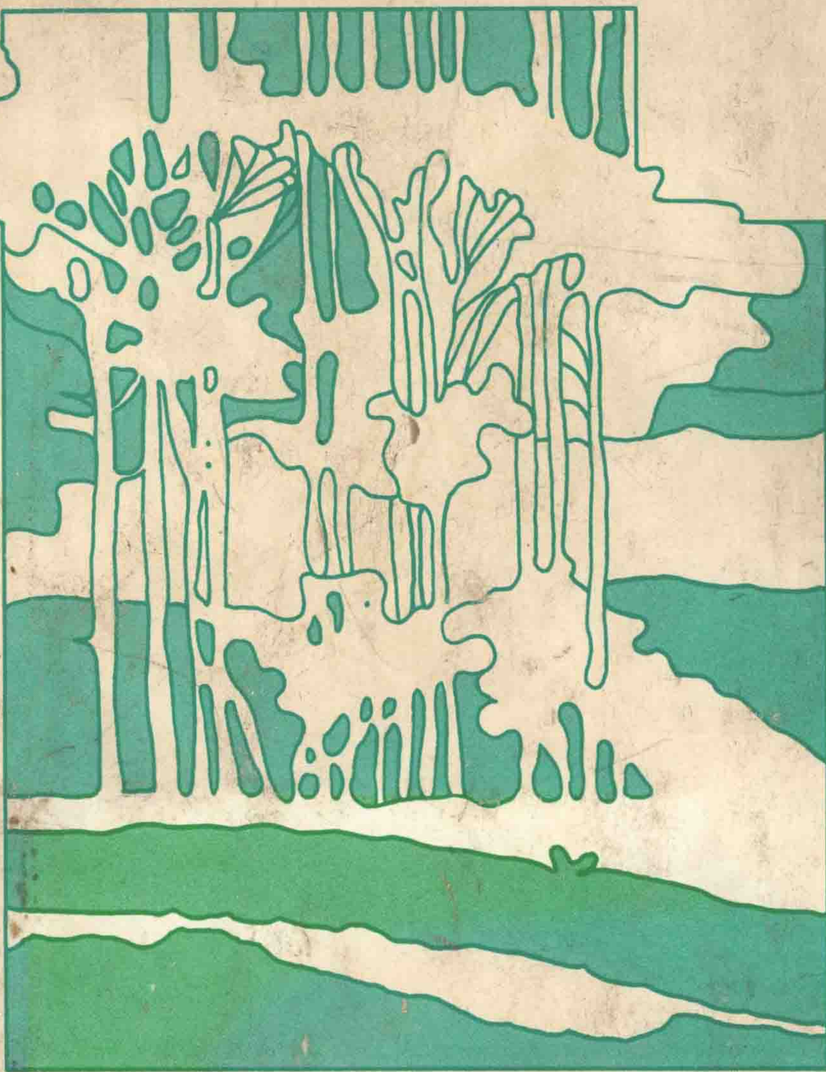

GEOBOTANY

EDITED BY ROBERT C. ROMANS

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GEOBOTANY

Preface

The papers in this volume were presented at the Geobotany Conference held at Bowling Green State University, Bowling Green, Ohio, on 21 February 1976. Though such diverse topics as anthropology and paleobotany are covered, all papers utilized the concept of geobotany as a unifying theme.

Nearly a decade ago, the first in this series of geobotany conferences was organized on this campus by Dr. Jane Forsyth of the Department of Geology. After considerable growth, culminating in an International Geobotany Conference at the University of Tennessee in 1973, it was decided to again organize a regional geobotany meeting. The melange of papers in this volume are products of that meeting.

Geobotany, by definition, is an interdisciplinarian approach to interpretational problems involving such investigators as geologists and botanists, archaeologists and stratigraphers, ecologists and palynologists. Interaction among these individuals is necessary for the satisfactory solution of a problem. Each can provide invaluable assistance to the other. The purpose of the meeting in Bowling Green was to provide a forum for the exchange of ideas and information.

Sponsors of the conference include the Department of Biological Sciences, the Department of Geology, the Environmental Studies Center, the College of Arts and Sciences, and the Graduate School. All of the sponsors are academic or administrative units of Bowling Green State University and each played an important role in the success of the conference.

Bowling Green
1976

Robert C. Romans

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LATE PLEISTOCENE AND POSTGLACIAL PLANT COMMUNITIES OF THE GREAT LAKES REGION

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ABSTRACT

The few available interglacial pollen studies from the southern Great Lakes region show developmental sequences and pollen assemblages with striking similarities to postglacial records. A five-stage cycle of glacial and interglacial vegetation phases is postulated and applied to data from this region. There is limited evidence, however, of late Pleistocene changes in genetic potential of certain species (e.g., *Picea mariana*). Also, some interglacial and interstadial (glacial age) pollen records indicate that ranges of certain tree genera or forest communities extended beyond their modern ranges.

Late-glacial (post-Wisconsinan) records in the glaciated Great Lakes region do not consistently give evidence of tundra vegetation; instead, "open forests" may have existed in ice-margin areas. The major climatic/ecologic break at about 10,500 B.P. initiated a developmental sequence of postglacial hardwood forests which is remarkably consistent throughout the region. Migration routes were influenced by both physiographic (Appalachians, Great Lakes) and climatic factors. The spread of *Fagus* and *Tsuga* to their present ranges in glaciated areas is re-examined; additional detailed radiocarbon-dated analyses are required to document these migrational patterns.

The strong correspondence of patterns of contemporary pollen spectra and vegetational distribution has been revealed by recent detailed studies; this restores confidence in the paleoecological validity of pollen analysis. By utilizing statistical procedures, both regional and local vegetational composition can, within limits,

be directly correlated with pollen spectra. Overall, paleoecological research suggests that plant communities of the Great Lakes region have had remarkable continuity throughout the late Pleistocene. Although climatic conditions, extensive glacial meltwater channels, and fluctuations in the level and drainage of the Great Lakes apparently explain certain extensions of range and novel plan assemblages, patterns of forest migrations and succession are predictable.

INTRODUCTION

It is especially appropriate, and a personal privilege for me, to include a review of palynological and related evidence of Pleistocene vegetation in the proceedings of an Ohio geobotany conference. Ohio is the ancestral home of North American geobotany, especially of pollen analysis. Paul B. Sears published his first paper on postglacial paleoecology in 1930, only 14 years after the emergence of the fledgling science in Europe (von Post, 1916). The early work of Sears in Ohio (1930, 1931) and John Voss in Illinois (1933, 1934) prompted Sears to publish the first review paper on this subject in 1935, over 40 years ago! This apparently stimulated an interest in palynological research.

The prodigious research of Sears (1935b, 1940, 1941, 1942a, 1942b, 1942c, 1951a, 1952, 1955, 1956) and Potzger (1945, 1946, 1948, 1951, 1952, 1953) and their associates (Sears and Clisby, 1952; Sears and Bopp, 1960, Potzger and Courtemanche, 1956a, 1956b; Potzger and Otto, 1943) led to a series of more comprehensive review papers on the history of vegetation of the Great Lakes and Eastern North America by Sears (1948, 1951b), Deevey (1949, 1957), Martin (1958a), and Just (1959), all prior to 1960.

Beginning in about 1960, a period of logrhythmic growth in the quantity and sophistication of research in both glacial geology and palynology began. Extensive research programs were initiated by Wright in Minnesota; Bryson in Wisconsin; Benninghoff and Margaret Davis in Ann Arbor; Frey, Gooding, and Wayne in Indiana; Goldthwait, Forsyth, and Ogden in Ohio; as well as Terasmae, Dreimanis, and their associates in Ontario. These studies of the past 15 years have confirmed the basic patterns revealed by the work of the early researchers. Moreover, the availability of radiocarbon determinations, studies of contemporary pollen dissemination and its statistical correlation with vegetation and with fossil pollen spectra have improved our understanding of the nature of late-glacial and postglacial vegetation. Reviews of these recent developments by Ogden (1965), M.B. Davis (1965), Cushing (1965, 1967), and Wright (1964, 1968, 1971) suggest that we may already have been surfeited by an abundance of overviews and syntheses. Despite these misgivings, a review of the evidence for late Pleistocene vegetation seems to be an appropriate part of this volume on the geobotany of the Great Lakes region.

The scope of this review is the last half of the Pleistocene. Although evidence is still sketchy, we can now begin reconstruction of vegetation of the second (Yarmouthian) and third (Sangamonian) interglacial stages in the southern Great Lakes region. Vegetation of the related glacial stages can only be determined by studies of deposits at ice-free sites (pre-glacial, interstadial, late-glacial) in the glaciated region or at depositional localities beyond the glacial border. The sequence of Pleistocene stages and substages to which reference is made is given below (youngest to oldest):

(Stages)		(Interstadials-Erie Lobe)
Holocene		
		Late glacial
	Main (Late)	
		Plum Point (= Sidney ?)
Wisconsinan glacial	Middle	
		Port Talbot I & II
		St. Pierre
	Early	

Sangamonian interglacial stage
Illinoian glacial stage
Yarmouthian interglacial stage
Kansan glacial stage

PRE-WISCONSINAN GEOBOTANY

Yarmouthian Interglacial Record

The Illinoian glacial drift is sufficiently thin in certain areas of southeastern Indiana that underlying Yarmouthian and Kansan deposits are exposed in stream cuts (Gooding, 1966). At the Handley Farm section in Fayette Co., Indiana, a stream bank exposure includes 8 m of pollen-rich lacustrine clay; these interglacial deposits have Kansan till beneath and are overlain by pro-Illinoian glacial outwash and Illinoian till. The pollen record (Kapp and Gooding, 1974) is dominated by deciduous species; the pollen diagram (Fig. 1) is divided into three pollen zones:

1. *The Oak-Ironwood Pollen Zone* is characterized by high *Ostrya-Carpinus* pollen (20-35%), *Quercus* (about 30%), and lesser amounts of *Picea*, *Pinus*, *Tilia*, *Corylus* and *Populus*.
2. *The Oak-Elm-Beech Zone* is characterized by decrease in *Ostrya-Carpinus* pollen and increases in Ulmus (to 20%), *Fagus* (to 20%) *Celtis*, *Carya*, *Fraxinus* and *Acer*; conifers, at least *Pinus* and *Picea*, were not in the region.

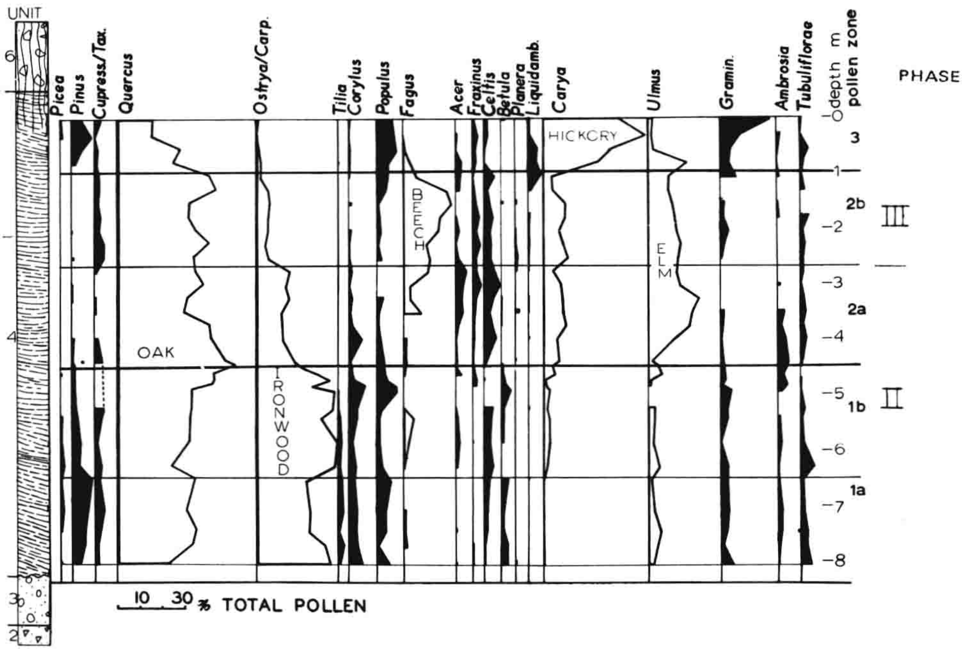

Figure 1. Yarmouthian interglacial pollen diagram from Handley Farm section, southeastern Indiana (adapted from Kapp and Gooding, 1974, p. 231).

3. The Sweetgum-Hickory Zone is characterized by a peak in Carya (50%), high frequencies of Liquidambar, Populus and Gramineae pollen, increased conifer representation and sharp declines in frequencies of Quercus, Fagus and Ulmus.

The sequence of development of this deciduous tree pollen record is strikingly similar to that seen in many postglacial pollen diagrams; commonly the deciduous types are represented by successive maxima in the sequence: Ostrya/Carpinus (usually with Betula) → Ulmus → Fagus/Acer → Carya (or Quercus, Gramineae, etc.) It is likely that this sequence is the result of several interlinked factors including: speed of migration, ease of establishment on youthful sites, climatic requirements and tolerance, ecological and successional characteristics. The hypothesis that the sequence of appearance of major pollen types is virtually the same throughout the deciduous forested sections of the Great Lakes region, both in interglacial and postglacial records, requires further testing. The Handley Farm diagram suggests that such may be the case.

In a yet broader generalization, it was postulated by Turner and West (1968) that a four-phased pattern typifies European interglacial sequences; Wright (1972) applied this model to eastern North America. The four phases are:

I. Late-glacial or pre-temperate phase
II. Early temperate phase (maximum warmth)
III. Late temperate phase
IV. Post-temperate (or pre-glacial) phase

For unglaciated sites, V. Full glacial phase, can be added.

The Yarmouthian pollen diagram from the Handley Farm site seems to include interglacial Phases II and III; persistence of low frequencies of pine and spruce pollen into Early temperate phase gives residual evidence of the end of the preceding Late-glacial phase. The reappearance of these two conifer genera near the top of Phase III reflects the beginning of climatic deterioriation of the Late-temperate phase.

Illinoian Glacial/Sangamonian Interglacial

At Pittsburg Basin in south-central Illinois, about 60 km south of the limit of Wisconsinan glaciation, E. Grüger (1970, 1972a, 1972b) analyzed a pollen sequence which includes all five vegetational phases (Fig. 2). The deposits, formed in a lake basin, are interpreted to extend from late-Illinoian to the present, with the uppermost horizon disturbed by plowing.

The record begins with Phase I, the Illinoian late-glacial phase, dominated by Picea (20-50%) and Pinus (15-35%) and including low frequencies of pollen of hardwood genera or of herbs. This is succeeded by Sangamonian interglacial phase II which is initially dominated by pollen of Quercus, Ulmus, Carya, Fraxinus and the Taxodiaceae/Cupressaceae groups and subsequently reflects the glacial maximum in the invasion of prairie species (Ambrosia and Gramineae). Phase III shows a reversion to dominance by hardwood forests. Interestingly, Liquidambar is not prominent in the record until this later phase, supporting the hypothesis that sweetgum requires mature, well-leached soils. Phase IV (Post-temperate) is probably only fragmentary due to an apparent hiatus in the record. The full-Wisconsinan record (Phase V) at the Pittsburg site seems to give a detailed record of the demise of the interglacial plant communities and their replacement by full-glacial vegetation. The mesophytic deciduous species (Juglans, Liquidambar, Platanus, Fagus, Ulmus, and even Carya) declined rapidly in south central Illinois at the end of the Sangamon. Deciduous forest communities were apparently supplanted again by prairie (high frequency of Artemisia, Ambrosia, other Compositae, Chenopodineae, Gramineae, and Cyperaceae) with scattered oak-hickory stands during the Altonian (early Phase V) substage 75,000 - 28,000

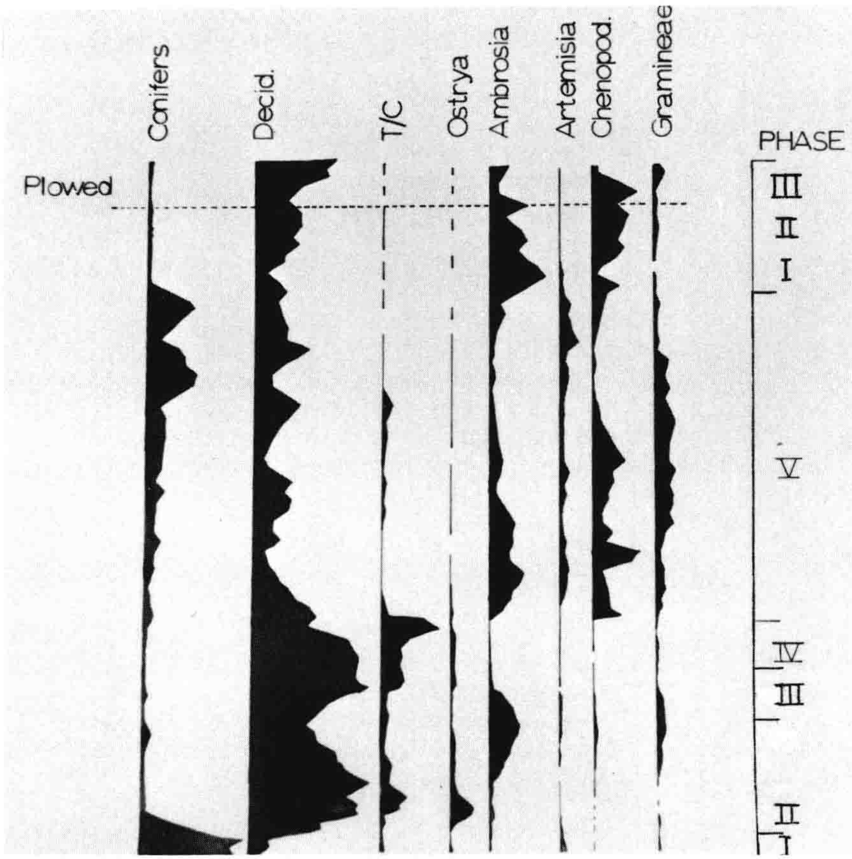

Figure 2. Pollen diagram from the Pittsburg Basin, Fayette Co., Illinois. Records begin in the late Illinoian glacial age (Phase I) and extend through an entire interglacial-glacial sequence into the postglacial (adapted from E. Grüger, 1972a).

years ago. During the Farmdalian (28,000 - 22,000 B.P.) and Woodfordian (22,000 - 12,500 B.P.) substages pine-hardwood and finally spruce-pine-hardwood communities developed.

The uppermost (Phases I, II, III) zones at the Pittsburg basin reflect the expected postglacial sequence for that area, dominated by prairie species with oak/hickory stands. It is significant that the postglacial of south-central Illinois was less favorable for deciduous forests than the equivalent period of the early Sangamonian interglacial. The climate of Phase II of the interglacial seems to have been sufficiently equable to permit establishment of the species-

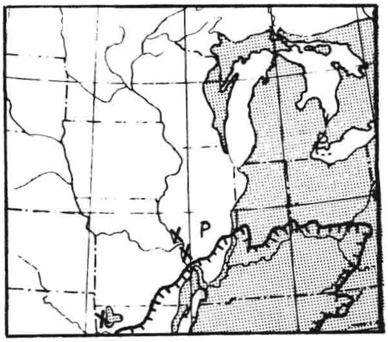

Figure 3. Location of Pittsburg Sangamonian interglacial site (P) in relation to the present ranges of Fagus (gray) and Liquidambar (x).

rich Western Mesophytic forest communities (sensu Braun, 1950) in that region; this is reflected by the extension of the ranges of Liquidambar and Fagus into south-central Illinois (Fig. 3).

Sangamonian pollen records have also been described from southeastern Indiana (Englehardt, 1962, Kapp and Gooding, 1964b) and from the Don Beds at Toronto (Terasmae, 1960). The Darrah and Smith Farm sections near Richmond, Indiana record the end of Late-glacial Phase I and Early-temperate phase II. The record is then truncated and overlain by involuted sediments which may represent scouring and disturbance by Wisconsinan ice. Dreimanis (1973) suggests that these uppermost conifer-pollen-rich sediments represent the Early Wisconsinan St. Pierre interval; they clearly correspond to vegetation of Full glacial Phase V.

While the validity of suggesting direct continuity between segments of pollen diagrams from such distant locations as southeastern Indiana and Toronto, Canada is most questionable, a diagrammatic representation of these two Sangamonian interglacial records is suggestive of the probable sequence. Figure 4 is such a composite diagram. The Smith Farm interglacial sequence from the Whitewater Basin of Indiana is shown at the base of Fig. 4 and, higher in the diagram, the glacial segments of this record is plotted.

The pollen record from the Don Beds of Toronto seems to record interglacial phases III and IV, beginning during the interglacial climatic optimum and subsequently reflecting the climatic deterioration and floristic changes which occurred with the approach of the Wisconsinan glacial stage. Terasmae (1960) concludes that the Don Beds assemblage "represents a mean annual temperature of 5° (3° C) warmer than the present."

Certain phytogeographical and autecological inferences can be drawn from these interglacial records. The presence of Liquidambar pollen in abundance in the Don Beds Sangamonian record is a substantial extension of range (Fig 5). Its presence along with a more southerly assemblage of deciduous species (Chamaecyparis, Maclura, Robinia, and Quercus muhlenbergii and Q. stellata) indicates a substantially different forest distribution at the Sangamonian maximum compared with present. I have already commented on the extension of

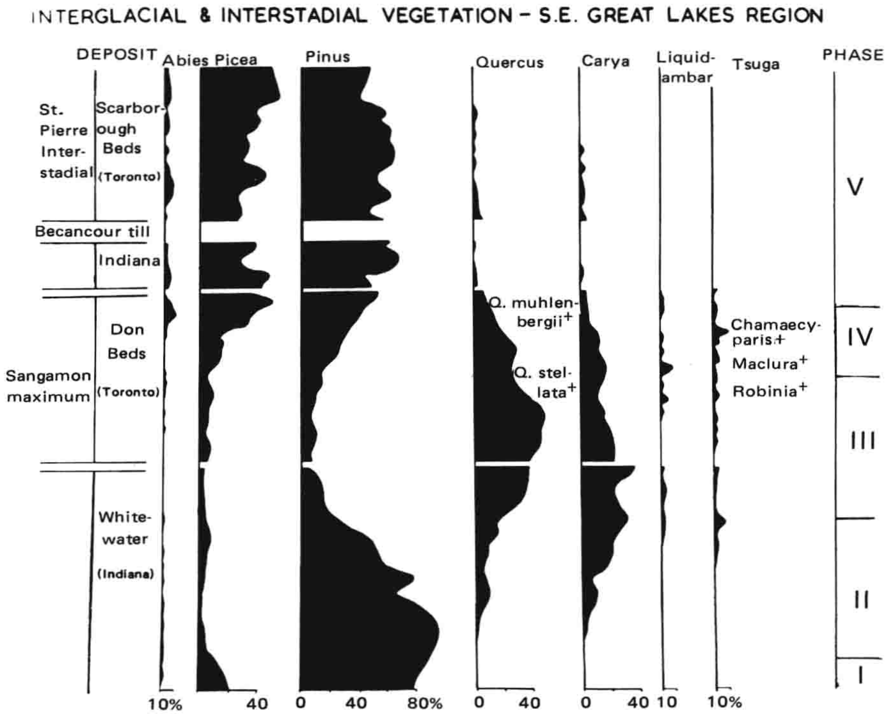

Figure 4. Composite Sangamonian pollen diagram from Smith Farm section (Wayne Co., Indiana) and Don Beds of Toronto. Macrofossil remains from the Don Beds, originally reported to Coleman (1933) include several species (marked +) whose ranges do not now extend as far north as Toronto.

the Western mesophytic assemblages (including sweetgum) northwest into south-central Illinois.

The Sangamonian record from Smith Farm in southeastern Indiana includes another autecologically significant feature. Picea (believed on the basis of size to be P. mariana) pollen persists in low but significant percentages throughout the interglacial record (see Fig. 6 for present range). I postulate that this reflects broader ecologic amplitude in that species during the last interglacial than is true of postglacial populations in the Great Lakes region. Postglacial pollen diagrams from the southern Great Lakes region have virtually no Picea pollen after 10,000 years B.P. The genotypic diversity and ecotypic flexibility of that species seems to have been reduced during the Wisconsinan. We should look for evidence of this type of biotype depauperation as pollen-analytical studies are pushed back into the earlier stages of the Pleistocene. Unfortunately, only very few pollen-rich interglacial deposits have

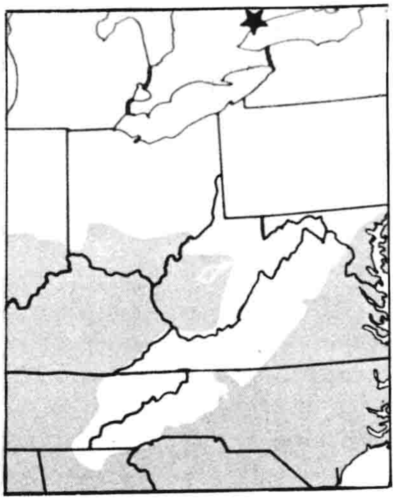

Figure 5. Modern distribution (gray) and Sangamonian interglacial record (star) of Liquidambar.

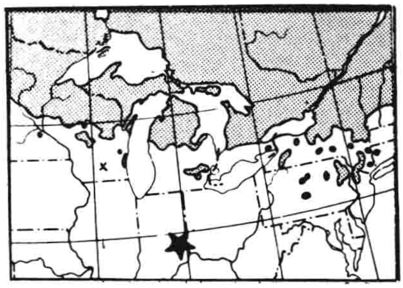

Figure 6. Modern distribution (gray) and Sangamonian interglacial record (star) of Picea mariana.

been discovered in North America and only the few described above are in the Great Lakes region. It is imperative that the vegetational patterns postulated above be tested at numerous additional sites.

WISCONSINAN FULL-GLACIAL AND INTERSTADIAL VEGETATION

The ecological conditions and vegetational distribution of the full-sized glacial stage is perhaps the most poorly understood, yet most widely described and misrepresented aspect of Pleistocene biogeography. Synthesizers from Darwin (1859) to Dorf (1959) and Martin (1958) have tended to present an oversimplified, but logically appealing portrait of full glacial vegetation in which broad belts of climate/vegetation were displaced southward by the advancing continental glaciers of eastern North America. These simplistic theories have too often found their way into ecology, geology and biogeographic textbooks.

Scattered evidence of white spruce and other northern species from such southern latitudes as Texas and Louisiana have served at once to both support these hypotheses and cause consternation regarding the means of survival of the floristically-rich eastern deciduous forests. The question posed by Deevey (1949) nearly 30 years ago still stands: where were the refugia for deciduous species, short of extensive migrations to southern Florida or central America? Many paleoecologists have come to explain the situation as a dynamic mixing of northern and southern species under stress of Wisconsinan continental glaciation.

It is beyond the scope of this paper to review all evidence of full-glacial vegetation for eastern North America; Whitehead (1973) and Watts (1970) have provided the most recent treatises on that subject. Brief examination of evidence for southern distribution of northern species, such as are now found in the Great Lakes region, will, however, give some clues regarding the fate of these northern communities during the full-glacial period. In the southern Appalachian Mountains, (northwestern Georgia, Watts, 1975) and at Singletary Lake, North Carolina (Whitehead, 1967) beech (Fagus grandfolia), along with a diverse mixture of mesophytic forest species may have coexisted with pine and spruce in mixed stands or at nearby valley and crest sites. It is unlikely that beech, or the mixed mesophytic forests, occupied sites in the southern Piedmont, Coastal Plain or Florida.

The well-known records of white spruce (Picea glauca) cones and tamarack (Larix) wood in the Tunica Hills region of Louisiana (Brown, 1938) and of spruce pollen from deposits in Texas (Potzger and Tharp, 1954; Graham and Heimsch, 1960) have focused attention on the Mississippi Valley as a Pleistocene plant migration route. Recent reexamination of the Muscotah Marsh sediments of northeastern Kansas by J. Grüger (1973) confirms the abundant presence of Picea pollen (originally misidentified as Abies by Horr, 1955) from 24,000 B.P. to as late as 12,000 B.P. This study and those of the Pleistocene spring deposits of western Missouri (Mehringer, et al., 1968, 1970; King, 1973) all verify the southern distribution of spruce during the Wisconsinan maximum (Main Wisconsinan). A considerable southerly extension of range of spruce along the Mississippi and its tributaries, and in the Ozark Mountains, is now undisputed. In a series of provocative papers Hazel and Paul Delcourt (1974, 1975, in press) have extended the paleoecological studies of the Tunica Hills area of Louisiana/Mississippi. They verify the existance of Picea glauca and Larix laricina macrofossils in these terrace deposits in association with oak, ash, hornbeam, elm, hickory, butternut (Juglans cinerea), black walnut (J. nigra), beech, cucumber magnolia (Magnolia acuminata), Liriodendron, sugar maple, birch, alder and pine. They contend that the dissected loess-covered blufflands which form a high ridge east of the Mississippi Valley served as a migrational route and glacial refugium for both northern (Great Lakes) plant assemblages and for the mixed mesophytic forests. The latter plant communities are also postulated to have occupied sites along other north-south trending streams of Mississippi and Alabama.

Figure 7 shows the modern distribution of black spruce (Picea mariana) in the Great Lakes region (white spruce, P. glauca, does not extend as far south), and reflects the Appalachian distribution of red spruce (Picea rubens). Extreme southerly and westerly Pleistocene localities are plotted; the spruce pollen records off the Florida coast (Davis, 1946), in Texas, Missouri, and Kansas are likely to include both Picea mariana and P. glauca, although presence of the former is paleoecologically more conservative since black spruce now