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Late Pleistocene and Holocene Distributional History of the Deciduous Forest in the Southeastern United States *, **

by

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1. Introduction

The species richness, complexity, and apparent antiquity of the vegetation of the southeastern United States has intrigued phytogeographers since the time of the earliest botanical explorations in North America (CORE 1970). Numerous eminent botanists, including Asa Gray and E. Lucy Braun, have adopted the view that the floristic diversity of the Southeast is directly related to the length of time this region has experienced a relatively stable climatic and geologic regime. The Appalachian Mountains traditionally have been considered a refuge for plant taxa characteristic of the eastern deciduous forest, both because of the great diversity of topographic and edaphic sites available for occupancy by vascular plant taxa and because of the north-south continuity of the mountain ranges providing a migration route available during times of climatic changes (BRAUN 1950). This is in contrast to the east-west trending Alps, which formed an effective barrier to north-south plant migrations in Europe (VAN DER HAMMEN et al. 1971).

It is now widely recognized that the climate of the last 10,000 to 12,000 years has been warmer than that characterizing 90% of the Quaternary Period (EMILIANI 1966, DAVIS 1976, WRIGHT 1977). During the successive glaciations of the Quaternary, progressive extinctions of vascular plant taxa occurred in Europe due to the extreme climatic conditions characterizing times of maximum glaciation (VAN DER HAMMEN et al. 1970). European full-glacial refuges for deciduous forest taxa are thought to have been localized in the Alps; however, little evidence has yet been found for full-glacial distributions in Europe of either temperate deciduous forest taxa or taxa today characteristic of the Mediterranean region (WRHIGHT 1976).

Knowledge concerning the composition and distribution of vegetation during the Wisconsinan Stage south of the Laurentide Ice Sheet in eastern North America is also sparse. Despite the paucity of sites, qualitative maps portraying full-glacial vegetation have been constructed (FLINT 1971, WHITEHEAD 1973). Both of these reconstructions include a tentative mapping of the deciduous forest formation in the southeastern United States. However, until the site along Nonconnah Creek, Memphis, Tennessee, was excavated in 1976 (P. DELCOURT 1978), no site had been found and radiocarbon dated that contained confirming paleobotanical evidence for the location of a full-glacial refuge for deciduous forest taxa anywhere in eastern North America. Results from the study of the Nonconnah Creek locality and from additional sites we have recently investigated in Tennessee, Alabama, and Louisiana (DELCOURT and DELCOURT 1977a, H. DELCOURT 1978, P. DELCOURT 1978) now yield major new insight into the history of the deciduous forest in the southeastern United States.

In this paper, we review the evidence for late Quaternary climatic and vegetational change in the southeastern United States that has been gathered since the last major review in 1973 (WHITEHEAD 1973). Our approach is based upon a perspective concerned with tracing the changes in distribution and composition of deciduous forests in the Southeast from the time of the last glacial maximum to the present day.

Acknowledgments

We would like to express our appreciation to Dr. H.E. Wright, Jr., University of Minnesota, for making the facilities of the Limnological Research Center available to us during the course of the research on Anderson Pond, Mingo Pond, Goshen Springs, and Nonconnah Creek. Financial assistance for this research was provided through NSF Grants BMS75-04999 and DEB77-20803.

2. The blufflands hypothesis: full-glacial refuges and late-glacial migration routes for deciduous forest taxa

The extent to which climatic cooling during continental glaciations affected the distributions of deciduous forest taxa and the composition of deciduous forest communities south of the glacial margin has been the subject of considerable speculation and disagreement in the North American literature. The traditional viewpoint of plant taxonomists and plant geographers is exemplified by the works of CAIN (1943), BRAUN (1950, 1955), and ILTIS (1965). Based principally upon inferences made from modern distributions of vascular plant taxa, these workers postulated that the glacial episodes of the Pleistocene had no major impact upon the southeastern flora. They argued that the central location of maximum species richness in the southern Appalachians, along with the presence of numerous endemics and taxa with distributions known only from the southeastern United States and southeastern Asia, constitute evidence that the flora and vegetation of the southeastern United States have remained intact and stable since the Tertiary Period. According to BRAUN, a full-glacial map of the distribution of the Mixed Mesophytic Forest region or other vegetation regions recognized today in the Southeast would differ little from a map of their modern ranges (Fig. 1).

The opposing point of view, held by DEEVEY (1949) and other palynologists, is that paleobotanical evidence for conditions in the Southeast during the Pleistocene indicates a severely cold climate during glacial maxima. DEEVEY (1949) postulated displacement of deciduous forest taxa as far south as Mexico and southern Florida during the Pleistocene.

Proponents of each of these two extreme views drew their suppositions from data gathered from several classical sites. One such area was the Tunica Hills of southeastern Louisiana. The Tunica Hills posed a major dilemma. Relict populations of indicator species of the Mixed Mesophytic Forest association, today primarily Appalachian in distribution, occurred in deep, moist ravines of the Tunica Hills, several hundred kilometers south of their main ranges (COCKS 1914, BROWN 1938). These "northern disjuncts" occur today with evergreen magnolias and genera such as *Pachysandra* and *Schisandra* that have strong affinities to the fossil taxa of the arcto-Tertiary geoflora reported from North America (GRAY and SOHMA 1964, GRAHAM 1972), in addition to several endemic vascular plant taxa (BROWN 1938). The "island refugium" of the Tunica Hills was cited by BRAUN (1950) as evidence for floristic and vegetational stability since the Tertiary. A second, similar "refugial" area harboring both northern disjuncts and endemic species (e.g. *Torreya taxifolia* Arn.) is located in the panhandle of Florida along the bluffs of the Apalachicola River (BRAUN 1950, MITCHELL 1963, DELCOURT and DELCOURT 1977b).

On the other hand, paleobotanical evidence concerning the vegetation and climate of the Tunica Hills during the Pleistocene (BROWN 1938) indicated that climatic cooling was severe even to low latitudes (DEEVEY 1949). Macrofossils including cones of white spruce (*Picea glauca*) and wood of larch (*Larix*) recovered from alluvial terrace deposits along Little Bayou Sara were cited by DEEVEY as evidence that major changes in distribution of North American taxa resulted from climatic change during the Quaternary.

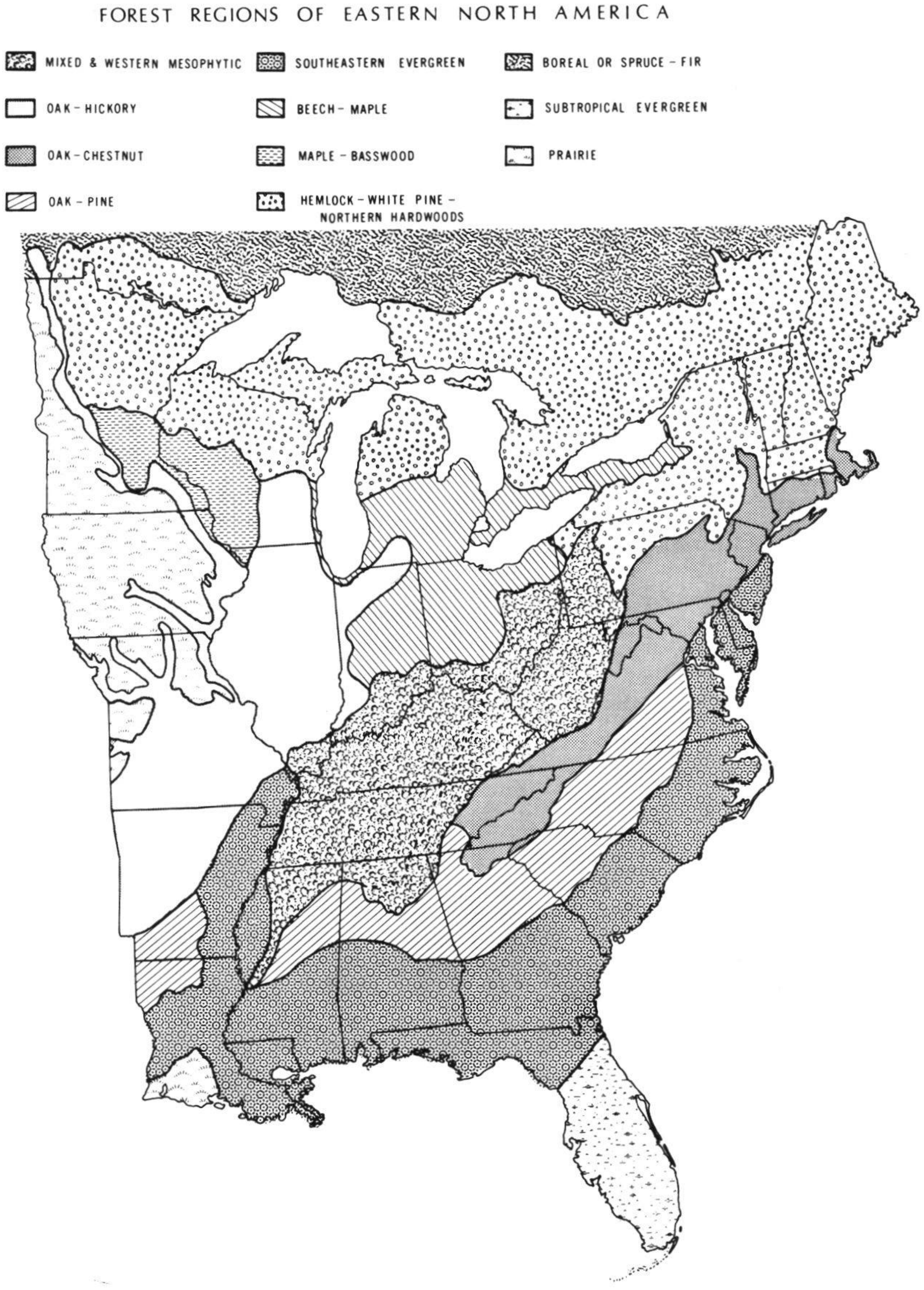

Fig. 1: Vegetation regions of eastern North America (after BRAUN 1950)

We have reinvestigated both the modern distributions of the "northern disjunct" Mixed Mesophytic Forest indicator species found in the Tunica Hills (DELCOURT and DELCOURT 1975) and the plant-fossil evidence from both original and new terrace localities (DELCOURT and DELCOURT 1977a). The current interpretation of the phytogeographic significance of the Tunica Hills is that of a pivotal point in understanding of Quaternary vegetation history in the southeastern United States. Rather than representing an "island refugium" during the Pleistocene and Holocene, the Tunica Hills may be viewed within the context of a larger natural region. The Tunica Hills represent the southern terminus of a north-south trending belt of dissected hills, the blufflands, that form a 20 to 50 km wide strip of unusually fertile, mesic habitat along the eastern escarpment of the lower Mississippi alluvial valley. The blufflands coincide with the thickest loess deposits in the states of Tennessee, Mississippi, and Louisiana. The loess provides calcareous silt loam soil and erodes to form precipitous ravines, banks, and cliffs which provide suitable edaphic and microclimatic sites for maintainance of Mixed Mesophytic Forest species south and west of their main ranges in the southern Appalachians (DELCOURT and DELCOURT 1975).

Terrace deposits along Little Bayou Sara and Tunica Bayou that contained abundant pollen and plant-fossil evidence for white spruce along with wood of larch have been radiocarbon dated as late glacial in age (DELCOURT and DELCOURT 1977a).Occurring with these boreal taxa in the deposits was an assemblage of plants that included a mixture of deciduous taxa, e.g. *Quercus, Fraxinus, Carpinus caroliniana, Ulmus, Carya, Juglans nigra, Fagus grandifolia, Magnolia acuminata, Liriodendron tulipifera, Acer saccharum, Betula,* and *Alnus*. The great species richness of the arboreal deciduous element of this late-glacial fossil assemblage can be readily explained in terms of the concept of the blufflands as refuge and pathway for cool-temperate and even boreal taxa during the late Pleistocene and Holocene. The late-glacial plant fossil assemblage from the Tunica Hills reflects at least localized climatic cooling along the Mississippi River valley during the late glacial. During the waning of the last continental glaciation, the waters of the glacial Mississippi River (KENNETT and SHACKLETON 1975) and associated cold air funneled past the uplands bordering the eastern escarpment of the Mississippi River alluvial floodplain (the blufflands). Contact of this cold air with relatively warm, humid air from the Gulf of Mexico could have given rise to extensive, persistent advection fogs (DONN 1965). We postulate that frequent fogs would have provided a cooling influence upon adjacent uplands, supplying moisture, increasing cloud (fog) cover, reducing evapotranspiration, and providing cooler summers in the blufflands. The loess, deposited before and during this time, provided optimal edaphic conditions, which, together with the local climatic cooling would have promoted the southward migrations of numerous Mixed Mesophytic Forest species along the blufflands. Eastward of the Mississippi River bluff edge, the decrease in available moisture (dispersion of fog) and loess thickness would have resulted in a transition from mesic, deciduous bluffland forest to a more xeric forest on upland sites. At the southern limits of its present range, white spruce is found in sites where fog ameliorates summer extremes of heat and evapotranspiration (SICCAMA 1974). White spruce and larch probably migrated southward along active braided streams within the Mississippi River valley (SAUCIER 1974) and onto tributary floodplains of the Tunica Hills, where deciduous forest species would not have competitive advantage. The assemblage of plant fossils of late glacial deposits in the Tunica Hills can be explained without postulating extended periods of extreme winter cold, provided that a mechanism such as persistent advection fog tempered the summer extremes in temperature and evapotranspiration (DELCOURT and DELCOURT 1977a).

Upon climatic amelioration at the beginning of the Holocene, deciduous forest species increased their populations in climatically and edaphically favorable areas. We hypothesized that the blufflands pathway served as a major route for northward Holocene migration for mesic deciduous trees and associated understory species. Numerous elements of the late-glacial cool-temperate deciduous forest communities have thus persisted throughout the Holocene within the favorable microhabitats provided by the deep ravines of the Tunica Hills and the blufflands (DELCOURT and DELCOURT 1974, 1975, 1977a).

WHITEHEAD (1973) mapped undifferentiated deciduous forest over the entire Gulf Coastal Plain during the full-glacial period. However, even under the modern warm, humid climatic regime the poor soils of the sandy uplands of the Gulf Coastal Plain did not support deciduous forests in presettlement times (BRAUN 1950, DELCOURT and DELCOURT 1977b). We postulated that during the last continental glaciation mesic deciduous forest taxa would have been restricted by lack of appropriate upland habitats to bottomlands and the dissected terrain adjacent to major north-south trending streams. They may have also persisted at low elevations in protected coves of the southern Appalachians (DELCOURT and DELCOURT 1975). The blufflands hypothesis thus adopts a moderate position, based upon available evidence, that considers climatic change to have had regional effects south of the glacial margin but yet allows for persistence in the southeastern United States of the many characteristic and endemic taxa of the modern deciduous flora through availability of local refuges on edaphically and microclimatically suitable sites. The hypothesis of the blufflands as both refuge and migration pathway thus establishes a new framework for designing further research to test the validity and usefulness of its several constituent postulates.

3. Tests of the blufflands hypothesis: results of three new Quaternary sites

The blufflands hypothesis implies that although deciduous forest taxa were not completely extirpated from the region of the Southeast, their boundaries were displaced southward from their general modern range limits due to climatic cooling associated with at least the last continental glaciation. In order to test the hypothesis that the effects were significant but moderate, sites with full-glacial records from several critical areas in the Southeast have been examined (H. DELCOURT 1978, P. DELCOURT 1978):

(1) Anderson Pond, White Co., Tennessee, located in the southern portion of the Mixed Mesophytic Forest - Western Mesophytic Forest regions of BRAUN (1950) (Fig. 2);

(2) Goshen Springs, Pike Co., Alabama, located on an interfluve in the sandy uplands of the Gulf Coastal Plain (Fig. 2);

(3) Nonconnah Creek, Shelby Co., Tennessee, situated in the northern blufflands (Fig. 2).

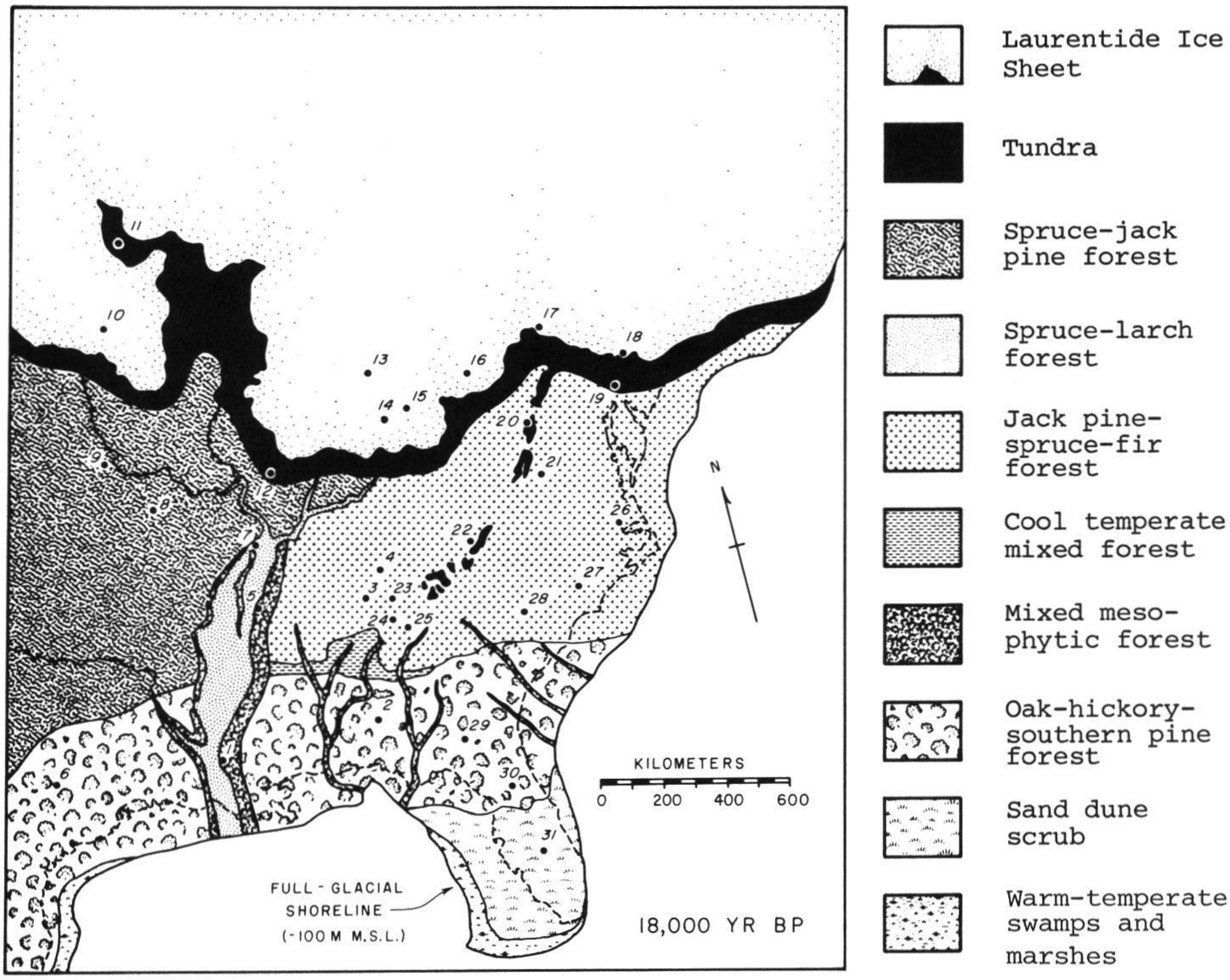

Fig. 2. Full-glacial vegetation map (18,000 BP) of eastern North America. Quaternary sites discussed in the text include: 1. Tunica Hills, LA (DELCOURT and DELCOURT 1977a). 2. Goshen Springs, ALA (P. DELCOURT 1978). 3. Mingo Pond, TN (H. DELCOURT 1978). 4. Anderson Pond, TN (H. DELCOURT 1978). 5. Nonconnah Creek, TN (P. DELCOURT 1978). 6. Boriack Bog, Texas (BRYANT 1977). 7. Old Field, MO (KING and ALLEN 1977). 8. Boney Springs, MO (KING 1973). 9. Muscotah Marsh, Kansas (J. GRÜGER 1973). 10. West Okoboji Lake, Iowa (VAN ZANT 1976). 11. Wolf Creek, Minnesota (BIRKS 1976). 12. Pittsburg Basin, IL (E. GRÜGER 1972). 13. Pretty Lake, Ind. (WILLIAMS 1974). 14. Carter and Stotzel-Leis sites, Ohio (SHANE 1976). 15. Silver Lake, Ohio (OGDEN 1966). 16. Battaglia Bog, Ohio (SHANE 1975). 17. Belmont Bog, N.Y. (SPEAR and MILLER 1976). 18. Wigwam Creek Bog, PA (SIRKIN 1977). 19. Marsh, PA (MARTIN 1958). 20. Buckle's Bog, MD (MAXWELL and DAVIS 1972). 21. Hack and Quarles Ponds, VA (CRAIG 1969). 22. Shady Valley, TN (BARCLAY 1957). 23. Friar Branch, TN (DESELM and BROWN 1978). 24. Pigeon Marsh, GA (WATTS 1975b). 25. Bartow County Ponds, GA (WATTS 1970). 26. Rockyhock Bay, N.C. (WHITEHEAD 1973, personal communication). 27. Bladen County Lakes, N.C. (FREY 1953). 28. White Pond, S.C. (WATTS, personal communication). 29. Lake Louise, GA (WATTS 1971). 30. Mud Lake, FLA (WATTS 1969). 31. Lake Annie, FLA (WATTS 1975a).

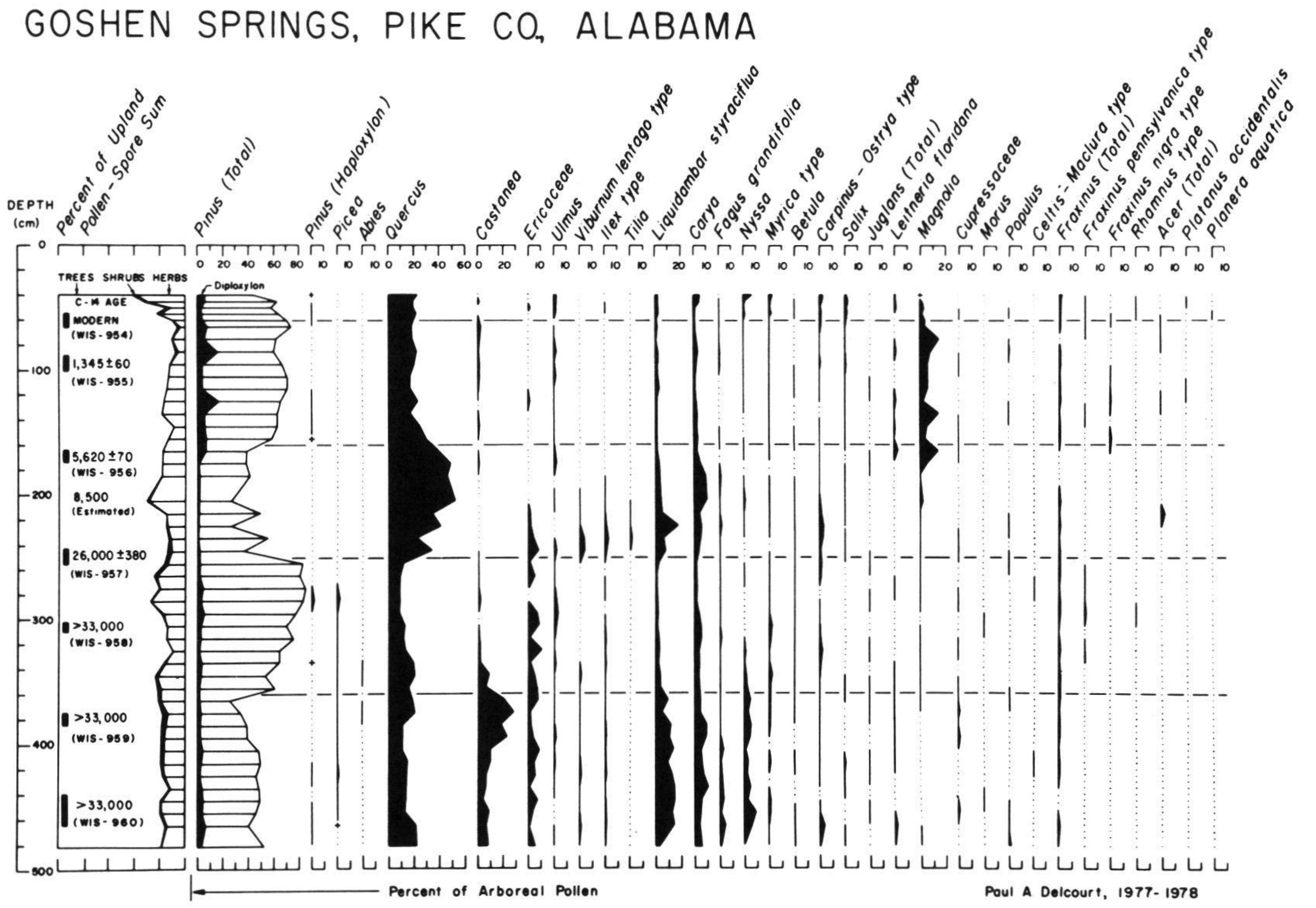

Fig. 3: Arboreal pollen percentage diagram, Anderson Pond, White Co., Tennessee

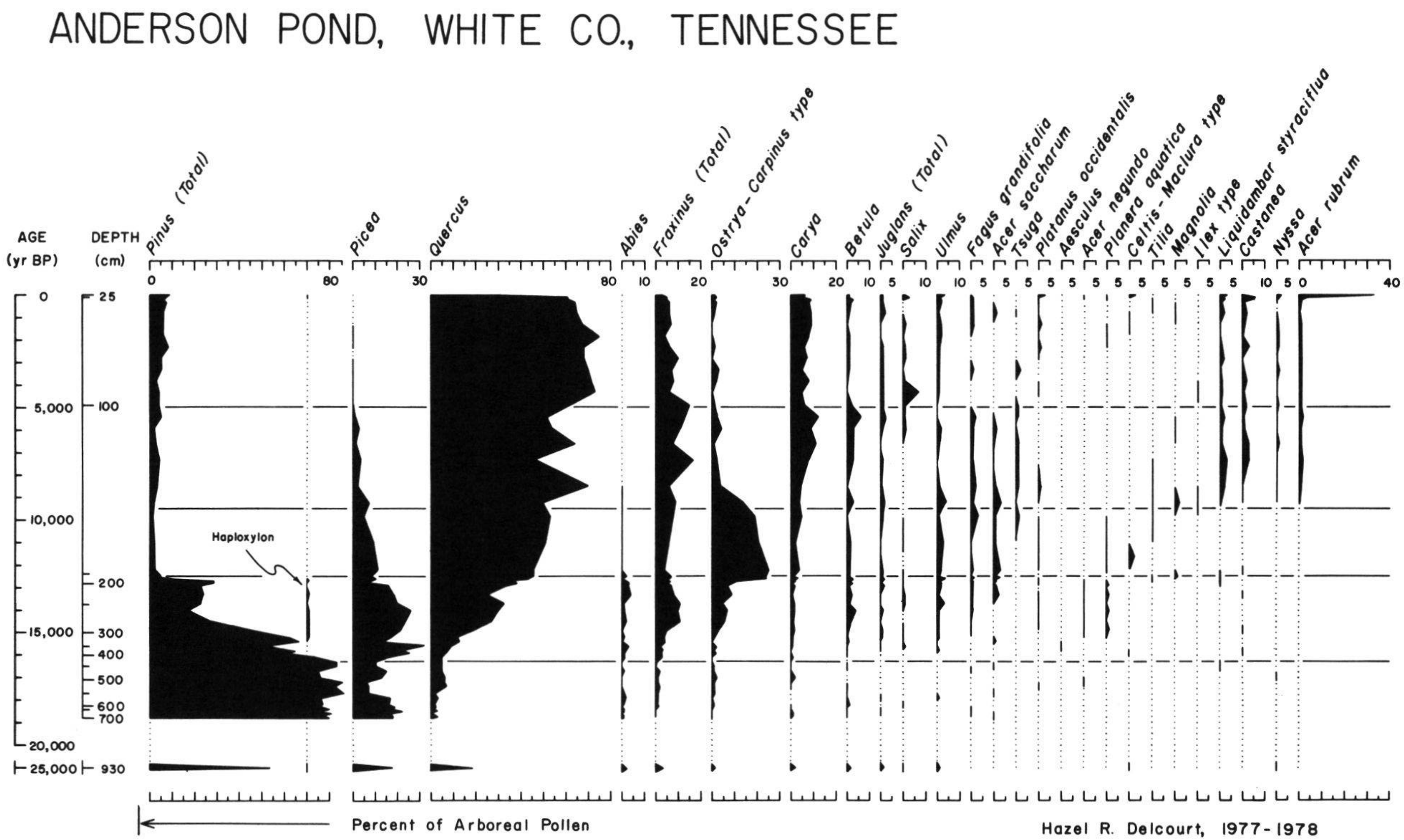

Fig. 4: Arboreal pollen percentage diagram, Goshen Springs, Pike Co., Alabama

The full-glacial vegetation at Anderson Pond (Fig. 3) was dominated by jack pine, as determined from size measurements of fossil pollen grains and anatomical characteristics of needle fragments (H. DELCOURT 1978). Pollen of *Picea, Abies, Quercus, Fraxinus,* and *Ostrya-Carpinus* type is consistently present throughout sediments of full-glacial age (Fig. 3). Pollen of additional deciduous forest taxa occurs only rarely between 19,000 BP and 17,800 BP, and pollen of deciduous trees composes only 6% of the total arboreal pollen at 18,000 BP. This plant-fossil assemblage reflects the full effects of climate change associated with the late Wisconsinan continental glaciation, during which boreal-like coniferous forest dominated the landscape of Middle Tennessee down to at least 300 m elevation. These data are consistent with either of two hypotheses: (1) during the full-glacial, mesic deciduous forest taxa existed farther south and west on edaphically favorable sites such as the blufflands of Mississippi-Louisiana and along bluffs and ravines of major river systems in Alabama and Georgia; or (2) mixed mesophytic forest taxa grew at the latitude of Anderson Pond throughout this time period (as well as possibly to the south), but their populations were too small to be recorded in the pollen assemblage, being restricted to protected, south-facing gorges in the eastern Highland Rim and adjacent Cumberland Plateau (H. DELCOURT 1978). The climatic conditions during the full-glacial at Anderson Pond may have been characterized by cool, long winters and a short growing season with periods of summer warmth. Mean annual temperature would have been as much as 15^{o} C lower than that of today, allowing "boreal" conifers to compete successfully with temperate deciduous tree taxa (H. DELCOURT 1978).

At Goshen Springs in south-central Alabama, the arboreal pollen record for the late Farmdalian Interstadial, full- and late-glacial period, and early Holocene is dominated by *Quercus*, *Carya*, and *Liquidambar styraciflua,* accompanied by moderate percentages of (southern) *Diploxylon Pinus* (Fig. 4). Xeric oak-hickory forests expanded in the upland vegetation mosaic at the expense of southern pine forests; the xeric oak-hickory forests presumably developed in response to a shift in the warm-temperate climate toward increased incidence of summer drought, with diminished fire frequency. Decreased thunderstorm activity during the summer would have reduced moisture available from precipitation, enhanced drought stress due to evapotranspiration, and lowered the number of lightning set fires. The full-glacial peak in aridity documented in the Gulf Coastal Plain (WATTS 1975a, P. DELCOURT 1978) favored expansion of xeric oak-hickory-southern pine forests on broad interfluves situated across the sandy uplands.

The pollen and plant-macrofossil stratigraphy of mesic and hydric plants records the progressive constriction then replacement of the pond by a rush-dock marsh in the Goshen Springs basin during the full-glacial period. Mesic deciduous forest taxa were virtually eliminated from the terrain surrounding Goshen Springs at this time. These data are consistent with the hypothesis that during late Wisconsinan glaciation, rich deciduous forest taxa were drastically restricted in habitat to fire-protected, mesic bluffs adjacent to the major river systems in deep South.

The Nonconnah Creek fossil localities are situated in Memphis, southwestern Tennessee, within the northern blufflands and adjacent to the lower Mississippi alluvial valley. From approximately 22,300 to 17,000 BP (corresponding with NC, TN-1-A-95 to 50 cm depth), the arboreal pollen assemblage was dominated by spruce (typically 73 to 76%) (Fig. 5). In addition, boreal components of *Abies* and *Larix* occurred consistantly at 1 to 2% of the arboreal pollen. Values for *Quercus* pollen fluctuated between 7 and 16%. Continuing in its trend of declining pollen percentages initiated during the preceding interstadial, total *(Diploxylon) Pinus* pollen counts dropped to a level of 2 to 4%. These extremely low values for *Pinus* indicate that pines were probably not growing within the Nonconnah Creek area during the full glacial. Throughout this time interval, low but stratigraphically persistent values occur in the Nonconnah Creek pollen record for *Carpinus-Ostrya* type, *Fraxinus, Carya, Betula, Fagus grandifolia, Acer rubrum, Acer saccharum, Populus, Salix, Ulmus, Viburnum lentago* type, and *Juglans*, all of which are tolerant of cool-temperate climatic conditions. The continuous pollen representation of many mesic deciduous forest taxa, consistently comprising about 13% of the total arboreal pollen sum, is considered evidence that populations of the deciduous tree species survived the full-glacial period in favorable habitats (e.g. south-facing slopes of the loess-capped uplands) within the Nonconnah Creek drainage area. This interpretation is further substantiated by the collection of

NONCONNAH CREEK, SHELBY CO., TENNESSEE

SECTION NC, TN-I-A

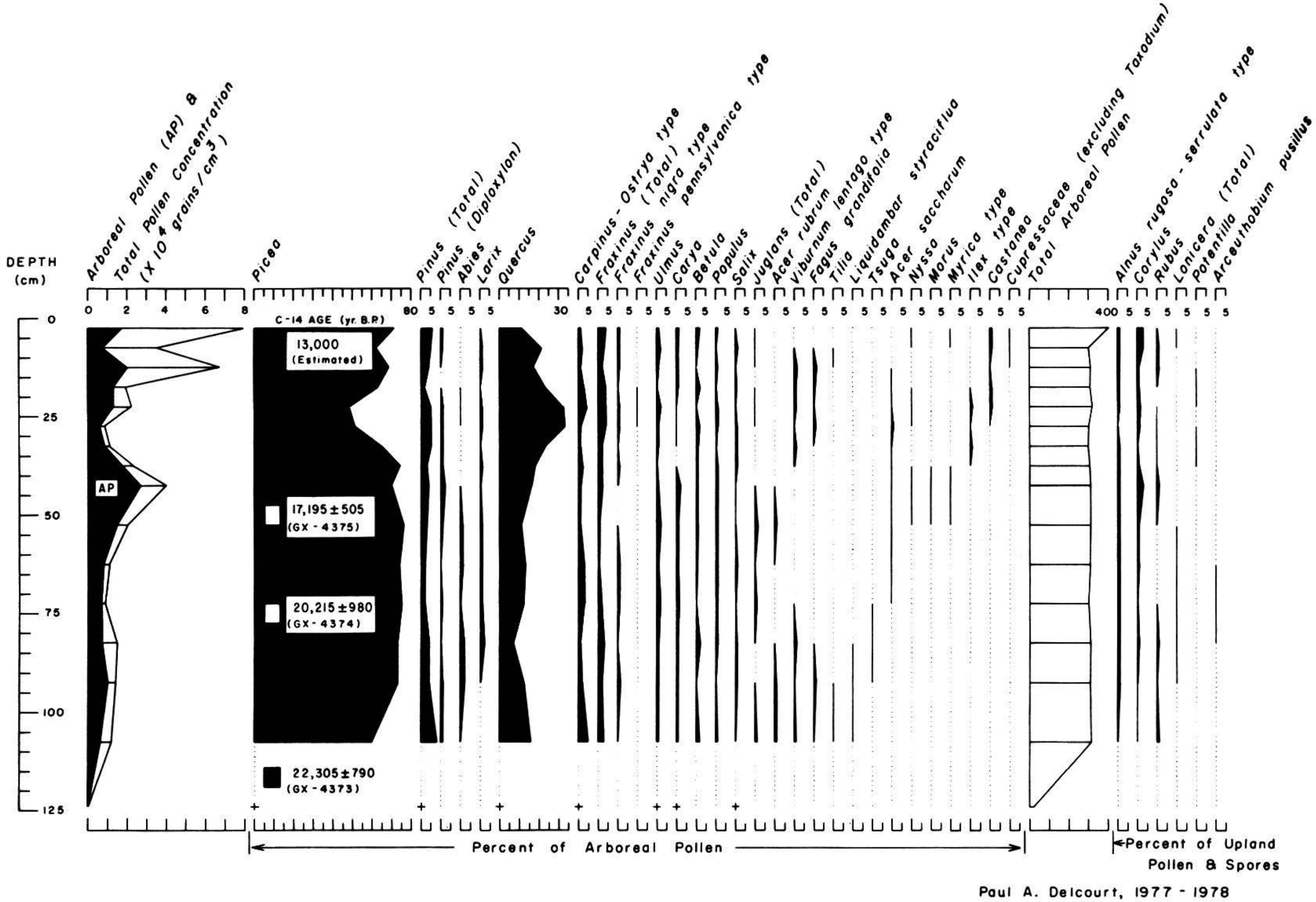

Fig. 5: Arboreal pollen diagram, Section NC, TN-1-A,Nonconnah Creek, Shelby Co., Tennessee

macrofossils including a hull and nut of *Fagus grandifolia*, a samara of yellow poplar (*Liriodendron tulipifera*), and *Carya* hulls from the dark gray clay layer of full-glacial age at locality NC, TN-1. A shell of *Juglans nigra*, associated with mastodon, was utilized with other organic material to provide a radiocarbon date of 17,195 ± 505 BP. Scattered hulls and nuts of several *Carya* species, *Quercus* nuts, and *Corylus* nuts were collected during the excavation of the fossil mastodon from the late-glacial layers of dark brown clay and blocky gray clay.

The great predominance of *Picea glauca* macrofossils and the high *Picea* pollen percentages, when compared with the stratigraphic record of cool-temperate mesic deciduous forest species, indicate that *Picea glauca* is relatively over-represented in the fossil assemblages because of the local proximity of spruce populations to the sedimentary environment of deposition. During the full-glacial, spruce and larch forests in alluvial bottomlands may have constituted a physical screen, filtering out pollen of *Quercus* and additional deciduous taxa occupying upland sites (CURRIER and KAPP 1974, TAUBER 1977). Extraordinarily large cones of *Picea glauca* (fossil cones up to 100 mm long) have now been collected from deposits of full- or late-glacial age from two sites: Nonconnah Creek and Percy Bluff in the Tunica Hills, southeastern Louisiana (BROWN 1938, DELCOURT and DELCOURT 1977a). It appears that an ecotype of white spruce was geographically isolated within the lower Mississippi alluvial valley, and spruce populations occupied alluvial habitats as far south as Louisiana until the late-glacial period. With major temperature increase in the early Holocene, this white spruce ecotype became extinct.

The plant hardiness for the suite of plant taxa recorded by fossil pollen, fruits, and seeds in the Nonconnah Creek locality NC, TN-1 places constraints upon the minimum winter temperatures for full-glacial winters in the Memphis region. The extremes in minimum winter temperatures were not lower than -40° C. Thus, during the late Wisconsinian continental glaciation, the winters were cooler but not severe within the Nonconnah Creek drainage area.

From 22,300 to 17,000 BP, arboreal pollen (calculated on the upland pollen-spore sum) dominated the Nonconnah Creek pollen record, with generally greater than 80%. This indicates widespread distribution of closed forests across the landscape and implies availability of soil moisture with low evapotranspiration stress during the summer season for the glacial period. During the full-glacial interval precipitation was probably available throughout the growing season, and periods of drought rarely occurred.

The palynological and plant-macrofossil evidence from Nonconnah Creek demonstrates that during the full-glacial period, boreal species of white spruce and larch occupied frequently disturbed alluvial sites within the lower Mississippi valley and tributary bottomlands immediately adjacent to the valley. Their distributions extended along the braided-stream surfaces as far as southeastern Louisiana (DELCOURT and DELCOURT 1977a). The blufflands provided suitable habitats for the persistence of populations of cool-temperate deciduous trees at least as far north as southwestern Tennessee during glacial times. The pollen and plant-macrofossil record from Nonconnah Creek provides the first documentation of a full-glacial locality for beech, yellow poplar, oak, hickory, and other mesic deciduous forest taxa in eastern North America. The Nonconnah Creek data support the hypothesis that the blufflands served as a major refuge for mesic deciduous forest taxa during the time of late Wisconsinan continental glaciation.

Very low percentages of *Pinus* pollen are observed in the full- and late-glacial sequence at Nonconnah Creek and the late-glacial record from the Tunica Hills (DELCOURT and DELCOURT 1977a). On the basis of this evidence, the lower Mississippi alluvial valley is postulated as a migrational barrier for pine during the late Wisconsinan, separating the jack pine population center in the Appalachian Mountains from populations of jack pine and possibly other pines distributed across the Great Plains and Ozarks.

4. Late glacial and Holocene history of the deciduous forest

Both the late-glacial and postglacial history of the eastern deciduous forest can now be traced from data available from numerous sites south of the glacial margin (Fig. 2). DAVIS (1976) examined the question of directions and rates of northward expansions of populations of individual deciduous forest taxa following the retreat of the Laurentide Ice Sheet. BERNADO and WEBB (1977) summarized the postglacial migration patterns of dominant tree taxa into the previously glaciated midwestern and northeastern regions of the United States. Compilation of data used in these studies was accomplished prior to discovery and analysis of Anderson Pond, Goshen Springs, and Nonconnah Creek, and hence before any definitive documentation was available for full-glacial and early late-glacial (beginning as early as 16'500 BP) locations of refugial areas for deciduous forest taxa (DAVIS 1976). The mapped migration patterns are thus highly speculative for the time period from 20,000 BP to 13,000 BP.

Additional significant data for conditions during the late glacial and Holocene near and south of the glacial margin have recently become available from the following sites (Fig. 2): the Tunica Hills, Louisiana (DELCOURT and DELCOURT 1977a); Mingo Pond, Tennessee (H. DELCOURT 1978); Rockyhock Bay, North Carolina (D. R. WHITEHEAD, personal communication); White Pond, South Carolina (W.A. WATTS, personal communication); Friar Branch, Tennessee (DESELM and BROWN 1978, H. DELCOURT 1978, H.R. DESELM, personal communication); Old Field, Missouri (KING and ALLEN 1977); Boriak Bog, Texas (BRYANT 1977); Battaglia Bog, Ohio (SHANE 1975); Carter and Stotzel-Leis sites, Ohio (SHANE 1976); Wigwam Creek Bog, Pennsylvania (SIRKIN 1977); and Belmont Bog, New York state (SPEAR and MILLER 1976). Additional radiocarbon-dated sites available for paleovegetation reconstruction for this time period south of the glacial margin are listed in Fig. 2.

Now for the first time it is possible to begin to document both the full-glacial distribution of deciduous forest in the deep South (Fig. 2) and to trace its subsequent history across unglaciated eastern North America. The reconstructions presented here are based upon pollen-stratigraphic and plant-macrofossil evidence from the network of well-dated sites located in Fig. 2.

The maximum displacement and areal restriction of the eastern deciduous forest occurred between 22,000 and 16,500 BP (Fig. 2). Based upon the limited evidence from Goshen Springs and Boriak Bog, we project that xeric oak-hickory woodland occupied the Gulf Coastal Plain from central Texas to southern Georgia during the full glacial, with southern *Diploxylon* pines persisting as subdominants at least on the Alabama Coastal Plain. Northward on the Atlantic coastal plain, oak-hickory woodland was replaced by xeric jack pine-spruce woodland in South Carolina and North Carolina. The southern Florida peninsula was occupied by open sand dune scrub vegetation. West and south of the Appalachian Mountains, the distribution of mesic deciduous forest is mapped to be consistent with the blufflands hypothesis. Across Missouri, Arkansas, Tennessee, and North Carolina, and extending northward to southern Minnesota, Wisconsin, Illinois, Indiana, Ohio, and across Pennsylvania to the eastern seabord, is mapped a broad belt of boreal-like coniferous forest dominated by jack pine and spruce with fir. White spruce dominated in the lower Mississippi alluvial valley and extended with larch southward as far as southeastern Louisiana. This wedge of spruce forest in the Mississippi valley corridor separated full-glacial populations of jack pine in Missouri to the west from those distributed eastward in Tennessee, North Carolina, South Carolina, and northern Georgia. Similarly, full-glacial oak-hickory-southern pine woodland in the Texas-Louisiana area was genetically isolated from populations of oaks in the southeastern coastal plain of Mississippi, Alabama, Georgia and northern Florida. Distinctive "Ozarkian" and "Appalachian" floristic elements associated with oak-hickory-southern pine forest may have arisen as a consequence of such genetic and geographic isolation at that time.

A belt of tundra and park-tundra bordered the ice margin and extended south along the crest of the Appalachian Mountains at least as far south as Maryland during the late Wisconsinan glacial maximum. Geomorphological evidence of periglacial conditions, including relict patterned ground features (P. KING 1964, CLARK 1968) were used to project areas at appropriate elevations in the central and southern Appalachians where tundra may have occurred during the full glacial (Fig. 2).

The nature of the vegetation in the full-glacial transition area between the boreal-like forests of Tennessee-North Carolina and the xeric oak-hickory-southern pine woodland of the Gulf Coastal Plain is still speculative, but we currently envision that this region was occupied by an ecotonal "tension zone" of mixed northern conifers and tolerant cool-temperate hardwoods, similar to the modern Great Lakes-Northern Hardwoods forest.

During the late glacial, beginning about 16,500 BP in the Southeast, spruce, pine, and fir forests declined in importance in mid-latitudes, as recorded in Missouri (J. KING 1973) and Tennessee (P. DELCOURT 1978, H. DELCOURT 1978). These taxa migrated northward rapidly, following the retreat of the Laurentide Ice Sheet (WRIGHT 1968, DAVIS 1976, BERNABO and WEBB 1977). The late-glacial arboreal pollen spectra at Hack Pond in the Shenandoah valley of Virginia are dominated by *Picea* and *Diploxylon* pine (CRAIG 1969). Tundra was replaced by spruce-fir forest at Carter and Stotzel-Leis sites by 14,000 BP (SHANE 1976), at Pretty Lake by 13,800 BP (WILLIAMS 1974), at Buckle's Bog by 12,700 BP (MAXWELL and DAVIS 1972), and at Belmont Bog by 12,500 BP (SPEAR and MILLER 1976).

Between 16,500 and 12,500 BP, mixed coniferous-deciduous forests covered the landscape between 34^{o} N and 37^{o} N latitude. For example, at Anderson Pond, oak, ash, ironwood, hickory, and then beech and sugar maple increased their populations during this time interval (H. DELCOURT 1978). At Shady Valley in East Tennessee, hemlock and chestnut were represented during the late glacial along with oak, pine, hickory, and spruce (BARCLAY 1957).

The earliest expansion of deciduous forest was in the south, beginning at about 16,500 BP at Nonconnah Creek, Anderson Pond, and Boney Springs. With climatic amelioration during the late glacial period and early Holocene, deciduous forest elements spread northward along the Appalachian Mountain chain and the Allegheny and Cumberland plateaus to the west. During the Holocene, dated at Anderson Pond at 12,500 to about 8,000 BP, cool-temperate mixed mesic forest prevailed throughout the region between 34^{o} N and 37^{o} N latitude. At Rockyhock Bay (WHITEHEAD, personal communication), the expansion of mesic cool-temperate deciduous-coniferous forest is dated at about 11,500 to 7,000 BP. At this site, *Tsuga, Betula, Fagus grandifolia,* and *Ostrya-Carpinus* type each increases to 2-4% of the arboreal pollen sum during this time, then decreases in abundance during the late Holocene. WHITEHEAD (1973) compares his early-Holocene arboreal assemblage with Braun's Northern Hardwoods Forest. At Shady

Valley, pollen of *Tsuga, Castanea,* and *Picea* were abundant at the time of the late-glacial *Pinus* fall, along with *Quercus,* and continued to indicate mesic conditions through the early Holocene (BARCLAY 1957). Quicksand Pond (WATTS 1970) contains a late-glacial to early Holocene record (post-13,500 BP) of increased percentages of *Picea* (to 5%) and *Carya* (to 5%), with 1-2% each of *Myrica, Betula, Ostrya-Carpinus* type, *Juglans, Fagus grandifolia,* and *Acer saccharum.* Pigeon Marsh, at 630 m elevation on Lookout Mountain near Chattanooga (WATTS 1975b), contains a peak in *Fagus grandifolia* pollen of nearly 20% of the tree pollen at 10,000 BP (Fig. 6), along with 50% *Quercus,* 10% *Carya,* over 5% *Ostrya-Carpinus* type, and several percent each of *Liquidambar styraciflua, Fraxinus, Ulmus, Acer saccharum, Castanea, Tsuga, Betula,* and *Picea.* In Chattanooga, at 200 m elevation, the Friar Branch alluvial section (Fig. 6) confirms a pollen assemblage at 10,000 BP similar to that of Pigeon Marsh, but with only a few percent of *Fagus grandifolia* and more *Carya* and *Ulmus* (H. DELCOURT 1978). A taxonomically rich assemblage of plant macrofossils recovered from the Friar Branch section, dated at 10,270 ± 100 BP and 9,515 ± 95 BP, includes numerous species of *Quercus* and *Carya* found growing in the vicinity of Chattanooga today, along with fruits of *Diospyros virginiana, Liriodendron tulipifera, Fagus grandifolia,* and *Tsuga* (DESELM and BROWN 1978, H.R. DESELM, personal communication). An unpublished pollen record from White Pond near Columbia, South Carolina (W.A. WATTS, personal communication) also contains an early-Holocene assemblage (dated from about 12,800 to 9,500 BP) rich in mesic forest taxa, including *Fagus grandifolia* (up to 15%), and several percent each of *Betula, Ostrya-Carpinus* type (to 6%), *Ulmus, Fraxinus pennsylvanica* type, *Tsuga, Acer saccharum, Juglans nigra, Platanus occidentalis, Castanea,* and *Ilex* type.

The early Holocene record of mesic, cool-temperate deciduous forest is now well documented from numerous sites of mid-latitudes in eastern North America. At this time, mesic deciduous forest was probably widespread as far west as Crowley's Ridge, a loess-mantled upland area situated within the Mississippi alluvial valley of Southeastern Missouri and Northeastern Arkansas. The plant-fossil evidence confirms speculations that isolated modern stands of mixed mesophytic forest in the Piedmont of the Carolinas, e.g. Stevens Creek (RADFORD 1959), are relicts of a formerly more areally dominant mesic,

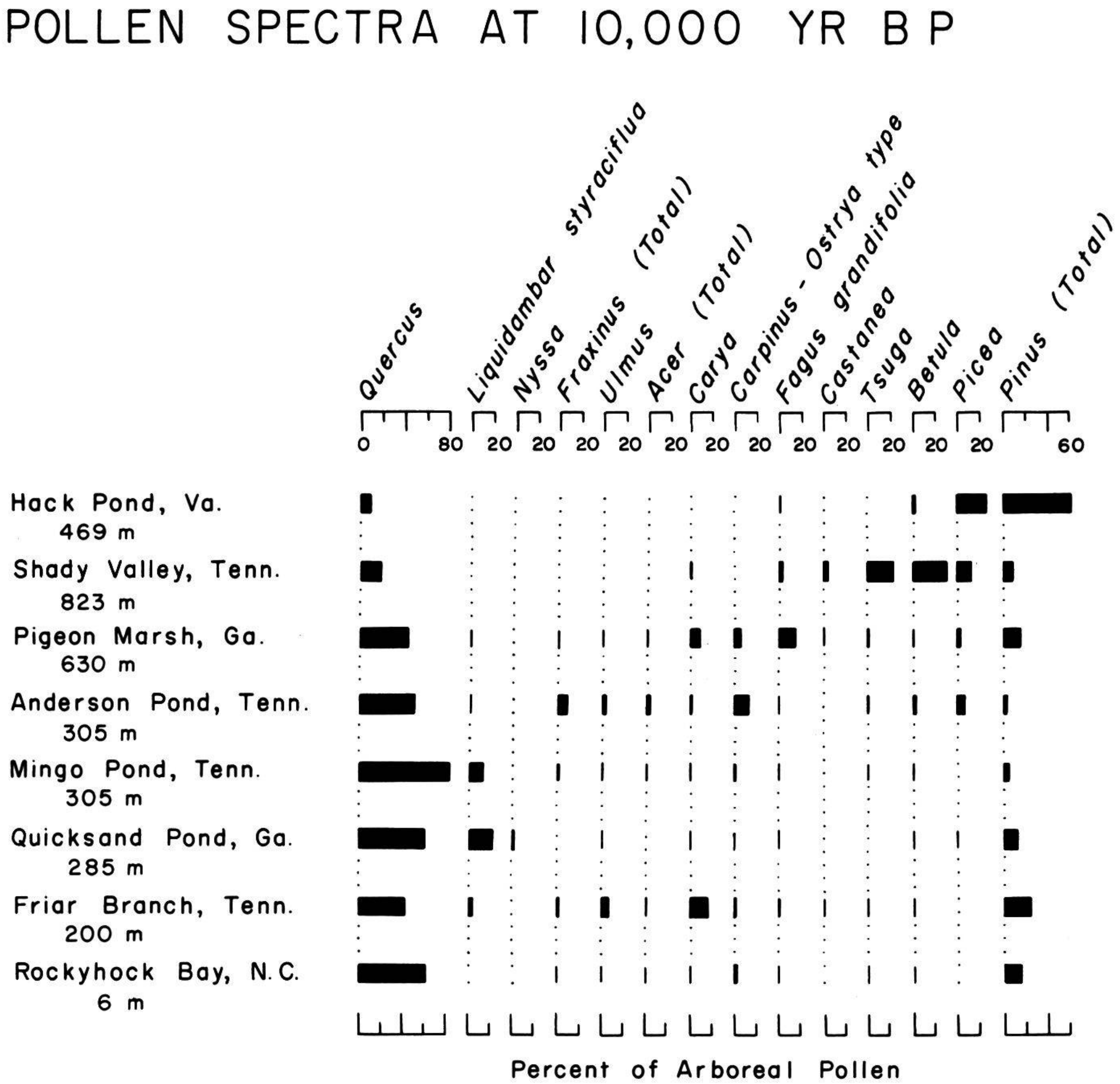

Fig. 6. Selected arboreal pollen spectra from sites in the Appalachian region, indicating the composition of the forests at 10,000 BP.

deciduous forest. This widespread, taxonomically diverse, predominantly deciduous forest of the mid-south, indicative of a cool and moist climate, prevailed there for nearly 5,000 years in the early Holocene. In contrast, early Holocene forests of the southern Atlantic and Gulf coastal plains were xeric, dominated by species of oak, hickory, and southern pine (WATTS 1969, 1971, BRYANT 1977, P. DELCOURT 1978).

During the early Holocene, Mixed Mesophytic Forest species migrated northward along the Cumberland and Allegheny plateaus and the Appalachian Mountain chain as far north as Ohio and Pennsylvania (KAPP 1977). At Hack

Pond in the Shenandoah valley, a rapid fall in *Pinus* pollen and a rise in *Quercus* pollen from 5% to 50% of the total upland pollen is dated at 9,500 BP (CRAIG 1969). The rise in *Quercus* pollen at Hack Pond is accompanied by increases in pollen of *Tsuga, Fagus grandifolia, Ulmus,* and *Juglans,* followed by *Castanea, Carya, Tilia, Acer,* and *Nyssa* (CRAIG 1969). At Buckle's Bog, replacement of spruce woodland by white pine northern hardwoods forest that included ash, ironwood, oak, birch, hemlock, and elm is dated at 10,500 BP. Mesic deciduous forest reached Silver Lake about 10,000 BP (OGDEN 1966) and Battaglia Bog in northeastern Ohio by 9,000 BP (SHANE 1975). Oak, birch, ironwood, beech, ash, elm, hemlock, and maple were representative constituents of the early Holocene forest of central and eastern Ohio (OGDEN 1966). At Pretty Lake, oak, elm, ironwood, maple, basswood, sycamore, and walnut were present by 9,700 BP, with beech arriving at 7,600 BP (WILLIAMS 1974, KAPP 1977). By 8,500 BP, hemlock, beech, sugar maple, and birch were abundantly represented by their respective pollen types at Belmont Bog, located just to the north of the present Mixed Mesophytic Forest region (SPEAR and MILLER 1976) (Fig. 1 and 2).

During the late glacial and early Holocene, the oak-hickory-pine woodland of central Texas was gradually replaced by prairie (BRYANT 1977). Climatic conditions favorable for the development of prairie, expanded eastward throughout the Great Plains region during the early Holocene, culminating in the Midwest in the maximum warmth and dryness of the Hypsithermal at 5,000 BP (WRIGHT 1976). Prairie was the dominant vegetation at Pittsburg Basin in south-central Illinois during the mid-Holocene (E. GRüGER 1972). The prairie-forest border spread as far east as the Old Field site in southeastern Missouri (KING and ALLEN 1977) and Silver Lake in central Ohio (OGDEN 1966).

At about 5,000 BP, the record of mesic deciduous forest diminishes across the central and eastern United States, and spruce pollen percentages fall to zero at mid-elevation sites in the Appalachian Mountains. From these data it may be inferred that the warming and drying trend of the Hypsithermal Interval (WRIGHT 1976) had widespread effects, not only in expanding the distribution of prairie eastward, but in changing the composition of forest in the central latitudinal belt of eastern North America. At Anderson Pond, in Middle Tennessee, forests became more xeric, dominated by oak, hickory, and ash (H. DELCOURT 1978). Cool-temperate deciduous forest taxa disappear from the Rockyhock Bay record by 5,000 BP and are replaced by pollen of warm-temperate, southern coastal plain elements such as *Taxodium* and *Nyssa* (WHITEHEAD personal communication).

During the mid-Holocene, Mixed Mesophytic Forest taxa become increasingly restricted in distribution and topographic position in areas peripheral to the Cumberland Mountains of eastern Kentucky. The center of distribution of the Mixed Mesophytic Forest shifted to the Cumberland Mountains in the mid-Holocene and probably remained there through the late Holocene. By 5,000 BP, boreal coniferous forest was restricted to territory farther north and to higher elevations in the Appalachian Mountains, occupying a smaller area on the landscape and contributing little to the late-Holocene pollen spectra from the southern Appalachian region.

In the late Holocene, after 5,000 BP, Appalachian pine species (*Pinus rigida, Pinus virginiana*) became locally important in the central Appalachians (CRAIG 1969). On the Atlantic and Gulf coastal plains, southern pines (*Pinus palustris, P. taeda, P. serotina, P. echinata, P. clausa,* and *P. elliottii*) became abundant in the late Holocene due to increased dominance of the tropical maritime airmass from the Gulf of Mexico, providing abundant precipitation throughout the year, along with high fire frequency due to lightning strikes (WATTS 1969, 1971, P. DELCOURT 1978). At the southern terminus of the Appalachians and west of the mountains, however, southern pines did not increase in importance, perhaps because of drought stress that prevented the coastal-plain species from migrating northward. Rather than exhibiting a uniform "southern pine rise" postulated by WATTS (1970, p. 28), the late Holocene arboreal pollen spectra from the Southeast illustrate gradients in vegetation composition within a diverse mosaic of deciduous and coniferous forest types. Late-Holocene dominance of southern pines appears to have been restricted to the coastal plains and to the central Appalachians (where local edaphic conditions permitted). Within the southeastern United States, several distinct floristic and vegetational provinces occurred at the time of settlement (BRAUN 1950, DELCOURT and DELCOURT 1977b), reflecting the diversity of climate, soils, and topography of this region.

Summary

In this paper, we review the evidence for late Quaternary climatic and vegetational change in the southeastern United States. We propose and test a hypothesis that postulates that climatic change had regional effects south of the glacial margin. This hypothesis allows for persistence of many endemic taxa within local refuges on edaphically and microclimatically suitable sites in the Southeast.

We propose that the blufflands along the eastern wall of the lower Mississippi alluvial valley served as both full-glacial refuge and subsequent migrational pathway for mesic deciduous forest species. The blufflands coincide with the thickest loess deposits in the states of Tennessee, Mississippi, and Louisiana. This north-south trending belt of dissected hills forms a strip of fertile, mesic habitat 20 to 50 km wide today occupied by Mixed Mesophytic Forest taxa. We speculate that during the last continental glaciation, mesic deciduous forest species would have been restricted by lack of appropriate upland habitats to bottomlands and to the dissected terrain adjacent to major north-south trending streams. Deciduous taxa may also have resisted at low elevations in protected coves of the southern Appalachian Mountains.

Pollen-stratigraphic evidence is presented from three sites located in areas critical to the testing of the blufflands hypothesis:

(1) Anderson Pond, White Co., Tennessee, located in the southern portion of the Mixed Mesophytic Forest-Western Mesophytic Forest regions;

(2) Goshen Springs, Pike Co., Alabama, located on an interfluve in the sandy uplands of the Gulf Coastal Plain; and

(3) Nonconnah Creek, Shelby Co., Tennessee, situated in the northern blufflands.

The full-glacial vegetation at Anderson Pond, Tennessee, was boreal-like coniferous forest dominated by jack pine and spruce. Only traces of deciduous tree pollen are represented in Anderson Pond sediments of full-glacial age; consequently, either the deciduous forest was displaced southward of 36° N or small populations of deciduous forest taxa persisted in protected coves of the Cumberland Plateau and southern Appalachian Mountains. At Goshen Springs, Alabama, the full- and late-glacial vegetation was xeric forest of oak, hickory, and southern pine with only sparse record of mesic deciduous trees. This site demonstrates that even with climatic cooling, the sandy uplands of the Gulf Coastal Plain did not support growth of rich deciduous forests. Nonconnah Creek, Tennessee, provides the first clear evidence of a full-glacial refuge for deciduous forest, with macrofossils of *Fagus grandifolia, Liriodendron tulipifera, Juglans nigra, Carya* ssp., *Quercus* ssp., and *Corylus*, as well as pollen of numerous additional deciduous tree taxa, recovered from sediments of full- and late-glacial age.

The earliest expansion of deciduous forest from restricted full-glacial refuges was 16,500 BP. With climatic amelioration, deciduous forest

elements spread northward along the blufflands, the Appalachian Mountain chain and the Allegheny and Cumberland plateaus. During the early Holocene, from 12,500 to 8,000 BP, cool-temperate mixed mesic forest prevailed throughout the region between 34° and 37° N. This early-Holocene expansion of deciduous forest is well-documented from numerous sites in the mid-latitudes of eastern North America. During the mid-Holocene, Mixed Mesophytic Forest taxa became increasingly restricted in distribution. The center of distribution of the Mixed Mesophytic Forest shifted to the Cumberland Mountains of eastern Kentucky by 5,000 BP and remained there through the late Holocene.

Zusammenfassung

In diesem Beitrag wird eine Uebersicht über die Klima- und Vegetationsänderungen während der späteren Quartärzeit in den südöstlichen Staaten der USA gegeben. Es wird die Hypothese vorgetragen und überprüft, dass regional und südlich des Eisrandes der Vergletscherung Klimawechsel stattfanden, so dass viele endemische Taxa nur lokal an edaphisch und klimatisch günstigen Orten des Südostens überdauern konnten.

Es wird angenommen, dass die "Blufflands" längs des östlichen Randes des alluvialen Mississippi-Tales als Glazialrefugium und als Wanderweg für die mesischen Laubwälder dienten. Die "Blufflands" umfassen die dicksten Lössablagerungen in den Staaten Tennessee, Mississippi und Louisiana. Dieser Nordsüd gerichetete Gürtel von freistehenden Hügeln bildet einen 20-50 km breiten Streifen von fruchtbarem Land mit mittleren Feuchtigkeitsbedingungen, der von Laubmischwald-Arten ("Mixed Mesophytic Forest") besiedelt wird. Während der letzten Vergletscherung waren wahrscheinlich die mesischen Laubwaldarten auf die tieferen Lagen längs dieses Streifens und auf die vorwiegend Nordsüd ziehenden Flusstäler innerhalb dieser Hügelzone beschränkt, da das angrenzende Hochland für eine Besiedlung nicht geeignet war. Ueberdauerungsmöglichkeiten waren wohl auch in besonders geschützten tieferen Lagen der südlichen Appalachen vorhanden.

Zur Stützung der Hypothese wurden die folgenden drei Pollenprofile analysiert:

1. Anderson Pond, White Co., Tennessee, im südlichen Teil der gemässigten Laubmischwälder (Mixed and Western Mesophytic Forets", siehe Fig. 1).
2. Goshen Springs, Pike Co., Alabama, auf dem sandigen Hochland der "Gulf Coastal Plain"
3. Nonconnah Creek, Shelby Co., Tennessee, in den nördlichen "Blufflands".

Die eiszeitliche Vegetation beim Anderson Pond, Tennessee, bestand aus borealen Nadelwäldern (vor allem Föhre und Fichte). Es wurden während der Hocheiszeit nur Spuren von Laubbaum-Pollen gefunden. Der Laubwald musste deshalb südlich über den 36. nördlichen Breitengrad ausweichen oder konnte höchstens an geschützten Stellen des Cumberland-Plateaus oder der südlichen Appa-

lachen überdauern. Bei Goshen Springs, Alabama, war die Vegetation während der Hoch- und Späteiszeit ein trockener Eichen-Hickory-Föhrenwald mit nur geringem Vorkommen von Bäumen des gemässigten Laubwaldes. Nonconnah Creek, Tennessee, ist der einzige Ort, der für das Hochglazial ein Refugium für den gemässigten sommergrünen Laubwald anzeigt, mit Makrofossilien von *Fagus grandifolia, Liriodendron tulipifera, Juglans nigra, Carya* spp., *Quercus* spp. und *Corylus* sowie mit Pollen von vielen zusätzlichen Laubbaumarten.

Die früheste Ausbreitung des sommergrünen Laubwaldes aus den eng umgrenzten Glazialrefugien begann etwa 16500 v.Chr. Mit der klimatischen Verbesserung wanderten die Laubwaldelemente längs der Blufflands,der Appalachen und des Allegheny- und Cumberland-Plateaus nach Norden. Während des frühen Holozäns(zwischen 12500 und 8000 v.Chr.) herrschte im Gebiet zwischen dem 34. und 37. nördlichen Breitengrad kühl gemässigter Laubmischwald vor. Die frühe Holozän-Ausbreitung des sommergrünen Laubwaldes ist heute von vielen Orten der mittleren Breiten der östlichen USA nachgewiesen. Während des mittleren Holozäns wurden diese Wälder von Süden her zunehmend eingeschränkt. Das Verbreitungszentrum der Laubmischwaldarten (Arten des Mixed Mesophytic Forest) verlagerte sich in die Cumberlandberge von Ost-Kentucky (etwa 5000 v. Chr.) und blieb dort während des späten Holozäns.

References

BARCLAY, F.H., 1957: The natural vegetation of Johnson County, Tennessee, past and present. Ph.D. dissertation, Univ. of Tennessee, Knoxville, 147 p.

BERNABO, J.C. and WEBB T., III. 1977: Changing patterns in the Holocene pollen record of northeastern North America: a mapped summary. Quat. Res. *8*, 64-96.

BIRKS, H.J.B., 1976: Late-Wisconsinan vegetational history at Wolf Creek, Central Minnesota. Ecological Monogr. *46(4)*, 395-429.

BRAUN, E.L., 1950 (Reprinted 1974): Deciduous forests of eastern North America. Hafner Press, MacMillan Publ. Co., Inc., New York, 596 p.

\- 1955: The phytogeography of unglaciated eastern United States and its interpretation. Bot. Rev. *21*, 297-375.

BROWN, C.A., 1938: The flora of Pleistocene deposits in the western Florida parishes, West Feliciana Parish, and East Baton Parish, Louisiana. Louisiana State Dept. Cons. Geol. Bull. *12*, 59-96.

BRYANT, V.M., 1977: A 16,000 year pollen record of vegetational change in Central Texas. Palynology *1*, 143-156.

CAIN, S.A., 1943: The Tertiary character of the cove hardwood forests of the Great Smoky Mountains National Park. Bull. Torrey Bot. Club *70*, 213-235.

CLARK, G.M., 1968: Sorted patterned ground: new Appalachian localities south of the glacial border. Science *161*, 355-356.

COCKS, R.S., 1914: Notes on the flora of Louisiana I. Plant World *17*, 186-191.

CORE, E.L., 1970: The botanical exploration of the southern Appalachians. In: The distributional history of the biota of the southern Appalachians, Part II: Flora, Research Div. Monogr. *2*, Virginia Polytechnic Institute and State Univ., Blacksburg, Virginia, 1-65.

CRAIG, A.J., 1969: Vegetational history of the Shenandoah Valley, Virginia. Geol. Soc. Am. Spec. Paper *123*, 283-296.
CURRIER, P.J. and KAPP, R.O., 1974: Local and regional pollen rain components at Davis Lake, Montcalm County, Michigan. Michigan Academician *7*, 211-225.
DAVIS, M.B., 1976: Pleistocene biogeography of temperate deciduous forests. Geoscience and Man *13*, 13-26.
DEEVEY, E.S., 1949: Biogeography of the Pleistocene. Geol. Soc. Amer. Bull.*60*, 1315-1416.
DELCOURT, H.R., 1978: Late Quaternary vegetation history of the eastern Highland Rim and adjacent Cumberland Plateau of Tennessee. Ph.D. dissertation, Univ. of Minnesota, Minneapolis, 210 pp.
- and DELCOURT, P.A., 1974: Primeval magnolia-holly-beech climax in Louisiana. Ecology *55*, 638-644.
-- 1975: The blufflands: Pleistocene pathway into the Tunica Hills. Am. Midl. Nat. *94*, 385-400.
-- 1977a: The Tunica Hills, Louisiana-Mississippi: late glacial locality for spruce and deciduous forest species. Quat. Res. *7*, 218-237.
-- 1977b: Presettlement magnolia-beech climax of the Gulf Coastal Plain: quantitative evidence from the Apalachicola River bluffs, north-central Florida. Ecology *58*, 1085-1093.
DELCOURT, P.A., 1978: Quaternary vegetation history of the Gulf Coastal Plain. Ph.D. dissertation, Univ. of Minnesota, Minneapolis, 244 pp.
DESELM, H.R. and BROWN, J.L., 1978: Fossil flora of the Friar Branch and Boyd Buchanan School sites. (Abstr.) Assoc. Southeastern Biol. Bull.*25*,83.
DONN, W.L., 1965: Meteorology. 3rd ed. McGraw-Hill, New York.
EMILIANI, C., 1966: Isotopic paleotemperatures. Science *154*, 851-856.
FLINT, R.F., 1971: Glacial and Quaternary Geology. John Wiley and Sons, Inc., New York, 892 p.
FREY, D.G., 1953: Regional aspects of the late-glacial and postglacial pollen succession of southeastern North Carolina. Ecol. Monogr. *23*, 289-313.
GRAHAM, A., 1972: Outline of the origin and historical recognition of floristic affinities between Asia and eastern North America. In: GRAHAM, A. (Ed.), Floristics and paleofloristics of Asia and eastern North America. Elsevier Publ. Co., Amsterdam, 1-18.
GRAY, J. and SOHMA, K., 1964: Fossil *Pachysandra* from western America with a comparative study of pollen in *Pachysandra* and *Sarcococca*. Amer. J. Sci. *262*, 1159-1197.
GRÜGER, E., 1972: Pollen and seed studies of Wisconsinan vegetation in Illinois, U.S.A. Geological Society of America Bulletin *83*, 2715-2734.
GRÜGER, J., 1973: Studies on the late Quaternary vegetation history of northeastern Kansas. Geological Society of America Bulletin *84*, 239-250.
ILTIS, H.H., 1965: The genus *Gentianopsis (Gentianaceae)*: transfer and phytogeographic comments. Sida *2*, 129-154.
KAPP, R.O., 1977: Late Pleistocene and postglacial plant communities of the Great Lakes region. In: ROMANS, R.C. (Ed.), Geobotany, Plenum Publ. Co., New York, 1-27.
KENNETT, J.P. and SHACKLETON, N.J., 1975: Laurentide Ice Sheet meltwater recorded in Gulf of Mexico deep-sea cores. Science *188*, 147-150.
KING, J.E., 1973: Late Pleistocene palynology and biogeography of the Western Missouri Ozarks. Ecol. Monogr. *43*, 539-565.

- and ALLEN, W.H. Jr., 1977: A Holocene vegetation record from the Mississippi River Valley, Southeastern Missouri. Quat. Res. *8*, 307-323.
KING, P.B., 1964: Geology of the Central Great Smoky Mountains, Tennessee. U.S. Geological Survey Professional Paper *349-C*, 1-148.
MARTIN, P.S., 1958: Taiga-tundra and the full-glacial period in Chester County, Pennsylvania. Amer. J. Sci. *256*, 470-502.
MAXWELL, J.A. and DAVIS, M.B., 1972: Pollen evidence of Pleistocene and Holocene vegetation of the Allegheny Plateau, Maryland. Quat. Res. *2*, 506-530.
MITCHELL, R.S., 1963: Phytogeography and floristic survey of a relic area in the Marianna Lowlands, Florida. Amer. Midl. Nat. *69*, 328-366.
OGDEN, J.G., III. 1966: Forest history of Ohio. I. Radiocarbon dates and pollen stratigraphy of Silver Lake, Logan County, Ohio. Ohio J. Sci. *66*, 387-400.
RADFORD, A.E., 1959: A relict plant community in South Carolina. J. Elisha Mitchell Sci. Soc. *75*, 33-34.
SAUCIER, R.T., 1974: Quaternary geology of the Lower Mississippi Valley. Arkansas Archeol. Surv., Publ. Archeol. Res. Ser. No. *6*, 1-26.
SHANE, L.C.K., 1975: Palynology and radiocarbon chronology of Battaglia Bog, Portage County, Ohio. Ohio J. Sci. *75*, 96-102.
- 1976: Late-glacial and postglacial palynology and chronology of Darke County, west-central Ohio. Ph.D. dissertation, Kent State Univ., Kent, Ohio, 221 p.
SICCAMA, T.G., 1974: Vegetation, soil, and climate on the Green Mountains of Vermont. Ecol. Monogr. *44*, 325-349.
SIRKIN, L., 1977: Late Pleistocene vegetation and environments in the middle Atlantic region. Ann. New York Acad. Sci. *288*, 206-217.
SPEAR, R.W. and MILLER, N.G., 1976: A radiocarbon dated diagram from the Allegheny Plateau of New York State. J. Arnold Arboretum *57*, 369-403.
TAUBER, H., 1977: Investigations of aerial pollen transport in a forested area. Dansk Botanisk Arkiv *32*, 1-121.
VAN DER HAMMEN, T., WIJMSTRA, T.A. and ZAGWIJN, W.H., 1971: The floral record of the Late Cenozoic of Europe. In: TUREKIAN, K.K. (Ed.) "The Late Cenozoic Glacial Ages". Yale Univ. Press, New Haven, 391-424.
VAN ZANT, K.L., 1976: Late- and postglacial vegetational history of northern Iowa. Ph.D. dissertation, Univ. of Iowa, Iowa City, 123 p.
WATTS, W.A., 1969: A pollen diagram from Mud Lake, Marion County, north-central Florida. Geol. Soc. Amer. Bull. *80*, 631-642.
- 1970: The full-glacial vegetation of northwestern Georgia. Ecology *51*, 17-33.
- 1971: Postglacial and Interglacial vegetation history of southern Georgia and central Florida. Ecology *52*, 676-690.
- 1975a: A late Quaternary record of vegetation from Lake Annie, south-central Florida. Geology *3*, 344-346.
- 1975b: Vegetation record for the last 20,000 years from a small marsh on Lookout Mountain, northwestern Georgia. Geol. Soc. Am. Bull. *86*, 287-291.
WHITEHEAD, D.R., 1973: Late-Wisconsin vegetational changes in unglaciated eastern North America. Quat. Res. *3*, 621-631.
WILLIAMS, A.S., 1974: Late-glacial - postglacial vegetational history of the

Pretty Lake region, northeastern Indiana. U.S. Geol. Surv. Prof. Paper *686-B*, 23 p.

WRIGHT, H.E., Jr., 1968: The roles of pine and spruce in the forest history of Minnesota and adjacent areas. Ecology *49*, 937-955.

- 1976: The dynamic nature of Holocene vegetation, a problem in paleoclimatology, biogeography, and stratigraphic nomenclature. Quat. Res. *6*, 581-596.

- 1977: Quaternary vegetation history - some comparisions between Europe and America. Ann. Rev. Earth Planet. Sci. *5*, 123-158.

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