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VEGETATION AND CLIMATE CHANGE IN EASTERN
NORTH AMERICA SINCE THE LAST GLACIAL MAXIMUM¹

I. COLIN PRENTICE

Institute of Ecological Botany, Uppsala University, Box 559, S-751 22 Uppsala, Sweden

PATRICK J. BARTLEIN

Department of Geography, University of Oregon, Eugene, Oregon 97403 USA

THOMPSON WEBB III

Department of Geological Sciences, Brown University, Providence, Rhode Island 02912 USA

Abstract. Response surfaces describing the empirical dependence of surface pollen percentages of 13 taxa on three standard climatic variables (mean July temperature, mean January temperature, and mean annual precipitation) in eastern North America were used to infer past climates from palynological data. Inferred climates at 3000-yr intervals from 18 000 years ago to the present, based on six taxa (spruce, birch, northern pines, oak, southern pines, and prairie forbs), were used to generate time series of simulated isopoll maps for these taxa and seven others (hickory, fir, beech, hemlock, elm, alder, and sedge). The simulations captured the essential features of the observed isopoll maps for both sets of taxa, including differences in migration patterns during the past 10 000 yr that have previously been attributed to differential migration lag. These results establish that the continental-scale vegetation patterns have responded to continuous changes in climate from the last glacial maximum to the present, with lags ≤ 1500 yr. The inferred climatic changes include seasonality changes consistent with orbitally controlled changes in insolation, and shifts in temperature and moisture gradients that are consistent with modelled climatic interactions of the insolation changes with the shrinking Laurentide ice sheet. These results pose new ecological questions about the processes by which vegetated landscapes approach dynamic equilibrium with their changing environment.

Key words: climatic change; eastern North America; equilibrium; individualism; migration; modelling; palaeoecology; palynology; response surface; response time; simulation; vegetation.

INTRODUCTION

Maps of changing pollen percentages in eastern North America and western Eurasia during the period since the last glacial maximum, $\approx 18\,000$ yr BP (measured as radiocarbon years),² have shown a complex vegetation history in which no two taxa have behaved alike (Huntley and Birks 1983, Jacobson et al. 1987, T. Webb 1987, 1988). Such maps demonstrate that each taxon has responded individually to the large changes in climate that have taken place during this period (Delcourt and Delcourt 1987, Huntley 1988, Webb 1988, Huntley and Webb 1989). The resulting patterns of change in vegetation are too complex to be explained by a simple increase in temperature causing a gradual displacement of the north–south vegetation gradient (Davis 1981). Two hypotheses have been put forward to explain this complexity (Prentice 1983, Ritchie 1984):

1) The *disequilibrium hypothesis* attributes the differential rates and directions of movement of different taxa to different distribution areas at the glacial maximum and different intrinsic rates of spread (Iversen 1960, Davis 1976, 1981). A variant (Iversen 1960, Bennett 1986, Bennett and Lamb 1988) emphasizes population dynamics and species interactions rather than dispersal and spatial spread. The disequilibrium hypothesis does not invoke complex changes in climate, and indeed it has sometimes been stated (or implied) that the observed changes in vegetation during the Holocene (the past 10 000 yr) mainly represent a delayed response to rapid changes in climate associated with the period of rapid deglaciation centered around 10 000 yr BP.

2) The *dynamic equilibrium hypothesis* explains the vegetation changes as a response to continuous climatic forcing (Solomon et al. 1981, Webb 1986). The use of pollen-based methods to reconstruct past climates is based on this hypothesis (Davis 1978, Prentice 1983). It implies that the processes by which ecosystems adjust to climatic changes must be fast enough for the broad-scale vegetation patterns to have kept up with the changes (Webb 1986), or, more precisely, that the

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² The *North American Stratigraphic Code* recommends the kiloannum (ka) as the preferred unit for ages of fossil materials. However, we have used the unit “years before present (yr BP)” in this paper to be consistent with *Ecology*’s usual style.

vegetation patterns have kept sufficiently close to equilibrium that most of the observed variance in a particular time frame (usually 10 000–20 000 yr) can be explained by a time-independent model (Prentice 1986, 1988). The fact that the geographic distributions of plant taxa have shifted in different directions at different rates is explained by the effects of non-parallel variations in the various climate variables to which plants respond (Prentice 1983, Webb 1986) and the individualistic responses of the taxa to these variables.

Several authors, including Prentice (1986), have pointed out that neither the disequilibrium nor the dynamic equilibrium hypothesis can be true for all spatial and temporal scales; the relative importance of autogenic vs. allogenic processes (succession, dispersal, and ecesis vs. environmental change) must depend on the space and time scale of the observed changes in relation to the characteristic spatial scale and response time of each process. In this paper, we analyze the Late-Quaternary pollen record for the whole of eastern North America in order to test the equilibrium hypothesis for the major continental-scale patterns of vegetation change since the last glacial maximum. Our analysis is based on small-scale “snapshot” maps constructed at 3000-yr intervals. All finer-resolution detail is ignored. Thus, we disregard the mechanisms of vegetation dynamics that are known to be important on the time and space scales of field observations and permanent plots, in order to focus on the causes of the big patterns observed in the pollen record of the continent.

THEORETICAL BACKGROUND

Recent palaeoclimatological research (e.g., Kutzbach 1987, Webb et al. 1987, COHMAP Members 1988) has shown that the spatial patterns of summer and winter temperature, precipitation, and potential evapotranspiration across the continents have varied through time as a result of continuous changes in the distribution of insolation across latitudes and seasons (produced by variations in the earth's orbit) and interactions of these direct orbital effects with the changing extent and height of the continental ice sheets (Imbrie and Imbrie 1980, Bartlein and Prentice 1989). Experiments with atmospheric general circulation models (GCMs) have indicated the complexity of the climatic changes that can be produced in this way. There are many instances where model experiments suggest that different regions within the temperate mid-to high latitudes experienced climatic changes of opposite sign, or that different variables (e.g., summer and winter temperatures) changed in opposite directions, and in several cases such predictions have provided convincing explanations for features of the palaeoclimatic record that had seemed paradoxical before (COHMAP Members 1988).

Research in palaeoclimatology has thus made the equilibrium hypothesis more plausible than it seemed

10–20 yr ago, when Quaternary climatic change was widely perceived in terms of a “glacial–interglacial cycle” of globally warm and cold periods (see discussion in Webb 1986). However, the question of how long vegetation takes to respond to climatic changes has remained open. Direct hypothesis testing has proved difficult because there is no other, independent source of palaeoclimatic data that is as comprehensive as the pollen record. Prentice (1983) therefore suggested an indirect method to explore the predictive power of the dynamic equilibrium hypothesis. First, response surfaces (Bartlein et al. 1986) would be constructed to fit empirical data on modern (surface) pollen percentages as a function of two or more climate variables with direct or indirect effects on plants. These surfaces would allow any climate within or close to the range of modern values to be used to predict pollen percentages. Hypothetical scenarios of past climatic change could then be translated into simulations of changes in pollen percentages. Such changes could be mapped and compared with observed isopoll maps. The simulated maps would resemble the observed ones if and only if (a) the climatic scenario were correct and (b) the patterns of vegetation had remained close to equilibrium with climate, both now (otherwise the response surfaces would be artefacts with no predictive utility) and in the past. Webb et al. (1987) used this deductive approach to test the predictions of a GCM experiment in which global boundary conditions were varied so as to approximate the situation at 3000-yr intervals from 18 000 yr BP to the present (Kutzbach and Guetter 1986, COHMAP Members 1988). The boundary conditions included key factors thought to be important in controlling climate change on a Quaternary time scale: orbital changes, ice sheet changes, and associated changes in sea-surface temperatures and sea ice extent (CLIMAP Project Members 1981, Bartlein and Prentice 1989). The varying combination of these factors in the GCM experiments produced a series of simulated global climates, each unique. Webb et al. (1987) used these simulated climates with response surfaces to generate isopoll maps of spruce (*Picea*) in eastern North America that closely resembled the observed maps. For some other taxa the discrepancies between observed and simulated maps pointed to possible inaccuracies in the specification of boundary conditions, and to imprecision in the simulated positions of airmass boundaries due to the limited spatial resolution of the models (Webb et al. 1987, Harrison 1989).

A set of response surfaces for several taxa can alternatively be used in an inferential mode, to estimate the combination of climate variables most likely to have produced any given pollen assemblage (Bartlein et al. 1986). Here we use this method of “non-linear calibration” (Ter Braak and Prentice 1988) to obtain a climatic change scenario for eastern North America during the past 18 000 yr. This scenario was used as input to the response surfaces to drive a simulation of

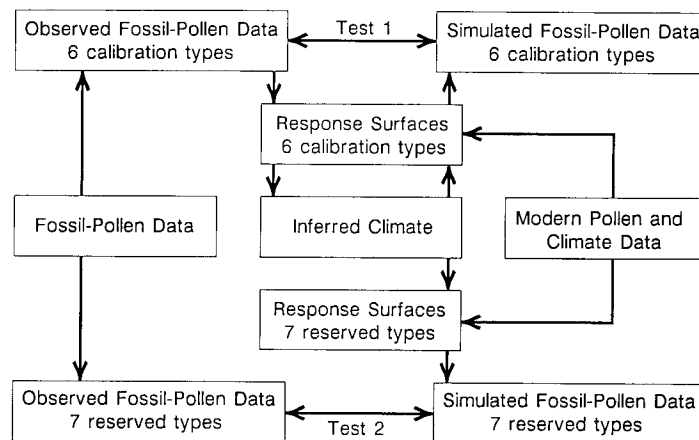


FIG. 1. The hypothesis-testing scheme, which uses 13 quantitatively important plant taxa of eastern North America.

the pollen record, for comparison with the data. Response surfaces were derived for 13 quantitatively important taxa. To avoid circularity, we used a subset of six taxa for climate reconstruction and reserved the other seven for an independent test. We then carried out two tests (Fig. 1).

The first test was to establish whether the climatic scenario could reproduce the isopoll maps for the six taxa included in the reconstruction procedure ("calibration types"). This test would fail if the pollen assemblages in the fossil record included combinations of abundances of the six taxa that were substantially different from any found today; such combinations could not be produced by response surfaces based on present-day conditions. The climatic reconstructions were also examined for climatological plausibility, and compared with specific predictions from the Kutzbach and Guetter (1986) series of GCM experiments. Vegetational disequilibrium would be likely to produce widespread no-analog conditions and/or climatologically implausible reconstructions, and consistency with the GCM results would be unlikely to arise by chance. This first set of comparisons can therefore be regarded as a weak test of the disequilibrium hypothesis.

The second test was designed to show whether the same climatic scenario could also predict the observed patterns of change for the other taxa ("reserved types"). This is a strong test of the equilibrium hypothesis because there is no prior reason why the patterns in the second set of taxa should be predictable from the patterns in the first. Agreement between simulated and observed isopoll maps for the second set of taxa would therefore provide strong evidence for an overall climatic control, common to both sets.

DATA AND METHODS

Pollen and climate data

We used a set of 982 surface pollen samples (Fig. 2) and 328 fossil pollen sites (Fig. 3) distributed throughout eastern North America. Site density for the fossil

pollen data ranged from 5 sites per 10^6 km² at 18 000 yr BP, to 12 sites per 10^6 km² at 12 000 yr BP, to 25 sites per 10^6 km² from 9000 yr BP to the present (Webb et al. 1987). The data were interpolated using age models fitted to depth and chronology data. All the pollen data were extracted from an updated (1990) version of the Brown University data base as described by Bartlein et al. (1986), Jacobson et al. (1987), and Webb et al. (1987). Climate data (mean January and July temperatures, and annual precipitation) for modern pollen samples were obtained from the nearest meteorological station (see Huntley et al. [1989] for a map of those stations). Bartlein et al. (1986) discuss the choice of these three commonly observed variables as measures of the climatic controls of plant distribution and abundance.

Response surfaces

Response surfaces for several eastern North American pollen types were presented by Bartlein et al. (1986). These surfaces were fitted by polynomial regressions of order two or three. A disadvantage of using global polynomials for response surfaces is that the shapes of the surfaces tend to fit the trends in the data much better in some regions of climate space than others. Also, it is not permissible to extrapolate the surfaces. Here we present new response surfaces obtained by a locally weighted averaging technique. The fitting method approximates the smoothing of a multi-dimensional scatter diagram by the robust locally weighted regression method (Cleveland and Devlin 1988: LOWESS). We moved a window over a $20 \times 20 \times 20$ point grid in the space defined by the three climate variables, and obtained "fitted values" (predicted values of each pollen type at the center of the window) at each grid point. The grid points were spaced at intervals of 1.5°C along the July temperature axis, 3°C along the January temperature axis, and 100 mm along the annual precipitation axis. The fitted values were obtained as locally weighted averages (using the tricube-weighting func-

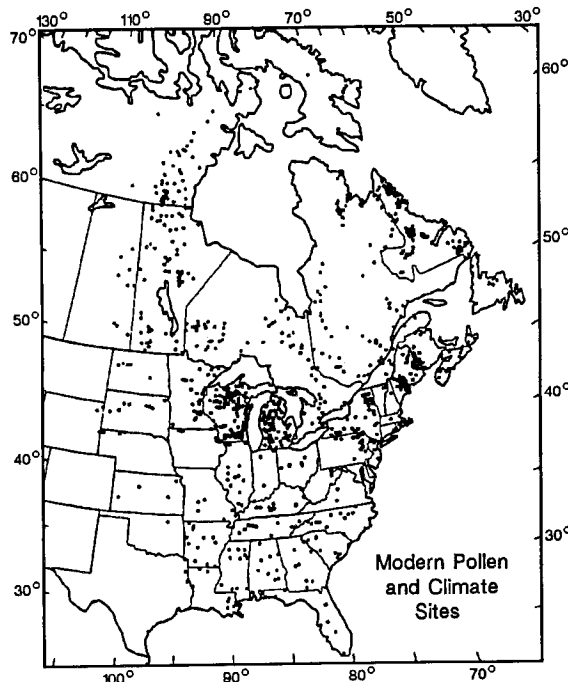


FIG. 2. Sites in eastern North America that were the sources of modern pollen and climate data.

tion, see, e.g., Huntley et al. 1989) of the pollen percentages for the observations contained within the window at each grid point. The window width was selected so that observations falling within one-twentieth of the length of the climate axis to either side of the window center contributed most heavily to each weighted average. The combination of grid point spacing and window width yielded surfaces that are relatively smooth while still flexible enough to portray the major patterns of variation of the pollen data in climate space.

Once the fitted values are obtained, the response surfaces can be depicted by interpolating among them. "Simulated" pollen abundances can be obtained analogously, for any combination of climatic values, simply by interpolating among the appropriate set of fitted values.

Because the surfaces are fitted locally rather than globally, the trend of the contours at the edge of the filled region of climate space is determined only by data points within a certain (climatic) distance from the edge. Extrapolation is therefore permissible, and the surfaces can be extended for a limited distance beyond the edge, in order to predict pollen assemblages expected in climates slightly different from any that exist in the region today. The surfaces were extrapolated by constructing weighted averages for grid points just outside the region in climate space where observations exist, based on the fitted values from just inside the region. The addition of one "layer" of fitted values was sufficient to generate analogs for those fossil spectra without good analogs in the modern data set. Good analogs for these artificially created pollen spectra exist

within the fossil data set (P. J. Bartlein, *personal observation*).

Surfaces were fitted for 13 pollen taxa: northern and southern pines (*Pinus*), spruce (*Picea*), birch (*Betula*), oak (*Quercus*), prairie forbs (*Artemisia*, Compositae and Chenopodiaceae), beech (*Fagus*), hickory (*Carya*), hemlock (*Tsuga*), fir (*Abies*), elm (*Ulmus*), alder (*Alnus*) and sedge (Cyperaceae). These taxa were selected because they are sufficiently abundant to allow quantitative mapping, and because their abundance patterns are not dominated by local, site-specific factors—as is the case for certain other sometimes-abundant taxa such as Gramineae or *Nyssa*. Northern and southern pines are ecogeographic rather than taxonomic groupings; they are not distinguishable palynologically, but isopoll maps show that their distribution areas have remained separate during the past 18 000 yr (Webb 1988). They were separated for the construction of response surfaces by dividing the modern distribution of pine pollen at 40° N. The three pollen types lumped as prairie forbs have similar distributions today and in the past; they are lumped to reduce noise (Webb et al. 1983).

Inferred climate

The reconstruction set of six pollen types (northern and southern pines, spruce, birch, oak, and prairie forbs) was chosen as the smallest set that would allow any pollen assemblage to define a unique position in climate space. The climates inferred in this way are pro-

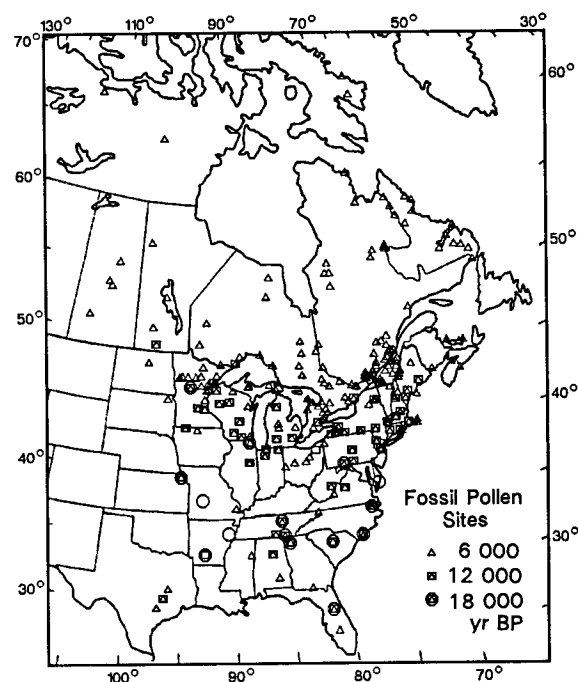


FIG. 3. Sites in eastern North America that were the sources of fossil pollen data. Δ = sites with records at 6 000 yr BP, □ = sites with records at 12 000 yr BP, and ○ = sites with records at 18 000 yr BP. All dates are based on radiocarbon analyses.

visional in the sense that they were based on the *smallest* possible number of taxa needed to obtain a robust reconstruction. The use of any smaller set would lead to indeterminacy. For example, many different combinations of summer and winter temperatures and precipitation could produce similar pollen percentages of, say, spruce and oak. The more types that are included, the more precisely the climate can be inferred.

Values of the three climate variables were inferred for each fossil pollen sample from the response surfaces for these six taxa by scanning the three-dimensional climate space at intervals of 1.5°C July temperature, 3°C January temperature, and 100-mm annual precipitation, and interpolating among the 10 combinations of values where the predicted pollen percentages of these six taxa were most similar to their fossil pollen percentages. Similarity was indicated by low values of a dissimilarity coefficient, squared chord distance (SCD; Prentice 1980, Overpeck et al. 1985). The final inferred climate value was taken as the centroid of these values, each inversely weighted by the SCD between the predicted and observed pollen percentages of the six taxa. The same procedure was also applied to the modern pollen data, as a check on the method's ability to reconstitute modern climate.

Simulated and observed isopoll maps

Simulated pollen percentages of all 13 taxa were obtained by evaluating the response surfaces at points corresponding to the inferred climate values. Isopoll maps were prepared by interpolating the observed or simulated pollen percentages of individual sites onto a 100-km² grid and recoding the value at each map gridpoint to four abundance levels. The resulting maps approximate the hand-contoured isopoll maps in, e.g., Jacobson et al. (1987) or Webb (1988). The smoothing (by interpolation onto a grid), spatial filtering (by presenting results at a small map scale), and generalization (by recoding) all help to focus attention on the continental-scale patterns.

Isopoll maps were prepared for both observed and simulated data at 3000-yr intervals from 18 000 yr BP to the present. To avoid distraction, we do not show site locations on each isopoll map.

RESULTS

Response surfaces

A response surface can be imagined as a solid of variable density, in which the pollen abundance of the taxon is represented by the density and the three-dimensional coordinates define the climate. The fitted surfaces (Fig. 4) are portrayed as a series of slices, each showing pollen abundance as a function of January and July temperatures at a particular value of annual precipitation. The shape of the whole surface can be imagined by mentally stacking the slices in order of increasing annual precipitation.

Each of the 13 surfaces is unique, implying that each

taxon has an individualistic relationship to present climate. The two most similar surfaces are those for beech and hemlock, but even these are not identical. Most of the surfaces are unimodal, i.e., they show a unique optimum at a point in climate space with abundances falling away in all directions. This applies to taxa that include many species (e.g., oak, pine) as well as to taxa represented by a single species (e.g., beech: *Fagus grandifolia*; hemlock: *Tsuga canadensis*). Some other taxa (e.g., prairie forbs) have increasing values towards one edge of the fitted surface, implying that their abundance maximum lies outside the included range of modern climates.

The goodness-of-fit statistics (Table 1) show that most of the variance in the pollen percentages of the most abundant taxa can be related to climate. The R^2 values are lower for the less abundant pollen types, but the surfaces can still predict the areas where these taxa are present and where they are abundant.

Inferred and observed modern climate

Climate values "re-inferred" from the surface pollen data (Fig. 5) are a good approximation to the observed modern climate. Correlation coefficients were $r = 0.94$ for July temperature, 0.84 for January temperature, and 0.76 for annual precipitation.

Inferred past climates

The maps of inferred past climates (Fig. 6) indicate discordant patterns of change through time in summer and winter temperatures and annual precipitation, and concomitant changes in the orientation of major climatic gradients. The gradient of winter temperature runs approximately northwest-southeast today; it apparently ran north-south between 18 000 and 12 000 yr BP, changing to its present orientation between 12 000 and 9000 yr BP. The summer temperature gradient, which runs northeast-southwest today, apparently ran north-south at 18 000 yr BP and changed to its present orientation earlier, between 15 000 and 12 000 yr BP. The present, generally northwest-southeast precipitation gradient was established between 9000 and 6000 yr BP, but was then steeper than at present, with conditions much drier than present in the Midwest. At 18 000 yr BP the region as a whole was apparently much colder and drier than present, but summer and winter temperatures and precipitation did not increase concurrently, and many areas appear to have had a greater seasonal temperature range at 9000 yr BP than today. Most northern areas show cooling summers and warming winters since 6000 yr BP.

The inferred July temperature and annual precipitation patterns for 6000 yr BP are in agreement with previous reconstructions obtained from pollen data by the transfer function method (Bartlein and Webb 1985). The spatial patterns of change in precipitation are also corroborated by independent evidence from palaeolake levels (Harrison 1989, Webb 1990).

Further support for the patterns reconstructed in Fig.

6 comes from dynamic climatology. The past 18 000 yr has seen a change from orbital conditions similar to today through a northern-hemisphere summer insolation maximum and winter-insolation minimum centered around 11 000 yr BP. During the same period the Laurentide ice sheet shrank from its maximum extent at 18 000 yr BP to a much reduced state \approx 9000 yr BP and had disappeared by 6000 yr BP. These two controls acting together would be expected to have produced very cold and dry conditions around 18 000 yr BP, with rapid warming during deglaciation towards a climate with a greater annual temperature range than at present occurring at 9000 yr BP. The time series of simulations at 3000-yr intervals by Kutzbach and Guetter (1986; see also Webb et al. 1987, COHMAP Members 1988, Harrison 1989) bear out these expectations, and indeed reproduce all of the broad features of spatial patterns in summer and winter temperatures and precipitation seen in Fig. 6.

Simulated and observed modern isopoll maps

Simulated isopoll maps based on the observed modern climate (Fig. 7) closely resemble the observed modern isopoll maps. This comparison demonstrates the ability of the response surfaces to reproduce the observed patterns. Any discrepancies found at this stage show the uncertainty associated with the response surface method and would have implications for the comparison of simulated and observed isopoll maps for the past.

The largest discrepancy shown in Fig. 7 is for sedge, which has some high local pollen abundances that are unrelated to climate and therefore smoothed over by the response surface. The simulations also show a general tendency to underestimate the higher abundance values, especially for taxa with low pollen representation such as beech, hickory, and fir. This tendency is an unavoidable consequence of the smoothing.

Simulated and observed isopoll maps for the past

Simulated isopoll maps for the past, based on the inferred climatic time series, also resemble the observed isopoll maps. The changing abundance patterns of the six taxa used in the reconstruction (Figs. 8, 10) are accurately reflected by the simulations (hypothesis Test 1). This result implies that the past combinations of abundances of these taxa all had reasonably close analogs among the modern assemblages used to derive the response surfaces. The fact that the inferred climates are climatologically plausible and qualitatively consistent with the Kutzbach and Guetter (1986) general circulation model (GCM) simulations is evidence against the disequilibrium hypothesis, at least for this set of taxa. Their changing abundance patterns can be explained more simply as a response to climatic changes induced by orbital variations and the dynamics of the Laurentide ice sheet.

Test 2 (Fig. 9) provides more direct support for the

TABLE 1. Goodness-of-fit statistics for pollen-climate response surfaces of 13 quantitatively important taxa over the past 18 000 yr.

Pollen type	R^2	Percentage of correct predictions of presence or absence
Taxa included in the climate reconstruction		
Spruce	0.89	88.5
Birch	0.76	92.4
Northern Pines	0.79	95.6
Oak	0.85	90.2
Southern Pines	0.86	96.8
Prairie Forbs	0.79	91.8
Taxa not included in the climate reconstruction		
Sedge	0.61	85.7
Fir	0.67	77.4
Hemlock	0.72	82.3
Beech	0.61	77.5
Hickory	0.74	83.1
Elm	0.69	84.6

dynamic equilibrium hypothesis. The simulated pollen percentages show a general tendency to underestimate the observed pollen percentages, and in particular to smooth out the higher percentages. Fig. 10 shows this most clearly. The slope of the relationship between simulated and observed percentages is typically <1 , and several taxa show a pronounced flattening at higher observed percentages. These distortions reflect the inherent smoothing in the response surfaces. Fig. 10 also shows greater scatter for the reserved types than for the calibration types, some of which may be due to the lower R^2 values of the response surfaces for the reserved types (Table 1). Yet the essential space-time patterns are preserved (Fig. 10). The same inferred climate changes that successfully reproduced the space-time patterns in the calibration types also serve to delineate those patterns for the reserved types. This result would not have been obtained unless both sets of taxa were subject to a common set of climatic controls. Inspection of the isopoll maps in conjunction with the simulated maps, the inferred climate maps, and the response surfaces thus allows us to postulate a climatic cause for the major features of *both* sets of maps. These climatic explanations are summarized in the following sections.

Test 1: taxa used in the reconstruction

Spruce was widely distributed south of the ice sheet at 18 000–15 000 yr BP due to the much colder than present climate. Its abundance was reduced in the southeast by 12 000 yr BP due to rising temperatures. By 9000 yr BP a further rise in summer temperature had eliminated spruce from the south, while the region farther north (the area of the present-day boreal forest) was still occupied by ice. This area became spruce covered after deglaciation. A decrease in summer temperatures caused the slight southward readvance of the southern boundary of spruce between 6000 yr ago and the present.

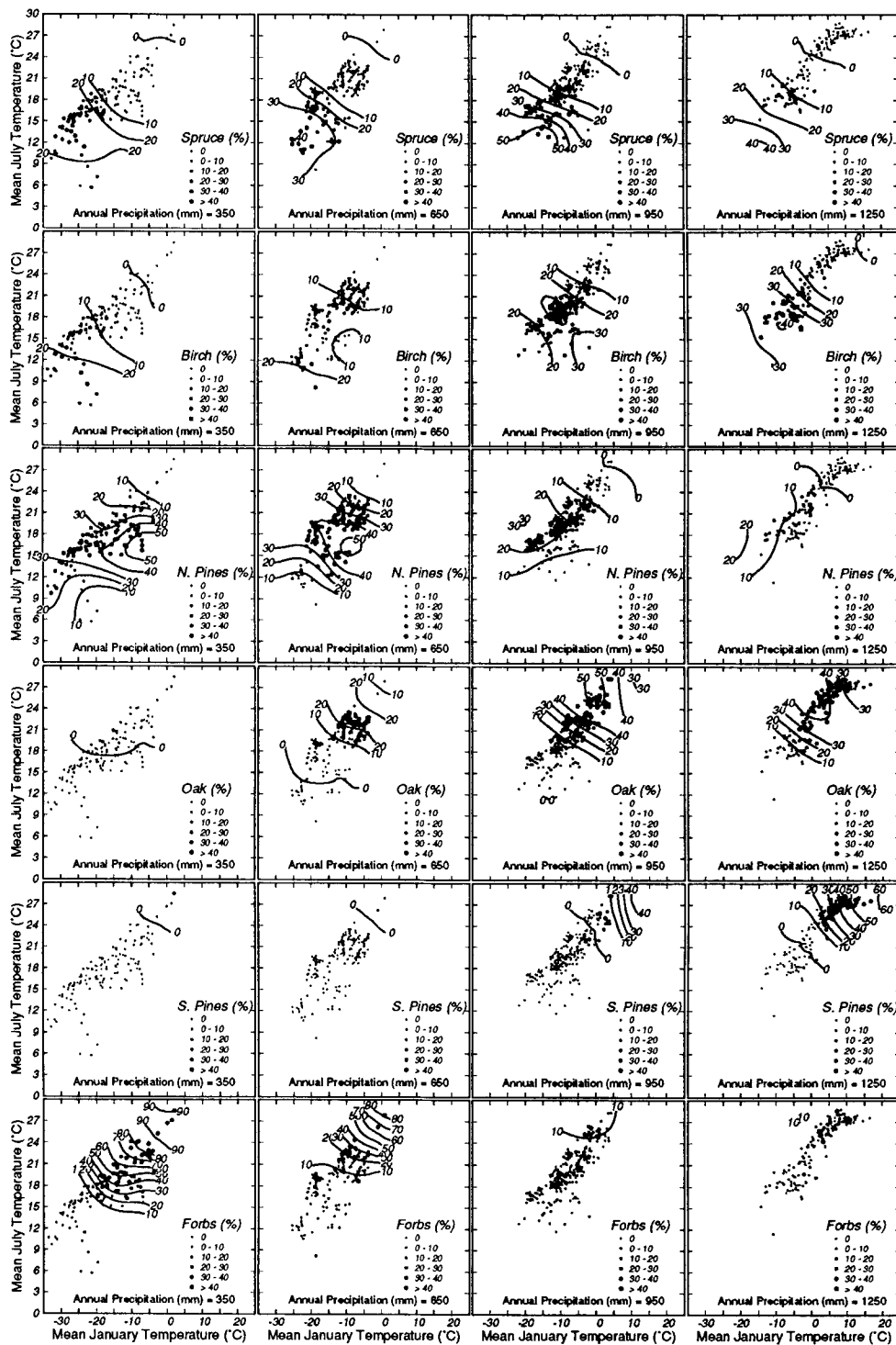


FIG. 4. Pollen-climate relationships and response surfaces. The modern pollen data were divided into four mean annual precipitation bands with midpoints at 350, 650, 950, and 1250 mm, and plotted against mean July and January temperatures within each band. Isolines illustrate the fitted three-dimensional surfaces.

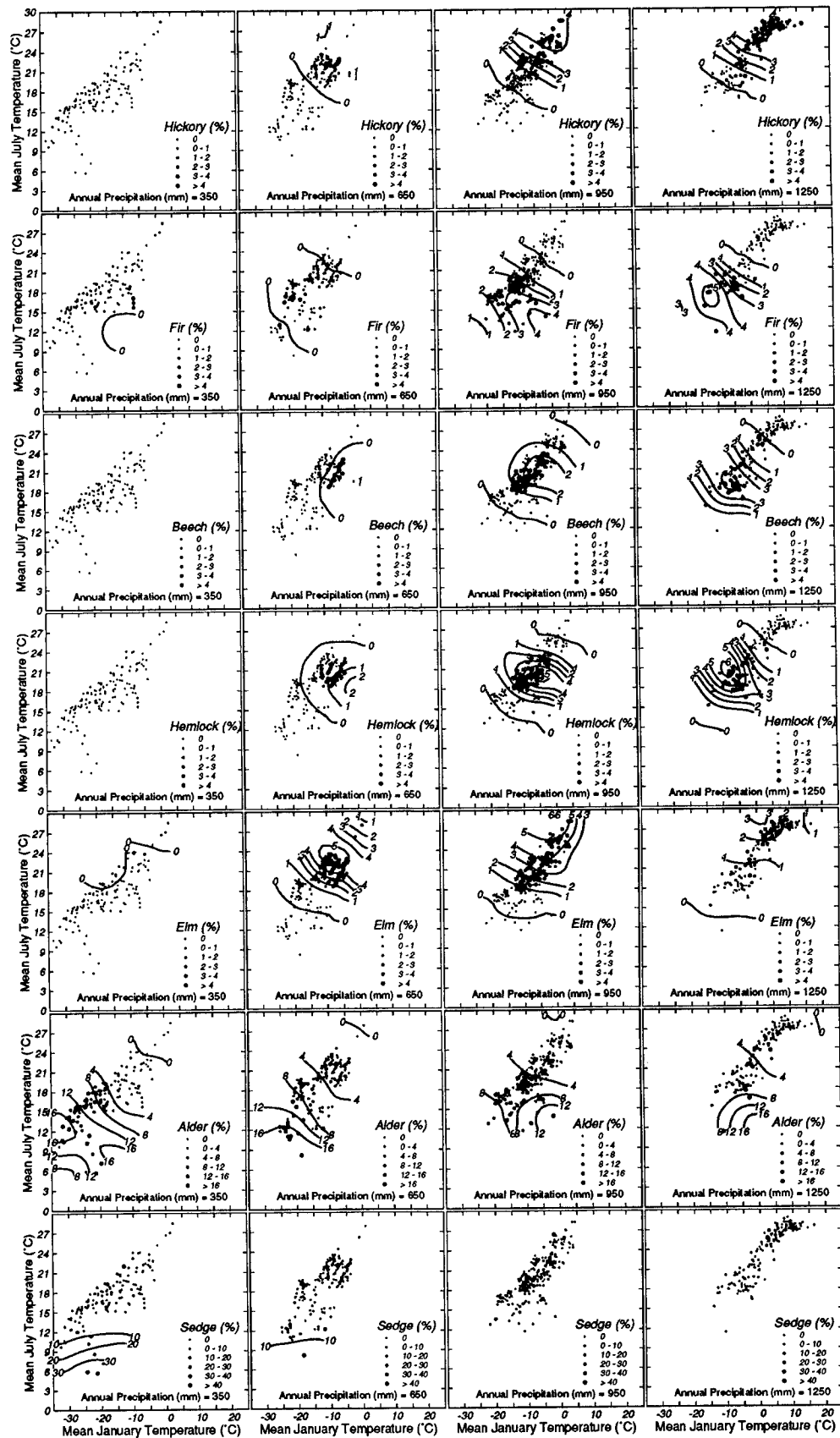
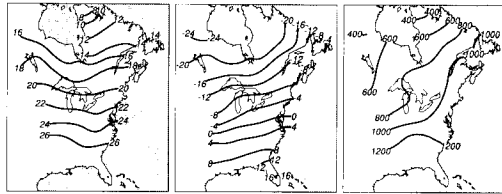
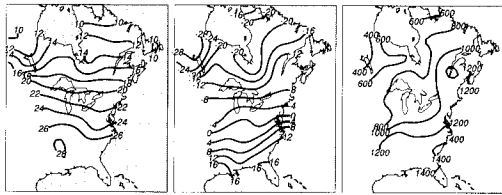


FIG. 4. Continued.

Observed**Inferred from Modern Pollen**

July Temp. (°C) Jan. Temp. (°C) Ann. Precip. (mm)

FIG. 5. Observed modern climate (top row), and modern climate inferred from the modern abundances of six pollen types listed in Table 1 (bottom row).

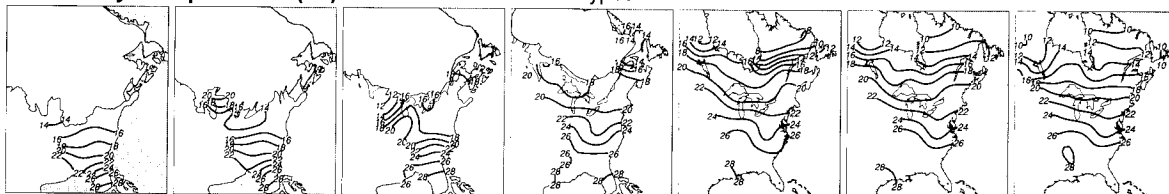
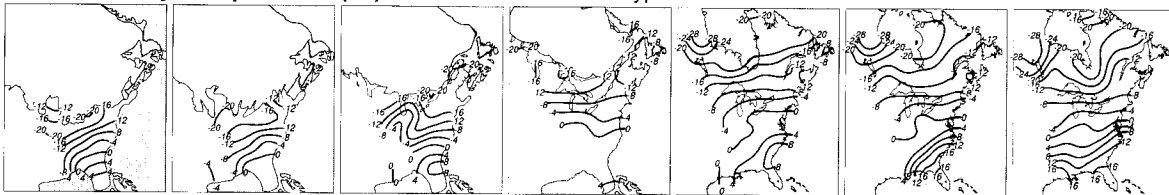
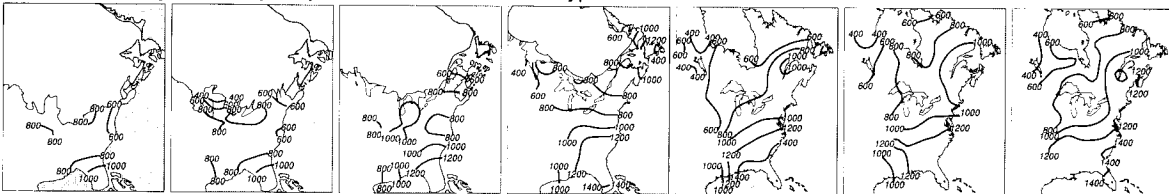
Birch was present south of the ice sheet at 18 000–15 000 yr BP, but in low abundance: temperatures were low enough but precipitation was only marginally adequate. Expansion of birch in the northeast by 12 000 yr BP is explained by rising precipitation, and a further increase by 9000 yr BP by a continuation of this trend. Birch expanded onto the formerly glaciated area after deglaciation.

Northern pines were abundant in the south at 18 000 yr BP due to the cool summers. They spread up the east coast during the period 18 000–12 000 yr BP in

response to increasing summer temperatures. The temperature increase was greatest west of the Appalachians and in the southeast, where summers became warm enough to exclude the northern pines. Between 12 000 and 9000 yr BP northern pines replaced spruce in a broad band south of the residual ice sheet in response to a further large increase in summer temperature. In contrast with spruce and birch, the northern pines had reached essentially their present distribution by 9000 yr BP; they increased in abundance, in response to increasing summer warmth and dryness between 9000 and 6000 yr BP, then decreased again after 6000 yr BP as precipitation increased and summer temperatures fell.

Oak was present in the south at 18 000–15 000 yr BP, but in low abundance because of the low temperatures. A slight northward expansion and increase in abundance by 15 000 yr BP is explained by a slight rise in summer temperature. Oak spread further northward and became much more abundant by 12 000 yr BP due to increases in temperature in both seasons. A continuing northward spread from 12 000–6000 yr BP is explained by a continuation of the warming trend. From 6000 yr ago to the present falling summer temperatures caused a slight southward retreat of the northern boundary, while rising winter temperatures (combined with high precipitation) caused a northward retreat along the southern boundary.

Southern pines were in low abundance at 18 000–15 000 yr BP because the climate of the whole region was too cold and dry. They appeared in Florida by

Mean July Temperature (°C) Inferred from Six Pollen Types**Mean January Temperature (°C) Inferred from Six Pollen Types****Annual Precipitation (mm) Inferred from Six Pollen Types**

18 000 15 000 12 000 9 000 6 000 3 000 0 yr BP

FIG. 6. Climates inferred from the fossil and modern abundances of six pollen types (listed in Table 1), from 18 000 yr BP to the present. The blank area is the Laurentide ice sheet (Dyke and Prest 1987).

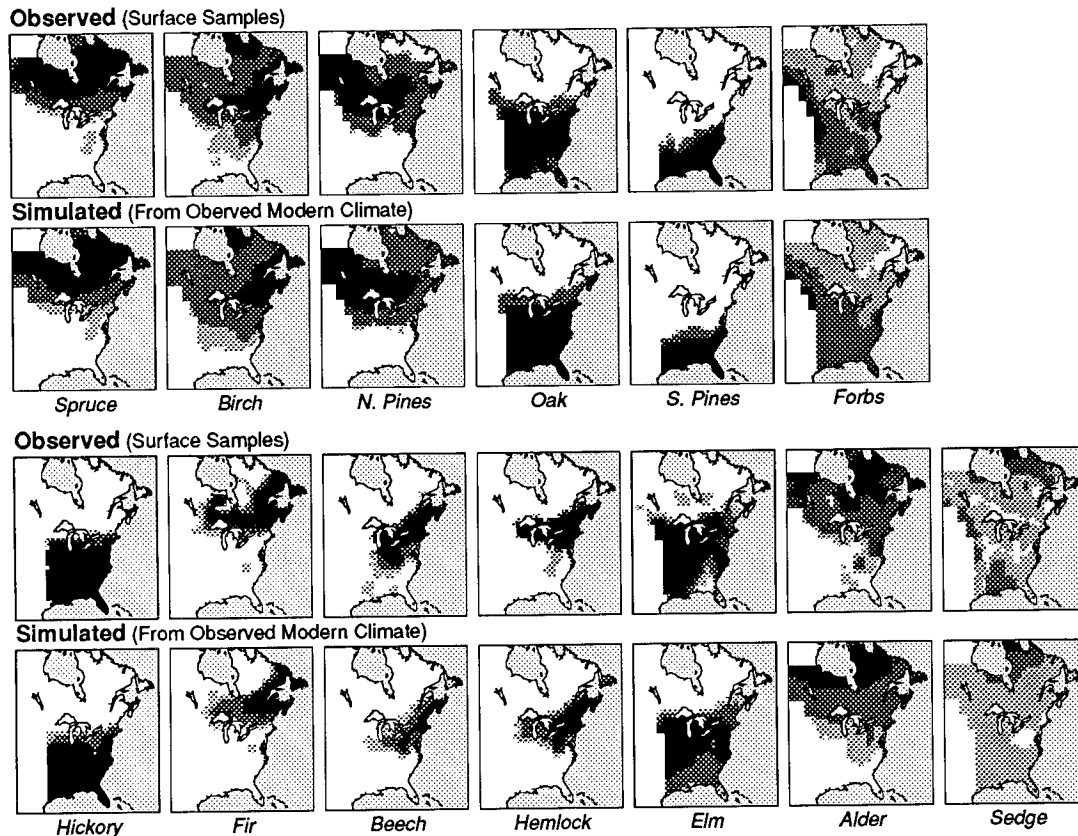


FIG. 7. Isopoll maps from surface samples, and simulated from the observed modern climate. For spruce, birch, northern pines, oak, southern pines, prairie forbs, and sedge the three terrestrial shading levels (light, medium, and dark) indicate pollen abundances greater than 1, 5, and 20% respectively. For fir, hemlock, beech, hickory, elm, and alder the corresponding levels are 0.5, 1, and 2%.

12 000 yr BP; here summer temperatures had almost reached modern values, and winter temperature and precipitation had risen enough to allow southern pines to grow. The subsequent expansion of southern pine from Florida towards the north and west is explained by a steady rise in winter temperatures throughout the southeast during the period from 12 000 yr ago to the present.

Prairie forbs were present in moderate abundance south of the ice sheet at 18 000–12 000 yr BP. A reduction in their abundance in the northeast between 12 000 and 9000 yr BP is explained by an increase in precipitation in the northeast. An area of high prairie forb abundance appeared in the northwestern part of the region by 9000 yr BP, due to a large increase in summer temperature while precipitation remained low. This prairie area expanded eastward between 9000 and 6000 yr BP and then retreated again, primarily in response to precipitation changes in the Midwest.

Test 2: taxa not used in the reconstruction

Hickory was restricted to the southeast at 18 000 yr BP due to the cold, dry climate. Its gradual expansion during 18 000–12 000 yr BP is explained by warming summers. The continuation of this warming trend

caused hickory to spread further north along the east coast and into the Midwest, and to increase in its abundance in the Midwest between 12 000 and 9000 yr BP. Increasing precipitation explains the continued northward expansion of hickory into the Appalachian region between 9000 and 6000 yr BP, while decreasing precipitation in the Midwest explains the slight eastward retreat of its western limit during the same period. Increasing precipitation in the Midwest after 6000 yr BP caused a westward readvance of its western limit.

Hickory and oak have similar but not identical distributions today. The differences in the climatic tolerances of the two taxa explain the differences in their distributional history. The response surfaces show that hickory has a slightly higher precipitation requirement. At 9000 yr BP the perceptible lag in the spread of hickory relative to oak along the east coast can be explained by precipitation there being lower than today.

Fir was present south of the ice sheet at 18 000 yr BP but in low abundance due to the coldness and dryness of the climate. Fir had expanded into the Midwest by 15 000 yr BP in response to slight increases in temperature and precipitation. The large increase in abundance and northeastward spread of fir between 15 000

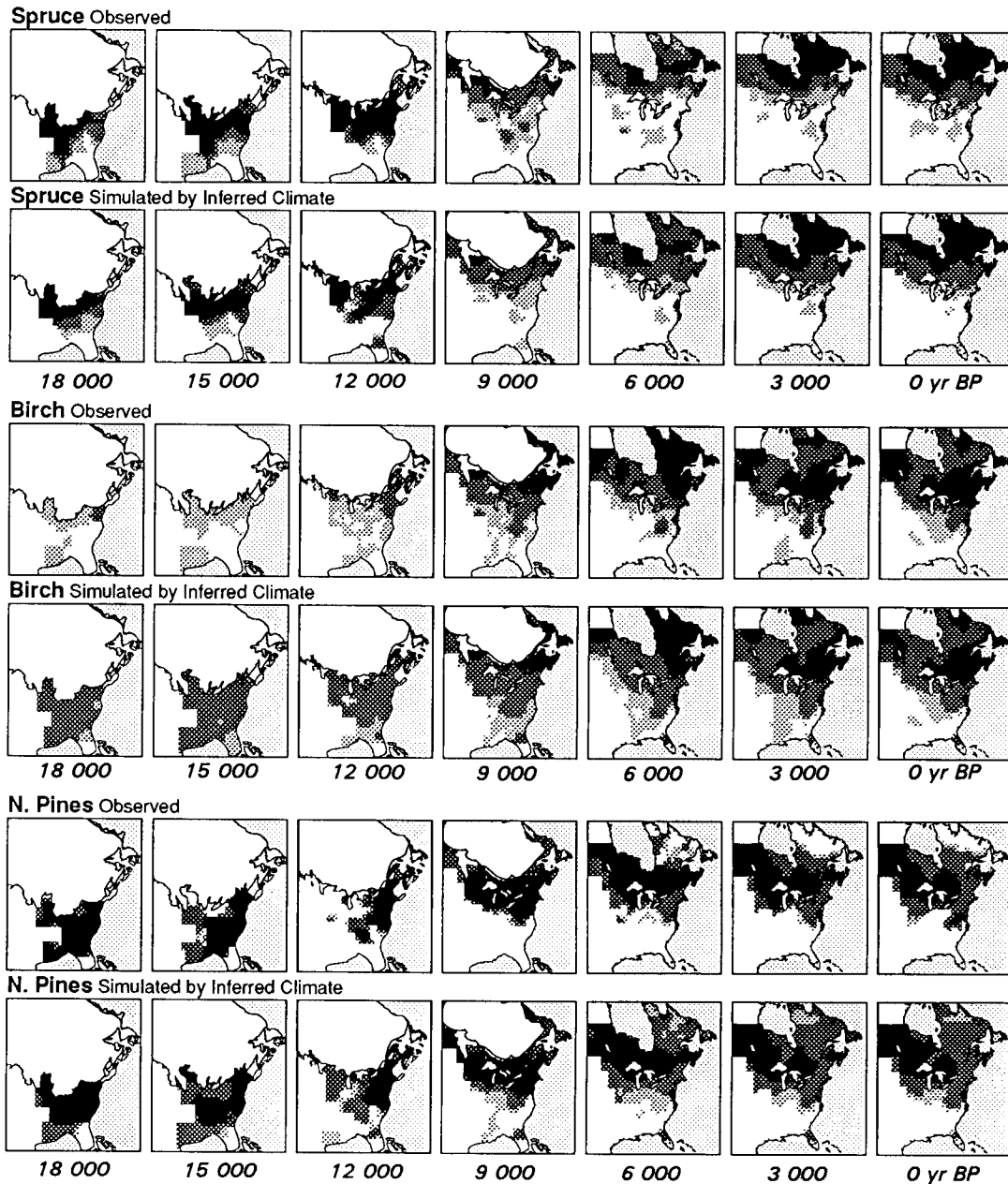


FIG. 8. Test 1: isopoll maps from fossil samples, and simulated from the inferred climates, from 18 000 yr BP to the present. Shading as in Fig. 7. These six taxa were used in the climatic reconstruction.

and 12 000 yr BP are explained by the increase in precipitation, especially in the northeast. Rising summer temperatures caused the northeastward shift of the population center of fir through 12 000–6 000 yr BP; falling summer temperatures and continuing high precipitation explain its increase in abundance and slight southward re-expansion from 6 000 yr ago to the present.

Fir and spruce have similar but not identical distributions today. Fir requires higher precipitation. Low precipitation during 18 000–12 000 yr BP explains why

fir was restricted at this time, when spruce was widespread.

Beech was very restricted during 18 000–15 000 yr BP because of the cold, dry climate. It appeared in greater abundance in the south by 12 000 yr BP in response to rising summer temperature and precipitation. This continuing trend allowed beech to expand toward the northeast during 12 000–9 000 yr BP, while reducing its extent in the south. Its westward expansion into the Midwest between 9 000 and 3 000 yr BP can be explained by a combination of rising winter tem-

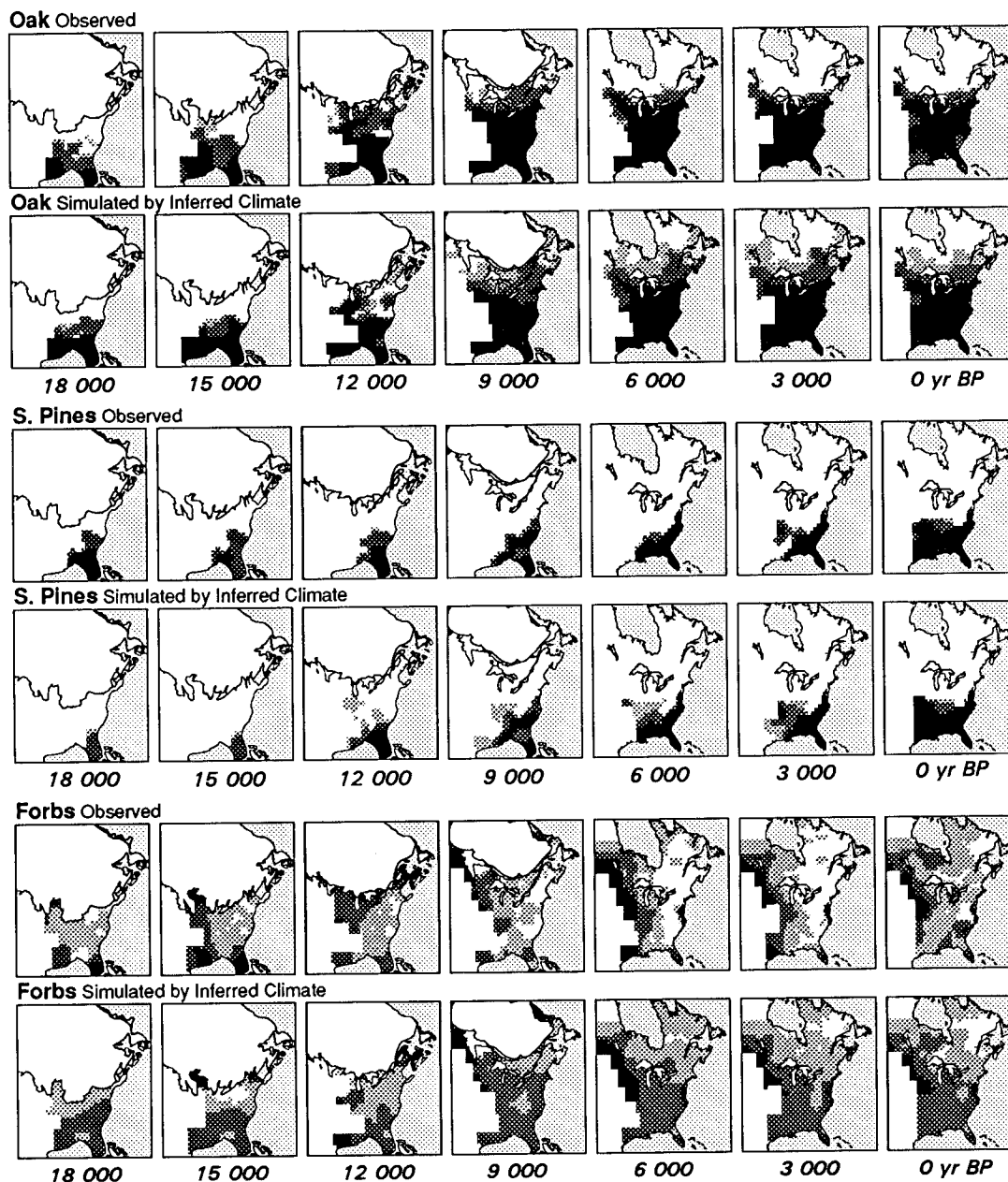


FIG. 8. Continued.

peratures (from 9000 to 3000 yr BP) and increasing precipitation (after 6000 yr BP). Rising precipitation throughout this period allowed beech to spread and increase in abundance in the northeast. Falling summer temperatures explain the slight retreat of its extreme northeastern limit between 3000 yr ago and the present.

Hemlock was extremely restricted during 18000–15000 yr BP but appeared in significant abundance by 12000 yr BP as summers warmed and precipitation increased. As this trend continued hemlock expanded

northeastward during 12000–9000 yr BP. Rising winter temperatures, and rising precipitation after 6000 yr BP explain its expansion into the Midwest during 9000–3000 yr BP. Falling summer temperatures explain a slight retreat in the northeast between 3000 yr ago and the present.

Hemlock tolerates slightly lower precipitation than beech. This difference explains the slight lead of hemlock over beech in their northeastward spread at 9000 yr BP.

Elm was present only in low abundance at 18000

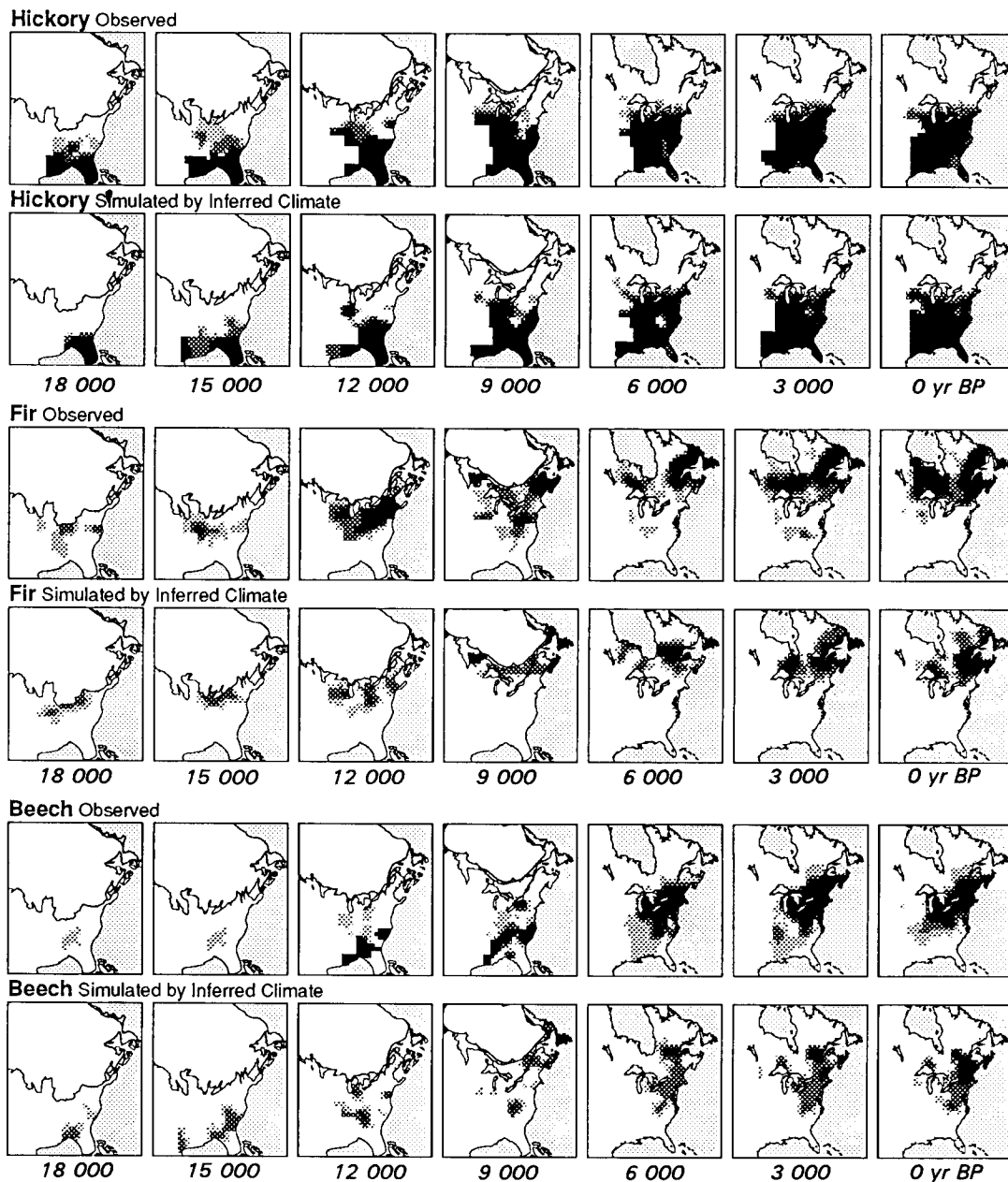


FIG. 9. Test 2: isopoll maps from fossil samples, and simulated from the inferred climates, from 18 000 yr BP to the present. Shading as in Fig. 7. These seven taxa were *not* used in the climatic reconstruction.

yr BP due to the cold climate. It increased in abundance south of the ice sheet and in the southeast by 15 000 yr BP in response to summer and winter warming. Between 15 000 and 12 000 yr BP its abundance maximum shifted towards the Midwest as summer temperatures and precipitation increased. The continued warming in both seasons between 12 000 and 9 000 yr BP caused elm to increase in abundance generally, and especially in the Midwest, but in the extreme southeast winters became too warm and precipitation too high for elm. Its present distribution was essentially in place by 9 000 yr BP.

Alder was present in low abundance, scattered throughout the region south of the ice sheet during 18 000–15 000 yr BP. The cold conditions allowed it to be distributed far to the south, but drought restricted its abundance. By 12 000 yr BP the distribution of alder had become confined further north because of warming summers in the southeast. By 6 000 yr BP alder had become abundant in the large deglaciated area. It decreased in abundance in eastern Canada in response to increasing winter temperatures between 6 000 yr ago and the present.

Alder and spruce have rather similar distributions

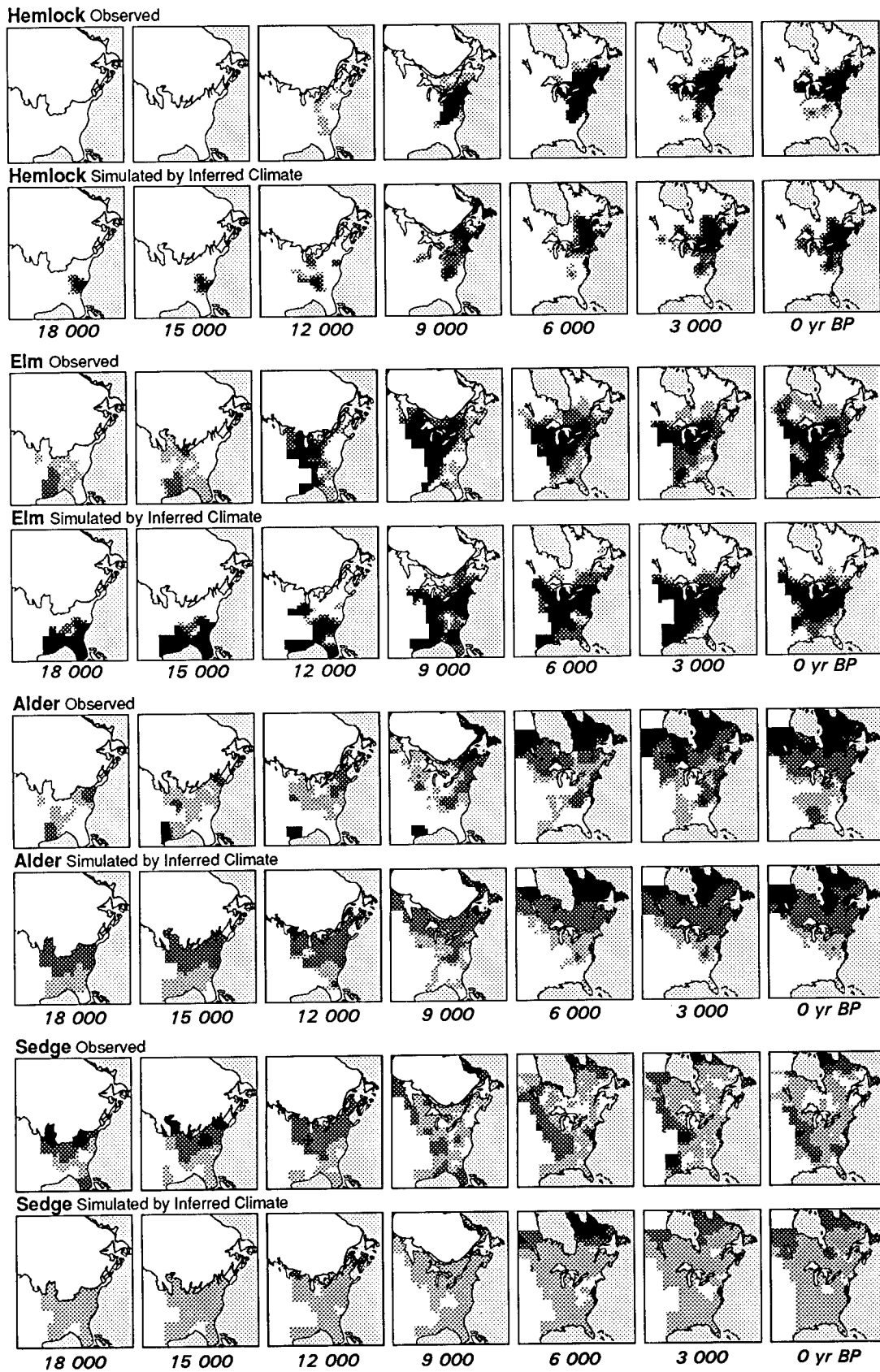


FIG. 9. Continued.

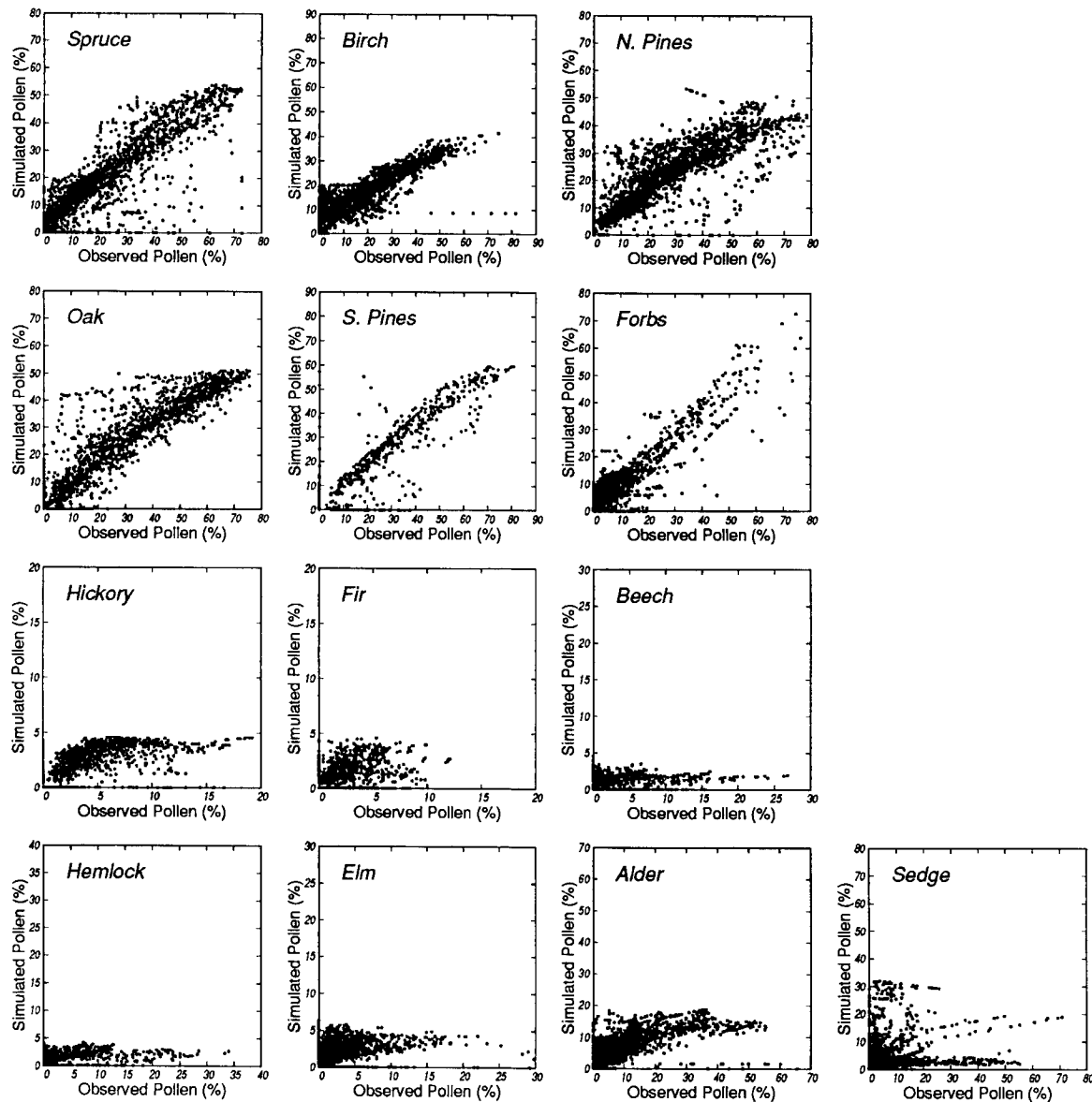


FIG. 10. Scatter diagrams of observed and simulated pollen percentages, for all taxa, sites, and times.

today and behaved in generally similar ways during the past 18 000 yr. However, spruce abundances are somewhat more sensitive to summer temperatures near the climatic optimum for spruce. This difference in sensitivity explains why the alder isopoll maps show relatively little change during the past 9000 yr in areas where spruce first increases, and then decreases, in response to changing summer temperatures.

Sedge shows highest abundances in the area of lowest temperatures, just south of the ice sheet, during 18 000–12 000 yr BP. Sedge became much reduced in abundance by 9000 yr BP due to rising summer temperatures, except in the northwestern part of the region where low precipitation allowed higher abundances to persist. Deglaciated areas in the far north became colonized by sedge during 9000–6000 yr BP.

Discrepancies between observed and simulated isopoll maps

Some systematic differences between simulated and observed isopoll maps occur at 18 000–15 000 yr BP where the simulations show too much birch, oak, beech, and hemlock and too little pine in the southeast. The closest modern analogs for the fossil assemblages of the southeast at this time are in the vicinity of the prairie–forest boundary in Minnesota and Manitoba, an area of steep climatic gradients where the climate inferred for the present day (Fig. 5) is somewhat too warm and wet.

Significant discrepancies occur along the east coast of Canada at 9000 yr BP for some of the taxa not included in the reconstruction set. The simulations

produce too much beech and hemlock and not enough pine, alder, or sedge, suggesting that the estimated summer temperatures may be too high for this area and time. The discrepancies are probably due to imprecision in climatic inferences that were derived from the pollen percentages of a small number of taxa. If, for example, alder or sedge had been added to the reconstruction set, then the simulations for the other taxa would have been more accurate.

Elm presents a special problem. Through the period from 18 000 to 12 000 yr BP, elm was present in part of the Midwest in assemblages with no modern analog. The simulations do not succeed in producing the observed high abundances of elm for this area and time because the best analogs inferred from the response surfaces do not contain abundant elm; this illustrates a limitation in the procedure used to extrapolate the response surfaces to climates different from those that exist in eastern North America today.

A discrepancy noted for sedge relates to the effects of variability in pollen percentages due to factors other than climate. Systematically low sedge abundances were simulated for the area south of the ice sheet at 18 000–12 000 yr BP and in the prairie region from 9000 yr ago to the present. This discrepancy is present in the reconstruction for the present day and has a technical explanation: the modern data show considerable site-to-site variability in sedge pollen abundances in the low-precipitation region, which is smoothed out by the response surface fitting procedure. Individual sites with high values have a strong effect on the appearance of the isopoll maps but less effect on the form of the response surface. Thus, the simulated isopoll maps show lower-than-observed abundances in the present-day prairie region, and in comparable climatic situations in the past.

DISCUSSION

Support for the dynamic equilibrium hypothesis

The agreement between observed and simulated isopoll maps for the six taxa included in the reconstruction set shows that it is possible to infer a climatic history that explains their movements during the past 18 000 yr. That this inferred climatic history is qualitatively similar to that independently simulated by general circulation model (GCM) experiments, and that these independently simulated climates could also correctly generate most of the major features of the isopoll maps (Webb et al. 1987), implies that the climatic change scenario is likely to be essentially correct.

Our further demonstration that most of the space-time variation in the abundances of several other taxa, independent of the reconstruction procedure, can be accounted for by the same climatic change scenario provides strong support for the dynamic equilibrium hypothesis at the time and space scales we are considering. Neither these results, nor those based on inde-

pendent GCM-based climate simulations by Webb et al. (1987) give any hint that the composition of the vegetation lagged behind the climatic changes when observed at the continental scale with a time resolution of 3000 yr. With snapshots 3000 yr apart, lags greater than ≈ 1500 yr would be clearly visible as major discrepancies (e.g., offsets) between the patterns seen in the simulated and observed maps. We conclude that the continental-scale vegetation patterns have responded to continuous climatic changes during the past 18 000 yr, with lags no greater than ≈ 1500 yr.

Other evidence

In a series of papers (Davis et al. 1986, Davis 1987, S. L. Webb 1987, Woods and Davis 1989), M. B. Davis and co-workers have analyzed the spread of hemlock and beech into and through the Midwest during the past 8000 yr. By providing information for a part of the continent with a much greater spatial and temporal precision than can be resolved on our maps, these results provide a complementary perspective on the processes by which vegetation reaches dynamic equilibrium with climate.

Davis et al. (1986) and Davis (1987) showed that the immigration of hemlock into Michigan between 7000 and 6000 yr BP was spatially incoherent, consisting of local increases of scattered populations over a large area. Hemlock then spread extremely rapidly throughout the area between 6000 and 5500 yr BP. It was inferred that the climate had changed sufficiently before 6000 yr BP to have caused a major expansion of hemlock's potential range, so that the species' actual distribution was partly dispersal limited between 7000 and 5500 yr BP. The later westward spread of hemlock was slower and more regular, suggesting that by then the species' range was in equilibrium with climate. A similar argument was used to suggest that the distribution of beech was in equilibrium with climate after 6000 yr BP. Woods and Davis (1989) traced the spread of beech in more detail and found alternating phases of stillstand and advance, suggesting close tracking of climatic changes from 5000 yr BP onwards. They concluded that the western range limit of beech was close to equilibrium with climate from at least 5000 yr BP, and possibly 8000 yr BP, to the present. Maximum lags in spread during this period were estimated to be on the order of 1000 yr (Woods and Davis 1989, S. L. Webb 1987).

Woods and Davis (1989) noted, on the basis of the modern biology of beech on its western limit, that low winter temperatures and precipitation were likely to have been factors limiting its Holocene spread. Our results suggest that this was so for hemlock as well as for beech. By 9000 yr BP, inferred July temperatures (Fig. 6) in the northern Midwest had already reached levels suitable for the growth of both taxa. In this range of July temperature (20° – 22°C), to get $\geq 1\%$ beech pollen requires January temperatures above $\approx -8^{\circ}\text{C}$ and

annual precipitation above ≈ 900 mm. The corresponding requirements for hemlock are -10°C and 800 mm. Thus both winter temperatures and precipitation in the northern Midwest were marginal or inadequate for beech and hemlock at 9000 yr BP, but the progressive winter warming from 9000 yr BP onwards, and the increase in precipitation from 6000 yr BP onwards, can explain the spread of these taxa, with hemlock spreading slightly in advance of beech because of its greater tolerance of drought and winter cold. Comparison of the observed and simulated isopoll maps suggests that neither species was geographically far from its equilibrium range during this time.

The work by Davis and others leaves unanswered the question of whether the distributions of these taxa were in equilibrium with climate before their immigration into the Midwest. Our results suggest that climate did not suddenly change at some earlier time so as to make a large area favorable for hemlock; rather the area of favorable habitat extended gradually, in response to continuous climatic change. Both our results and those of Davis and co-workers are consistent with lags no greater than 1500 yr during the entire period since the last glacial maximum.

Woods and Davis (1989) also pointed out that the vegetation is probably in disequilibrium with climatic changes on a shorter time scale (centuries). The persistence of individual trees may prevent the range boundaries from changing more rapidly in response to short-term fluctuations in climate. This inertia presumably increases the proportion of spatiotemporal variance in the pollen record that can be explained by longer-term climatic changes of the kind documented in this paper.

Implications for palaeoecological research

Remarkably, we have been able to use the pollen percentages of just six taxa to infer a climatic scenario that is both qualitatively consistent with our understanding of the causes of Late-Quaternary changes in climate, and capable of explaining major patterns of Late-Quaternary change in vegetation—including differences between taxa in migrational history, such as the patterns of spread of oak and hickory between 12 000 and 9000 yr BP, that had previously been attributed to migrational lag (Davis 1976, 1981). If we now accept the equilibrium hypothesis for these broad space and time scales, then we can in the future use response surfaces for all of the major taxa in the pollen record to derive the most accurate available estimates of past climatic trends on these scales. Climatic changes inferred in this way should provide a palaeoenvironmental background for interpreting changes in pollen abundances on finer space and time scales, which can potentially resolve the vegetation's transient response to the changes in climate (Prentice 1988).

Long-term climatic changes during the past 18 000 yr have evidently been substantial, continuous, and

responsible for the large vegetational changes that are a major feature of the Late-Quaternary pollen record, including the Holocene record. Although the results presented here apply specifically to eastern North America, there is no reason to expect that the conclusions would be fundamentally different if a similar study were carried out for another region of comparable extent. It follows that information about climatic changes at this space and time scale can validly be obtained from the pollen record, and used to test physical models of climate dynamics (COHMAP Members 1988). On the other hand, our results pose new ecological questions about the processes that allow a dynamic equilibrium to be maintained in a changing environment.

That vegetation patterns can be in dynamic equilibrium with climate may seem paradoxical, because non-equilibrium processes (succession and gap-phase dynamics) are considered paramount on the time scales normally studied by plant ecologists (Shugart 1984, Pickett and White 1985). The resolution of the paradox lies in the fact that dynamic equilibrium applies to continental-scale patterns, which change only on long time scales, whereas ecologists predominantly study the finer-scale (and more readily observable) patterns, which are dynamic on much shorter time scales. Vegetation observed on these different spatial scales has quite different dynamic characteristics (Prentice 1986, McDowell et al. 1990). Species abundances measured over, say, a 100-km² landscape represent averages over many habitat types. One effect of climatic change is to alter the competitive balance of species within any given stand, but another—at least equally important—is to alter the amount of suitable habitat for each species. Landscapes also include patches that have been disturbed at different times; climatic changes affect the natural disturbance regime and thereby alter the proportions of the landscape in different successional stages. For example, an increase in precipitation may decrease the fire return time and so shift the balance in favor of late-successional species such as beech and hemlock (this may be part of the explanation for their sensitivity to precipitation, shown in the response surfaces). In the long run, effects of climatic change on the relative suitability of different topographic and edaphic situations for different species, and on the relative frequency of stands of different successional age, must cause gradual changes in the average species composition of the landscape.

The simultaneous operation of several mechanisms linking landscape-scale species abundances to climate means that the processes by which broad-scale vegetation patterns respond to climatic change cannot simply be equated with succession, as was done, e.g., by Iversen (1960). The properties of species that determine their long-term spatial dynamics in response to climatic changes are not the same properties that determine their behavior during succession (Prentice, *in press*). We need to consider these additional processes

and properties in order to understand how entire landscapes respond to changes in climate.

The response surfaces developed in this paper are purely empirical functions; they tell us how much of each taxon to expect to find on the landscape under a particular set of climatic conditions, but they cannot tell us why; nor do they model the transient response of the landscape. Our demonstration that Late-Quaternary patterns of change in vegetation have been persistently close to equilibrium with climate poses new ecological problems. Why do species co-occur in the abundances they do in any given climate, and what are the processes that allow vegetation to respond so rapidly to changes in climate? These questions require a different kind of model building. We need to model landscape-scale vegetation dynamics as an outcome of species' physiological and life-history characteristics, interspecific competition, landscape heterogeneity, natural disturbance regimes, and the response of species' growth rates and disturbance frequency to changes in climate (Davis and Botkin 1985, Solomon and Webb 1985, Prentice 1988). Palaeoecological data can provide powerful tests of such models, which are also required if we are to understand how natural landscapes will respond to rapid, human-induced changes in climate.

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