

Is vegetation in equilibrium with climate? How to interpret late-Quaternary pollen data

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Abstract

Current methods for estimating past climatic patterns from pollen data require that the vegetation be in dynamic equilibrium with the climate. Because climate varies continuously on all time scales, judgement about equilibrium conditions must be made separately for each frequency band (i.e. time scale) of climatic change. For equilibrium conditions to exist between vegetation and climatic changes at a particular time scale, the climatic response time of the vegetation must be small compared to the time scale of climatic variation to which it is responding. The time required for vegetation to respond completely to climatic forcing at a time scale of 10^4 yr is still unknown, but records of the vegetational response to climatic events of 500- to 1 000-yr duration provide evidence for relatively short response times. Independent estimates for the possible patterns and timing of late-Quaternary climate changes suggest that much of the vegetational evidence previously interpreted as resulting from disequilibrium conditions can instead be interpreted as resulting from the individualistic response of plant taxa to the different regional patterns of temperature and precipitation change. The differences among taxa in their response to climate can lead a) to rates and direction of plant-population movements that differ among taxa and b) to fossil assemblages that differ from any modern assemblage. An example of late-Holocene vegetational change in southern Quebec illustrates how separate changes in summer and winter climates may explain the simultaneous expansion of spruce (*Picea*) populations southward and beech (*Fagus*) populations northward.

Introduction

Over the past 20 000 years, most plant species have changed their range and abundance in the face of major climatic changes. Geographic networks of

pollen samples record these changes. The question raised in interpreting the pollen data is whether the vegetation has been in equilibrium with climate and has therefore tracked the long-term climate changes with relatively short-term lags or whether the lags have been long, perhaps comparable in time to the climate variations, and thus caused the vegetation to be in disequilibrium with climate. Under the latter circumstance, communities would be growing in certain climates without all the species present that can grow in those climates. These two possible interpretations pose a major interpretive problem to Quaternary palaeoecologists and palaeoclimatologists. The problem has at least three complicating elements: 1) climate change is complex and its late-

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Quaternary history is incompletely known, 2) vegetational dynamics are complex and not fully understood, and 3) pollen data provide an imperfect record of vegetational dynamics.

Climates change continuously, and different variables change in different ways, although covariance among certain variables can increase the impact of small climatic changes (Mitchell, 1976). Climate change has many superimposed components, corresponding to different frequencies (time scales) of variation. Vegetation responds differently to specific climatic variables and to their variations at differing time scales. The nature and rate of the response depends upon what aspect of the vegetation is monitored: individual plants, whole populations, or communities. Individual plants adjust their growth and reproductive rates. Plant populations change in abundance, genetic composition, and geographic distribution, and plant communities change in composition. These changes form a spectrum of botanical variation on time scales of tens to tens of millions of years, and palaeoecologists have several ways of sampling that spectrum. Tree-ring widths respond to annual variations in growth rates; pollen and plant-macrofossils in sediments record the 100-yr or longer changes in abundance, distribution, and association among taxa. Plant macrofossils and pollen from rocks record long-term evolutionary changes. Palaeoclimatologists working with these data must learn to decipher each of the different botanical responses to climatic change. They also must learn to identify the various responses to nonclimatic factors that may complicate the extraction of the climatic signal in the data. For selected time scales, these other responses can potentially obscure the climatic signal or can at least cause the full vegetational response to lag significantly behind certain climatic changes.

Continental- and regional-scale maps of pollen percentages at 1000-yr intervals through the late-Quaternary (last 20000 years) show many broad-scale patterns associated with climatic change in eastern North America (Wright, 1968; Bernabo & Webb, 1977; Bartlein *et al.*, 1984). Major pollen types such as spruce (*Picea*), pine (*Pinus*), and oak (*Quercus*) exhibit broad-scale patterns of changes that are similar from the East Coast to the Midwest (Bernabo & Webb, 1977). The systematic alignment of patterns along climatic gradients that cut across regions of widely differing soils implicates climate

as a major causative factor behind the changes (Webb, 1980).

Other evidence on the maps raises the question of major lags (i.e. disequilibrium) between vegetation and climate (Davis, 1978; Birks, 1981). Isochrone maps of species range boundaries show different rates and directions of movement among the various species (Davis, 1976, 1981a, 1983). Comparison of data from modern and fossil samples have revealed 'no-analog pollen assemblages', i.e. assemblages of fossil pollen unlike any modern assemblage (Overpeck *et al.*, 1985). When combined with a particular view of how the climate changed in the late-Quaternary, this evidence is used to deduce disequilibrium conditions as follows: 1. the assumption is made that the rapid changes in climate between 11 000 and 10000 yr B.P. led to certain climatic variables attaining early-Holocene patterns markedly different from their late-Pleistocene patterns (Davis, 1978) and that the changes were so rapid that the spatial movement of the climatic limits for certain species far outstripped their rates of dispersal and establishment, 2. species that were still moving away from their full-glacial locations in the mid- to late-Holocene may therefore have required thousands of years to reach their climatic limits (Davis, 1978; Birks, 1981), 3. because climate may not have controlled their rates of spread, the distribution of these species during the early- to mid-Holocene was probably not in equilibrium with climate (Davis, 1981a), 4. the absence of these species from vegetation in climatic regions in which these species presumably could grow meant that this vegetation was not in equilibrium with climate because the floral list was incomplete and species that were present had different realized niches than they have in modern forest communities (Birks, 1981), and 5. no-analog pollen assemblages were one consequence of this disequilibrium vegetation (Birks, 1981). Nonclimatic factors, such as disease, have also influenced Holocene vegetational patterns (Anderson, 1974; Davis, 1981b; Webb, 1982) and created situations in which the climatic interpretation of the vegetation can be difficult (Davis, 1978).

Two explanations have been developed to account for what the pollen data show (Prentice, 1983): one emphasizes the slow dynamic processes in vegetation and postulates *complex dynamic vegetational responses* to simple changes in climate

(Iversen, 1973; Davis, 1981a); the other assumes that the broad-scale vegetational patterns have remained in approximate equilibrium with climate but postulates *complex past climatic changes* to explain the complexities in the observed vegetational response (Howe & Webb, 1983). The first explanation has focused attention on endogenous vegetation factors such as differences between taxa in growth rates, longevity, shade tolerance, fire susceptibility, and seed dispersal. If these factors slow the vegetational response to certain time scales of climatic change, then palaeoclimatic maps and time series derived from pollen data by multiple regression methods (e.g. Howe & Webb, 1983) might be inaccurate records of climatic change at these time scales. The alternative explanation has emphasized the complex nature of (exogenous) climatic change in which temperature and precipitation can vary independently of each other both seasonally and spatially. The unique climatic response of each taxon (Chapin & Shaver, 1985) could then be the cause of differential movement and of the other major patterns of change apparent in the available late-Quaternary pollen records. For example, assemblages of fossil pollen without modern analogs could be the result of past climates without modern analogs.

For data sets representative of either extremely long or short periods of time, the choice between these two explanations is trivial. Few people would dispute that climate has forced the major vegetational changes during each 100000 yr glacial/interglacial cycle or that the generation times of trees can cause significant lags in the vegetational response to decade by decade changes in climate. It is the response to intermediate time scales that is harder to analyze and that raises important conceptual and factual issues. One conceptual issue concerns which definition to use for equilibrium, which Chorley & Kennedy (1971, p. 201) described as 'a highly ambiguous state' with '... many different aspects and ... the subject of a wide variety of definitions'. I have chosen here a definition for dynamic (vs static, stable, steady state) equilibrium, and this definition leads to discussion of six other topics: 1) dynamic models for climatic forcing of vegetational changes, 2) the effect of spatial and temporal scale (i.e. coverage and resolution), 3) data characteristics and methods of data display, 4) the likely response times of vegetation to climate

change at a specified scale, 5) the likely nature and pattern of climatic change during the late-Quaternary, and 6) the representation of the climatic relationships of the taxa under study.

Vegetation-climate equilibrium

The distribution and composition of vegetation is a sensor of climatic variations at selected spatial and temporal scales. No sensor, however, is ever in perfect equilibrium with the system being sensed, especially when the system is as dynamic as climate, which varies continuously on all time scales (Kutzbach, 1976). The full vegetational response must lag any change in climate. Bryson & Wendland (1967) illustrated a hypothetical example of an exponential-decay response to a step-function climatic change; Davis & Botkin (1985) have recently simulated this type of response with a forest succession model. An exponential response is identical in form to the response of a mercury thermometer when subjected to a step-function temperature change on the time scale of minutes (Middleton, 1947).

What then constitutes an equilibrium state between vegetation and climate? How can such a state be recognized in the behavior of two dynamic systems? A necessary first step toward a definition of dynamic equilibrium involves splitting the spectrum of climatic variations into its constituent frequency bands (time scales of variation) and then posing the question in terms of specific frequency bands (Chorley & Kennedy, 1971). For each frequency band, the judgement about equilibrium between the time series of two dynamic systems will then depend upon the ratio of the response time in one system (vegetation as recorded at a particular spatial scale) and the time scale of variation in the other system (climate) to which it is responding (Imbrie & Imbrie, 1980; Clark, 1985; Ritchie, 1986).

This ratio definition pits the alternative explanations for late-Quaternary vegetation change against each other. The ratio for a particular time scale will be large if lag times dominate the response and small if the time scale of climate change dominates. For extremely short-term climatic changes, the vegetational response may be too slow for a compositional change to record them (Davis & Botkin, 1985). For certain other choices of spatial and tem-

poral scale, these ratios may be as low as 1/50 to 1/100. Under such conditions, the vegetation would effectively be in equilibrium with the designated scale of climatic change, because the vegetational response would be an adequate approximation to an equilibrium response and the vegetation would 'track' changes in its climatic environment (Fig. 1, see the next section for the theory that underlies this figure). Palaeoclimatologists need to choose data sets and to filter or analyze their records such that the records depict a given frequency of climatic variation with as low a ratio as possible. When the ratio is low for a certain vegetational data set, then those data should be highly sensitive to the frequency band of climatic variation being monitored.

This ratio definition for equilibrium is appropriate because both systems being studied are dynamic (Figs. 1, 2). For time scales within which the ratio is low, a *dynamic equilibrium* will exist between vegetation and climate in which secondary succession and other short-term vegetational fluctuations will appear as 'balanced fluctuations about a constantly changing system condition [the vegetational composition] which has a trajectory of unrepeatable "average" states through time' (Chorley & Kennedy, 1971, p. 203). This type of equilibrium contrasts with *steady-state equilibrium* which exists for an open system whose average '... properties are invariant when considered with reference to a given time scale. . .', but whose instantaneous properties may oscillate about the average values (Chorley & Kennedy, 1971, p. 202). Chorley & Kennedy (1971, p. 204) also note that when a dynamic equilibrium exists between two systems, 'the equilibrium state can only be satisfactorily specified . . . with strict reference to a given length or scale of time'. Clark (1985) has shown that the concepts of relative scale, in which the temporal and spatial scales of two systems are compared, and of dynamic equilibrium have a well established history in geography, population ecology, oceanography, and climatology.

Under the conditions of dynamic equilibrium for a certain time scale, if the climate at that scale has changed continuously, then the composition of the vegetation will also have changed continuously, and stable vegetation (i.e. vegetation of constant composition) will only have existed if the climate was stable. Evidence for vegetational instability (i.e. continuous compositional change) is therefore not necessarily evidence for disequilibrium conditions.

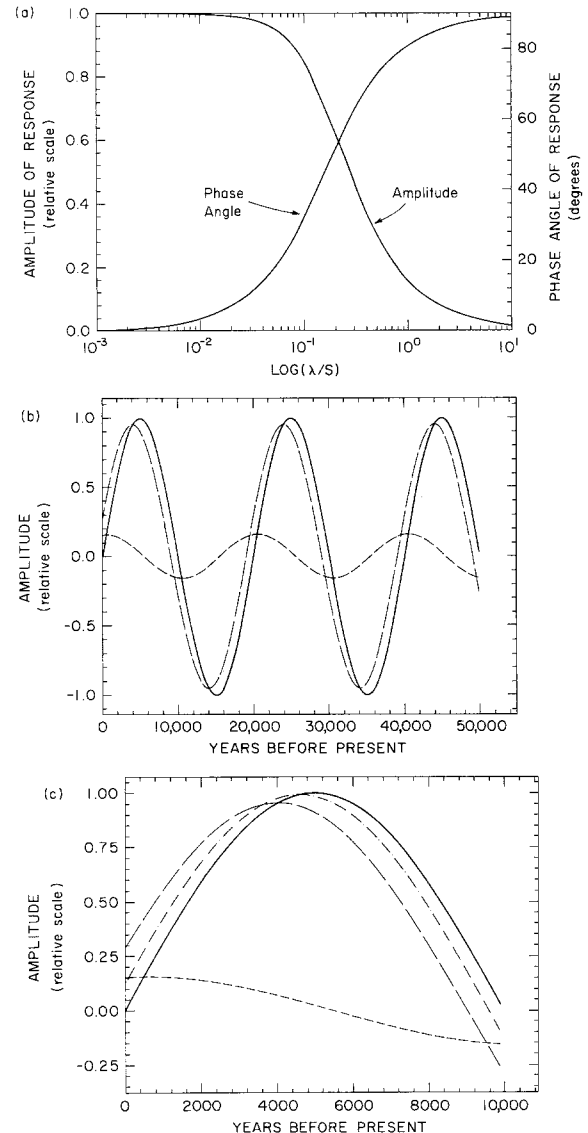


Fig. 1. a. Plot showing how the amplitude and phase angle of response change as λ/S increases, where λ is the vegetational response time and S is the period of climatic forcing. The phase angle is a measure of the offset or time lag between the forcing function and the response curve. λ/S is plotted on a log scale to make the distance from 10^{-2} to 10^{-1} equal to the distance from 1 to 10. The amplitude has an arbitrary scale from 0 to 1.0.

b. Vegetational response to sinusoidal climatic forcing as predicted by equation (4) in the text. Solid line represents climatic forcing with a period (S) of 20000 yr, and the long and short dashed lines represent the vegetational response for λ/S ratios of 1/20 and 1/1 respectively. The amplitude is scaled from -1.0 to 1.0.

c. Sample plot as b, but enlarged to show the results for the 10000 years before present. Long and short dashed lines as in b). The line of dashes and dots is for $\lambda/S=1/50$.

By using a different definition for equilibrium conditions and equating disequilibrium with instability and continuous compositional change, Delcourt & Delcourt (1983) concluded that the continuous compositional changes in the Holocene vegetation of the Midwest resulted from disequilibrium vegetational dynamics. Their definition for equilibrium seems appropriate for either stable or steady-state climatic conditions that have been assumed in studies of secondary succession, but changes in seasonal radiation guarantee that such conditions did not exist over the length of the Holocene in the Midwest or Southeast (Kutzbach & Guetter, 1984).

Models for climatic forcing of vegetation change

The formulation of a differential equation for the vegetational response to climatic variation can help clarify the above discussion of dynamic equilibrium. This formulation begins with an initial model that follows directly from the intuition that the rate of vegetational change is greater after a large climatic change than after a small climatic change. This intuition is captured in a differential equation in which the rate of the vegetational response (dV/dt) is proportional to the difference in the vegetational composition ($V - V_1$), where V is the composition at time t and V_1 is the composition required for the vegetation to be in equilibrium with the climate after a sudden step-function climatic change at $t=0$, i.e.,

$$dV/dt = -(1/\lambda)(V - V_1) \quad (1)$$

(This and the following equations are direct modifications of those Middleton, 1947, described in his consideration of time lags in thermometers and are similar to equations discussed by Imbrie, 1985.) Response functions exist that can estimate V_1 for a known climatic state (Bartlein *et al.*, 1985). Integration of equation (1) between $t=0$ (when $V=V_0$) and t yields

$$V - V_1 = (V_0 - V_1)\exp(-t/\lambda) \quad (2)$$

When $t = \lambda$, the difference between V and V_1 is $1/e$ of the original difference (where e is the base of the natural logarithm), and λ , a measure of the vegetational response time, is therefore called the $1/e$ fold-

ing time, i.e. the time for the compositional difference to decrease exponentially by 63%.

The model can be modified to incorporate continuous as well as periodic climatic changes by expressing V_1 as follows:

$$\begin{aligned} V_1 &= f(\text{climate}) = a_0 + a_1 \sin(2\pi t/S) \\ dV/dt &= -(1/\lambda)(V - (a_0 + a_1 \sin(2\pi t/S))) \end{aligned} \quad (3)$$

where S is the period for the sinusoidal forcing and a is its amplitude. The simple harmonic forcing is used here as an adequate first approximation for the climatic variations resulting from the orbitally driven variations (Berger, 1981). This equation becomes

$$V - V_1 = C_1 \exp(-\lambda/t) + (a_1/C_2) \sin((2\pi t/S) - \gamma) \quad (4)$$

where C_1 is a constant that depends on initial conditions, but the term it multiplies can be ignored if t is very much larger than λ ,

$$\begin{aligned} C_2 &= (1 + (2\pi\lambda/S)^2), \\ \tan \gamma &= 2\pi\lambda/S \text{ and } \gamma \text{ is the phase angle.} \end{aligned}$$

The vegetational response in equation (4) is sinusoidal with an amplitude reduction (a/C_2) and phase lag (γ) that depend on λ/S , the ratio of the vegetational response time (λ) to the period of the forcing (S). For 'Milankovitch' orbital forcing, S has values between 20000 and 100000 yr (Imbrie & Imbrie, 1980; Ritchie, 1986), and λ 's of 400 to 1000 yr can therefore be tolerated because they only cause small reductions in the amplitude of the response (Fig. 1).

Model (3) explicitly represents the continuous nature of the climatically forced vegetational change during the Quaternary and earlier times. No taxa could evolve and survive for long without their λ being short enough for the taxa to track the continuously changing location of their growth habitats (Good, 1931). Given this fact, the main concern about disequilibrium conditions must narrow from concern about long-term tracking of habitats to concern about selected time intervals during which regional changes in climate might have been so rapid that the lags in vegetational response significantly affected vegetational composition for 1000 yr or more. Sinusoidal forcing, however, includes times of relatively rapid change,

during which the vegetation also would have changed rapidly. During these times, the time lag in the response is most evident (Fig. 1), which may explain, in part, why the period of inferred rapid climatic change from 14000 to 9000 yr B.P. is such a focus concern for the vegetation lagging climate.

Importance of scale

The sensitivity and response time of vegetation to variations in climate depend on the spatial and temporal scales at which the vegetation is observed (Ritchie, 1986). Conclusions about whether the vegetation is in equilibrium with climate will vary depending upon whether the focus is upon either high frequency short-term climate changes or low frequency long-term changes. For pollen data, the climatic forcing may include a) short-term changes involving both decade-scale changes (Dust Bowl climatic change in the Midwest) and century-scale changes (Little Ice Age and short-term glacial advances including the Younger Dryas), and b) long-term changes involving millennial scale and longer changes such as post-glacial warming, ice-sheet retreat, and other orbitally induced climatic changes (Fig. 2). As the observational time scale is lengthened, the vegetational response to climatic variations changes both in kind and in quantity. Monthly and annual climatic variations induce physiological responses in trees that are recorded in tree rings, but the abundance changes recorded by pollen data generally require century or longer changes in climate.

The spatial scale of pollen studies can also influence the conclusions about whether equilibrium conditions exist because the relative importance of climate in influencing vegetational variations varies with spatial scale (Delcourt *et al.*, 1983). Different conclusions about which factors control pollen variations can arise if the primary concern is to interpret each level-by-level variation in a pollen diagram, whose pollen-source area is ca. 10^2 to 10^3 km² (Bradshaw & Webb, 1985), rather than understanding the major long-term (>1000 yr) pollen changes across a continent (10^7 km²) or region (10^5 km²). Many nonclimatic factors, e.g. near-site (within 30 km) soil development and secondary succession, can influence both the short-term and even some of the long-term variations in a single

pollen diagram. At a continental scale all of these near-site variations should appear as unique occurrences at individual sites, and the broad scale patterns (covering distances of 1000 km or more) that relate to climatic patterns will dominate (Fig. 3).

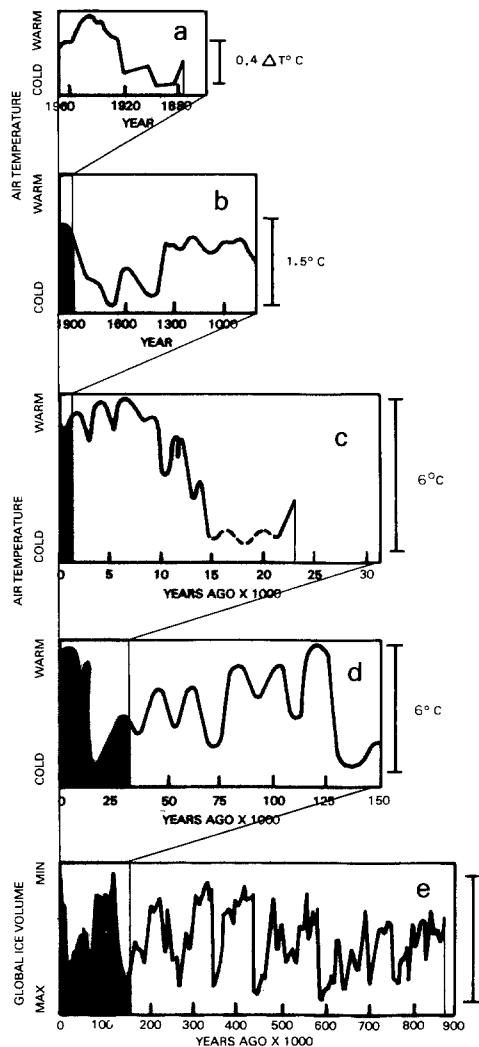


Fig. 2. Estimated variability of the global mean temperature for various time scales from decades to hundreds of millennia (modified from National Research Council, 1975 and Bernabo, 1978). Time series are based on a) averages from instrumental data, b) general estimates from historical documents, emphasis on the North Atlantic region, c) general estimates from pollen data and alpine glaciers, emphasis on mid-latitudes from eastern North America and Europe, d) generalized oxygen isotope curve from deep-sea sediments with support from marine plankton and sea-level terraces, and e) oxygen-isotope fluctuations in deep-sea sediments (volume indication = 5×10^{16} m³).

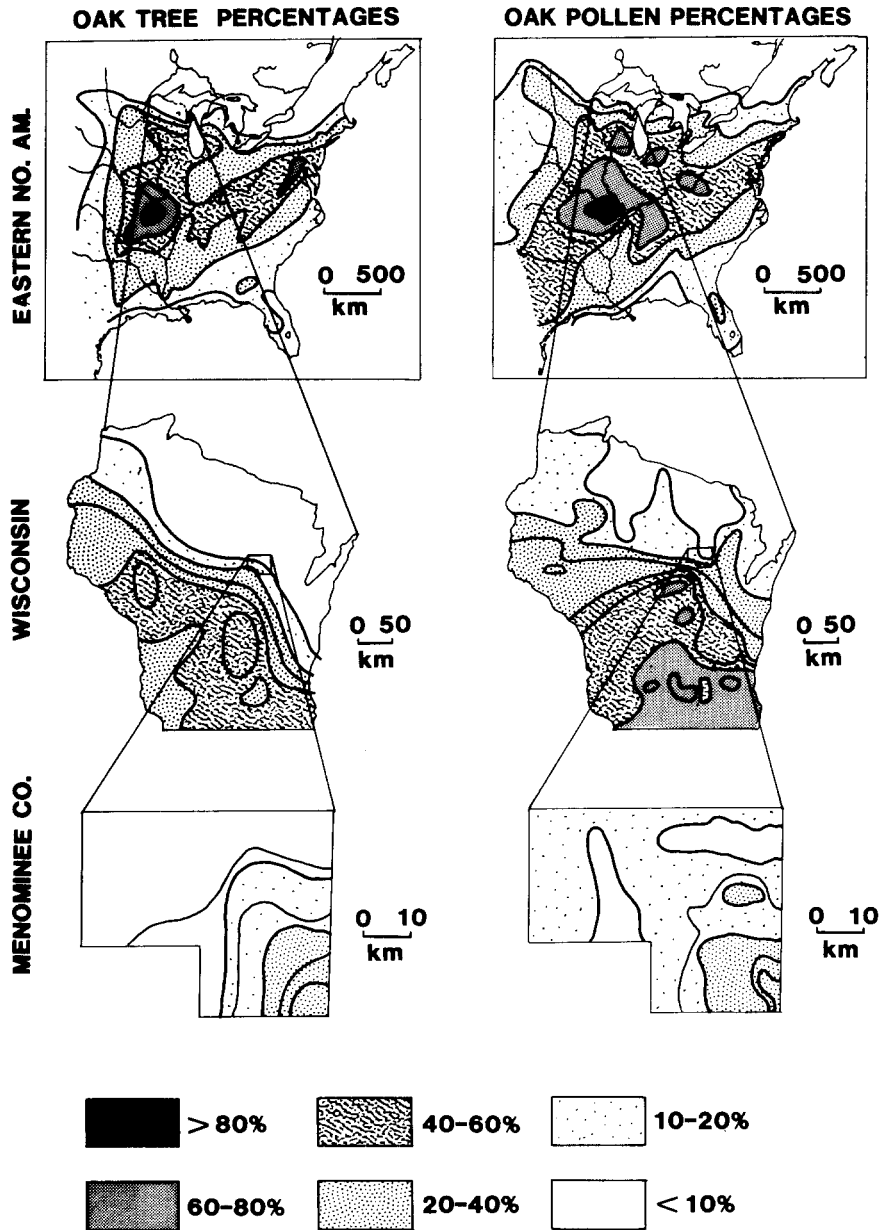


Fig. 3. The geographic distribution of oak (*Quercus*) pollen as percent of total tree pollen and oak trees as percent of total growing stock volume (eastern North America) or of total basal area (Wisconsin and Menominee) for subcontinental (5×10^6 km²), regional (10^5 km²), and subregional (10^3 km²) scales. (Note: the data from Menominee are not to be included in the data from Wisconsin, but the latter are included in the data from eastern North America, thus making the contour patterns in Wisconsin similar at both the subcontinental and regional scales.) Data from Delcourt *et al.* (1984) and Bradshaw & Webb (1985). Figure from Solomon & Webb (1985) and republished with permission from the Annual Reviews of Ecology & Systematics, Vol 16 © 1985 b, Annual Reviews, Inc.

For instance, at the subcontinental (5×10^6 km²) and regional (10^5 km²) scales, the contemporary abundance gradients for oak (*Quercus*) pollen and trees in eastern North America reflect the broad-scale temperature and moisture gradients (Fig. 3; Bartlein *et al.*, 1984). In contrast, at a subregional (10^3 km²) scale, the abundance gradients for *Quercus* grade outward from a region of sandy outwash soils and are unrelated to climatic patterns (Fig. 3; Bradshaw & Webb, 1985).

Data characteristics and methods of data display

By choosing a particular data set and the methods for displaying its variations, an investigator can influence how clearly a potential climatic signal is displayed. For pollen data, these choices include the total time span and area of coverage, the sampling frequency and the stratigraphic resolution of individual samples, and the taxonomic precision and numerical nature of the data (Webb *et al.*, 1978; Webb, 1982). The effect of these choices can be illustrated by extreme cases. Pollen percentages and even pollen accumulation rates in a series of short cores of varved sediment in lakes from a small area can reveal local variations in soils (Fig. 3; Brubaker, 1975; Bernabo, 1981) or fire frequency (Swain, 1978). These local variations are hardly evident in the continent-wide gradients of pollen percentages from long cores with radiocarbon dates (Fig. 3; Webb, 1981).

Different methods of data display also affect the types of variability evident in the data. For example, filtering the data by averaging and contouring smooths out variations including local site effects or soil variations and thus can increase the signal-to-noise ratio when macroscale climatic variability is of prime interest (Fig. 3). Maps showing isochrones of range boundaries focus attention on range extensions and contractions free of major abundance variations, but maps of the changing abundance patterns for each taxon offer a much greater potential for providing climatic information (Davis, 1978). These latter patterns are illustrated on isopoll and difference maps (Bernabo & Webb, 1977; Webb *et al.*, 1983a). A focus on range extensions rather than abundance changes reflects an interest in floristics and an emphasis on the climatic controls of species limits rather than on the

climatic control of species abundances throughout a geographic area. Ecologists have focused on climatic correlation with species limits because many maps are available that show geographic distributions (Little, 1971), whereas fewer maps of taxon abundances have been readily available (Webb, 1974; Bernabo & Webb, 1977; Delcourt *et al.*, 1984). In contrast to the range-limit maps, however, the maps of taxon abundances provide a clearer format for identifying which climatic variables influence the plant distribution patterns, because both the range boundary (a single line) and the abundance gradients can be used in establishing whether a pollen type or plant taxon is aligned with a particular climate variable and its spatial gradients (see Figs. 2 and 3 in Bartlein *et al.*, 1984 and Fig. 2.1 in Davis, 1978). Models of density-dependent competition have made ecologists wary of trusting the climatic sensitivity of species abundances within a given community, but Enright (1976) has discussed this problem and shown why this distrust is unwarranted.

The use of pollen data for sensing past climatic change requires many decisions guided by an interest in extracting the climatic information within the data. For the study of late-Quaternary climates, networks of pollen data are needed from regional to continental areas. Average sampling density in these data sets ranges from 1 sample per 10^4 – 10^5 km², and the sampling frequency in individual cores averages 1 sample per 200–500 yr (Table 1). The uncertainty in radiocarbon dates for correlating synchronous levels in a network of cores is about 300 yr (Webb, 1982). Within these data sets, the smallest reliable time intervals for mapping are therefore 500–1000 yr. Lags between vegetation and climate that result from certain ecological processes (e.g. secondary succession or dispersal) may not be resolvable within data sets from large regions and continents, if the lags are shorter than 500 yr or involve distances of 100 km or less for the densest of available networks of sites (e.g. southern Quebec, Fig. 5) or 200 km or less for subcontinental regions (e.g. eastern North America). Paired sites from different soil types within 30 km of each other can reveal significant differences in pollen composition and the timing of vegetational changes (Brubaker, 1975; Bernabo, 1981), but these subgrid-scale variations are often small when contrasted with the climatically controlled composi-

Table 1. Sampling characteristics in space and time.

	Grid size km ²	Area sampled by each sample km ²	Sampling density (samples per area) no./10 ⁵ km ²	Total time span yr	Stratigraphic resolution for each sample yr	Sampling frequency no./1000 yr
Pollen records						
Lake sediments	10 ⁷	10 ² – 10 ³	1	2 × 10 ⁴	10 – 50	2 – 5
Lake sediments	10 ⁵	10 ² – 10 ³	10	10 ⁴	10 – 50	2 – 5
Varved-sediments	2 × 10 ⁶	10 ² – 10 ³	1	2 × 10 ³	2 – 10	20 – 100
Mor humus or Small basin in canopy	N.A.	10 ⁻³ – 10 ⁻²	N.A.	10 ³ – 10 ⁴	5 – 50	2 – 5
Plant macrofossils						
Lake sediments	N.A.	10 ⁻⁵ – 10 ⁻²	N.A.	10 ⁴	20 – 40	2 – 5
Lake sediments	N.A.	10 ⁻⁵ – 10 ⁻²	N.A.	10 ³	20 – 40	20 – 40
Peat middens	5 × 10 ⁶	10 ⁻⁴ – 10 ⁻²	1 – 2	2 × 10 ⁴	2 – 10	1
Tree rings						
Climate network	10 ⁷	10 ⁻⁴ – 10 ⁻²	10	3 × 10 ²	1	10 ³

tional contrasts over 300–1000 km in large data sets (Fig. 3).

Vegetation response times

An exact definition for the vegetation response time (λ) depends upon the mathematical form of the vegetational response to a given climate change and upon the types of vegetational response that must occur for the response to be considered complete. For situations in which step-function climate changes induce an exponential lag-response in the vegetation (equation 1), the vegetation response time can be defined as the time the vegetation takes to reach 1/e of the total response (Clark, 1985). If the functional form of the response is unknown, then the response time can still be defined by the general term relaxation time, which is the time required for the vegetation to complete some fraction or all of its total response to a step or pulse change in climate (Chorley & Kennedy, 1971).

In considering situations in which the vegetational response depends upon several factors from seed dispersal to rates of disturbance, I have found it useful to distinguish between two types of vegetational response: 1) an 'immediate' Type A response in which range extensions and soil development are not necessary for the vegetation to reach its new composition (V_1) and 2) a 'full' Type B response in which range extensions and soil development are key factors. When several species are present in the vegetation, each with different ecological relation-

ships to climate, most climatic changes should elicit an immediate (i.e. 1/e folding time of 50–80 yr) response in the vegetation by altering the competitive balance among the species that are present (Type A response). Even if only one tree taxon were present, e.g. *Populus* or *Picea*, with an ability to tolerate a wide variety of climates, a shift in climate would elicit a relatively rapid response in the mixture and abundance of shrub and herb taxa. In most environments, the response would be immediate whether or not all species that can grow in the environment are present. At a subregional scale (10³ to 10⁴ km²), immediate responses to climatic change should be evident within species-abundance gradients along edaphic or topographic gradients (Brubaker, 1975; Bernabo, 1981; Davis *et al.*, 1980; Gaudreau, 1986). A given climatic change may also induce certain species to expand their range on a regional to continental scale (Type B response). When these new species appear in a region, the vegetational composition (i.e. species list and abundance of various species) will change. The effect of the range extensions can be to lengthen the time for a full response of the regional vegetation and to alter its final composition, but some type of observable, immediate response should still have occurred with a response time of 50–80 yr.

If the total response time is less than 400 yr, then dispersal and establishment lags should not affect climatic calibration studies that produce maps for each 1000-yr interval and record orbitally induced changes in climate (Fig. 1). Problems may arise if the total response time is longer. But even if total

response times were to be 1000 yr or longer, immediate responses would guarantee some sort of compositional changes on very short time scales (100 yr or less), and maps of these changes over 10^4 – 10^6 km² should show patterns that contain climatic information.

Vegetation has responded to short-term climatic change like the 'Little Ice Age' of 1450 to 1850 A.D. Several relatively high-resolution palynological studies in the Midwest have indicated vegetational changes for this time interval. Davis (1981b) described beech (*Fagus*) expanding its range in upper Michigan (Type B response), Swain (1978) and Bernabo (1981) illustrated compositional changes in Wisconsin and Michigan (Type A responses), and several studies have recorded prairie retreat and forest development in central Minnesota (McAndrews, 1968; Waddington, 1969; Grimm, 1983). Such sensitivity implies short response times with $1/e$ -folding times of 50–100 yr. Recent research with a forest-stand-simulation model for northeastern forests is supportive of response times for Type A responses being this short (Davis & Botkin, 1985). For climatic change with a period (S) of 10000 yr or more, these lags are too small to cause disequilibrium conditions (Fig. 1).

If response times of 1000 yr or longer are claimed, then seed dispersal, seedling establishment (Davis, 1981), and soil formation (Pennington, 1986) must be among the main factors causing the lags. Can they be the cause of such long lags? Studies of seed dispersal by birds indicate rapid local dispersal rates. During one field season, Darley-Hill & Johnson (1981) observed blue jays (*Cyanocitta cristata*) caching acorns at a mean distance of 1.1 km from the seed producing trees, and in another field season, Johnson & Adkisson (1986) observed blue jays depositing beechnuts up to 4 km from the seed producing trees. Because the preferred cache sites were open areas, the blue jay behavior favors both dispersal and establishment. Over a longer observation period, longer dispersal by rare events becomes possible and might involve distances of 10 km or more in one year. Vander Wall & Balda (1977) observed the Clark's nutcracker carrying pine seeds up to 22 km. Tornadoes at the right season could transport seeds of all sizes 50 km or more. The combination of these and other dispersal processes (e.g. wind blown seeds on ice- or snow-covered surfaces) should yield maxi-

imum dispersal rates that exceed the average rates of population expansion estimated from isochrone or isopoll maps (Davis, 1981a; Bennett, 1984). Were a rapid large change in climate to shift the climate limits for several taxa by 500 to 1000 km, then the opportunities for rare events dispersing seeds for long distances would be much enhanced. Over 500–1000 yr the prevalence of disturbance (either fires or blow-downs) would continuously create open areas in which seedlings of new taxa could become established once the climate was favorable.

The initial development of soil sufficient for tree growth can be rapid in recently deglaciated terrain. In studies patterned on Cooper's (1931, 1939) classic work, Jacobson & Birks (1980) and Wright (1980) provided evidence for spruce trees growing on such terrain within 100–300 yr after the retreat of the Klutlan glacier in the Yukon. However, Pennington (1986) estimated soil-related lags of 500–1500 yr at selected British sites from 10000–12000 yr B. P., but her estimates depend upon certain assumptions about the timing and uniformity of climatic change at that time. A clear message from her study is that the timing of vegetational changes can vary among regions with different soils and that careful site selection can provide the data with the fastest and largest vegetational response to a particular change in climate (Brubaker, 1975; Bernabo, 1981).

Another potential control on climatic response times for various taxa is their ability to evolve in the face of environmental change. Selective pressures have changed during the past 20000 yr, and these changes have surely induced changes in gene frequency within the taxa as they migrated. These evolutionary changes probably led to changes in the environmental response of each taxon, but the differences resulting from these short-term within-taxon changes have probably been relatively small compared to the differences in environmental tolerances between taxa. Were within-taxon genetic changes large and the dominant response, the differentiation of new ecotypes would buffer the effects of climatic change (Good, 1931), and these ecotypes would resist competitive replacement by other taxa. The empirical evidence for rapid replacement among taxa during the past 20000 yr, however, suggests that the within-taxon genetic changes are far from dominant. Evolution within taxa has surely occurred during the past 20000

Table 2. Time scales and magnitudes of a hypothetical change in mean July temperature and the effects of response times or rates of various processes (e = effect significant, p = possible effect, n = no significant effect, x = observation unlikely).

Vegetational process		Compositional change induced by								
Process or factor	Growth of single tree	Succession after disturbance	Type A response ^a		Type B response ^a		Soil development			
			80 yr ^b 5°, 2°, 1°C	80 yr ^b 5°, 2°, 1°C	Fast dispersal 1.0 km/yr ^c 5°, 2°, 1°C	Slow dispersal 0.2 km/yr ^c 5°, 2°, 1°C	Micro-evolution 0.1°C/1000 yr ^d 5°, 2°, 1°C	Fast 100 yr ^b 2°C	Medium 1000 yr ^b 2°C	Slow 10000 yr ^b 2°C
Rate of response	annual	80 yr ^b	80 yr ^b	80 yr ^b	1.0 km/yr ^c	0.2 km/yr ^c	0.1°C/1000 yr ^d	100 yr ^b	1000 yr ^b	10000 yr ^b
Temperature change	5°, 2°, 1°C	5°, 2°, 1°C	5°, 2°, 1°C	5°, 2°, 1°C	5°, 2°, 1°C	5°, 2°, 1°C	5°, 2°, 1°C	2°C	2°C	2°C
Duration of climatic change										
10 yr	n, n, n	e, e, e	e, e, e	e, e, e	e, e, e	e, e, e	n, n, n	e	e	e
100 yr	x, n, n	e, e, e	e, e, e	e, e, e	e, e, e	e, e, e	n, n, n	e	e	e
1000 yr	x, n, n	n, n, n	n, n, n	n, n, n	n, n, n	e, e, n	n, n, n	n	n	e
10000 yr	x, x, x	n, n, n	n, n, n	n, n, n	n, n, n	n, n, n	n, p, e	n	n	e

^a Type A and B responses to climate change are defined in the text under Vegetation response times.

^b 1/e – folding time.

^c Maximum rate of dispersal. With mean July temperature gradients of 4°C/550 km in eastern north America, a 1°C change will induce a potential movement of 140 km, a 2°C change implies 280 km, and a 5°C change implies 700 km.

^d Hypothetical rate of temperature adjustment in a population. Such a gradual change seems unlikely but permits comparison with other effects.

yr, but its influence on the climatic response times of most taxa has probably been small.

Given the several time scales of climatic change (Fig. 2), a matrix of comparisons is required to determine which processes are rate limiting to the vegetational response at selected time scales (Clark, 1985). Table 2 aids this evaluation but is simplistic because, for illustrative purposes only, temperature change was used as a univariate proxy for the past multivariate changes in climate. Many processes limit the total response of vegetational compositional changes to short-term climatic changes of 10–100 yr, but only species with slow maximum dispersal rates or soils with development rates of 1000 yr or more have major effects on the vegetational response to climate changes of 1000 yr or longer (Table 2). Other processes such as secondary succession or evolution occur either too fast or too slow to have major effects at these long time scales.

Climatic change

To reason that differential migration rates and no-analog conditions imply that the vegetation is out of equilibrium with climate requires some independent knowledge or model of how climate has changed. Quaternary climatologists do not yet know the details of Holocene climatic change at the local to regional scale (10^2 – 10^5 km²) at which climate affects the vegetation recorded by one to several pollen diagrams. But evidence independent of pollen data is accumulating that shows 1) regional patterns in climatic changes on all time scales, 2) temperature and moisture conditions changing independently, 3) major changes in seasonality during the late-Quaternary, and 4) late-Holocene climatic patterns that are different from early Holocene patterns (Kutzbach, 1981; Street & Grove, 1979; Webb *et al.*, 1985).

Spatial patterns are evident in the sea-surface temperature map for 18000 yr B.P. (CLIMAP, 1981) just as they are in monthly and decadal anomaly maps (Reitan, 1971, 1974; Blasing & Fritts, 1977; Diaz & Quayle, 1980). On all time scales (Fig. 2), global climatic changes, whether they be abrupt or gradual, have been expressed differently in different regions, because they induced spatial patterns in temperature, precipitation, and other meteorological variables. Some areas became

wetter, others drier, warmer, or colder, and some areas registered larger changes whereas others registered no change in temperature, moisture, or both. These spatial patterns can lead to spatial variations in the perceived abruptness of the regional changes. Global changes that are gradual can induce abrupt changes in certain regions, and abrupt global changes can induce gradual changes locally or regionally.

Lake level data from the tropics and various continents indicate changes in regional water budgets and provide evidence for changes in the combination of temperature and moisture conditions in many regions (Smith & Street-Perrott, 1983; Street-Perrott & Harrison, 1985). The recent work of Kutzbach (Kutzbach, 1981; Kutzbach & Otto-Bliesner, 1982; Kutzbach & Guetter, 1984; Webb *et al.*, 1985) has demonstrated the potential importance of the orbitally induced seasonal variation in solar radiation as a forcing function for climatic change during the past 20000 yr. In the northern hemisphere, the seasonal radiational contrast increased until between 12000 and 9000 yr B.P. and then decreased (Fig. 4). Given the contrast in heat capacity between land and sea, the 8% increase in summer-season solar radiation at 9000 yr B.P. is likely to have increased the summer monsoons in Africa and Asia. Climate simulations from general circulation models support this inference (Kutzbach, 1981; Kutzbach & Guetter, 1984), and lake level and marine plankton data from 9000 yr B.P. provide evidence for markedly enhanced monsoon flow in Africa and Asia during the summer (Street-Perrott & Harrison, 1985; Prell, 1984; Webb *et al.*, 1985).

The changes in solar radiation also affected North American climates (Ritchie *et al.*, 1983; Heusser *et al.*, 1985), but the long-term retreat of the Laurentide ice sheet led to a more complicated climatic response than the response in tropical regions. At its maximum extent at 18000 yr B.P., the Laurentide ice sheet not only was a highly reflective surface to solar radiation but also acted as an orographic barrier to atmospheric circulation (Bryson & Wendland, 1967; Wright, 1984). As the ice sheet retreated, the climatic impact of its role as an orographic barrier decreased faster than its role as a reflective surface. The climatic consequences were therefore complex but are beginning to be understood (Kutzbach & Wright, 1985).

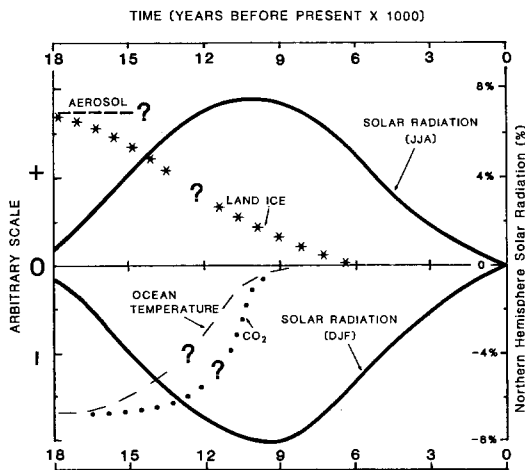


Fig. 4. Schematic diagram of the major changes of external forcing (northern hemisphere solar radiation for June and August and December to February, in percent difference from present, right-hand scale) and internal climatic boundary conditions not explicitly simulated by general circulation models (land ice, ocean temperature, CO₂, aerosols – arbitrary left-hand scale of plus or minus departure from present conditions). Question marks indicate uncertainty concerning the exact magnitude, timing, and, where appropriate, location of the boundary condition changes. (Diagram from J. E. Kutzbach, modified from version in Webb *et al.*, 1985).

Even without knowing the details, one can use meteorological theory along with the history of ice sheet retreat in order to describe some of the probable complexity in the climate changes in eastern North America since the last glacial maximum at 18000 yr B.P. When the temperature field across a subcontinental area is considered for some date (e.g. 12000–18000 yr B.P.), three features require description: 1) the mean temperature for the field, 2) the extreme temperatures and the direction of the main temperature gradient (i.e. the two sites with the highest and lowest temperature should be located), and 3) the regions within the field with steeper than average (or flatter than average) thermal gradients and the orientation of these steep (or flat) gradients within the study area. The position and orientation of the thermal gradients are important to meteorological dynamics because steep temperature gradients define the location of mean frontal positions and hence the regions in which storms

form and track. Such regions mark the boundaries between contrasting air masses.

When the vegetation responded to increasing temperatures after a postulated temperature minimum during full glacial times (see Peterson *et al.*, 1979 for evidence from 18000 yr B.P.), the mean temperature for eastern North America increased and the difference in temperatures between the northern and southern ends of the continent changed. The magnitude of the temperature changes in the north and south were not the same, but radiational differences guarantee a north to south temperature contrast at all times. The presence and slow retreat of the Laurentide ice sheet from 18000 to 6000 yr B.P. also guarantees that certain regions warmed faster than others. Within this framework of change, if one region warmed faster than another region, then the position and orientation of the steep thermal gradients would change. The increasing temperatures would change the characteristics of the air masses, and the changing location of the thermal gradients would necessitate changes in the location of storm tracks and in the frequency and duration of the air masses. Rainfall patterns and magnitude would also be affected by the increasing temperatures, the changes in the air masses, and the changes in the thermal gradients.

In light of all these changes and their varying effects, I would label any model for Holocene climatic change simplistic if it emphasizes mere increases and decreases in mean annual temperature and implies a similar timing and magnitude for this increase and decrease at all sites across North America. The northward movement of the July and January isotherms was not uniform in space and time; and, with changes in precipitation and seasonality, few or no species ranges should have moved northward in a uniform manner. The many interacting elements of late-Quaternary climatic change are quite sufficient to allow for the observed criss-crossing patterns and differential rates of range-boundary movements that Davis (1978, 1981a) and Birks (1981) have interpreted as evidence for migration lags and non-equilibrium distributions. Under the complex nature of past climatic changes, individualistic behavior by the different species should be expected (Chapin & Shaver, 1985).

Pollen-climate response functions and their application

Bartlein *et al.* (1985) have recently developed a series of multiple regression equations that use temperature and precipitation data to estimate the abundance of selected pollen types. These ecological equations (*sensu* Imbrie & Kipp, 1971) represent linear combinations of climatic variables that can reproduce the modern abundance patterns of these pollen types at the continental scale over which their past distributions have been mapped (Bernabo & Webb, 1977). The equations illustrate the unique 'individualistic' relationship between each pollen type and climate and show how the relative importance of the various climatic variables varies across the range for each taxon. An example in the next paragraph illustrates how these ecological equations can help in explaining past changes in the vegetation. Although further testing is required to show whether the ecological and climatic explanations are correct, the example demonstrates the type of interpretations that become possible when a complex and plausible model for climatic change is entertained.

Isochrone maps of pollen variations in southern Quebec show that beech (*Fagus*) populations increased northward over distances of 200 km after 6000 yr B.P. while *Picea* populations increased southward 200 km after 4000 yr B.P. (Fig. 5). These changes could be considered as evidence for delayed range and abundance expansion in beech, because its population was still moving northward after the climate had begun to cool enough for the spruce population to move south. An alternate interpretation is supported by the evidence for how spruce and beech abundances are related to July and January mean temperatures (Fig. 6). The variations in the earth's orbit since 6000 yr B.P. have decreased July solar radiation in the northern hemisphere by 5% but increased January solar radiation by 5% (Fig. 4; Berger, 1981; Kutzbach & Guetter, 1984). These radiation changes probably decreased the seasonal contrast in temperatures in southern Quebec (Fig. 6). For this type of seasonal climatic change, the ecological equations indicate that beech values would increase from 0 to 2% and *Picea* values would increase from 1 to 8%. Both increases are statistically significant (Bartlein, pers. comm.). Independent physiological evidence indi-

cates that the vernalization mechanism for *Fagus* trees does not work for winter temperature extremes below -40°C (Burke *et al.*, 1976). Warmer winters with fewer occurrences of temperatures below -40°C would therefore favor more *Fagus* trees growing further north during the late-Holocene.

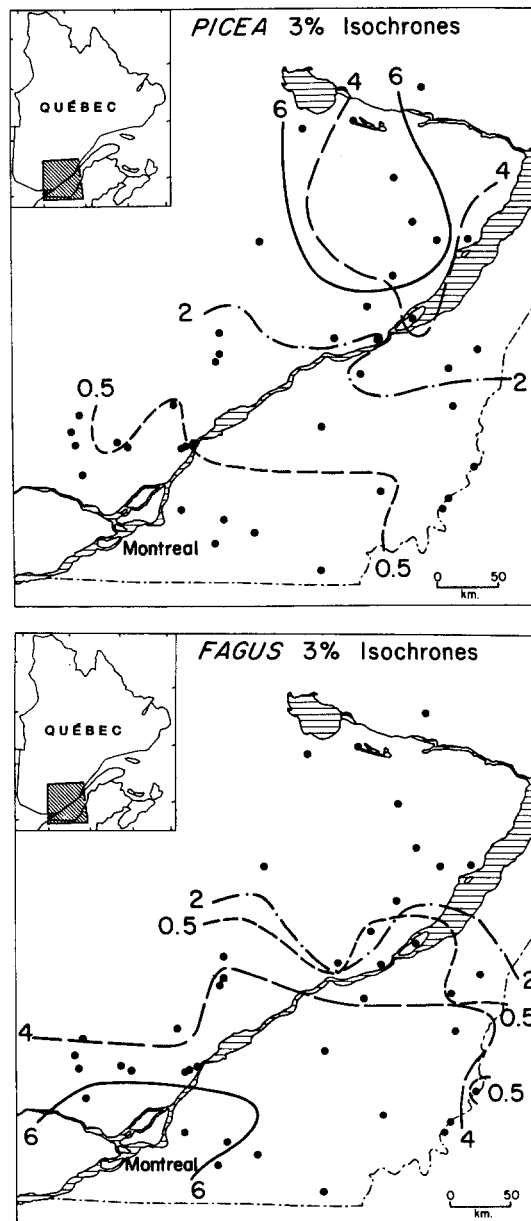


Fig. 5. Isochrone maps in 10^3 yr B.P. for the southward extension of the 5% isopoll for spruce (*Picea*) pollen and for the northward extension of the 3% isopoll for beech (*Fagus*) pollen in southern Quebec (from Webb *et al.*, 1983b).

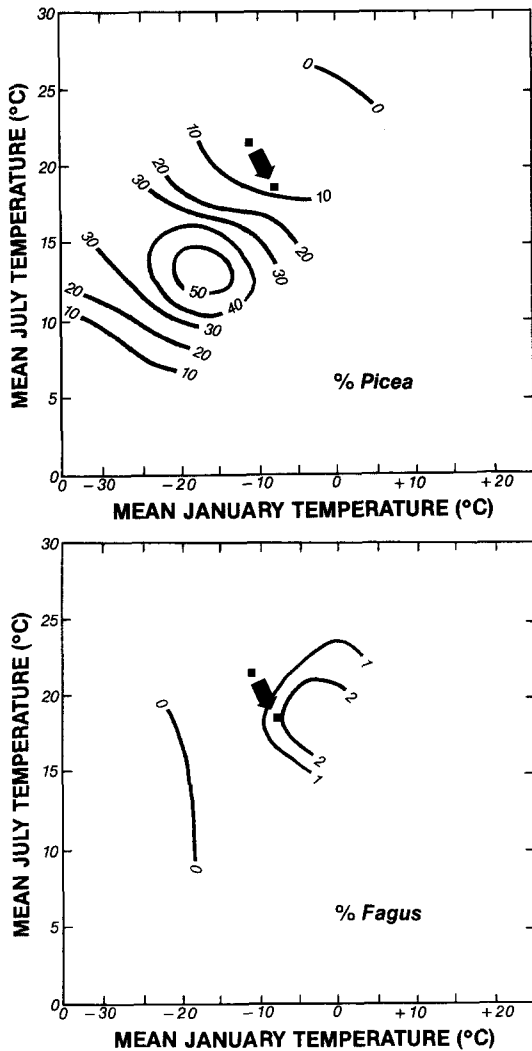


Fig. 6. Scatter diagram showing the smoothed distribution of percentages of spruce (*Picea*) and beech (*Fagus*) pollen from sediment samples with modern pollen data in eastern North America when the pollen percentages are plotted at coordinates for modern January and July mean temperature (P. J. Bartlein, unpubl.). The arrow indicates the direction and approximate magnitude of temperature change at Montreal since 6000 yr B.P.

Conclusions

Climate changes during the late-Quaternary have been complex, and the details of the vegetational response to climate change are also complex. Many processes are involved (Table 2). Both the time scale and magnitude of the climatic change affect wheth-

er each process might influence the vegetational response to climate (Figs. 1, 2; Table 2). Pollen data can record vegetation change at several different scales of time and space (Fig. 3; Brubaker, 1975; Webb *et al.*, 1978; Jacobson & Bradshaw, 1981), and the available analytical techniques can emphasize different aspects of the data (Solomon & Webb, 1985). For certain of these scales and data displays, endogenous processes may dominate and the effects of climatic change may be obscure (Table 2). At such scales, the data are relevant to the study of endogenous vegetation processes and their effects on climatic response times. In those studies that illustrate secondary succession as the dominant dynamics, the definition of steady-state equilibrium may best describe the equilibrium state. At other time and space scales and with a different display of the data, direct climatic interpretation of the data may be appropriate. Endogenous processes still determine the climatic response in the vegetation, but the response times are short compared to the time scale of the dominant climatic change, and the conditions for a dynamic equilibrium can be assumed.

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