Midwestern Holocene Paleoenvironments Revealed by Floodplain Deposits in Northeastern Iowa

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Pollen analysis of pond deposits in the upper reaches of a stream from northeastern Iowa, an area beyond the last glacial margin, provides a nearly complete record of vegetational changes during the last 12.5 thousand years. Sixty-one radiocarbon dates provide good chronological control. Spruce forest was replaced by deciduous forest before 9.1 thousand years ago, followed by prairie from 5.4 to 3.5 thousand years ago, and oak savanna from 3.5 thousand years ago until presettlement times. The prairie invasion was nearly 3 thousand years later here than at other sites in Iowa and Minnesota, documenting a late Holocene, rather than an early-middle Holocene, period of maximum warmth and dryness for the southern part of the upper Midwest.

SITES FOR LATE-GLACIAL AND HOLOCENE paleoecological studies are rare beyond the Wisconsinan glacial margin in the upper Midwest. Lakes and bogs, the usual sources for fossil pollen data, are virtually absent. Pack-rat middens, a fruitful source of paleoecological materials in the southwestern United States (*1*), are not encountered in the Midwest. Sinkhole ponds that can provide pollen sequences in other areas of the country (*2*) are not present. As a result, few data on climatic change are available in this region, and many aspects of Holocene paleoclimates are uncertain.

We describe palynological data from deposits along Roberts Creek in the Paleozoic Plateau (*3*) ("Driftless Area") of northeastern Iowa (Fig. 1). These deposits contain abundant, identifiable organic remains spanning the last 12.5 thousand years and are within 8 km of the source (hence have local provenance). The topography of the Roberts Creek area is gently rolling, with a maximum local relief of about 30 m; therefore, it is unlikely that such anomalous microhabitats as fir or pine on north-facing slopes and goat prairies on south-facing slopes (common in steeper parts of the plateau) have been contributing regionally anomalous fossils to the record. Little entrenchment or valley-filling has occurred since late-glacial time, and only 2 to 3 m of late-glacial and Holocene alluvium underlies both the modern floodplain and low Holocene terraces. Organic preservation is dependent on a consistently high water table, and the remains occur only along parts of the creek where the piezometric surface is near the bed of the stream.

Depositional environments of the deposits include (i) beaver ponds (beaver-gnawed wood is abundant at 3 of the 42 sites examined, and one site contains a 10,700-year-old beaver dam constructed entirely of spruce); (ii) small oxbow lakes; and (iii) pool deposits between riffles. Thus the sites are more properly designated small-pond deposits, rather than alluvium, even though they occur in an alluvial setting. Pollen, vascular-plant macrofossils, bryophytes, insects, mollusks, and, in some cases, small vertebrates are preserved. Similar sediments have been reported from southwestern Wisconsin (*4*), but no paleoecological work has been done on them.

Pollen samples and wood for radiocarbon dating were dug from stream banks, placed in plastic bags, and returned to the laboratory. Standard methods of processing with KOH, HCl, HF, and acetolysis solution (*5*) were augmented by screening with a 7-μm sieve (*6*), flotation with $ZnCl_2$, and treatment with 0.2% Clorox bleach (*7*). Pollen samples were mounted in silicone fluid (2000 centistokes), and pollen was identified by comparison with the reference collection at the University of Iowa Geology Department.

We obtained 61 radiocarbon dates, at least one for each site. Because 52 of the dates are on wood, which is considered to be the most reliable material to date, the chronology is probably better than those from most lake and bog sequences, where whole-sediment dates may yield spurious ages (*8*). Individual deposits ranged from about 10 to 100 cm in thickness, and pollen analysis of several levels within sites revealed little or no change in pollen content from top to bottom. Multiple dates on five sites are in agreement to within ±100 radiocarbon years and show that most deposits accumulated in 100 to 200 years. Pollen spectra from separate sites of the same age are similar. These observations indicate that each site represents a detailed view of the biota during essentially a point in time.

The lower pollen zone dating from 12.5 to 9.1 thousand years ago (ka) is dominated by spruce (*Picea*) and sedge (Cyperaceae) pollen, and black ash (*Fraxinus nigra*) and larch (*Larix*) are relatively abundant (Fig. 2). Zone 2 (9.1 to 5.5 ka) records the dominance of pollen from deciduous trees, including elm (*Ulmus*), oak (*Quercus*), ironwood or blue beech (*Ostrya-Carpinus*), sugar maple (*Acer saccharum*), and hickory (*Carya*). In zone 3 (5.4 to 3.5 ka), pollen of ragweed (*Ambrosia*) and grasses (Gramineae), both nonarboreal elements, replaces tree pollen. Nonarboreal pollen (NAP) is much more abundant in this zone than arboreal pollen (AP). Zone 4 (3.5 to 0.15 ka) records the return of oak pollen to prominence, along with willow (*Salix*). The top zone, the postsettlement period, is dominated by ragweed and grass.

Spruce, larch, and black ash were apparently the dominant late-glacial trees in the area. Both black spruce (*Picea mariana*) and white spruce (*P. glauca*) cones were recovered. Black spruce probably grew in wetter areas along with black ash and larch, where-

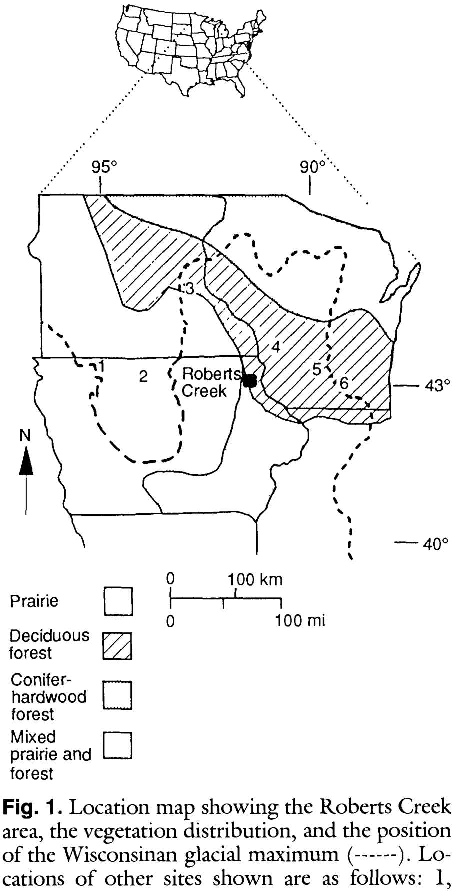

Fig. 1. Location map showing the Roberts Creek area, the vegetation distribution, and the position of the Wisconsinan glacial maximum (------). Locations of other sites shown are as follows: 1, Lake West Okoboji, Iowa; 2, Zuehl Farm, Iowa; 3, Kirchner Marsh, Minnesota; 4, site of McDowell's alluvial study, Wisconsin; 5, Devils Lake, Wisconsin; and 6, four lakes and bogs near Madison, Wisconsin.

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as white spruce was probably present both on dry parts of the floodplain and in upland areas.

As climate became warmer, deciduous trees replaced the upland spruce forest, and mesic forest was present, probably with elm on the floodplain, oak and hickory on south-facing upland slopes, and maple, basswood, and ironwood in other upland areas. Spruce remained in wetland habitats until nearly 9 ka, more than 1 ka later than the time of its regional disappearance from upland sites (*9*).

The duration of the deciduous forest at Roberts Creek is unlike that documented elsewhere in the upper Midwest, where prairies expanded eastward between 9 and 6 ka (*9, 10*) because of an increased presence of dry Pacific air (*11*). The warmest, driest part of the middle Holocene is thought to have occurred between 7 and 6 ka (*12*). In contrast, the most mesic period of deciduous forest at Roberts Creek occurred between 7 and 5.5 ka. Two hypotheses may account for this contrast. (i) A sharp climatic boundary may have developed between central and eastern Iowa. A comparable boundary in northwestern Minnesota is currently responsible for an abrupt ecotone, from prairie to savanna to deciduous forest to conifer hardwood forest within a distance of 50 km (*13*). In northeastern Iowa, moist air from the Gulf of Mexico remained dominant in the middle Holocene at the same time that Pacific air was dominant to the north and west. (ii) Moist floodplains may have been able to support local mesic forests in northeastern Iowa throughout the warmer, drier climatic conditions of the early-middle Holocene. The piezometric surface on the floodplain finally dropped sufficiently so that the surface became dry enough to allow prairie to replace the forest at 5.4 ka.

The demise of this forest between 5.5 and 5.4 ka indicates that a significant change occurred in the local environment. Such a sudden change from mesic to xeric vegetation is difficult to explain solely on the basis of a change to warmer climate. The direct cause of this change may have been fire, although charcoal was not abnormally abundant in sediments of this age. Charcoal counts elsewhere suggest that Holocene fires were common in prairies (*14*), which were present in north-central Iowa between 9 and 4.5 ka; maple-basswood forest (dominant at 5.5 ka at Roberts Creek) is susceptible to fire (*15*). In addition, a drier climate after 5.4 ka would have increased fire susceptibility. The relative importance of fire and climate in maintaining a prairie environment after the demise of the forest is still uncertain. Abundant charcoal does occur in sediments dating from 4.8 and 2.8 ka.

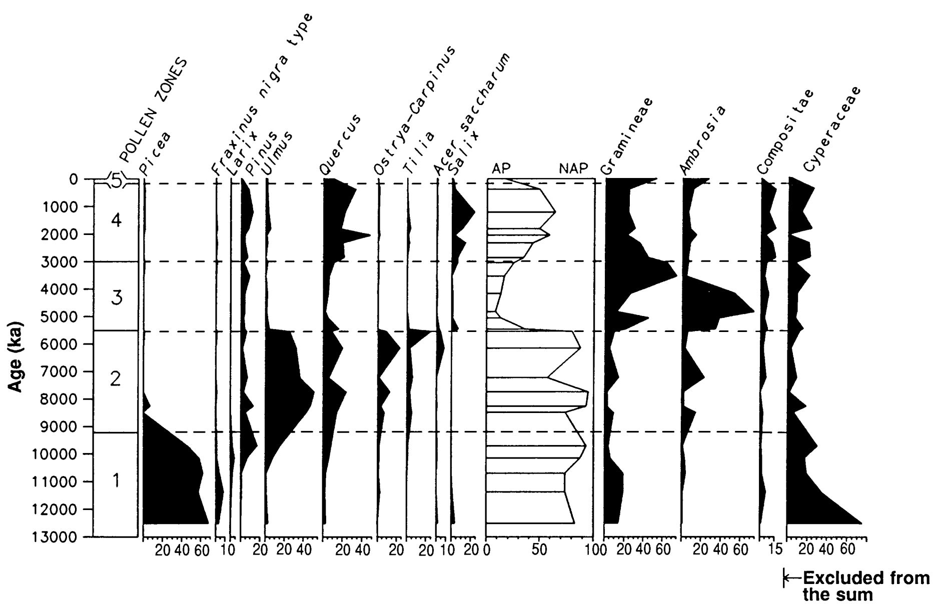

Fig. 2. Pollen diagram compiled from 23 radiocarbon-dated sites along Roberts Creek. This analysis was conducted by C. A. Chumbley, 1986 to 1989.

Although the change from mesic forest to prairie took place 2 to 3 ka later in northeast Iowa than at sites to the west and north, pollen records in south-central Wisconsin (Fig. 1) show a pattern similar to that at Roberts Creek. Two lake and two bog sequences, all well dated, record a sudden decline in mesic forest elements (*Ulmus*, *Acer*, *Tilia*, and *Ostrya-Carpinus*) at about 5.5 ka (*16*). However, at these sites, the mesic forest was replaced by a more xeric forest dominated by oak. Apparently prairie never reached as far east as south-central Wisconsin, but the change in forest type was toward warmer, drier conditions as at Roberts Creek. Thus the hypothesis that the late forest demise at Roberts Creek was due to local moist floodplain conditions can probably be eliminated. The mid-Holocene prairie-forest border must have been between central and eastern Iowa sites and was much sharper in the southern Midwest than it was in presettlement times. A sharp climatic gradient was thus present in this region.

The return of oak pollen after 3.5 ka signals the establishment of oak savanna in the area. Nonarboreal pollen remains abundant in deposits of this age and indicates that open ground was still common. The reestablishment of oak probably signaled a return to a wetter or cooler climate, a shift that is indicated in many Midwestern paleoecological records. The final vegetational change in the Roberts Creek basin was the establishment of ragweed and other weeds as a result of agricultural activities. This change was also widespread in northeastern North America.

Deposits similar to those at Roberts Creek are known from southwest Wisconsin (*17*) and eastern and central Iowa. McDowell tied the alluvial chronology in the northern part of the "Driftless Area" to climatic change as deduced from pollen records available at the time. She concluded that a minimum in precipitation between 7.8 and 5.7 ka corresponded with an episode of erosion, and that a rapid increase in precipitation between 5.7 and 5.5 ka was correlated with floodplain construction. The more complete Roberts Creek sequence indicates that moist climate prevailed between 7.8 and 5.5 ka with little or no change in stream regimen. If these climatic conditions prevailed throughout northeastern Iowa and southern Wisconsin, the relation between climatic models and alluvial chronologies will need to be revised.

REFERENCES AND NOTES

1. W. G. Spaulding *et al.*, in *Late-Quaternary Environments of the United States*, vol. 1, *The Late Pleistocene*, S. C. Porter, Ed. (Univ. of Minnesota Press, Minneapolis, 1983), pp. 259–293.
2. H. R. Delcourt and P. A. Delcourt, in *Pollen Records of Late-Quaternary North American Sediments*, V. M. Bryant, Jr., and R. G. Holloway, Eds. (American Association of Stratigraphic Palynologists Foundation, Dallas, 1985), pp. 1–38.
3. J. C. Prior, *Iowa Landforms* (Educational Series 3, Iowa Geological Survey, Iowa City, 1976).
4. J. C. Knox, P. F. McDowell, W. C. Johnson, in *Quaternary Paleoclimate*, W. C. Mahaney, Ed. (Geo Abstracts, Norwich, England, 1981), pp. 107–127; P. F. McDowell, *Quat. Res.* **19**, 100 (1983).
5. K. Faegri and J. Iversen, *Textbook of Modern Pollen Analysis* (Hafner, New York, 1975).
6. L. C. Cwynar, E. Burden, J. H. McAndrews, *Can. J. Earth Sci.* **16**, 1115 (1979).
7. C. A. Chumbley, thesis, University of Iowa (1989).
8. T. A. Brown, D. E. Nelson, R. W. Mathewes, J. S. Vogel, J. R. Southon, *Quat. Res.* **32**, 205 (1989).
9. H. K. Kim, thesis, University of Iowa (1986).
10. K. L. Van Zant, *Quat. Res.* **12**, 358 (1979); T. Webb III, E. J. Cushing, H. E. Wright, Jr., in *Late-Quaternary Environments of the United States*, vol. 2, *The Holocene*, H. E. Wright, Jr., Ed. (Univ. of

Minnesota Press, Minneapolis, 1983), pp. 142–165; H. E. Wright, Jr., T. C. Winter, H. L. Patten, *Geol. Soc. Am. Bull.* 74, 1371 (1963).

11. P. J. Bartlein, T. Webb III, E. Fleri, *Quat. Res.* 22, 361 (1984); P. F. McDowell, in (*4*); T. Webb III and R. A. Bryson, *ibid.* 2, 70 (1972).
12. P. F. McDowell, in (*4*); K. L. Van Zant, in (*10*); W. A. Watts and T. C. Winter, *Geol. Soc. Am. Bull.* 77, 1339 (1966).
13. J. H. McAndrews, *Bull. Torrey Bot. Club* 22, 1 (1966).
14. J. C. B. Waddington, in *United States Contributions to Quaternary Research*, S. A. Schumm and W. C. Bradley, Eds. (Special Paper 123, Geological Society of America, Boulder, CO, 1969), pp. 263–282.
15. E. C. Grimm, *Ecol. Monog.* 54, 291 (1984).
16. M. G. Winkler, *Ecology* 69, 1032 (1988); ——, A. M. Swain, J. E. Kutzbach, *Quat. Res.* 25, 235 (1986); L. J. Maher, Jr., in *Quaternary History of the Driftless Area*, J. C. Knox, L. Clayton, D. M. Mickelson, Eds. (Wisconsin Geological and Natural History Survey, Madison, 1982), pp. 119–135.
17. P. F. McDowell, in (*4*); J. C. Knox, P. F. McDowell, W. C. Johnson, in (*4*).
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Transmembrane Helical Interactions and the Assembly of the T Cell Receptor Complex

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Studies of the subunit interactions of the multicomponent T cell antigen receptor (TCR) revealed that specific pairs of chains have the ability to assemble after transfection into fibroblasts. For one such pair, TCR-α and CD3-δ, their ability to assemble was encoded by their transmembrane domains. The specificity of this interaction suggests that well-defined helical interactions in the membrane can explain the assembly of some multichain membrane complexes.

MANY MEMBRANE PROTEINS EXIST as part of multicomponent complexes (*1*). These range in complexity from the homodimeric transferrin receptor to the T cell antigen receptor (TCR), which is comprised of at least seven transmembrane subunits encoded by six different genes (*2*). These complexes may be held together by either covalent (disulfide) bonds or noncovalent interactions. Correct assembly is most likely required for function. To prevent the cell surface expression of unassembled subunits or partially assembled complexes, the cell imposes an effective set of mechanisms that prevent the transport or survival or both of all but completely assembled complexes (*3*). Transmembrane proteins can conveniently be divided into three domains; extracellular, membrane-spanning, and intracellular. For proteins that cross the membrane once, these domains are arranged as uninterrupted segments along the primary sequence.

This is the situation for the seven chains of the TCR, which are all single membrane-spanning proteins with their amino termini facing the external milieu (*2*). The external domains of the TCR-α and TCR-β subunits are responsible for antigen recognition (*4*) whereas the cytoplasmic domain of ζ has been directly implicated in signal transduction (*5*). The hydrophobic transmembrane domains of the TCR chains and other membrane proteins anchor them in the membrane and negotiate the hydrophobic lipid bilayer. The transmembrane domains of each of the TCR subunits have the unusual characteristic of possessing single (or in the case of TCR-α, two) charged amino acids (*2*). Mutation of the positively charged amino acid residues of TCR-α and TCR-β transmembrane domains failed to allow reconstitution of surface expression of the TCR in α- or β-deficient T cells (*6*). It has been proposed that these charged amino acids may be involved in subunit assembly. These observations along with the high degree of sequence conservation of these domains between mouse and human suggest more specific structural information resides in the membrane-spanning regions than merely the ability to sit in a lipid environment. That the transmembrane domain of TCR-α contains specific sequence and structural information is supported by the recent identification of this region as containing information that causes targeting for rapid degradation in the endoplasmic reticulum (*7*). In this study we demonstrate that the transmembrane domains of the TCR-α and

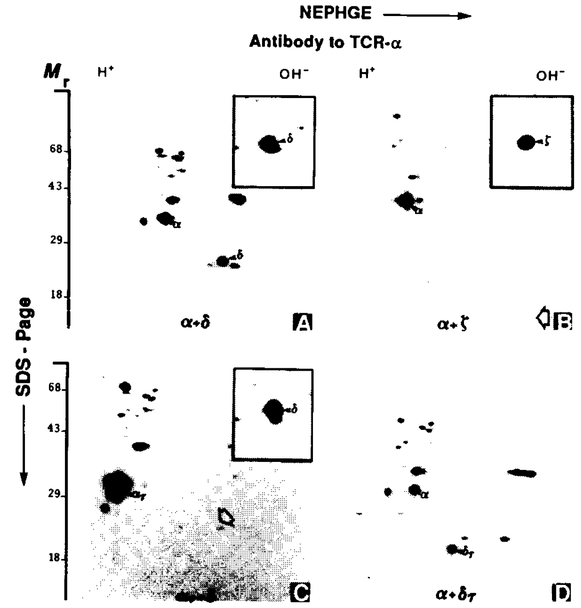

Fig. 1. Assembly of TCR-α (α) with CD3-δ (δ). COS-1 cells were cotransfected (*12*) with expression plasmids encoding: (**A**) full-length TCR-α and CD3-δ; (**B**) full-length TCR-α and TCR-ζ (ζ); (**C**) truncated TCR-α ($α_T$) lacking 41 carboxyl-terminal amino acid residues and full-length CD3-δ; and (**D**) full-length TCR-α with a truncated CD3-δ lacking 41 carboxyl-terminal amino acid residues ($δ_T$) (*13*). At 48 hours after transfection, cells were treated for 16 hours with 5 mM sodium butyrate and metabolically labeled for 2 hours at 37°C (*14*). Cells were removed from the plates, solubilized with lysis buffer containing 0.5% Triton X-100, and supernatants were added to antibody beads (*15*). The immunoprecipitated TCR chains were resolved by 2-D nonequilibrium pH gel electrophoresis (NEPHGE)/SDS-PAGE, as previously described (*2, 16*). Panels (A) through (D) show immunoprecipitates with antibody to TCR-α. Insets in (A) and (C) show the amount of total CD3-δ expressed in the same cells as analyzed by direct immunoprecipitation with antibodies to CD3-δ. The inset in (B) shows total TCR-ζ immunoprecipitated with antibodies to TCR-ζ. The positions of molecular weight (M_r) markers (kilodaltons) are indicated on the left. The positions of TCR-α, CD3-δ, and TCR-ζ are indicated. In (B), the expected position of TCR-ζ is marked by the open arrow. In (C), the expected position of CD3-δ is shown by the open arrow. The spot just below the arrowhead in (C) is not TCR-δ, but a nonspecific band. A truncated TCR-α lacking the transmembrane and cytoplasmic domains (TCR-$α_t$) failed to assemble with CD3-δ (C). However, a truncated CD3-δ lacking the cytoplasmic domain assembled normally with full-length TCR-α (D). Truncated CD3-δ could not be directly assessed by immunoprecipitation.

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