

The appearance and disappearance of major vegetational assemblages: Long-term vegetational dynamics in eastern North America

Thompson Webb III*

Department of Geological Sciences, Brown University, Providence, RI 02912–1846, USA

Keywords: Dynamics, Fossil pollen, Isopoll map, Late Quaternary, Long-term vegetation change

Abstract

Contoured maps of pollen percentages from eastern North America illustrate that the vegetation changed continuously during the past 18000 years. The maps show that the geographic distribution for selected pollen types from 500 years ago parallels the major patterns in the vegetation, and that the correspondence is good enough to justify using maps of fossil pollen to interpret the patterns and composition of the broad-scale vegetation from earlier times. Data for *Artemisia*, Cyperaceae, *Picea*, *Betula*, *Alnus*, *Abies*, and *Pinus* pollen illustrate how the changing location and abundance of their plant taxa and populations altered the spatial pattern, local composition, and the overall structure of the vegetation and thus led to the disappearance as well as appearance of major biomes and ecotones. For example, the *Picea* parkland biome that existed from 18000 to 12000 yr B.P. within a broad region south of the ice sheet disappeared within 2000 years after 12000 yr B.P., and the modern boreal forest biome began to develop across a large area of central Canada only after 6000 yr B.P. On a time scale of 10^4 to 10^6 yr, these types of vegetation changes involve a continual overlapping and separation of the abundance distributions for different taxa. Such changes are likely to have been a feature of vegetational dynamics for millions of years.

Introduction

Contoured maps of pollen percentages from networks of radiocarbon-dated sediment cores illustrate how the vegetation has changed during the

past 18000 years within eastern North America and Eurasia (Bernabo & Webb, 1977; Gaudreau & Webb, 1985; Huntley & Birks, 1983; Peterson, 1983; Ralska-Jasiewiczowa, 1983; Webb, 1985). Temporal sequences of the maps record the numerical as well as spatial expansion and contraction of individual plant taxa and depict the changing pattern of abundance gradients as the range boundaries and density centers for various taxa change in location and areal coverage leading to new associations among taxa. During the past 18000 years, the changes were large enough to result in the appearance and disappearance of major biomes and ecotones (Ritchie, 1976; Davis, 1983b).

Recent paleoclimatic studies have indicated the extent of climatic change during the past 18000 years (CLIMAP, 1981; Hecht, 1985; Street & Grove,

* An NSF grant (ATM-8406832) to COHMAP from the Climate Dynamics Program supported this research. I thank J. Avizinis, K. Hauschildt, T. Judd, S. Klinkman, F. Lefkowitz, M. Prestas for technical assistance; and A. M. Solomon, B. Huntley, S. T. Jackson, and I. C. Prentice for constructive comments on the manuscript. The maps were produced from data available as of Nov. 1983. R. E. Bailey, R. G. Baker, E. J. Cushing, R. P. Futyma, D. C. Gaudreau, R. O. Kapp, G. King, H. F. Lamb, J. H. McAndrews, R. J. Nickmann, J. G. Ogden III, W. A. Patterson III, P. J. H. Richard, L. C. K. Shane, S. K. Short, K. M. Trent, K. L. Van Zant, and D. R. Whitehead kindly contributed unpublished pollen data.

1979), and various studies are showing what the past climatic patterns were (Kutzbach & Guetter, 1986; Kutzbach & Wright, 1985). In eastern North America, much of the climatic change from 18000 to 6000 yr B.P. was strongly influenced by the retreat and disappearance of the Laurentide ice sheet, which was near its maximum extent at 18000 yr B.P. The large climatic changes during this time period make it an ideal one to use in developing theory about how long-term climatic change affects the vegetation (Bartlein *et al.*, 1984, 1986; Davis *et al.*, 1986; Prentice, 1983, 1986; Ritchie, 1986; Overpeck *et al.*, 1985; Solomon & Webb, 1985; Webb, 1986). Radiocarbon dating within this time span has a precision fine enough to permit mapping in intervals upto 500 years (Webb, 1982). Because mapping at this time scale is impossible for any previous 18000 year interval, the past 18000 years gains added importance in providing a window for viewing comparable intervals during the more distant geological past.

The focus of my paper is on describing some of the changes in vegetational composition and structure in the areas of eastern North America where *Picea* trees have been numerous within the past 18000 years.

Data and methods

A sequence of isopoll maps with contours of equal pollen percentage illustrates the distribution of the pollen types at each 2000 year interval from 18000 to 2000 yr B.P. The final map in the series is for 500 yr B.P., which is just before European settlement in North America, and thus illustrates the 'pre-settlement' vegetation patterns before widespread logging and agriculture modified the pollen record in much of eastern North America south of 50°N (Bernabo & Webb, 1977; Van Zant *et al.*, 1979; Gaudreau & Webb, 1985).

The pollen data came from a network of lakes and bogs where sediments had been collected and radiocarbon-dated, and the data set represents the work of over 80 palynologists since 1960. The maps were produced from computer files listing the pollen counts and radiocarbon dates for each site (Webb *et al.*, 1983a, b; Gaudreau & Webb, 1985). First, the dates were used to estimate the age for each pollen sample, and then the pollen percentages from adjacent pollen samples were linearly interpolated to obtain estimates of the pollen percentages for each 500 year interval (e.g. 500, 1000, 1500, ..., 18000 yr B.P.) for which data existed at each site. In general, no data were mapped

at a site for time intervals more than 500 years older than the oldest radiocarbon data at that site. The pollen percentages were calculated from a pollen sum of all tree, shrub, and non-aquatic herb pollen. At a few sites, locally over-represented wetland taxa (e.g. *Nyssa*, *Larix*) were deleted from the pollen sum. Initial versions of the maps showed anomalously high values for these taxa at single sites.

Site density varies depending on the dates being mapped. The total number of available sites increases from 15 at 18000 yr B.P. to 70 at 12000 yr B.P. and to over 250 from 10000 yr B.P. to 500 yr B.P. (Fig. 1). See Webb (1985) for a table and bibliography for the sites with data available at 6000 yr B.P.; Webb *et al.* (1983a, b) and Gaudreau & Webb (1985) provide lists of the sites and their dating control in southern Quebec and in central and northeastern United States. Three contours for each pollen type were chosen to illustrate the key features of the distribution for that taxon. The differential scaling of pollen types depended upon the overall abundance of the type in the pollen record. *Pinus* pollen is the most abundant type. Its maps had contours of 20% and 40%, but it is too ubiquitous for a low-valued contour to be informative. For most taxa, the contour with the lowest value lies near or outside the range boundary for the plants, the intermediate contour marks areas where the plants are in low to moderate numbers, and the contour with the highest value identifies the region of high abundances (i.e. the density center) for the taxon.

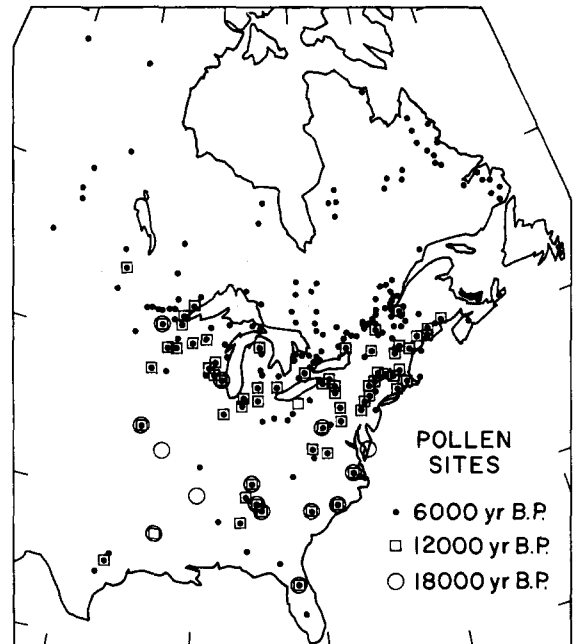


Fig. 1. Location of sites with pollen data for 6000 yr B.P. (black dots). Open squares mark sites with data for 12000 yr B.P. and open circles mark sites with data for 18000 yr B.P.

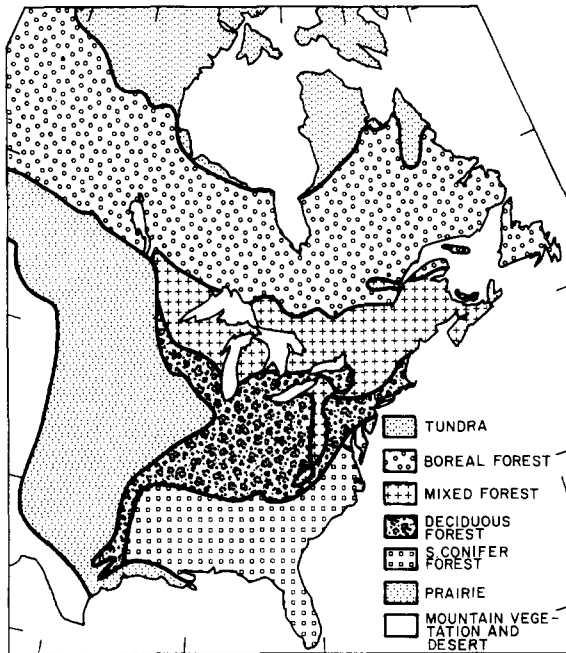


Fig. 2. Generalized vegetation map for eastern North America (modified from Webb & Bernabo, 1977).

Results

500 yr B.P.

Maps of pollen data for 500 yr B.P. show that patterns in the abundances for major pollen types parallel the patterns in the major vegetational regions (Figs. 2, 3). The pollen samples in the region of prairie vegetation contain high values of *Artemisia* and Cyperaceae pollen; the sites in the tundra and forest-tundra have high values of Cyperaceae, *Betula*, and *Alnus* pollen; the sites in the boreal forest exhibit high values of *Picea*, *Abies*, and *Betula* pollen; the sites in the mixed conifer-hardwood forest contain high values of *Betula* and *Tsuga* pollen in the east and of *Pinus* pollen in the west; the sites in the deciduous forest are dominated by high values of *Quercus* pollen; and the sites in the southern conifer forests have high values of *Pinus* pollen. Steep gradients in the pollen abundances mark the ecotones between the vegetation regions. Six biomes and five ecotones are evident, and the mixed

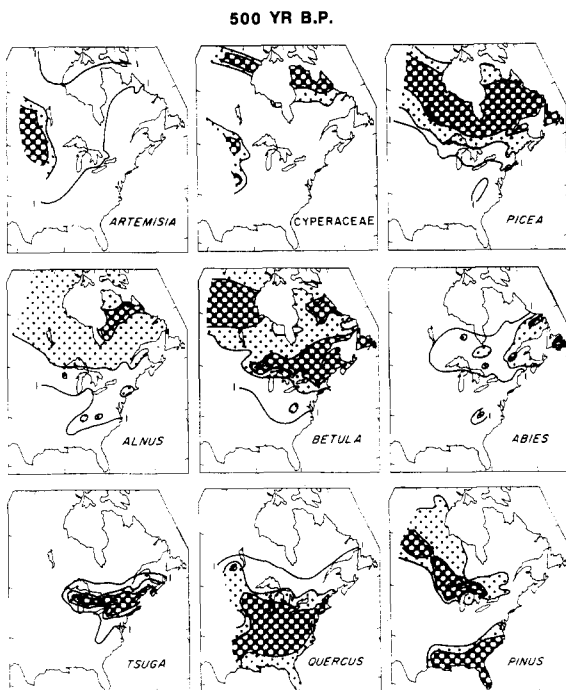


Fig. 3. Maps with isopolls (contours of equal pollen percentage) for 500 yr B.P. for *Artemisia* (1, 5, 10%), *Cyperaceae* (1, 5, 10%), *Picea* (1, 5, 20%), *Alnus* (1, 5, 20%), *Betula* (1, 10, 20%), *Abies* (1, 2, 6%), *Tsuga* (1, 5, 20%), *Quercus* (1, 5, 20%), and *Pinus* (20, 40%) pollen. Numbers in parentheses give percentages for isopolls. Stippling highlights regions with intermediate (white with black dots) and high (black with white circles) percentages.

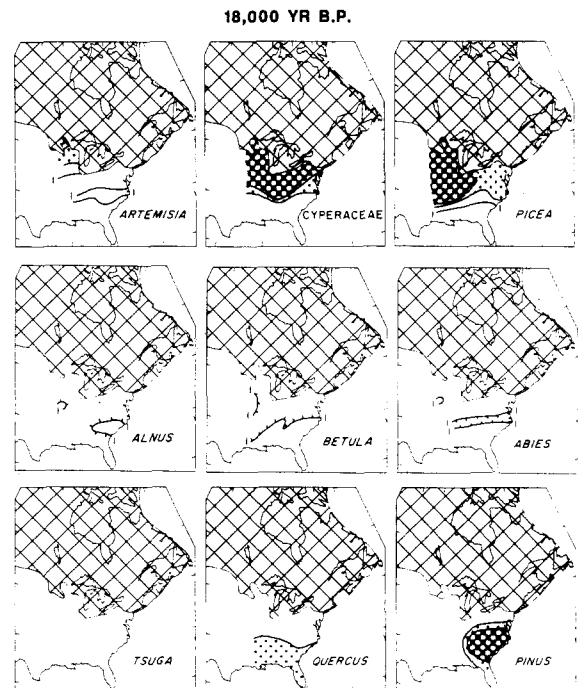


Fig. 4. Maps with isopolls for 18,000 yr B.P. for *Artemisia*, *Cyperaceae*, *Picea*, *Alnus*, *Betula*, *Abies*, *Tsuga*, *Quercus* and *Pinus* pollen. See Fig. 3 for labeling of isopolls and stippled regions for each pollen type.

conifer-hardwood forest is further divided into eastern and western sectors with *Pinus* pollen highest in the west. The ability of pollen data to record the modern patterns in the vegetation demonstrates the general sensitivity of the data to vegetational patterns and makes it likely that isopoll maps from past times record the prevailing vegetational patterns. In describing the isopoll maps, I therefore followed the practice of Webb *et al.* (1983a, p. 142) and provided a narrative description of the vegetation changes illustrated by the maps of pollen percentages.

18000 yr B.P.

The patterns in the 9 pollen types at 18000 yr B.P. (Fig. 4) differ strongly from those at 500 yr B.P. (Fig. 3). These differences are evident despite a de-

crease in site number from 250 (Fig. 2) to 15 (Fig. 3). The ice sheet extended south to about 41°N and was probably over 3 km in maximum height in central Canada (Denton & Hughes, 1981). South of it *Artemisia*, Cyperaceae, and *Picea* pollen were abundant over a wide region and indicate growth of a *Picea* parkland quite different from the boreal forest of today. The *Picea* trees must have grown far enough apart to allow for the relatively abundant growth of herbs and the ready dispersal of herb pollen. Neither *Betula* nor *Alnus* pollen were abundant in this region or elsewhere. Northern pines grew abundantly in forests from Georgia to the Carolinas (Watts, 1983), and Smith (1985) has recently provided evidence of abundant *Pinus* pollen from a site in the Ozarks that dates back to 17000 yr B.P. Along the ecotone between the *Picea* parkland and the *Pinus* forests, three sites possessed greater than 1% *Abies* pollen. This evidence

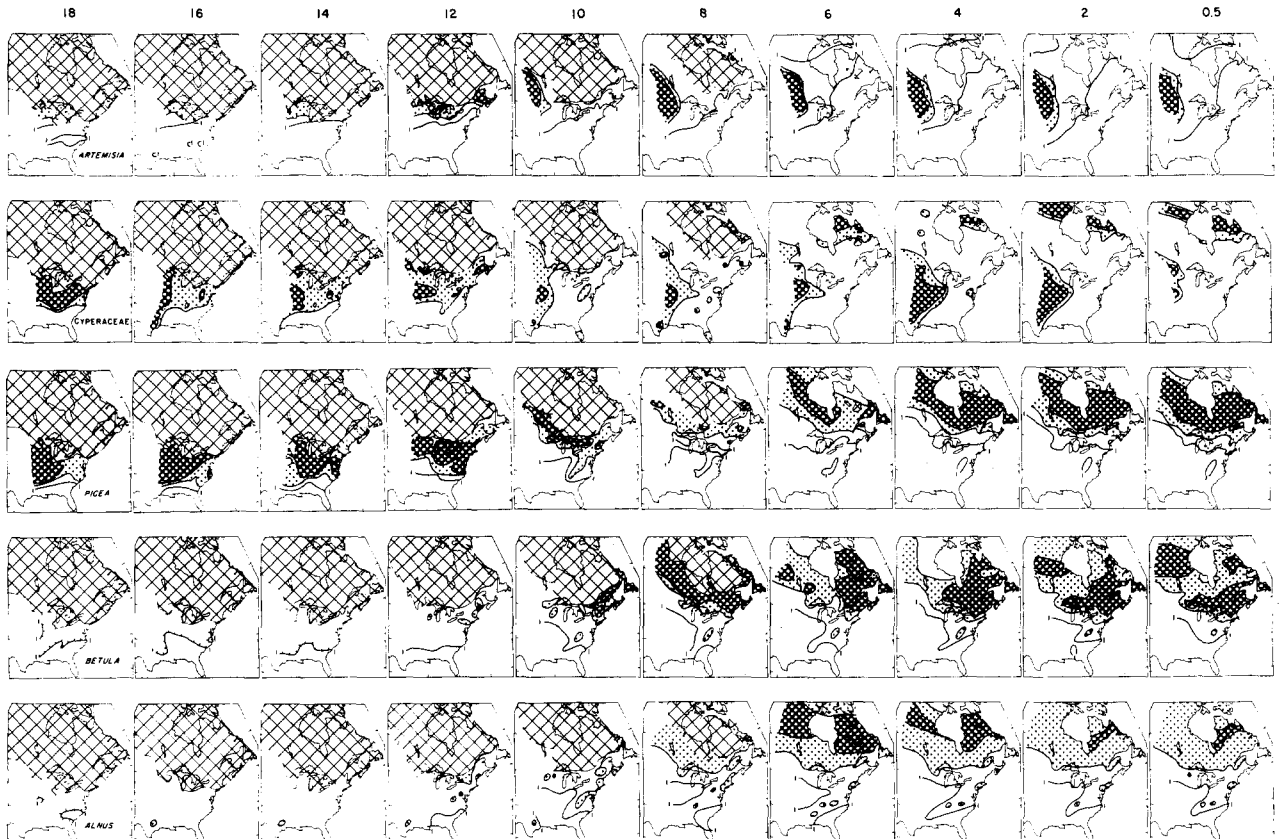


Fig. 5. Isopoll maps from 16000 to 500 yr B.P. for *Artemisia*, Cyperaceae, *Picea*, *Betula* and *Alnus*. See Fig. 3 for labeling of isopolls and stippled regions for each pollen type.

may indicate a center for *Abies* populations at a low level of overall abundance (Delcourt & Delcourt, 1984), but the strong under-representation of *Abies* tree abundances by *Abies* pollen abundances (Webb *et al.*, 1981) makes this interpretation tentative at best.

Quercus and *Carya* pollen were somewhat abundant east of Louisiana, but no published terrestrial site south of 32°N has provided information on these taxa for 18000 yr B.P. (Watts, 1983). The best fossil pollen data published so far are from Sheelar Lake (Watts & Stuiver, 1980) in north Florida, which recorded 9% *Quercus*, 3% *Carya*, and 75% *Pinus* pollen at 18500 yr B.P. but had an hiatus in sedimentation from then to 14500 yr B.P. I used these data but not those from Goshen Springs. Evidence for a full glacial pollen assemblage similar to the Holocene deciduous forest is therefore lacking (Davis, 1983b).

Several pollen types that are fairly abundant over broad areas today have either low values at isolated sites at 18000 yr B.P., e.g. *Tsuga* (Fig. 4) and *Fagus*, low values at several adjacent sites, e.g. *Betula*, *Alnus*, and *Abies* (Fig. 4) and also *Ostrya/Carpinus*, *Fraxinus*, *Ulmus*, and *Castanea*. The climatic conditions 18000 yr B.P. were colder and drier than today (Kutzbach & Wright, 1985) and were probably unfavorable to wide-spread growth of large numbers of individuals of these taxa. The main vegetation pattern at 18000 yr B.P. was the contrast between the *Picea* parkland in the north and *Pinus* forest or woodland in the south.

Map sequence from 18000 to 500 yr B.P.

Maps between 18000 and 500 yr B.P. show the timing and patterns of change as the vegetation shifted from its full glacial distribution to its distribution just before European settlement. These maps illustrate temporal changes in location and abundance for various taxa and the resultant changes in the overlapping of distributions among taxa. These individualistic changes among the different taxa led to profound changes in the pattern, composition, and structure of the vegetation that produced maximum amounts of *Picea* pollen. Similar changes have occurred in other vegetational regions (Davis, 1983b).

Picea, Artemisia, and Cyperaceae. At 18000 yr B.P. the highest values of *Picea* pollen were centered in Missouri (King, 1973), but a second population center also existed on the east coast as is evident in the map for 16000 yr B.P. (Fig. 5). By 12000 yr B.P., *Picea* values had increased over a broad region south of the ice sheet, and the orientation of the main abundance gradients for *Picea* pollen was primarily north-south. This orientation changed to northeast-southwest by 10000 yr B.P. as the band of high values became narrower and was located just in front of the ice sheet in the west. After 10000 yr B.P. the values of *Picea* pollen generally decreased until 7000 yr B.P. when only 5 isolated sites had values above 20%. By 6000 yr B.P., with central Canada free of ice, new regions with high

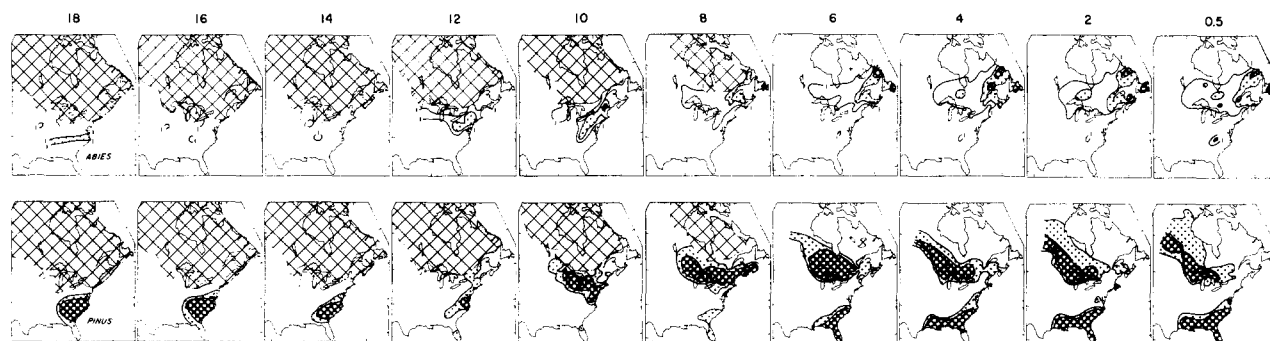


Fig. 6. Isopoll maps from 18000 to 500 yr B.P. for *Abies* and *Pinus* pollen. See Fig. 3 for labeling of isopolls and stippled regions for each pollen type. Cross-hatching marks area with Laurentide ice sheet.

values of *Picea* pollen appeared both along the Labrador coast and south and west of Hudson Bay. *Picea* populations then expanded both to the north and south as the modern boreal forest developed. The changes for *Picea* populations were gradual from 18000 to 12000 yr B.P., abrupt from 12000 to 10000 yr B.P., gradual from 10000 to 7000 yr B.P., abrupt between 7000 and 6000 yr B.P. and again gradual up to 500 yr B.P.

Evidence from other pollen types indicates the nature of the vegetational changes associated with these changes in *Picea* populations. *Artemisia* and Cyperaceae pollen had high to intermediate values in the north and low values in the south from 18000 to 12000 yr B.P. (Fig. 5). The distributions of both of these herbaceous types coincide with part or all of the region with high *Picea* pollen. At 18000 yr B.P., high values of *Artemisia* pollen occurred only in Minnesota, but by 12000 yr B.P., its region of high values extended as a narrow band all along the southern edge of the ice sheet and had a marked north-south gradient. Cold, dry environmental conditions along the ice front probably favored the prolific growth of arctic *Artemisia* plants.

In this same region and much further to the south, Cyperaceae plants grew in moderate to high numbers, and the coincidence between the patterns of *Picea* pollen and these herbaceous types suggests that a broad region of *Picea* woodland or parkland existed south of the ice sheet from 18000 to 12000 yr B.P. (Fig. 5). The spacing of the *Picea* trees was wide enough to permit the growth of the herbs and the dispersal of their pollen. Few *Betula* or *Alnus* shrubs or *Abies* trees grew in this region until 12000 yr B.P. when moderate values for the pollen of each of these types first appeared in the northeastern United States (Figs. 5, 6). This vegetation differed markedly in both composition and structure from the modern boreal forest or forest-tundra. In these, *Picea*, *Pinus*, *Abies*, *Betula*, and *Alnus* are prominent today, but *Artemisia* is infrequent (Fig. 3). The *Picea* parkland was a favorable region for browsing by mastodons, and loess accumulated in it near major river systems in the mid-western United States (Porter, 1983).

Between 12000 and 10000 yr B.P., a major change occurred in the vegetation. The band of

high values of *Picea* pollen at 10000 yr B.P. marks a region of closed forest for the first time because the distributions of *Picea* pollen and herb pollen cease to overlap. The main orientation of the abundance gradients for *Artemisia* and Cyperaceae pollen shifted from north-south to east-west as the region of modern prairie developed. The arctic and boreal species producing the *Artemisia* and Cyperaceae pollen in the west were probably replaced by prairie species. This 90° change in the abundance gradient for these types suggests a major environmental change as hot dry summer conditions became important on the central plains and the cool dry conditions in front of the ice sheet became less pronounced.

Betula and Alnus. Between 12000 and 10000 yr B.P., the values for *Betula* and *Alnus* pollen increased in the east north of the highest *Picea* values. High values of Cyperaceae pollen also occurred in southern Labrador as the modern tundra and forest tundra began to develop. This development continued when the region of high values of Cyperaceae, *Betula*, and *Alnus* moved northward along the Labrador coast at 8000 yr B.P. and then expanded across the recently deglaciated parts of central and northern Canada by 6000 yr B.P. South of the ice sheet, the vegetational composition changed relatively quickly from 10000 yr B.P. when *Picea* populations were prominent to 8000 yr B.P. when *Betula* trees and shrubs were prominent to 6000 yr B.P. when *Alnus* populations expanded rapidly across the deglaciated central region (Fig. 5). After 6000 yr B.P., the modern boreal forest developed (Ritchie, 1976) with the expansion of *Picea* populations both north and south, the confinement of high *Alnus* values to the modern forest-tundra zone, and the separation of the *Betula* pollen densities into three centers. Shrub-*Betula* populations became dominant in the northeastern forest-tundra zone, *Betula papyrifera* populations grew in the western region of boreal forest, and *B. papyrifera* populations graded southward into dominant *B. leutea* populations in the east-central region. The *B. papyrifera* populations grow today with the *Picea* and *Abies* in the southern boreal forest, and the *B. leutea* populations grow most

prolifically in the mixed conifer-hardwood forests of the east. During this same time period, the modern tundra also developed in the north. Note the westward expansion of the region with high values of Cyperaceae pollen after 8000 yr B.P.

Abies and Pinus. Today in the southeastern boreal forest, *Abies* populations are prominent along with *Picea* populations. The *Picea-Abies* association in the east first appeared at 12000 yr B.P. in the mid-Atlantic region. It expanded north and south to form a band along the Appalachians at 10000 yr B.P. (Fig. 6). By 8000 yr B.P., the geographic distribution of *Abies* populations was similar to their distribution today. In contrast, the regional distribution of *Picea* trees became similar to their modern one sometime after 6000 yr B.P. After 6000 yr B.P., *Abies* populations expanded north of the Great Lakes and also in New England (Davis *et al.*, 1980), southern Quebec (Webb *et al.*, 1983b), and the central Appalachians (Delcourt & Delcourt, 1985). Although significant numbers of *Picea* and *Abies* trees have grown together in some part of their range since 12000 yr B.P., each taxon followed a separate history in gaining its modern distribution (Davis, 1983b).

Just as the association between *Picea* and *Abies* populations varied through time, so too has the association between *Picea* and *Pinus* populations. Today, *Pinus* pollen percentages are highest in south-central Canada and overlap the region of moderate to high values of *Picea* pollen west of Hudson Bay (Figs. 5, 6). At 18000 yr B.P., the arrangement was quite different; the region of highest *Pinus* values was along the east coast, *Picea* values were highest in the west, and *Abies* values were low everywhere.

Between 18000 and 12000 yr B.P., *Pinus* populations decreased in abundance and area and became confined to the east coast. In the next 2000 years, the population center for *Pinus* broadened and shifted westward. A region of *Pinus* forests developed south of the narrow band of *Picea* forests. By 8000 yr B.P., the population center for *Pinus* had expanded northward, and *Pinus* forests grew over a wide area from Nova Scotia to Manitoba while just to the north *Picea* populations had declined. By

6000 yr B.P., *Pinus* populations had decreased in the east, and the population center had shifted westward to its present location in the northern Great Lakes region and central Canada. At the same time, the number of *Pinus* trees increased in the southeastern United States as a well-pronounced ecotone with *Quercus* forests and a new biome became established there (Figs. 4, 6).

Discussion

Recent research concerning climatic changes within the past 10^4 to 10^7 years indicates how orbitally induced seasonal changes in solar insolation have produced major climatic changes with periodicities of 20000 to 400000 years (Hays *et al.*, 1976). These changes arise from small, but regular, variations in the tilt of the earth's rotational axis (period of 41000 yr) and in the elliptical nature of the earth's orbit about the sun (period of 100000 yr) as well as from the precession of the axis of the earth's orbit (period of 20000 yr). Within the precession cycle, the earth moves from being closest to the sun in January, as it is now, to being closest in July, as it was 10000 years ago. At that time the northern hemisphere on average received 8% more radiation in summer than it does today (Kutzbach & Street-Perrott, 1985). The land-sea contrast in specific heat results in these changes in seasonal radiation alternately weakening and strengthening the monsoons in the tropics, where immediate climatic changes are induced (Kutzbach, 1981; Kutzbach & Street-Perrott, 1985).

The orbitally induced changes in monsoonal climates have always influenced global climates, with a major impact in the tropics (Berger *et al.*, 1984). Since at least the Miocene, the radiation changes have also induced the build up and melting of ice sheets in high latitudes. The long response times (10^3 to 10^4 yr) of the ice sheets introduced major lags into the climate system and its response to external forcing, but the imprint of orbital forcing is still clear in pacing of the variations in global ice volume (Imbrie & Imbrie, 1980; Imbrie, 1985).

By use of climate models and physical reasoning, paleoclimatologists are beginning to be able to

sketch out how the relatively simple radiational forcing (the sum of three periodic processes), which is uniform within latitudinal belts, produces a spatially regular but more heterogenous response in the atmosphere, oceans, and ice sheets. This response includes (1) continuous and sometimes abrupt changes in the atmospheric circulation; and (2) spatial patterns of different size for temperature and moisture differences between today and past times. The vegetation then imposes a whole new set of patterns by its response to these temporal and spatial variations in climatic variables (Bartlein *et al.*, 1986). Not only does each plant species respond differently to climate, but it is also differentially sensitive to seasonal variations in moisture and temperature within its range as well as at its range boundary (north vs. south or east vs. west). No single climatic variable controls the spatial and temporal distribution of a pollen type or plant species.

The pollen maps (Figs. 5, 6) show how the associations among taxa varied as their constituent plant populations changed in location and abundance in response to climatic change. On time scales of 10^4 to 10^5 years, formations and their associated ecotones are ephemeral features, and plant taxa are capable of growing in a variety of locations and associations (Watts, 1973; Davis, 1983b). The individualistic behavior of taxa was prominent over the past 18000 years, and the changing mixture of taxa caused the composition and patterns to vary within the vegetation across eastern North America (Davis, 1976). During times of rapid climatic change, e.g. 12000 to 10000 yr B.P., the vegetation responded rapidly, and distribution patterns of individual taxa changed in orientation to reflect the new climatic gradients (Figs. 5, 6). For example, the movement of the pine populations between 12000 and 10000 yr B.P. indicates strong climatic control as seasonal temperature and atmospheric circulation patterns responded both to the retreating and lowering ice sheet and to the changing seasonal radiation (Webb, 1984; Webb, Bartlein Kutzbach, in press). After 8000 yr B.P., increased winter temperatures probably favored the increased numbers of pine trees in the previously oak-dominated forests of the southern United States (Webb *et al.*, in press).

The magnitude and kinds of vegetational changes between 18000 yr B.P. and 500 yr B.P. (Figs. 3–6) presumably have occurred many times during the Quaternary (1.8×10^6 yr B.P. to present day) as the populations of plant taxa tracked the environments favorable to their growth. The specific sequence and timing of vegetation changes during the past 18000 years are unique to this interglacial, and mainly reflect the unique sequence of regional climate changes induced by the particular combination of orbital forcing (i.e. changes in precession, tilt, and eccentricity of the earth's orbit) that differentiates the past 18000 years from previous interglacials (Berger, 1978; Imbrie, 1985). Because the unique aspects of the past 18000 years arise from a unique combination of established processes and not from a set of unique processes, observations about the general behavior of climate and of taxa during this time period provide insights applicable to any 18000 year period within the Quaternary and even the Tertiary. This conclusion holds even though the presence and retreat of the Laurentide ice sheet had a major impact on North American climates during the past 18000 years. Certain areas and time intervals within this period experienced climate changes little influenced by the presence of the ice. For instance, the climate changed significantly in the tropics where the climatic effects of the large ice sheets are minimal (Kutzbach & Street-Perrot, 1985), and the climate and vegetation also changed significantly during the past 6000 years (Fig. 5) when global ice volume was relatively constant. These climate changes are not unique to the Quaternary, and their associated vegetational responses may be representative of vegetation changes from the Tertiary and earlier.

The vegetational dynamics recorded on the pollen maps (Figs. 5, 6) pose an interesting problem for modeling. Webb *et al.* (in press) have recently used response functions that can estimate pollen percentages from linear combinations of temperature and precipitation values. The challenge is whether a synoptically consistent set of climatic conditions can be found that, via the response functions, can generate the spatial and temporal patterns illustrated on the maps. Initial research to explore this possibility has used the response functions to esti-

mate pollen diagrams from the patterns of past climatic change that have been simulated by general circulation models (Webb *et al.*, in press). Model simulations exist for each 3000 year interval from 18000 yr B.P. to present (Kutzbach & Guetter, 1986). Preliminary results for data from eastern North America indicate that certain of the model-generated results match many of the observed changes in the pollen record. The model results show the abrupt change in patterns between 12000 and 10000 yr B.P. and reproduce many of the changes in the abundances of *Picea* and *Quercus* pollen. Other features on the pollen maps, especially those sensitive to precipitation changes, are not as well reproduced by the model results. The implications of these initial results are under investigation.

The role of succession and disturbance

Ecological texts generally restrict their discussion of vegetational dynamics to primary and secondary succession (e.g., Mueller-Dombois & Ellenberg, 1974; Kershaw & Looney, 1985). These processes occur, but the eastern North American pollen maps as well as comparable maps for Europe (Huntley & Birks, 1983) show that neither process explains the major vegetational changes of the past 18000 years. The maps would have to be drawn for each 50 year interval in order for variations due to gap-phase processes and fire-induced succession to appear in a sequence of maps. Such variations would little affect the broad-scale patterns and would appear as a rapid flickering of the mapped values, were a film made from such a sequence of maps from the past 20000 years. Although important within stands over decades and centuries, successional changes comprise a continuously active but relatively minor component of the continent-wide variations in ancient vegetation.

Fires, disease, and wind-throws continuously create either gaps within forests or bare patches in open vegetation and thus produce openings that can be colonized by new taxa as well as exploited by established taxa. Invading species depend upon the continual occurrence of openings. At the scale of a

woodland stand, fire, disease and wind-throws often appear as singular events, but at the continental scale, these disturbance factors are continuously active agents with characteristic frequencies that change in space and time. Climatic change can alter these frequencies, and individual disturbances can be the agents that accelerate vegetation change once the climate has changed. Disturbance events tend to affect small areas ($<10^3$ km²). In some cases, however, pollen data record synchronous (± 300 yr) wide-ranging disturbance events, such as a large decrease in abundance over an entire species range, that may have resulted from the rapid spread of a disease (Davis, 1981; 1983a). The pattern of these abundance changes in time and space contrasts with those that are climatically induced, because the latter tend to be time-transgressive and to result in shifts in the location of both the population center and the range boundaries of the taxon (Webb, 1982).

Vegetation dynamics and evolution

Evolutionary change has occurred within the context of these millennial-scale climatic and vegetational dynamics of the past million or more years. The development of new genotypes is probably a continuous process as taxa adapt to their new locations and associations, but speciation within a genus is a relatively rare event, because the paleontological record reveals an average life time for plant species of 1 to 10 million years (Tiffney, pers. comm.). Each species must therefore be capable a) of tracking these millennial-scale changes in climate (Davis, 1983b; Webb, 1986) and b) of coping with major changes in vegetational composition and structure. For certain species, this has involved alternation between growing in dense populations across wide areas and growing in sparse populations in isolated microhabitats. The latter situation is a precondition for allopatric speciation, but its time scale of occurrence may be too short for the separate populations (a) to develop major morphological differences; (b) to become genetically isolated from the other populations. Millennial-scale climatic change can therefore create some of the necessary condi-

tions for plant speciation, but the environmental changes may be too frequent to allow the process to go to completion. Longer term geological and environmental processes (e.g. plate tectonics) probably play an important role in speciation.

As research into the effects of climatic variations on evolution continues, the different vegetative and vegetational responses to climatic change on various time scales must be recognized. On an annual time scale, trees are sessile organisms that use phenological and physiological mechanisms to survive annual changes in climate. On time scales of 10^4 to 10^5 years, tree species are comprised of many populations with dispersal and establishment capabilities that allow the species to be mobile enough to track the millennial-scale changes in climate. On time scales 10^3 to 10^4 times longer, most tree species can no longer survive the full range of climatic change, and speciation (whether rapid or gradual) becomes an important mechanism in allowing the genus or higher taxon to continue. Evolutionary processes are active on all time scales; but, on relatively short time scales, phenological, physiological, and ecological processes dominate and modify the rate of evolution by allowing species to survive large environmental changes. In light of the ephemeral nature of vegetational assemblages, research is needed to demonstrate the specific ways in which vegetational dynamics, such as succession or the changing composition and structure of communities or formations, affect evolutionary processes.

References

- Bartlein, P. J., Prentice, I. C. & Webb III, T., 1986. Climatic response surfaces based on pollen from some eastern North American taxa. *J. Biogeogr.* 13: 35–57.
- Bartlein, P. J., Webb III, T. & Fleri, E. C., 1984. Holocene climatic change in the northern Midwest: pollen-derived estimates. *Quat. Res.* 22: 361–374.
- Berger, A., 1978. Long term variations of daily insolation and Quaternary climatic changes. *J. Atmos. Sci.* 35: 2362–2367.
- Berger, A., Imbrie, J., Hays, J., Kukla, G. & Saltzman, B. (eds), 1984. *Milankovitch and climate*. Reidel, Dordrecht.
- Bernabo, J. C. & Webb III, T., 1977. Changing patterns in the Holocene pollen record from northeastern North America: a mapped summary. *Quat. Res.* 8: 64–96.
- CLIMAP Project Members, 1981. Seasonal reconstructions of the Earth's surface at the Last Glacial Maximum. *Geol. Soc. Amer. Map and Chart Series* 36.
- Davis, M. B., 1976. Pleistocene biogeography of temperate deciduous forests. *Geosci. Man* 13: 13–26.
- Davis, M. B., 1981. Outbreaks of forest pathogens in Quaternary history. IV International Palynological Conference, Lucknow (1976–77) 3: 216–227.
- Davis, M. B., 1983a. Holocene vegetational history of the eastern United States. In: H. E. Wright Jr (ed.), *Late Quaternary environments of the United States*. Vol. 2. The Holocene, pp. 166–181. University of Minnesota Press, Minneapolis.
- Davis, M. B., 1983b. Quaternary history of deciduous forests of eastern North America and Europe. *Ann. Missouri Bot. Gard.* 70: 550–563.
- Davis, M. B., Spear, R. W. & Shane, L. C. K., 1980. Holocene climate of New England. *Quat. Res.* 14: 240–250.
- Davis, M. B., Woods, K. D., Webb, S. L. & Futyma, R. B., 1986. Dispersal versus climate: expansion of *Fagus* and *Tsuga* into the upper Great Lakes region. *Vegetatio* 69: 93–103.
- Delcourt, H. R. & Delcourt, P. A., 1984. Late-Quaternary history of the spruce-fir ecosystem in the Southern Appalachian Mountain region. In: P. S. White & J. Wood (ed.), *The southern Appalachian Spruce-Fir ecosystem: its biology and threats*. U.S. Research Resource Management Report Ser-71: 22–35.
- Delcourt, H. R. & Delcourt, P. A., 1985. Quaternary palynology and vegetational history of the southeastern United States. In: V. M. Bryant & R. G. Holloway (eds), *Pollen records of Late-Quaternary North American sediments*, pp. 1–37. American Association of Stratigraphic Palynologists Foundation, Dallas.
- Denton, G. H. & Hughes, T. J. (eds), 1981. *The last great ice sheets*. J. Wiley & Sons, New York.
- Gaudreau, D. C. & Webb III, T., 1985. Late-Quaternary pollen stratigraphy and isochrone maps for the northeastern United States. In: V. M. Bryant & R. G. Holloway (eds), *Pollen records of Late-Quaternary North American sediments*, pp. 247–280, American Association of Stratigraphic Palynologists Foundation, Dallas.
- Hays, J. D., Imbrie, J. & Shackleton, N., 1976. Variations in the earth's orbit: pacemaker of the ice volume cycle. *Science* 194: 1121–1132.
- Hecht, A. D. (ed.), 1985. *Paleoclimate analyses and modeling*. J. Wiley & Sons, New York.
- Huntley, B. & Birks, H. J. B., 1983. *An atlas of past and present pollen maps for Europe: 0–13000 years ago*. Cambridge University Press, Cambridge.
- Imbrie, J. & Imbrie, J. Z., 1980. Modeling the climate response to orbital variations. *Science* 207: 943–953.
- Imbrie, J., 1985. A theoretical framework for the Pleistocene ice ages. *J. Geol. Soc. London* 142: 417–432.
- Kershaw, K. A. & Looney, J. H. H., 1985. *Quantitative and dynamic plant ecology*. E. Arnold Ltd., London.
- King, J. E., 1973. Late Pleistocene palynology and biogeography of the western Missouri Ozarks. *Ecol. Monogr.* 43: 539–565.
- Kutzbach, J. E., 1981. Monsoon climate of the early Holocene:

- climate experiment with the earth's orbital parameters for 9000 years ago. *Science* 214: 59–61.
- Kutzbach, J. E. & Street-Perrott, F. A., 1985. Milankovitch forcing of fluctuations in the level of tropical lakes from 18 to 0 kyr B.P. *Nature* 317: 130–134.
- Kutzbach, J. E. & Wright Jr, H. E., 1985. Simulation of the climate of 18000 yr B.P.: results for North American/North Atlantic/European sector and comparison with the geologic record. *Quat. Sci. Rev.* 4: 147–187.
- Kutzbach, J. E. & Guetter, P. J., 1986. The influence of changing orbital parameters and surface boundary conditions on the climate simulations for the past 18000 years. *J. Atms. Sci.* 43: 1726–1759.
- Mueller-Dombois, D. & Ellenberg, H., 1974. Aims and methods of vegetation ecology. *J. Wiley & Sons*, New York.
- Overpeck, J. T., Webb III, T. & Prentice, I. C., 1985. Quantitative interpretation of fossil pollen spectra: dissimilarity coefficients and the method of modern analogs. *Quat. Res.* 23: 87–108.
- Peterson, G. M., 1983. Holocene vegetation and climate in the western USSR. Ph.D. Thesis, University of Wisconsin, Madison.
- Porter, S. C. (ed.), 1983. Late-Quaternary environments of the United States. Vol. 1. The Late Pleistocene. Univ. of Minnesota Press, Minneapolis.
- Prentice, I. C., 1983. Postglacial climatic change: vegetation and the pollen record. *Progr. Phys. Geogr.* 7: 273–286.
- Prentice, I. C., 1986. Vegetation responses to past climatic variation mechanisms and rates. *Vegetatio* 67: 131–141.
- Ralska-Jasiewiczowa, M., 1983. Isopollen maps for Poland: 0–11000 yr B.P. *New Phytol.* 94: 133–175.
- Ritchie, J. C., 1976. The late-Quaternary vegetational history of the western interior of Canada. *Can. J. Bot.* 54: 1793–1818.
- Ritchie, J. C., 1986. Vegetation-climate equilibrium in relation to palaeoecology. *Vegetatio* 67: 65–74.
- Smith Jr, E. N., 1985. Paleovegetation zonation and tree-species migrations in southeastern Missouri: 17110 yr B.P. to the present. *Palynology* 9: 253.
- Solomon, A. M. & Webb III, T., 1985. Computer-aided reconstruction of late-Quaternary landscape dynamics. *Ann. Rev. Ecol. Syst.* 16: 63–84.
- Street, F. A. & Grove, A. T., 1979. Global maps of lake-level fluctuations since 30000 B.P. *Quat. Res.* 10: 83–118.
- Van Zant, K. L., Webb III, T., Peterson, G. M. & Baker, R. G., 1979. Increased *Cannabis/Humulus* pollen, an indicator of European agriculture in Iowa. *Palynology* 3: 229–233.
- Watts, W. A., 1973. Rates of change and stability in vegetation in the perspective of long periods of time. In: H. J. B. Birks & R. G. West (eds), *Quaternary plant ecology*, pp. 195–206. Blackwell, Oxford.
- Watts, W. A., 1983. Vegetational history of the eastern United States 25000 to 10000 years ago. In: S. C. Porter (ed.), *Late-Quaternary environments of the United States*. Vol. 1. The late Pleistocene, pp. 294–310. University of Minnesota Press, Minneapolis.
- Watts, W. A. & Stuiver, M., 1980. Late Wisconsin climate of northern Florida and the origin of species-rich deciduous forest. *Science* 210: 325–327.
- Webb III, T., 1982. Temporal resolution in Holocene pollen data. Third North American Paleontological Convention, Proc. 2: 569–572.
- Webb III, T., 1984. Late-Quaternary changes in climate seasonality in eastern North America. *American Quaternary Association. Program and Abstracts*, Boulder, CO, pp. 138–139.
- Webb III, T., 1985. A Global paleoclimate data base for 6000 yr B.P. U. S. Department of Energy Report TR-018. Department of Energy, Washington, DC.
- Webb III, T., 1986. Is vegetation in equilibrium with climate? How to interpret late-Quaternary pollen data. *Vegetatio* 67: 75–91.
- Webb III, T. & Bernabo, J. C., 1977. The contemporary distribution and Holocene stratigraphy of pollen in eastern North America. In: W. C. Elsik (ed.), *Contributions of stratigraphic palynology*. Vol. 1. Cenozoic Palynology, pp. 130–146. American Association of Stratigraphic Palynologists, Contr. Ser. No. 5A, AASP Foundation, Dallas.
- Webb III, T., Howe, S. E., Bradshaw, R. W. H. & Heide, K. M., 1981. Estimating plant abundances from pollen percentages: the use of regression analysis. *Rev. Palaeobot. Palyn.* 32: 269–300.
- Webb III, T., Cushing, E. J. & Wright Jr, H. E., 1983a. Holocene changes in the vegetation of the Midwest. In: H. E. Wright Jr (ed.), *Late-Quaternary environments of the United States*, Vol. 2, The Holocene, pp. 142–165. Univ. of Minnesota Press, Minneapolis.
- Webb III, T., Richard, P. J. H. & Mott, R. J., 1983b. A mapped history of Holocene vegetation in southern Quebec. *Syllogeus* 49: 273–336.
- Webb III, T., Bartlein, P. J. & Kutzbach, J. E., in press. Climatic change in eastern North America during the past 18000 years: comparisons of pollen data with model results. In: H. E. Wright, Jr. & W. F. Ruddiman (eds.), *North America and adjacent oceans during the last deglaciation*. Geol. Soc., Amer., Decade of North American Geology.