecotone of the prairie, deciduous forest, and mixed coniferous-deciduous forest formations. The conceptual model of the ecotone passing over a site as it migrated from northeast to the southwest in the late Holocene (Webb et al., 1983) is a valid interpretation of the paleoecological data from any single site in this study. However, the asynchrony of vegetational change among these six study sites with regard to their geographic position suggests that the concept of vegetation tracking a migrating climatic boundary does not apply at the scale of this investigation and should be used with caution whenever an ecotone passes over spatially heterogeneous landscapes. It is proposed that climatic change was not the direct cause of the late-Holocene vegetation change at the study sites, and that estimates of past climatic parameters from the pollen spectra of these closely spaced sites would yield conflicting results. Resolution of such conflicts requires a functional understanding of the relationship between climate and the proximal cause of vegetation change.

The analysis of Public Land Survey records, the modern vegetation, and the autecology of the community dominants all point to changes in fire frequency as the proximal cause in a shift from prairie to jack pine forest (Almendinger, 1985). The formation of water-related firebreaks in previously dry basins is hypothesized to be the event that insulated patches of outwash from prairie fires, thus allowing reforestation to proceed. The coincidence of the rise in pollen from woody taxa and the initial deposition of non-humified sediment at Wentzel's Pond, Big John Pond, and Stevens Pond supports this hypothesis. It is also hypothesized that linear firebreaks such as peat-filled channels were more effective at isolating patches of outwash from fire than were scattered lakes and depressions, as evidenced by the more rapid reforestation at Lake Minnie and Mud Lake, where these peat-filled channels occur. The rise in the water table, which initiated the formation of the lakes and wetlands, is almost certainly the result of climatic change in the form of increased precipitation or other parameters that lead to increased infiltration. Apparently local hydrologic and physical characteristics of outwash plains determined the absolute magnitude of the climatic change necessary for depressions to fill with water or peat. That is, climatic thresholds necessary to invoke the same vegetational change (as perceived palynologically) can vary locally. It follows, then, that when climatic inferences are to be drawn from palynological data some knowledge of the mechanistic link between climate and vegetation change is important, as is an understanding of the range of locally influenced climatic thresholds necessary to achieve that vegetational change.

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