

## 2. CLIMATIC INTERPRETATION OF POLLEN IN QUATERNARY SEDIMENTS

by Margaret B. Davis

### SUMMARY

Paleoclimatic interpretation of the fossil pollen record uses both the distribution limits of species and their abundances. In each case the relationship of the plants to modern climate is used to interpret past occurrences. Problems arise in using pollen to determine accurately either the distribution of a species in space or its abundance, but the real limitation of the method seems to be lack of understanding of the role of climate in controlling plant species. The distribution data seem to give more precise paleoclimate estimates, but the approach leads to consideration of each species in isolation. The use of abundances, because it relies so heavily on interpretation of pollen assemblages, places more emphasis on the entire community and its relation to regional climate. Here the major difficulty comes in understanding unique communities that differ from modern analogues. They may differ because of biological factors such as immigration lag yet reflect a climate fully analogous to modern climate. Or they may indicate a unique combination of climatic conditions that has evoked a unique vegetation response. Complicating these interpretations are interactions among species, which can produce changes in abundance that mimic the effect of climatic change. Species interactions, although difficult to unravel from climatic effects in the fossil record, have potential for showing how changes in the physical environment influence the outcome of competition in plant communities.

### INTRODUCTION

Reconstructions of ancient climate that are based on distributions of plants or animals rely on the generalization that each species tolerates a particular set of climatic conditions. The occurrence of fossils implies ancient climate within that particular species' range of tolerance. The assumed relationship of a species to climate is shown in figure 2.1a, where the abundance of an organism is plotted against a climatic parameter. Where conditions are optimal the organism will be abundant (region A), where conditions are marginal the organism will be rare (regions B and B'), and at the upper and lower limits of tolerance (points C and C') the organism will not survive.

Typically, interpretations of fossils use only a part of the information shown in figure 2.1a. The limits of the distribution are emphasized when interpretations are based on presence or absence. For example the presence of a fossil may be used to indicate a paleotemperature within the range C to C'. In practice, one is often dealing with one edge of the range of a fairly widespread species, thus arguing, for example, that the temperature exceeded C (fossil present) or was less than C (fossil absent). In order to gain more specific information, investigators sometimes use two or more species with overlapping tolerances (figure 2.1b). The presence of species 1 alone indicates temperature ranging between C and D, species 1 and 2 together temperatures ranging between D and C'. The classic example in palynology is Iversen's (1944) study of the changing occurrence of holly, ivy and mistletoe in the Danish Holocene. He concluded that mean temperatures in the coldest month four thousand years ago were above  $-2^{\circ}\text{C}$  (the lower limit for ivy, which was present) but below  $-0.5^{\circ}\text{C}$  (the lower limit for holly, which was absent), while mean temperatures during the warmest month were above  $17^{\circ}\text{C}$  (the lower limit for mistletoe, which was present). Since that time the climate has become more maritime; temperatures in the coldest month now average above  $-0.5^{\circ}\text{C}$  and both holly and ivy are present, while the mean July temperature has fallen below  $17^{\circ}\text{C}$ , and mistletoe has become extinct. Iversen based his conclusions on summer and winter temperatures in regions where each species

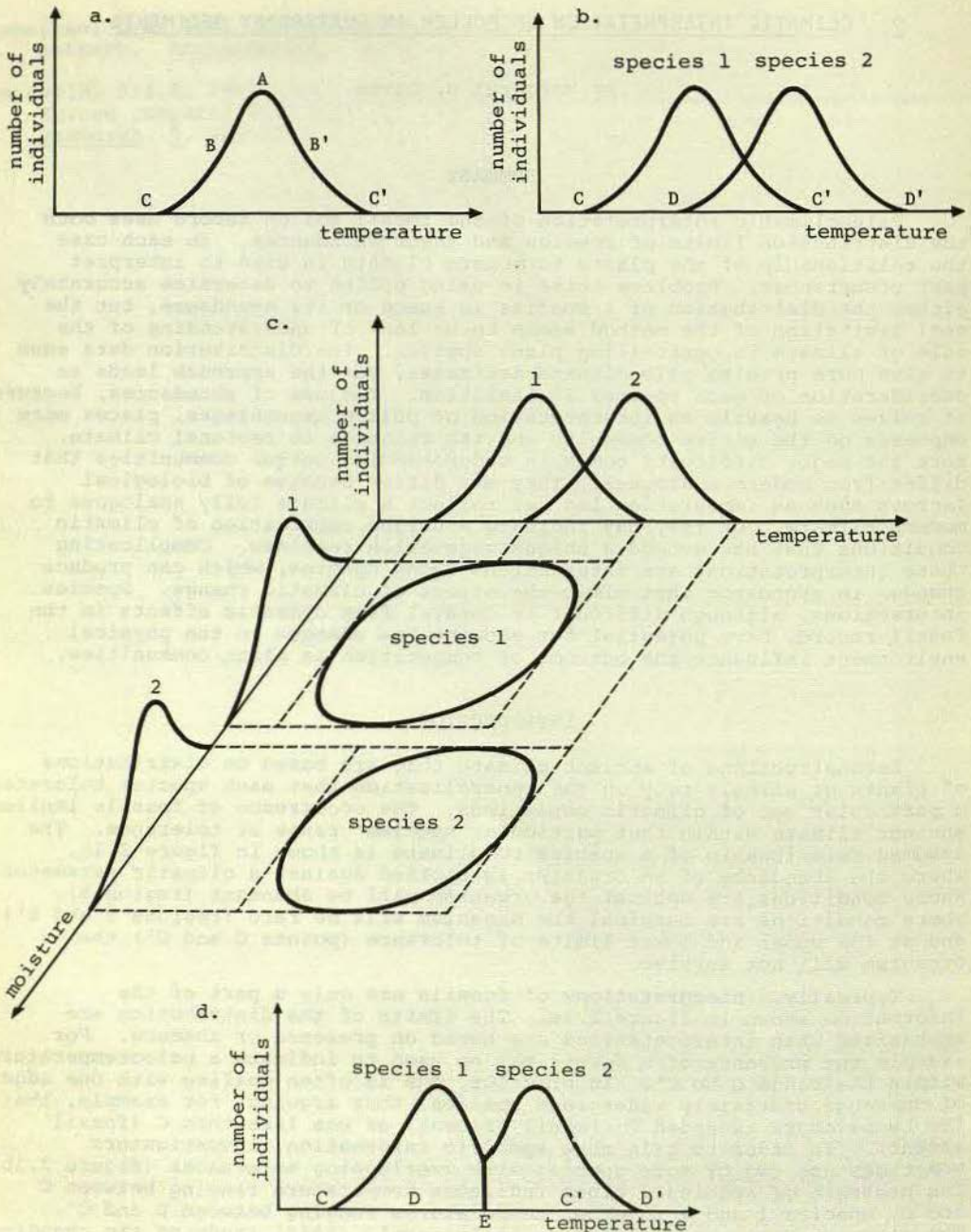


Figure 2.1 (a) Hypothetical relationship between the abundance of an organism and an environmental factor. (b) Hypothetical relationship between the abundances of two non-interacting species and an environmental factor. (c) Hypothetical relationships between the abundances of two, non-interacting, species and two environmental factors; the abundances are projected onto a surface that represents the two gradients; the ellipses outline the occurrences of the two species. (d) Hypothetical relationships between abundances of two species and a single environmental factor; species 1 and species 2 interact; each excludes the other over a portion of the environmental gradient.

occurs today. He observed damage to holly and ivy along their respective range limits during an unusually cold winter, thus demonstrating that the two species have different ranges of tolerance for the same limiting factor. This last point is important; figure 2.1c shows how species with overlapping tolerances for one factor can still be separated in the environment by a second, perhaps unknown, niche dimension. Identification of the environmental variable limiting both species is therefore essential for interpretation of co-occurrences of species in the fossil record.

Competition between species poses problems in this methodology that seldom are discussed by paleoecologists. If species interact, they may never co-occur even though their potential limits overlap (figure 2.1d). Potential and realized tolerance limits are seldom distinguished when paleoecologists attempt to define the relationship of a species to the physical environment. Tree species clearly compete with one another in forests, although the degree to which a species can completely exclude competitors is not really known. Even without complete exclusion a species might become so rare that it appears "virtually" absent from the region. One might conclude erroneously that it cannot tolerate the climate there. Forest communities have changes through time, raising the possibility that the realized niche for a particular species has expanded as it was released from competition or has contracted as new competitors have entered the community.

The potential for climatic information is much greater when abundances of species are considered. Using abundances, one can utilize all the points along the curve between C and C' (figure 2.1a) instead of the limits of distribution only. Most palynologists rely heavily on interpretations of abundance. The quantitative implications of pollen abundance give pollen a major advantage over traditional paleobotanical materials such as leaves, seeds and wood. Although pollen is notoriously imprecise as an estimator of population size (Davis et al. 1978), one can deduce that a species is rare or that it is very abundant without precise information. Much greater precision is necessary to know whether a species is present or absent, especially as many plants are rare near the limits of their geographic range. Consequently pollen is more useful in giving information on abundance than in pinpointing the exact limits of distribution. I shall endeavour to show in this essay, however, that both presence/absence, and abundance can be determined from the fossil pollen record, and that each kind of information has potential for determining climates of the past. The limitations of the method seem to reside in the incompleteness of our understanding of the relationship of plants to their biological and physical environment.

#### DISTRIBUTION LIMITS AS CLIMATIC INDICATORS

Pollen is usually dispersed far beyond the range of the plant. Consequently, the mere presence of a few pollen grains cannot be construed as evidence that the plant grew nearby. The dispersal of pollen of *Ephedra* 1200 km across the central plains of the United States from the southern Rockies to Minnesota is a spectacular example of this phenomenon (Maher 1964). Nevertheless, there are circumstances where pollen can be used to trace species distributions. The consistent presence of pollen from small, low-growing, insect-pollinated plants (ivy, for instance) might be construed as evidence of presence provided that surface sediments show that modern dispersal occurs close to parent plants. Pollen frequencies supported by the presence of macrofossils might also be used, although in this case it is the macrofossil, not the pollen, that forms the basis for interpretation. Under special circumstances, it has been possible to demonstrate a quantitative relationship between pollen frequencies and a species range limit. An example of this is shown in figure 2.2, a map showing the percentages and influx rates for beech (*Fagus grandifolia*) pollen in Upper Michigan. The pollen measurements were made in modern lake sediment. A map of the distribution of beech in the modern forests, as measured in the U.S. Forest Service Inventory, is

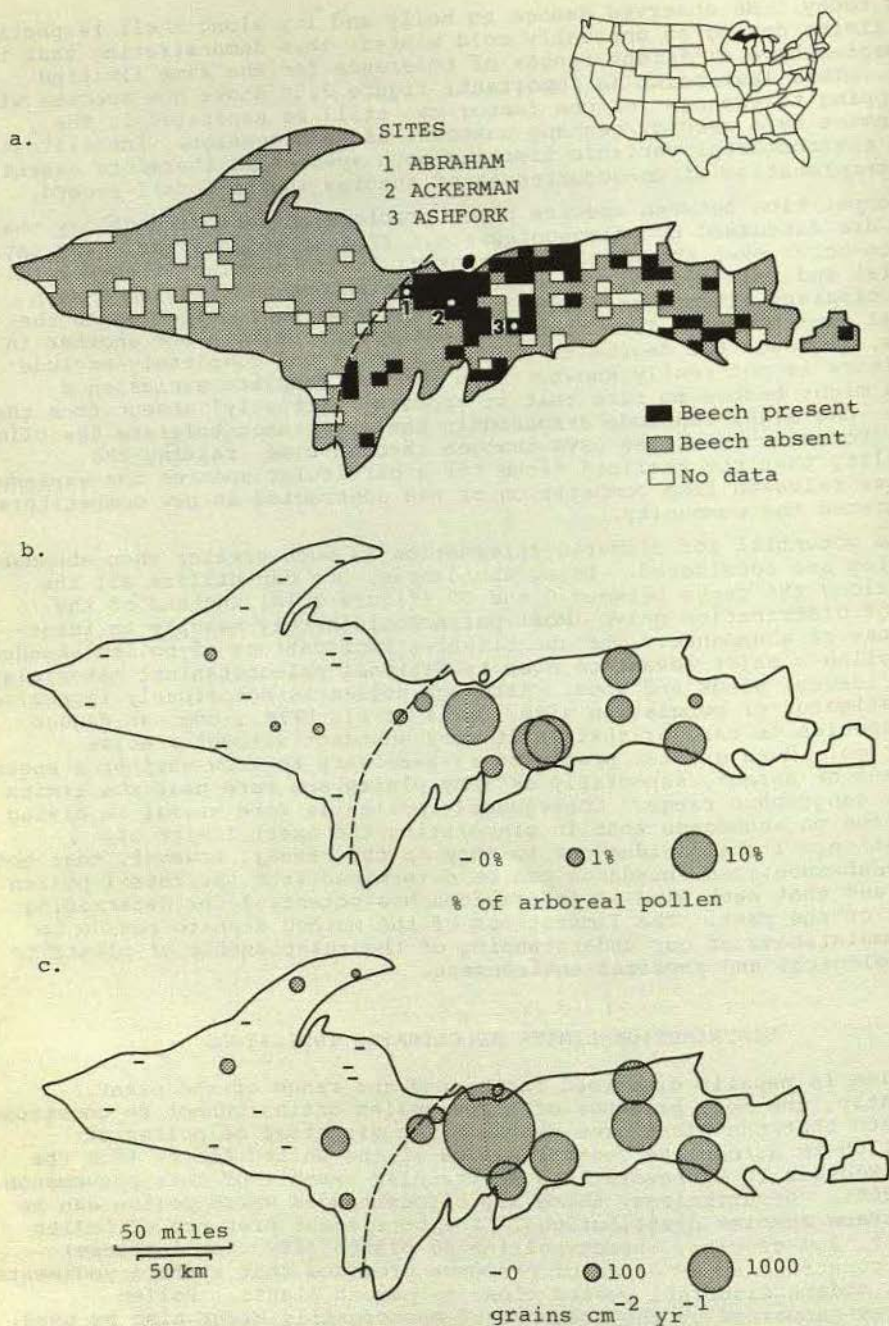


Figure 2.2 Maps of Upper Michigan, U.S.A. showing (a) Distribution of beech trees in modern forests; dashed line represents the western species limit. (b) Beech pollen percentages in surface sediment from a number of lakes. (c) Average beech pollen influx since the time of settlement, about 70 years ago, at the same sites.

shown for comparison. The dashed line indicates the western distribution limit for beech. The beech boundary is unusually sharp: beech is abundant (basal area greater than  $14 \text{ m}^2 \text{ ha}^{-1}$ ) only a few miles from its absolute limit. Except for beech, the forests are similar in composition on both sides of the boundary. Many lakes west of the boundary contain no beech pollen at all; those that do, contain less than 1%, or accumulation rates less than  $200 \text{ grains cm}^{-2} \text{ yr}^{-1}$ . In contrast all lakes east of the boundary show beech pollen in percentages greater than 1% and accumulation rates greater than  $200 \text{ grains cm}^{-2} \text{ yr}^{-1}$ .

Fossil pollen was studied in sediments from the three lakes indicated in figure 2.2a. Beech pollen was absent from all three sites until 3500 years ago, when it appeared at the easternmost site (figure 2.3). At this time the percentage rose to exceed 1%, indicating the presence of beech trees nearby. Beech distribution then remained stable for about 3000 years. About 500 years ago, when the Little Ice Age began in much of the northern hemisphere, beech extended its range 43 km to the west. A 35 km extension to the westernmost site followed within a few centuries. (The date of extension is imprecise because it was estimated by extrapolating ages of sediment between pollen culture horizons a few cm below the surface and radiocarbon dates at 1-1.5m depth.) The westernmost site, Abraham Lake, is at the very limit of beech today. The rapid extension of range to this site, averaging  $175 \text{ m yr}^{-1}$ , seems to represent a response to climatic change associated with the "Little Ice Age" documented by resurgence of glaciers in many parts of the world within the last four or five centuries (Porter and Denton 1967).

These changes in the geographical limits for beech in Upper Michigan should provide climatic information, indicating that climatic conditions at the two westernmost sites, formerly unsuitable for the survival of beech, are now within the range of tolerance for the species. Although this conclusion seems justified, stating it in specific climatic terms is more difficult. The particular climatic factors that limit the distribution of beech in Michigan at the present time are unknown. The situation is all too typical of the dearth of autecological information on the very plants we should like to use as climate indicators. Geographical patterns of precipitation, snow depth and temperature, recorded by the U.S. Weather Bureau over the last 40 or more years in this region, are not correlated with the distribution pattern for beech. It seems likely that beech is affected by the magnitude of the differences in temperature between summer and winter. This difference increases westward and is therefore correlated with the species boundary. Moisture at critical seasons of the year is another possibility. Intuitively this seems important because beech is abundant right along the shore of Lake Superior, when frequent fogs may influence the moisture regime. On the other hand, the lake may be exerting a tempering effect on seasonal temperature differences. The western limit of beech at present coincides with the boundary between Paleozoic shales and limestones to the east of Pre-Cambrian basement rocks to the west. The coincidence suggests that soils are important, yet climate must also influence beech, otherwise we cannot explain the easterly location of the limit of beech 500 years ago nor the extension of range since that time. An interaction of climate and soils as the control on the present distribution of beech cannot be ruled out. The history of beech shows how it might be possible to use a changing species limit as a sensitive assay of climatic change, monitoring subtle changes that have occurred from one century to the next, provided one has understanding of the modern relationship of the organism to climate and soils sufficient for interpretation.

The geographical limit for beech distribution in Upper Michigan, despite ambiguities in interpretation, appears at least to be in equilibrium with the climate of this century. There is no evidence of movement at the present time, as trees at the very limit of distribution near Abraham Lake are producing few seedlings and sprouts relative to beech in forests in the central part of the species' range (Davis unpublished data; Ward 1961). However, there are many examples in the Holocene record of species boundaries that were not in equilibrium with climate for many thousands of years, due to lag in the extension of ranges

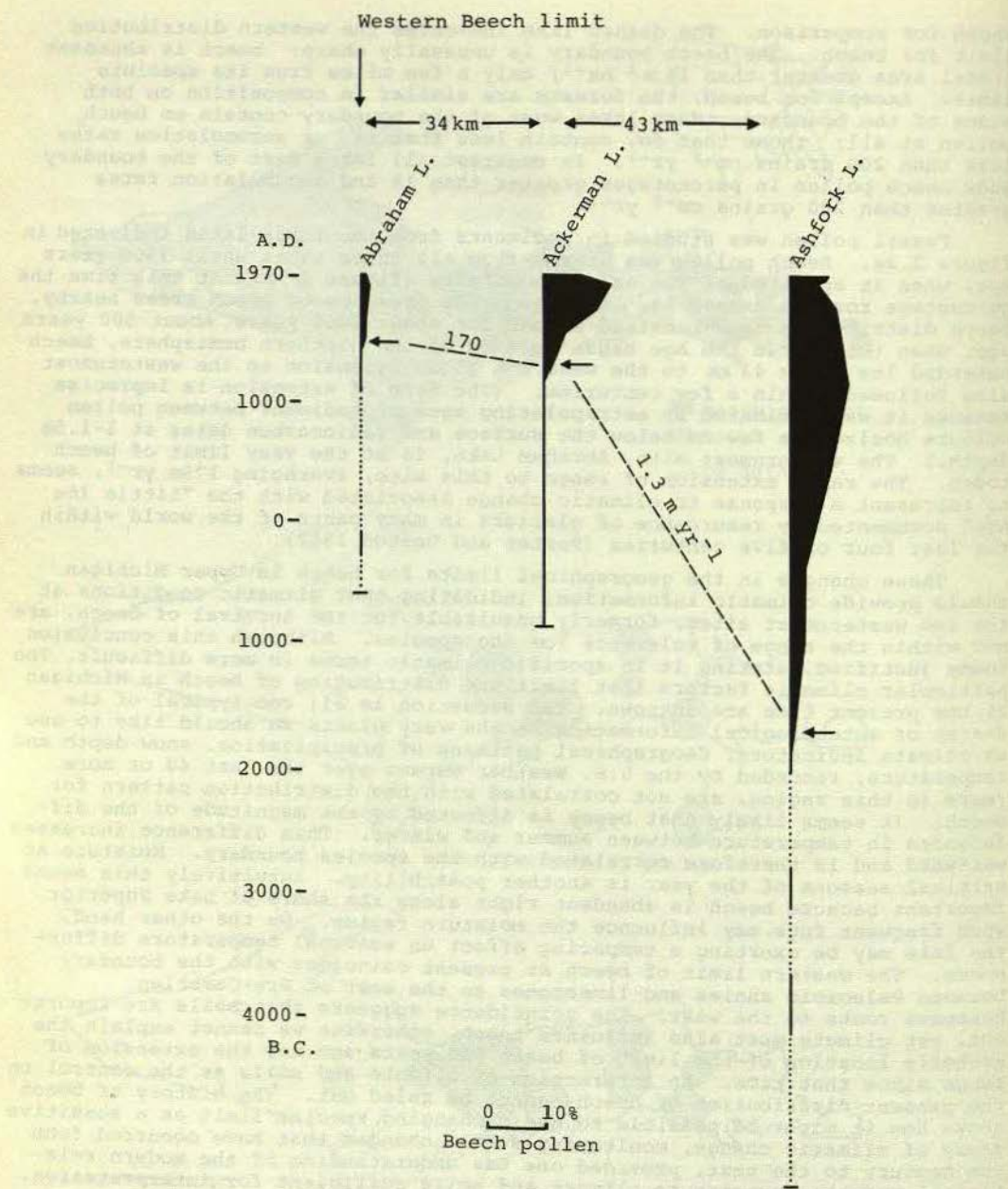


Figure 2.3 Beech pollen percentages plotted against time at the three sites indicated in figure 2.2a.

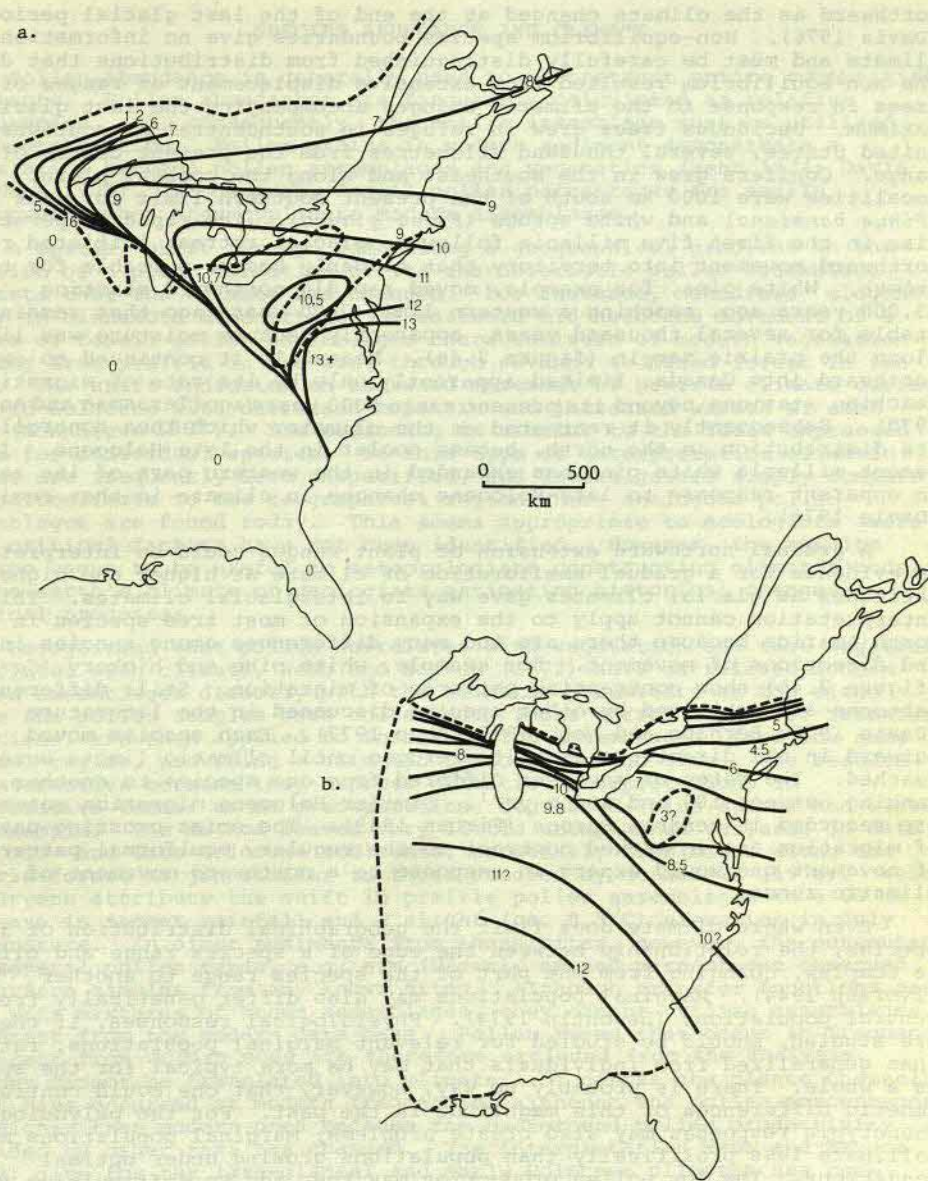


Figure 2.4

(a) Migration of white pine. (b) Migration of hickory.

The dashed lines enclose the modern ranges of the species. Solid lines represent the frontier of each species at 1000-year intervals during the late-Pleistocene and the Holocene. Small numbers on the maps represent radiocarbon ages in thousands of years B.P. at sites where the rational limit was exceeded. (Redrawn from Davis 1976).

northward as the climate changed at the end of the last glacial period (Davis 1976). Non-equilibrium species boundaries give no information on climate and must be carefully distinguished from distributions that do. The non-equilibrium resulted from extensive displacement of ranges of trees in response to the climatic changes accompanying the last glacial maximum. Deciduous trees grew in refuges in southcentral or southwestern United States, several thousand kilometres from the present centre of their range. Conifers grew in the southeast and along the coastal plain. These localities were 1000 km south of the present southern limit for jack pine (*Pinus banksiana*) and white spruce (*Picea glauca*). The rapid temperature rise in the first five millenia following glacial retreat initiated rapid northward movement into territory that suddenly became suitable for tree growth. White pine, for example, moved rapidly northward starting 13,000 years ago, reaching a western limit 7000 years ago that remained stable for several thousand years, apparently because moisture was limiting along the prairie margin (figure 2.4a). Meanwhile it continued to expand northward into Canada, limited apparently only by its rate of migration, reaching stations beyond its present range 5000 years ago (Terasmae and Anderson 1970). Subsequently it retreated as the climate, which then controlled its distribution in the north, became cooler in the late Holocene. In recent millenia white pine has expanded in the western part of its range, an apparent response to late-Holocene changes in climate in that region (Davis 1976).

A gradual northward extension of plant ranges could be interpreted as evidence for a gradual amelioration of climate at higher and higher latitudes as glacial climates gave way to interglacial climates. This interpretation cannot apply to the expansion of most tree species in North America because there are too many differences among species in rates and directions of movement. For example, white pine and hickory (*Carya*) (figure 2.4b) show contrasting patterns of migration. Still different patterns are exhibited by other species discussed in the literature (Davis 1976; Bernabo and Webb 1977; Kapp 1977). Each species moved outward in all directions from its refuges until climatic limits were reached. The rates of movement differed from one species to another, ranging between 100 and 400 m yr<sup>-1</sup>. Similar Holocene migration rates are recorded in central Europe (Firbas 1949). The criss-crossing patterns of migration are in marked contrast to the regular, equiformal patterns of movement one would expect in response to a northward movement of climatic zones.

Even where climate does limit the geographical distribution of a plant species, the relationship between the edge of a species range and climate is complex, changing from one part of the species range to another (Iversen 1944). Marginal populations may also differ genetically from central populations (Lewontin 1974). Physiological responses, if they are studied, should be studied for relevant marginal populations, rather than generalized from individuals that may be more typical for the species as a whole. There is probably no way, however, that one could control for genetic differences of this magnitude in the past. For the palynologist, phenotypic responses may also create problems; marginal populations may pollinate less prolifically than populations growing under optimal conditions. The low pollen production may then add to difficulties in detecting the position of the species boundary. Nichols (1976) speculates, for example, that "relict" stands of spruce growing in the arctic, beyond the limit of continuous forest, produce few or no pollen grains and have reproduced vegetatively by layering for hundreds or thousands of years.

Species boundaries can give climatic information only a) when the species boundary is detectable by pollen analysis, b) when the species boundary is in equilibrium with the climate and c) when it is controlled by a known climatic parameter. Such information is available in very few instances.



## SPECIES ABUNDANCE AND CLIMATE

Pollen abundance is generally used to reconstruct entire communities of plants. Pollen abundances are frequently calculated as relative frequencies, and, consequently, the entire assemblage must be utilized in interpretation. Pollen grains in modern sediment demonstrate a correlation between pollen assemblages and vegetation (Webb 1974; Davis and Webb 1975). In general, fossil pollen percentages are easily interpreted when they duplicate modern assemblages.

A spatial shift through time along a geographical gradient in the position of a plant formation or its characteristic pollen assemblage suggests that the climate has changed. For instance, McAndrews' elegant study in Minnesota demonstrated an eastward mid-Holocene movement of a series of fossil pollen assemblages characteristic of modern vegetation ranging from prairie in the west through savanna to mixed forest in the east. The shift indicates an eastward movement of prairie climate during the mid-Holocene with decreased moisture and increased warmth at each site (McAndrews 1967). The reasoning is similar to the ideas expressed above for individual species. In this type of interpretation climatic values are frequently left unspecified, and investigators simply compare the paleoclimate to the geographical region where analogous pollen assemblages are found today. This seems appropriate to ecologists aware that critical factors have not been identified. However, the results are too vague to be useful to meteorologists constructing climatic models of the earth's climate or geologists estimating historical changes in physical processes.

Recognizing that pollen correlates with vegetation and that vegetation correlates with climate, Webb and Bryson (1972) have correlated modern pollen assemblages directly with the climatic parameters at the sites where the pollen samples were collected. These correlations, or transfer functions, are then applied to fossil pollen assemblages from the same general region, providing a climatic readout through time. The results are attractive because they express climatic interpretations in quantitative terms: as mm precipitation, degrees Celsius summer and winter, for example. The method leaves very little unexplained variance in data from mid- and late-Holocene sediments, especially from sites along the prairie-forest margin similar to those studied by McAndrews (1976). Webb and Bryson attribute the shift in prairie pollen assemblages to a 50 mm decrease in summer rainfall and a slight (ca. 0.5°C) elevation in July temperature. In older sediments from these sites, however, the percentages for several pollen types, e.g. elm (*Ulmus*), exceed percentages observed in surface samples from any known sites. Although transfer functions can deal with mixtures of known assemblages, they cannot utilize assemblages different from the modern data base. Pollen types that occur in frequencies different from modern ones are therefore excluded from the analysis, as they cannot be translated into climate. Of course the plants themselves might have occurred at modern frequencies although the pollen percentages are higher than modern ones because the background pollen productivity provided by other taxa has changed. The interpretation Webb and Bryson (1972) give for the late-glacial and early Holocene climates has been based exclusively on the understudied pollen types which make up about 70% of the assemblage. Spruce (*Picea*) is the major component in the interpretation. The degree to which omission of pollen types can cause errors is not really known, since there is as yet no independent way to check the accuracy of paleoclimatic interpretations of pollen based on transfer functions. Clearly omission of certain types does not interfere with correlations of modern material with climate, in fact the correlation may be enhanced. However, the unusual percentages of pollen observed in the late-glacial and early Holocene may have climatic significance, indicating a unique combination of climatic conditions; this information should be utilized in some way rather than discarded if a full picture of past environments is to be obtained.

Interpretation of fossil pollen frequencies by any method tends to break down when pollen assemblages represent a community different from any found today. Early Holocene communities in many parts of North America were unique. Forests at that time were species-poor due to the lag in the northward migration of forest dominants. Immature soils may have affected the success of some species. Another cause may have been unique climatic conditions. Several different methods have been used in attempts to interpret pollen assemblages that have no modern analogue. Where pollen dispersal is not a factor, e.g. very small sites beneath a forest canopy, corrections can be made for differences in pollen productivity (Andersen 1970, 1973). Very detailed interpretations have been possible in these instances. Most analyses, however, are from sediments in larger basins where pollen dispersal is important. Present data indicate that pollen dispersal is so variable and difficult to measure that it seems unlikely that correlations for pollen representation can be made accurately in these situations. Some authors have suggested that measurements of the absolute rate of accumulation of pollen grains (pollen influx) show promise for interpreting unique pollen assemblages (Davis et al. 1973). Influx in existing lakes can be calibrated against plant abundances in the modern forest and used as a very rough estimate of population size. The estimates for each genus can be added together to reconstruct unknown communities (Davis et al. 1973). The accuracy of the result is probably not very high because sedimentary processes produce large variance in pollen influx from site to site, and sometimes at the same site through time.

Despite the difficulty inherent in interpreting pollen assemblages produced by plant communities that have no modern analogue, attempts must be made to understand their meaning. They disprove the idea that communities merely shift position along geographical and climatic gradients whenever the climate changes. Striking changes in composition are documented for example by the fossil history of spruce-fir forests on the slopes of the White Mountains in northeastern United States. The spruce-fir forests today are one of a series of forest communities arranged along an elevation gradient. The spruce-fir zone is conspicuous, partly because the coniferous forests stand out in contrast to the deciduous forests on the lower slopes. Spruce (*Picea rubens* and *P. mariana*) and fir (*Abies balsamea*), with patchy admixtures of paper birch (*Betula papyrifera*) in disturbed sites, are dominant from about 750 m to 1500 m elevation. Above these elevations, alpine tundra extends to the summits at about 1800 m. Below the spruce-fir forests deciduous trees are dominant. Paleoecologists used to assume that the Boreal Forest of Canada had been pushed southward as the glaciers advanced, and that it had moved northward again as the glaciers retreated (e.g. Martin 1958). It was therefore natural to interpret the spruce-fir forest on the mountain slopes as a relict of the Boreal Forest that had moved through the area. The descriptive term "Boreal" is often applied to montane spruce-fir forest, despite some differences in species composition from the Canadian Boreal Forest (Whittaker 1956; Siccama 1974). However, fossil pollen data from the White Mountains shows that although both spruce and fir have been abundant at various times in the past in this region, they have had different histories and only recently have come to grow together in abundance as a distinctive community on the mountain slopes. The spruce-fir forest is therefore not a relict of a previous formation but is instead a new community that has existed as a conspicuous forest zone for only about 2000 years.

Although spruce and fir occupy a distinctive elevation belt, climate is not the only factor limiting their occurrences. Competition with hardwood species seems to play a part in limiting red spruce at the lower limit of its elevation distribution (Bormann et al. 1970). Whittaker (1956) concluded that competition was occurring in the southern Appalachians, too, because deciduous trees grow there at much higher elevations on mountains where spruce is absent than where spruce is present. Factors controlling the upper limit for spruce are not so clear. The upper limit is diffuse, as patches of spruce become increasingly rare in fir forest

500 m or so below tree line. At these elevations fir competes successfully with spruce; fir is a short-lived tree and precedes spruce in biological succession. Apparently the lower limit for fir is determined by competition with spruce and at lower elevations in competition with deciduous trees. The upper limit for fir, however, is the upper limit for trees of any kind. Both fir and black spruce grow as krummholz at treeline. The upper limit of fir is doubtless controlled by the physical environment.

Spruce and fir pollen both occur in maximal abundance in surface sediments from the spruce-fir zone. Spruce pollen can be found in low percentages at sites at lower elevations, but fir pollen is quite local in its distribution (Davis et al. in preparation).

The history of spruce and fir is shown by the absolute accumulation rates of pollen from spruce and fir at a series of sites in northeastern United States (figure 2.5). Two of the localities are located several hundred km south of the White Mountains (figure 2.6). The other three localities are at various elevations in the mountains, from the valley floor (200 m) to the spruce-fir zone (1000 m).

As the ice left northeastern United States 13,000 to 14,000 years ago, tundra vegetation developed on the newly deglaciated landscape. After one or two thousand years spruce became established, first in the south and then moving northward. The absolute rate of spruce pollen deposition (probably not significantly different at the three low-elevation sites) was less than 5000 grains  $\text{cm}^{-2} \text{yr}^{-1}$ , suggesting an open spruce woodland extending from Connecticut northward to northern New Hampshire (Davis et al. 1973). Above 500 m in the mountains influx values are much lower, indicating that spruce grew only sparsely at these elevations. The presence of spruce needles at the 1000 m site (Linda Shane, University of Minnesota, personal communication) shows that spruce trees or krummholz did grow at this elevation, which must have been close to treeline at that time. About 10,000 years ago, spruce declined sharply in abundance at all elevations. Over the next millenium, it disappeared at low elevations, but spruce needles in the sediment show that it persisted near the higher sites at 650 and 1000 m elevation (Linda Shane, personal communication). The low pollen influx at these sites indicates that spruce was rare at these elevations and sites still higher on the slopes, now under study by Ray Spear, contain even fewer spruce pollen grains in late-glacial and mid-Holocene sediments (Ray Spear, University of Minnesota, personal communication).

Fir entered Connecticut about 11,000 years ago, becoming abundant at low elevations in both Connecticut and New Hampshire just as spruce declined. It remained abundant there a full 1000 years after spruce disappeared. It persisted somewhat longer near the 200 m site in the White Mountains. Fir is a poor pollen producer; hence, even though the influx rates in figure 2.5 are low, fir was more abundant than spruce. About 10,000 years ago fir arrived at higher elevations in the White Mountains including the site at 1000 m where it became abundant and has persisted as the dominant species to this day. Birch pollen and seeds indicate that paper birch arrived at about the same time.

Spruce became abundant again 2000 years ago. Its pollen increased sharply at all sites in the White Mountains. Macrofossil remains also increased in abundance at the sites at 650 m and 1000 m (Linda Shane, personal communication). Spruce grows today along the shore of the 650 m site, although the forests there as a whole are dominated by deciduous trees. Spruce is more common in forests just below the 1000 m site, although fir dominates the forest very near the lake. It should be noted that throughout the early history of this region, spruce and fir only briefly coincided; the peak in fir at low elevations persists after the decline of spruce. At high elevations fir remained as abundant as now throughout the mid-Holocene when spruce was rare. Only in the last two millenia has spruce become abundant at elevations where fir is common to form the spruce-fir forest. In this case, forest history does not involve a shift along the elevation gradient, but instead a complex series

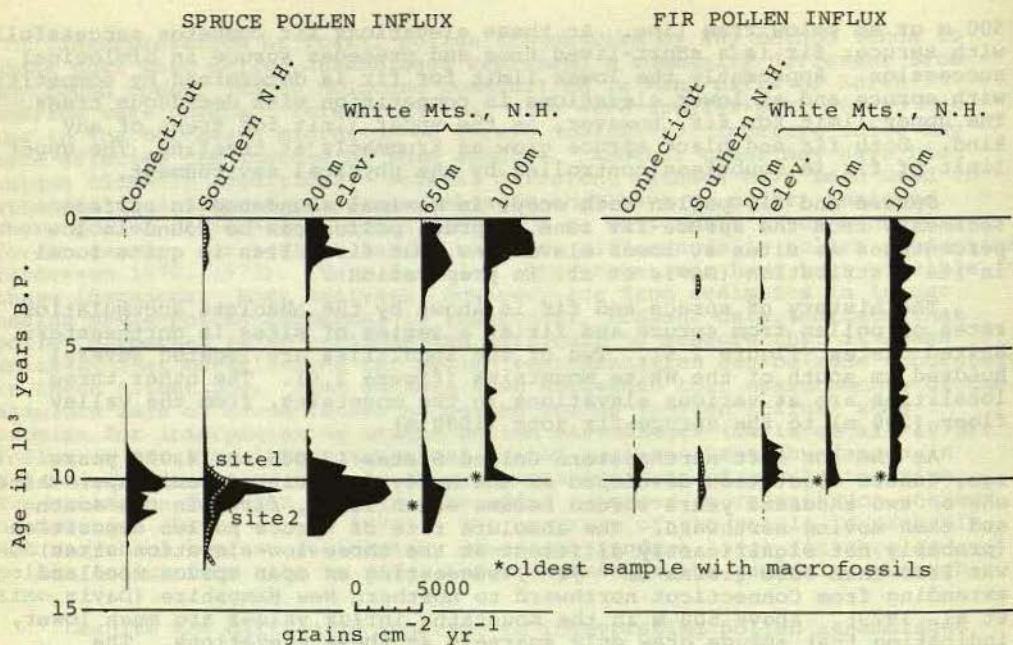


Figure 2.5 Absolute accumulation rate (influx) of spruce and fir pollen grains during the last 13,000 years at 5 localities in northeastern United States: Rogers Lake in Connecticut, Pout and Sandogardy Ponds in Southern New Hampshire, and Mirror Lake, Lost Pond and Carter Pond in White Mountains. The contrasting values at Pout and Sandogardy, which are only a few km apart, indicate the variability characteristic for pollen influx values.

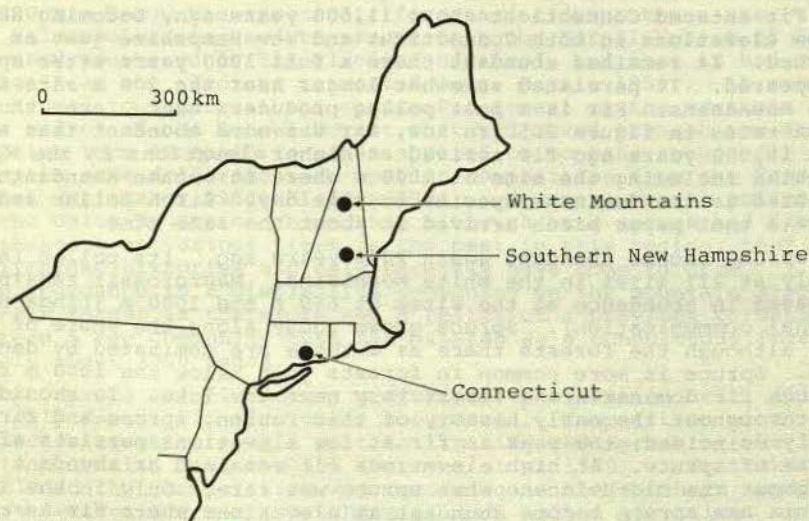
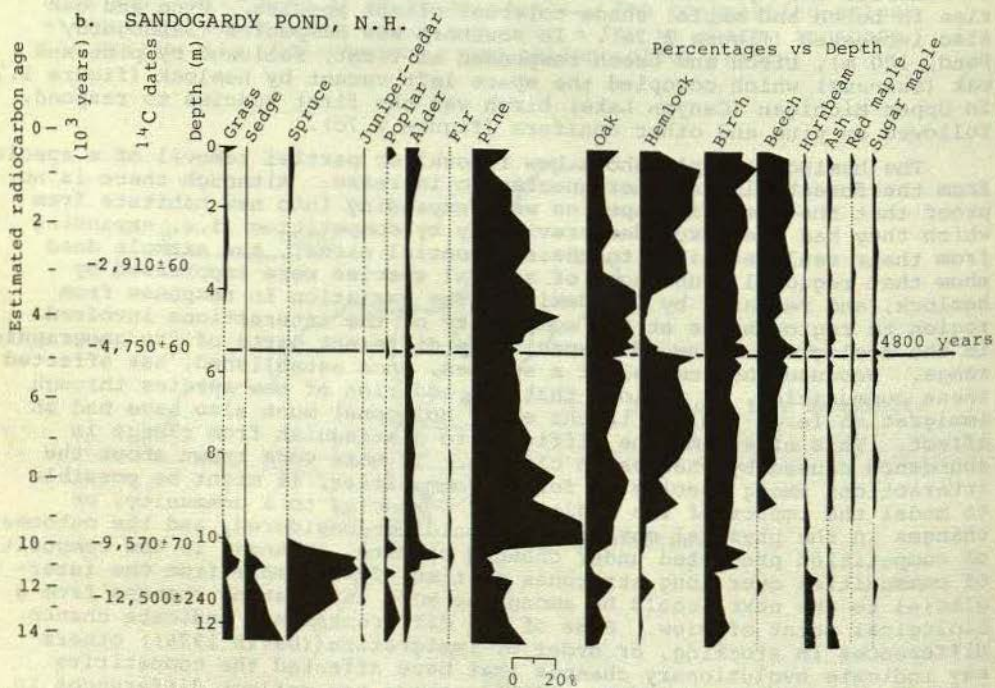
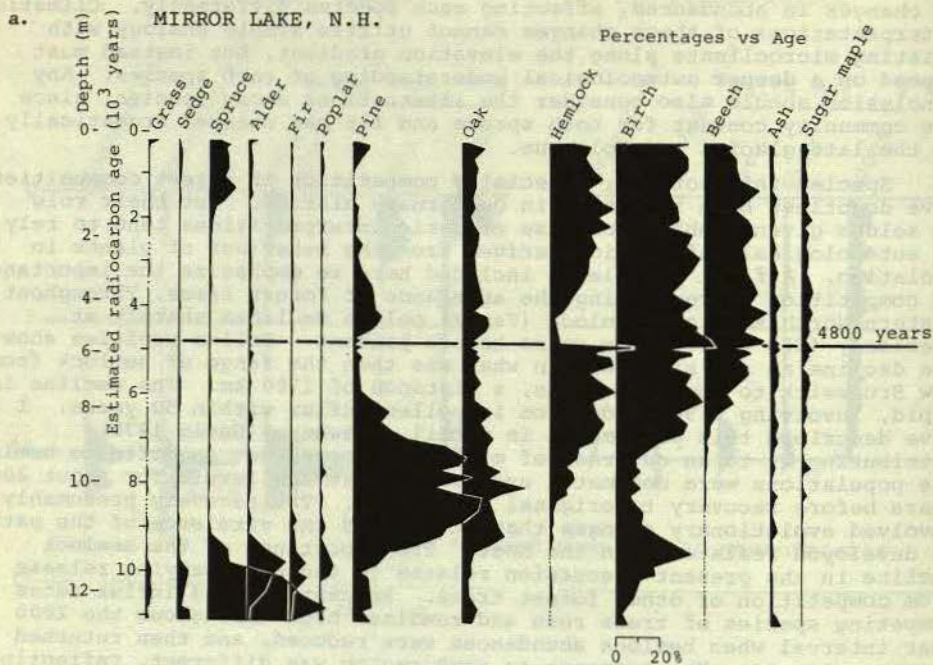


Figure 2.6 Outline map of northeastern United States, showing locations of sites in figure 2.5.

of changes in abundances, affecting each species differently. Climatic interpretations of these changes cannot utilize simple analogy with existing microclimate along the elevation gradient, but instead must depend on a deeper autecological understanding of each species. Any conclusion should also consider the interactions among species, since the community context for both spruce and fir has changed dramatically in the late-glacial and Holocene.

Species interactions, especially competition in forest communities, have doubtless been important in Quaternary history. Yet their role is seldom given emphasis because climatic interpretations tend to rely on autecological information derived from the behaviour of plants in isolation. A final example is included here to emphasize the importance of competition in regulating the abundance of forest trees. Throughout eastern North America, hemlock (*Tsuga*) pollen declines sharply at precisely 4800 radiocarbon years before present. Pollen profiles show the decline at all sites within what was then the range of hemlock from New Brunswick to Upper Michigan, a distance of 1700 km. The decline is rapid, involving a 90% reduction in pollen influx within 50 years. I have described this phenomenon in detail elsewhere (Davis 1976), attributing it to an outbreak of a pathogen or insect specific to hemlock. The populations were decimated and remained at low levels for about 2000 years before recovery to original abundances. The recovery presumably involved evolutionary changes that attenuated the virulence of the pathogen or developed resistance in the host. The importance of the hemlock decline in the present discussion relates to the accompanying release from competition of other forest trees. Percentages and influx rates for competing species of trees rose and remained high throughout the 2000 year interval when hemlock abundances were reduced, and then returned to previous levels. The response in each region was different, reflecting the diversity of competitors experienced by hemlock in different parts of its range. In the valleys of the White Mountains (Mirror Lake, 200 m elevation), the hemlock fall was followed by a brief increase in birch (a numerous seed producer) which, in turn, was followed by a long term rise in beech and maple, shade-tolerant climax species. Pine and oak also increased (figure 2.7a). In southern New Hampshire (Sandogardy Pond, 100 m), birch and beech responded at first, followed by pine and oak (*Quercus*) which occupied the space left vacant by hemlock (figure 2.7b). In Upper Michigan (Canyon Lake) birch was the first species to respond, followed by pine and other conifers (figure 2.7c).

The hemlock example shows how removal or partial removal of a species from the forest allows other species to increase. Although there is no proof that the competing species were expanding into new habitats from which they had been excluded previously by competition (i.e. expanding from their realized niche to their potential niche), the example does show that regional abundances of several species were suppressed by hemlock, and released by its demise. The variation in response from region to region hints at the complexity of the interactions involved in the ecological niche of a species in different parts of its geographical range. Because the removal of a species, once established, has affected these communities, it follows that the addition of new species through immigration (e.g. hemlock in the early Holocene) must also have had an effect. This effect may be difficult to distinguish from change in abundance caused by changes in climate. If more were known about the interactions among species in forest communities, it might be possible to model the impact of the addition of a species to a community, or changes in the physical environment could be considered, and the outcome of competition predicted under changed climate. Changes in the composition of communities over long stretches of time, for example from one interglacial to the next, could be among the most interesting changes from a biological point of view. Some of the differences may indicate chance differences in stocking, or order of immigration (Davis 1976); others may indicate evolutionary changes that have affected the competitive success of the dominant trees. Still others may reflect differences in



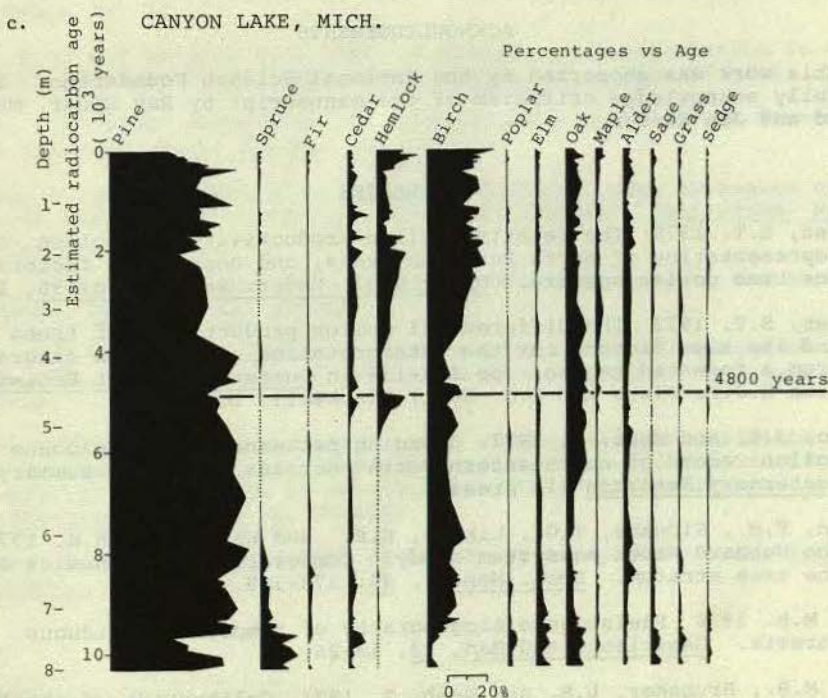


Figure 2.7 Pollen diagrams from three regions in northern United States showing the fall of hemlock pollen 4800 years ago, and the succession following it that is characteristic for each region. Pollen influx diagrams from these sites prove that a real increase in competing species occurred between 4800 and 3000 years ago when hemlock was rare. Geographical locations are shown in figures 2.2 and 2.6 (a) Mirror Lake, 200 m elevation, White Mountains in northern New Hampshire. (b) Sandogardy Pond, 100 m elevation in southern New Hampshire. (c) Canyon Lake, Upper Michigan, about 50 km west of the limit for beech.

climate from one interglacial to the next. In the long run, our best hope for valid estimates of paleoclimate will come from understanding these complex and difficult, but very real, interactions among species as they are affected by the physical environment.

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