Dispersal versus climate: Expansion of *Fagus* and *Tsuga* into the Upper Great Lakes region*

M. B. Davis[1], K. D. Woods[2], S. L. Webb[1] & R. P. Futyma[3]
[1]*Department of Ecology and Behavioral Biology, University of Minnesota, Minneapolis, MN 55455, USA;*
[2]*Department of Biology, University of California Santa Barbara, CA 93106, USA;*
[3]*Division of Biological Sciences, University of Michigan, Ann Arbor, MI 48109, USA*

Abstract

Pollen records for American beech (*Fagus grandifolia*) and eastern hemlock (*Tsuga canadensis*) compiled from 50 sites in Michigan and Wisconsin, USA, show that both species entered the Upper Great Lakes region about 7000 yr B.P., reaching their western and southwestern boundaries between 2000 and 1000 yr B.P. *Fagus* advanced northward into lower Michigan as a continuous front, except where Lake Michigan posed a geographic barrier. Colonies were established on the far side of the lake after a 1000 year lag, implying that long-distance dispersal across a 100-km wide barrier can occur. The *Fagus* range may not have been in equilibrium with climate for one or two thousand years before this time, when seeds were dispersed across the lake to Wisconsin. *Tsuga* seeds may have been dispersed 150 km or more from Ontario to reach Upper Michigan. Scattered colonies were established 6000–7000 yr B.P. on either side of Lake Michigan, which did not pose a significant barrier to this wind-dispersed species, *Tsuga* spread rapidly over a large region prior to 5000 yr B.P. Subsequent expansion to the west occurred more slowly, and may reflect gradual climatic changes in northern Wisconsin during the second half of the Holocene. *Tsuga's* range may have been limited by dispersal, rather than climate, for an unknown length of time prior to 5000 yr B.P. During this period *Tsuga* was expanding its range rapidly. The study shows, however, that it is difficult to devise rigorous tests to distinguish between dispersal limitations and climate as factors limiting range limits in the past.

Introduction

The rapid rates of range extension of forest trees in the early Holocene have led palynologists to speculate that the rate at which seed could be dispersed to new habitats limited the expansion rate of trees (Iversen, 1954; Davis, 1981a, 1983b; Huntley & Birks, 1983). If so, species could have been absent for short or long periods from areas where the climate was suitable for their growth. This possibility casts doubt on reconstructions of Holocene climate that assume equilibrium relationships between species ranges and climate.

In this paper we try to determine whether climate or seed dispersal was the factor limiting the colonization of the Upper Great Lakes region by two mesic tree species. We compare the history of the American beech, *Fagus grandifolia,* and eastern hemlock, *Tsuga canadensis.* These two trees entered the Upper Great Lakes region between 5000 and 7000 yr B.P. and reached their western limits less than 2000 yr B.P. They are both long-lived, shade-tolerant species characteristic of mesic, old-growth forests (Fowells, 1965). *Fagus* nuts are dispersed by mammals and birds (Johnson & Adkisson, 1986; Ridley, 1930) while *Tsuga* seeds are dispersed by wind (Fowells, 1965).

The Great Lakes are each more than 100 km in width. They pose barriers to the dispersal of seed, providing an opportunity to identify any lags in the range expansion of *Fagus* and *Tsuga* that might be

attributed to dispersal limitations. For example, the colonization of southern Wisconsin by *Fagus* was delayed for 1000 years after equivalent latitudes in southern Michigan were colonized (S. L. Webb, 1983). Was this delay due to difficulties in the dispersal of seed across Lake Michigan? Or can it be attributed to other factors, such as climate? We review here a number of cases where the data seem to imply the importance of seed dispersal as a factor limiting the range expansion of *Fagus* and *Tsuga*.

Methods

Spatial resolution

Our goal was to design a method to detect local populations of *Fagus* and *Tsuga* and to date the time of their establishment. Pollen grains in lake sediment show a quantitative relationship to the density of trees in the surrounding landscape (Webb *et al.*, 1981). However, because the numbers of grains reaching a site depend not only on population density but also on the distance of the population from the site of deposition, data from a single lake cannot distinguish between a small, nearby colony, and a far-distant but very large population of trees (M. B. Davis *et al.*, 1986). In order to make this distinction we used an irregular grid of small (3–10 ha) lakes about 50 km apart. Within the grid, the establishment of a new colony should be detectable as increased pollen concentrations or percentages at one, and only one site, while the advance of a continuous front should be detectable by increased pollen at a series of sites bordered on one side by sites without pollen and on the other by sites with significant pollen. Fig. 1 shows an ideal case, where the boundary of the main population is recorded by a continuous series of sites with 'significant' (+) amounts of pollen, adjacent to a series of sites with no (−) pollen. A disjunct colony is registered by 'significant' (+) percentages at one site. The surrounding sites with no (−) pollen provide evidence that the colony is in fact isolated from the main population. In reality the situation is more complicated because very small populations produce few pollen grains and populations located between sites might not have been detected. Because we were not always able to find suitable sites at the precise locations where we wanted them,
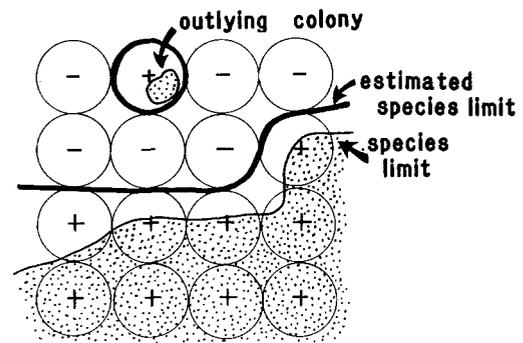

Fig. 1. Model sampling scheme. The stippled areas represent populations of trees, with a species limit and a small outlying population. Each + or − represents a lake used for pollen analysis, and the surrounding circle is the area of landscape from which pollen is contributed to the lake sediments. The symbol + means that significant quantities of pollen are present, − means that pollen is absent.

our grid is very irregular, and sites in parts of our study area are more than 100 km apart (Fig. 2). Recent studies suggest that small (3–10 ha) lakes should be located less than 20 km apart to provide more or less complete coverage for *Tsuga*, and even closer for *Fagus* (Schwartz, 1985).

At each site, the local arrival of a species was recorded by a succession of (1) no pollen (2) trace quantities of pollen and (3) 'significant' quantities of pollen. What range of values of pollen abundance should be considered 'significant'? Davis *et al.* (1986) determined the amounts of *Fagus* and *Tsuga* pollen that characterize lakes near local populations of these trees by comparing pollen percentages in lake sediments deposited in the early 19th century to the distances of the lakes from the 19th century range limits of source trees. Range limits were reconstructed from the occurrences of *Fagus* and *Tsuga* as witness and bearing trees in the United States Land Office Survey. The land survey was done in the mid-1800's before the forests were cleared. Approximately 50 sites near the range limits were uniform in size (3–10 ha), while an additional 50 sites well within the range limits include a few much larger lakes. Occasional grains were found in lakes more than 100 km from the species' limits, although most sites were devoid of pollen from *Tsuga* and *Fagus*. Percentages varied between 0 and 1% (*Tsuga*) or 0 and 0.5% (*Fagus*) in lakes 20–100 km outside the species boundaries. Closer
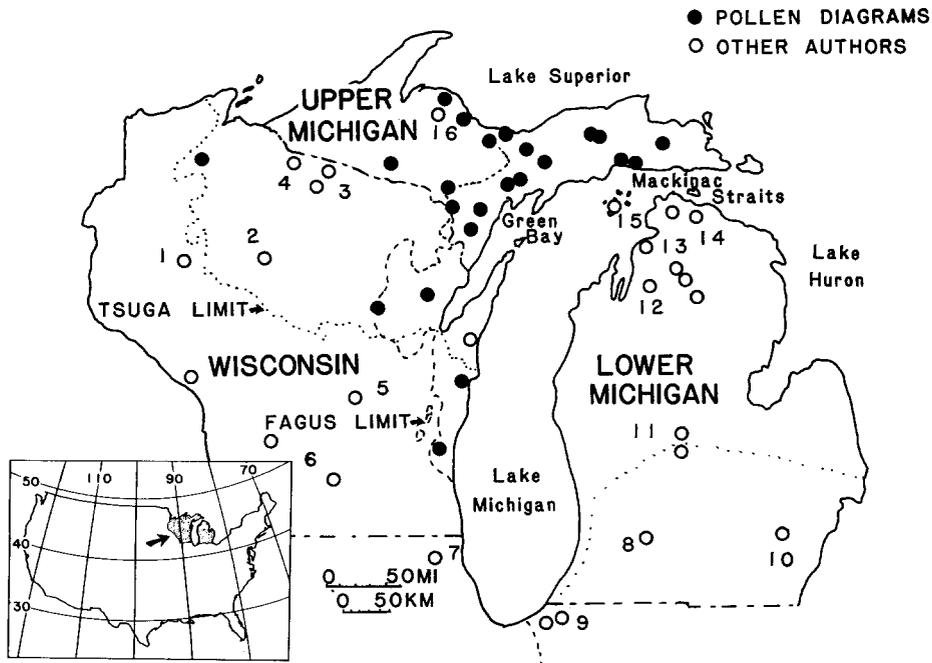
Fig. 2. Map of the Upper Great Lakes region indicating the locations of lakes used in this study (Woods & Davis, unpubl., S. L. Webb 1983; Futyma 1982). Open circles represent pollen analyses from the literature: 1) Peters & Webb, 1979; 2) Heide, 1984; 3) Webb, 1974; 4) Swain, 1978; 5) Maher, 1982; West, 1961; 6) Davis, 1977; 7) King, 1981; 8) Bailey, 1977; Manny *et al.* 1978; 9) Bailey, 1972; 10) Kerfoot, 1974; 11) Kapp, 1977; Gilliam *et al.* 1967; 12) Lawrenz, 1975; 13) Bernabo, 1981; 14) Futyma & Miller, unpubl.; 15) Kapp *et al.* 1969; 16) Brubaker, 1975. The four sites in eastern Upper Michigan are from Futyma, 1982.

to the boundaries they varied from trace amounts to 2–3%. Within the range limits, percentages rose as high as 20% (Davis *et al.,* 1986). These results mean that fossil pollen percentages higher than 1% (*Tsuga*) or greater than 0.5% (*Fagus*) that occur consistently at a series of stratigraphic levels (thus reducing the possibility of random events) can be considered evidence that the species boundary is located within 20 km. If the lake was surrounded by sites with little or no pollen from that taxon, these values are evidence for the establishment of an isolated local population. For example *Fagus* pollen is found in percentages greater than 0.5% at all levels younger than 6000 yr B.P. at sites in Wisconsin, on the west shore of Lake Michigan. These low percentages can be considered evidence for local *Fagus* trees, because there was no large population nearby (the closest known was 100 km distant) that could have served as a source for windblown pollen grains. Similar pollen values in contemporaneous sediment in northern Lower Michigan, however, could have been transported from the large popula-

tions that were growing further south — therefore they are not unequivocal proof of local presence of *Fagus* trees. We are using the term local here to mean within a radius of 5 km of the sampling site.

Temporal resolution

The accuracy of radiocarbon age determinations on lake sediment affects the precision with which we can date the establishment of new populations. The primary source of uncertainty is non-equilibrium carbon from calcareous bedrock or drift dissolved in lake water and incorporated into lake sediments via the uptake of CO_2 by submerged aquatic plants (Broecker & Walton, 1959; Deevey *et al.,* 1954). Non-equilibrium carbon is a problem throughout eastern Wisconsin and Upper Michigan where Paleozoic rocks, some of them calcareous, occur. Fortunately, most of the events that interest us occurred just before or just after the *Tsuga* decline, a pollen change that provides a convenient absolute time horizon dated at 4850 yr B.P.
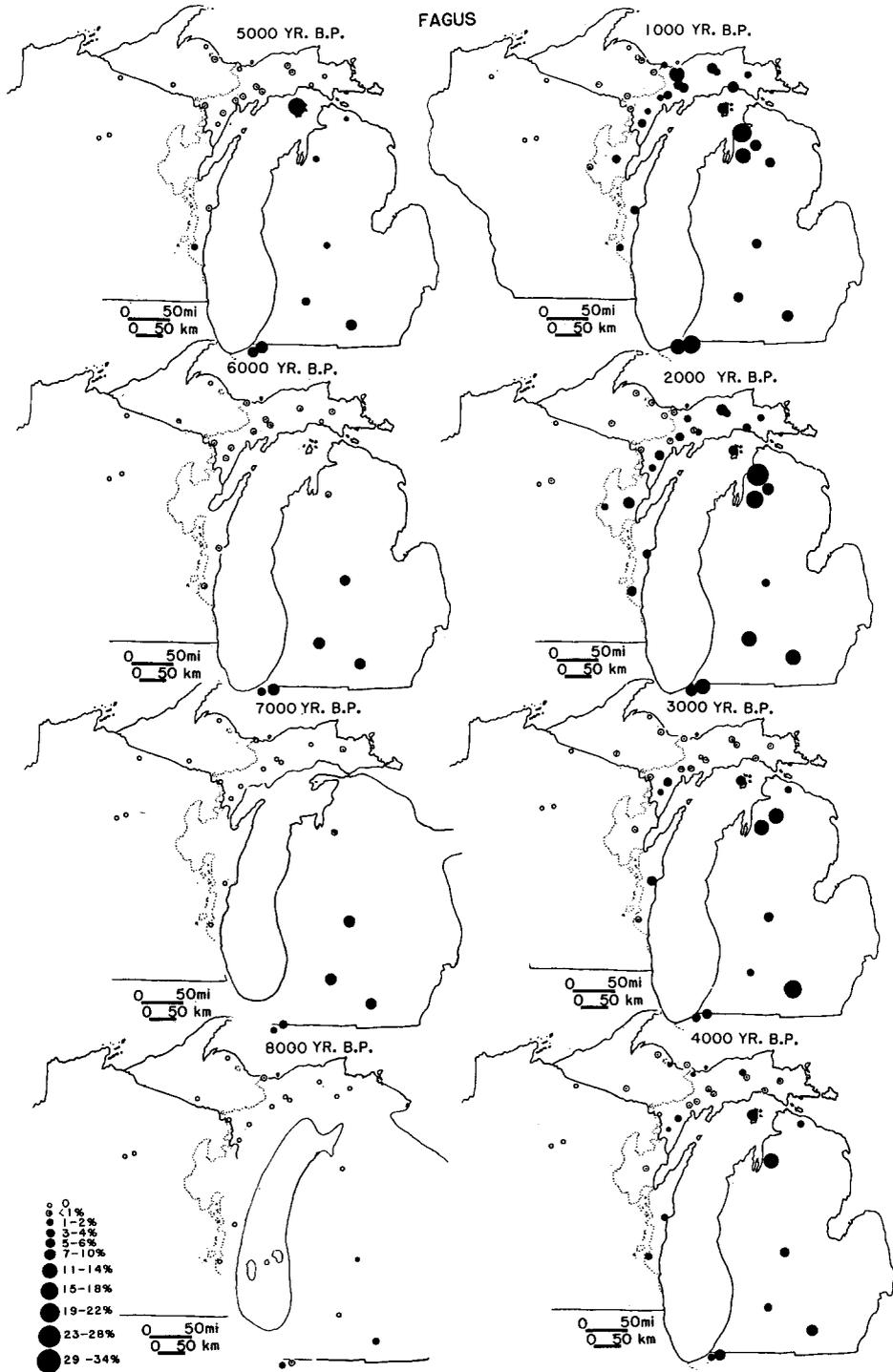
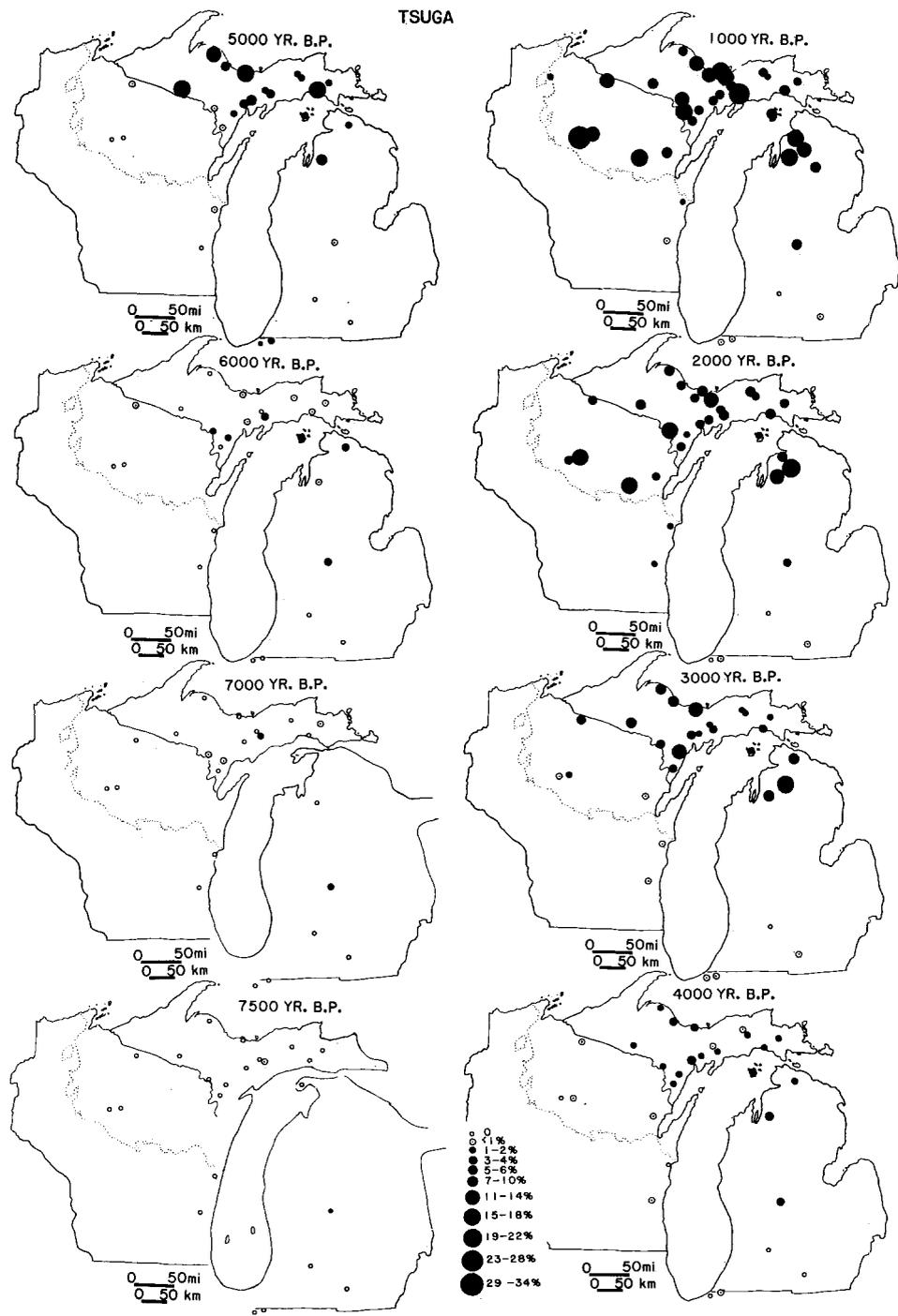*Fig. 3. Fagus* pollen percentages (as % total pollen from terrestrial plants) at 1000-yr intervals.

Fig. 4. *Tsuga* pollen percentages (as % total pollen from terrestrial plants) at 1000-yr intervals.

(Davis 1981b, Webb 1982, Allison *et al.*, 1986) to use for correction of radiocarbon dates. Nevertheless, we estimate that we cannot resolve events more closely than ±250 yr.

Results

Fagus

Maps of fossil *Fagus* pollen percentages at 1000-yr time intervals summarize our results. Published and unpublished data from other investigators are included on the maps; references appear in the figure legend for Fig. 2. Data shown in Figures 3 and 4 are pollen percentages interpolated between the two samples closest in estimated age to the datum for the map. *Fagus* pollen first appeared in lower Michigan 7000 yr B.P. By 6000 yr B.P., *Fagus* pollen percentages were ranging between 0.5 and 1.0% at two sites in southern Wisconsin, indicating that *Fagus* has become established on the western side of the lake (S.L. Webb, 1983). (This is the example mentioned above; there was no large population west of the lake from which pollen could have been dispersed. Therefore the low percentages must indicate local trees). This population was established by seeds which were dispersed either directly across the lake, or around its southern end. Because during this period the prairie-forest border in Minnesota had moved eastward from its present position and *Quercus* scrub or savanna grew in western Wisconsin and northern Illinois (Webb *et al.* 1983), continuous prairie may have been widespread in Illinois in areas that in presettlement time were prairie or savanna. Consequently the dispersal of *Fagus,* if it occurred around the southern end of the lake, must have involved dispersal of seeds between discontinuous patches of woodland growing in pockets of favorable habitat within a prairie landscape (S. L. Webb, 1983). These discontinuous patches could have been located among dunes or in ravines near the lake shore, or on moraines, where the irregular topography afforded protection from fire.

On the eastern side of Lake Michigan, *Fagus* expanded northward. It reached the straits of Mackinac and became established on a large island in Lake Michigan by at least 4500 yr B.P.; at this time trace quantities of pollen appeared at many sites in the Upper Peninsula (Fig. 3). After a lag of 500–1000 yr, populations became established 100 km to the west, near the western shore of Lake Michigan beyond Green Bay. At this time, however, populations had apparently not become established immediately to the north across the lake. *Fagus* pollen appeared at several sites in central Upper Michigan between 5000 and 3000 yr B.P., but the pollen occurrences are not continuous from one sample to another, and the percentages are very low. They may represent random pollen dispersal events, or small local populations that later became extinct. As late as 3000 yr B.P., significant amounts of pollen still occurred *consistently* only at the two sites west of Green Bay. Between 3000 and 2500 yr B.P., however, *Fagus* expanded rapidly (Woods & Davis, 1982). By the end of this 500-year interval *Fagus* was widespread across upper Michigan and extended southward into Wisconsin, where it came into contact with the older populations established 3500 yr earlier. A stable western boundary became established at this time. No further expansion took place until 500-1000 yr ago, when new populations became established as much as 50 km west of the frontier, at the present species limit (Woods & Davis, 1982). Fig. 5 shows a generalized map of *Fagus* spread into Michigan and Wisconsin.

Tsuga

Maps of fossil *Tsuga* pollen percentages at 1000 yr time intervals (Fig. 4) show the history of establishment of this species in Michigan and Wisconsin.

Tsuga pollen was absent from the region before 7000 yr B.P., when significant quantities of pollen appeared at two sites, one in lower and one in upper Michigan. Over the next 1000 years, pollen appeared at 4 additional sites. 6000 yr B.P. there were small quantities of pollen at widely scattered locations both north and south of the northern part of Lake Michigan, suggesting the establishment of small scattered outlying colonies, similar to those presently occurring today west of the main range of *Tsuga*. If these early occurrences are dated correctly, always a question in a region where the underlying bedrock is calcareous, they suggest the establishment of a number of separate populations through long-distance dispersal of seeds. The source area was apparently to the east and south-
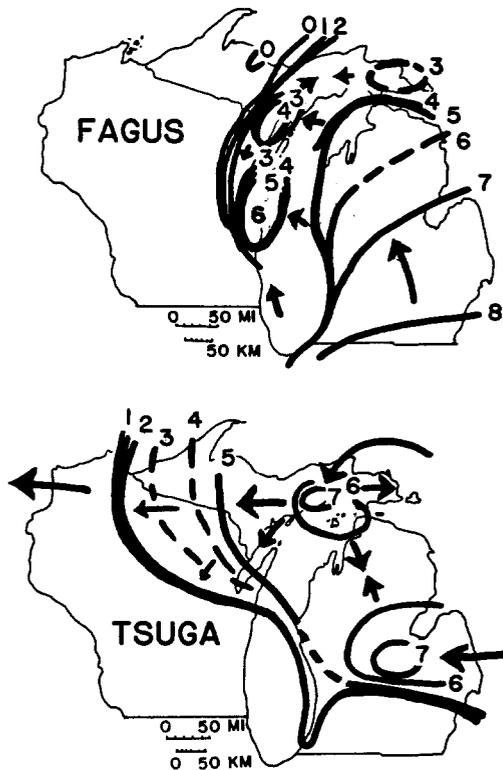
Fig. 5. Simplified reconstruction of the expansion of *Fagus* and *Tsuga* into the Upper Great Lakes Region. Lines show the position of the species limit at 1000-yr intervals.

east. Liu (1982) reports that by 7000 yr B.P. *Tsuga* pollen was present at low frequency in Ontario north of Lake Huron. This region was 150-200 km distant from the Michigan occurrences, although at that time the Lake Huron basin was partially drained and forests might have grown somewhat nearer, within the lake basin itself. The dispersal distances are not unreasonable, however, as colonies of *Tsuga*, apparently established within the last several thousand years, exist today in Minnesota, 50-150 km west of the main range limit in Wisconsin. Dispersal might also have occurred to lower Michigan over the shorter distance from southern Ontario, where *Tsuga* was established 8000 yr B.P. (Kapp, 1977; McAndrews, 1981). Farther south, in southernmost Michigan, only trace quantities of pollen occurred in lake sediments. *Tsuga* apparently never grew there, and migration did not occur from this direction, as one of us implied in earlier migration maps (Davis, 1981a, 1983b).

Tsuga then expanded rapidly. During the interval between 6000 and 5500 yr B.P. it colonized all sites in the eastern half of upper Michigan, with high pollen percentages suggesting population densities similar to today.

Tsuga pollen percentages decreased suddenly at all sites 4800 yr B.P. The *Tsuga* decline resembles a response to a pathogen outbreak, as it was synchronous throughout the range of *Tsuga* (Davis, 1981b; Webb, 1982), and its time course was similar to that for *Castanea* during the blight that occurred in the early decades of this century (Allison et al., 1986). The decline is shown in Fig. 4 by the decrease in *Tsuga* percentages at all sites between 5000 and 4000 yr ago. As populations recovered again over the next 2000 years *Tsuga* extended its range westward and southward. By 3000 yr B.P. it had reached central Wisconsin, and by 1800 yr B.P. significant quantities of pollen occurred at Hemlock Lake (Fig. 2), recording the arrival of *Tsuga* at its westernmost limit of continuous distribution in Wisconsin.

A generalized map (Fig. 5) suggests initial colonization 7000-6000 yr B.P., and rapid spread 6000 – 5000 yr B.P. within eastern Upper Michigan and throughout the northern part of Lower Michigan. During the next 5000 years, however, range extension proceeded much more slowly. The data are insufficient to indicate whether expansion during this latter interval occurred continuously, or at a variable rate.

Discussion

We have identified two different time lags in the expansion of *Fagus*, one of which is related to dispersal across Lake Michigan. Can these time lags be used as evidence that dispersal of seeds, and not another factor, limited the distribution of *Fagus*? S.L. Webb (1983) has discussed the problem of establishment of *Fagus* in southern Wisconsin. She argues that beechnuts had to be carried over barriers 25 – 100 km wide to reach Wisconsin, no matter what route was used – through xeric habitats around the southern end of Lake Michigan, or directly across the lake (Fig. 5). The probabilities of dispersal over such great distances are sufficiently low that dispersal constraints alone could have caused a 1000-yr delay in *Fagus* establishment in

southern Wisconsin, after the initial buildup of extensive stands in southern Michigan.

An alternative explanation for the delay in the establishment of *Fagus* in Wisconsin is that climate was unfavorable 7000 yr ago, changing and becoming more hospitable to *Fagus* by 6000 yr B.P. One can speculate that the decrease in seasonality that apparently characterized the mid-Holocene (T. Webb, 1986) could have caused the climate of Wisconsin to become more suitable for *Fagus*. Note, however, that pollen percentages in Michigan, where *Fagus* should have been favorably affected by the same change, were actually *declining* at this time. Arguments in favor of the climate hypothesis are the restricted range of *Fagus* in Wisconsin, and the fact that *Fagus* never spread westward from the areas initially colonized, suggesting that climate has always been as strongly limiting as it appears to be now (Ward, 1956, 1958, 1961). In fact, however, *Fagus* in Wisconsin and Michigan appears to be limited to particular soil types, especially calcareous soils. Possibly a combination of soil factors and climate prevent *Fagus* from expanding westward today. Another problem with the climate hypothesis is that even if we postulate that the climate suddenly changed 6000 years ago, making eastern Wisconsin habitable for *Fagus,* we are still faced with the problem of transporting seeds 100 or more km across open water of prairie. Blue jays (*Cyanocitta cristata*) have been observed to carry *Fagus* nuts distances of 4 km or more from *Fagus* forests to their nesting areas (Johnson & Adkisson, 1986). The extinct passenger pigeon probably dispersed seeds occasionally (S. L. Webb, 1986), but was primarily a seed predator. Thus a lag period during which the species range is not in equilibrium with climate seems reasonable. There is no way to estimate the probability of a rare event like long-distance dispersal except by using fossil data. In the absence of direct observation, a 1000 yr time lag seems reasonable to us, but we have not disproved the idea that the lag was partly caused by climate.

Colonization of most of Upper Michigan was delayed for about 2000 years after *Fagus* arrived in northern Lower Michigan. A dispersal lag is possible in this case also, although the water barrier was relatively narrow; there are several islands in the northern part of Lake Michigan that could have served as stepping stones. In fact a pollen diagram from Beaver Island (Kapp *et al.,* 1969) shows appreciable quantities of *Fagus* pollen at the time of

the *Tsuga* decline 4500–5000 yr ago, about the same time that *Fagus* was becoming abundant in the northern part of Lower Michigan. Yet *Fagus* was not established at most sites in the Upper Peninsula for another 1500 years.

To entertain a climate hypothesis to explain the lag in *Fagus* establishment in Upper Michigan, it is necessary to postulate a significant north-south climatic gradient across the lake, a distance of less than 50 km. There is evidence to support this idea, derived from the types of soils first colonized. The sites west of Green Bay, where *Fagus* was established early (3500–4000 yr B.P.), are in a region of glacial till over limestone bedrock. All but one of the lakes we have studied in eastern upper Michigan are in regions of sandy glacial outwash (Farrand *et al.,* 1982). We have not studied sediments in the easternmost part of the peninsula, where clay-rich soils exist. Our network of sites is thus not sufficiently dense nor sufficiently representative of soil types, to rule out the possibility that *Fagus* was established early throughout Upper Michigan wherever heavy soils existed, expanding later to dry, sandy soils near the sites we have investigated. An initial restriction to one soil type, and later relaxation of the soil preference, could imply a climatic change from strongly limiting soil moisture to conditions that were less limiting. This hypothesis will be tested by investigating sites of clay-rich soils in the eastern part of the peninsula. Pennington (1986) has shown that the late-glacial distribution of *Betula* was controlled by the rate of soil development. Because *Fagus* moved into Michigan during the late Holocene, we doubt that the rate of actual soil development was a controlling factor, but rather the moisture-retaining capacity of the parent materials.

The western limit of *Fagus* that was established 2500 yr B.P. was stable for the next 1500 years, expanding within the last 500–1000 years when regional climatic changes occurred that were associated with the Little Ice Age (Bernabo, 1981). A stable frontier, followed by expansion when climate change occurred, is convincing evidence that the species limit has been in equilibrium with climate for the last 2500 years.

Was the geographical range of *Tsuga* in equilibrium with climate? After its initial colonization of the region 7000–6000 yr B.P., its spread between 6000–5500 yr B.P. was so rapid that it is essentially instantaneous over a 70 000 km^2 area. The same

arrival time is seen on sands and finer-grained till soils, suggesting that soil moisture was not a limiting factor. If this explosive expansion was due to climate, it records a large step-change in temperature that occurred throughout an extensive region. A large step-change in temperature 5500–6000 yr ago is not recorded in the Great Lakes region by other kinds of evidence, however (Webb et al., 1983). We postulate that a non-equilibrium situation for hemlock existed 7000–5000 yr B.P., with populations first being established through long-distance dispersal of seeds, and then expanding exponentially in a climatically favorable region. There is no basis on which to speculate how long the region might have been favorable for hemlock prior to 7000 yr B.P., and we know of no way to rigorously investigate this idea.

After 5000 yr ago, however, westward and northward expansion of Tsuga occurred more slowly. From this time until the present, it seems likely that climate controlled the geographical distribution of Tsuga. Some of the outlying populations were established long ago but have not expanded, indicating that the climate has not been favorable for Tsuga beyond its limit except in special habitats. Radiocarbon-dated wood indicates that Tsuga was established 4500 yr B.P. in the driftless area of central Wisconsin (Johnson, 1976). Colonies exist there today, 100 km south of the main species boundary. At the time of its apparent establishment 4500 yr B.P., the outlier was about 150 km beyond the species boundary, a distance comparable to the farthest outlying colonies in Minnesota today.

The westward and southward expansion of Tsuga into Wisconsin occurred at the same time that Pinus strobus was moving westward in Minnesota (Jacobson, 1979). A westward movement of the prairie-forest border has been detected on a regional scale, starting about 6000 yr B.P. (Webb et al., 1983). We believe that the westward movement of Tsuga after 4000 yr B.P. might have been caused by similar climatic trends in northern Wisconsin.

Conclusions

We believe there is evidence that the geographical limit of Fagus was in disequilibrium with climate in southern Wisconsin 7000–6000 yr B.P., whereas the distribution of Tsuga in Michigan may also have been in disequilibrium with climate prior to 5000 yr B.P. The evidence is largely inferential, however. We have found it difficult to devise rigorous tests for these hypotheses. Lake Michigan poses a geographical barrier, suggesting that dispersal may have been responsible for the delay in Fagus arrival on the far side of the lake. However, this argument has no bearing on the possibility that climatic conditions in Wisconsin were also unfavorable. Different kinds of evidence are needed to assay the climate, and they must perforce be independent of the distribution of Fagus.

The delay in colonization of northern Michigan presents a similar dilemma. In this case it is possible to devise a means for testing the effect of soil moisture: in future studies we will look for differential colonization of fine-textured and coarse-textured soils by Fagus 4000–2500 yr B.P. We should emphasize, however, that when this is eventually done, the answer may still fail to distinguish between our two hypotheses. That is, if the answer is negative and we fail to demonstrate that soil moisture was important, we will not have *proved* that seed dispersal was limiting. Climate and dispersal are particularly difficult to distinguish because they are not mutually exclusive causes for colonization delays.

We are dissatisfied with arguments that the most 'parsimonious' explanation can be considered correct until proven wrong. The two hypotheses we have considered here are not mutually exclusive ideas; it seems likely to us that both factors were operating most of the time. Dispersal must always limit range expansion, but the resulting lag may be so short as to be unimportant for paleoclimatic reconstruction (Webb, 1986). Those exceptional circumstances when climatic changes were so large that extensive areas became suitable for growth before trees were able to colonize them probably occurred only during the early Holocene for most tree species. We postulate here that conditions like this might have existed in Michigan as late as 5000 yr B.P. for Tsuga, and as late as 6000 yr B.P. for Fagus in southeastern Wisconsin, and possibly as late as 2500 yr B.P. in Upper Michigan. We emphasize, however, that we have no way of knowing when the climate in Michigan and Wisconsin first became suitable for these species, and therefore we do not know how long disequilibrium conditions might have existed.

Both species we have investigated reached their western limits rather late in the Holocene, but our data suggest they were in equilibrium with climate along their western boundaries for several millennia prior to reaching modern limits. We know of no tree species in North America that is still expanding at the rapid rates recorded in the fossil record (Davis, 1981a). We are therefore lacking modern analogs for the rapid range extensions of temperate forest species recorded by fossil pollen during the Holocene.

References

Allison, T., Moeller, R. E. & Davis, M. B., 1986. Pollen in laminated sediments provides evidence for a mid-Holocene forst pathogen outbreak. Ecology, in press.

Bailey, R. E., 1972. Vegetation history of northwest Indiana. Ph.D. Thesis, Indiana University, Bloomington, Indiana.

Bailey, R. E., 1977. Pollen stratigraphy of Wintergreen Lake. In R. O. Kapp (ed.) 'Handbook for Paleoecology Field Trip in Central Lower Michigan'. Ecol. Soc. Amer., AIBS, East Lansing, MI.

Bernabo, J. C., 1981. Quantitative estimates of temperature changes over the last 2700 years in Michigan based on pollen data. Quat. Res. 15: 143–159.

Broecker, W. S. & Walton, A., 1959. The geochemistry of C14 in freshwater systems. Geochem. Cosmochim. Acta 16: 15–38.

Brubaker, L. B., 1975. Post-glacial forest patterns associated with till and outwash in Northcentral Upper Michigan. Quat. Res. 5: 499–527.

Davis, A. M., 1977. The prairie-deciduous forest ecotone in the upper Middle West. Ann. Assoc. Amer. Geogr. 67: 204–213.

Davis, M. B., 1976. Pleistocene biogeography of temperate deciduous forests. Geoscience and Man 13: 13–26.

Davis, M. B., 1981a. Quaternary history and the stability of deciduous forests. In D. C. West, H. H. Shugart & D. B. Botkin, (eds.) 'Forest Succession', p. 132–177. Springer-Verlag, N.Y.

Davis, M. B., 1981b. Outbreaks of forest pathogens in Quaternary history. Proc. 4th Int. Palynol. Conf. Lucknow, India 3: 216–227.

Davis, M. B., 1983a. Holocene vegetation history of the eastern United States. In H. E. Wright (ed.) 'Late-Quaternary Environments of the United States. Vol. 2, The Holocene', p. 166–181. Univ. of Minnesota Press, Minneapolis.

Davis, M. B., 1983b. Quaternary history of deciduous forests of eastern North America and Europe. Ann. Missouri Bot. Gard. 20: 550–563.

Davis, M. B., Schwartz, M. W., Woods, K. D. & Webb, S. L., 1986. Detecting beech and hemlock species limits from pollen in sediment. AMQUA Abstr. (1986) p. 76.

Deevey, E. S., Jr., Gross, M. S., Hutchinson, G. E. & Kraybill, H. L., 1954. The natural C14 contents of materials from hardwater lakes. Nat. Acad. Sci. Proc. 40: 285–258.

Farrand, W. R. & Bell, D. L., 1982. Quaternary geology of northern Michigan. Map, 1:500,000, MI Dept. Nat. Res., Geological Survey, Lansing.

Fowells, H. A., 1965. Silvics of forest trees of the United States. U.S. Dept. of Agriculture, Agr. Handbook 271, U.S. Govt. Printing Office, Washington, D.C.

Futyma, R. P., 1982. Postglacial vegetation of eastern Upper Michigan. Ph.D. thesis, University of Michigan, Ann Arbor, Michigan. 426 pp.

Gilliam, J. A., Kapp, R. O. & Bogue, R. D., 1967. A post-Wisconsin pollen sequence from Vestaburg Bog, Montcalm County, Michigan. Michigan Acad. Sci., Arts Lett 52: 3–17.

Heide, K. M., 1984. Holocene pollen stratigraphy from a lake and small hollow in north-central Wisconsin, USA. Palynology 8: 3–20.

Huntley, B. & Birks, H. J. B. 1983. An atlas of past and present pollen for Europe 0–13,000 years ago. Cambridge Univ. Press. Cambridge.

Iversen, J., 1954. The late-glacial flora of Denmark and its relation to climate and soil. Danmarks Geol. Unders. Ser. II, No. 80, p. 87–119.

Jacobson, G. L., 1979. The paleoecology of white pine (Pinus strobus) in Minnesota. J. Ecol. 67: 697–726.

Johnson, W., 1976. Impact of environmental change on fluvial systems: Kickapoo River, Wisconsin. Ph.D. diss., University of Wisconsin, Madison.

Johnson, W. C. & Adkisson, C. S., 1986. Dispersal of beech nuts by blue jays in fragmented landscapes. Am. Midl. Nat. 13: 319–324.

Kapp, R. O., 1977. Late Pleistocene and post-glacial plant communities of the Great Lakes Region. In R. C. Romans (ed.), 'Geobotany', p. 1–27, Plenum, New York.

Kapp, R. O., Bushouse, S. & Foster, B., 1969. A contribution to the geology and forest history of Beaver Island, Michigan. Proc. 12th Conf. Great Lakes Research 1969, p. 225–236.

Kerfoot, W. C., 1974. Net accumulation rates and the history of cladoceron communities. Ecology 55: 51–61.

King, J. E., 1981. Late Quaternary vegetational history of Illinois. Ecol. Monogr. 51: 43–62.

Lawrenz, R. W., 1975. The development of Green Lake, Antrim County, Nucgugan, Michigan. M.S. Thesis. Central Michigan University, Mount Pleasant, Michigan.

Liu, K., 1982. Palynology and paleoecology of the boreal forest/Great Lakes-St. Lawrence forest ecotone in northern Ontario. AMQUA Abstracts (1982) p. 122.

Maher, L. J., Jr. 1982. The palynology of Devil's Lake, Sauk County, Wisconsin. In Quaternary History of the Driftless Area, Fieldtrip Guide Book 5, p. 119–135, Univ. Wisc. Ext. Geol. and Natl. History Survey.

Manny, B. A., Wetzel, R. G. & Bailey, R. E., 1978. Paleolimnological sedimentation of organic carbon, nitrogen, phosphorous, fossil pigments, pollen, and diatoms in a hypereutrophic, hardwater Lake: A case history of eutrophication. Polsk. Arch. Hydrobiol. 25: 243–267.

McAndrews, J. H., 1970. Fossil pollen and our changing landscape and climate. Rotunda 3: 30–37.

McAndrews, J. H., 1981. Late Quaternary climate of Ontario: temperature trends from the fossil record. In W. C. Mahaney (ed.), Quaternary Paleoclimate. Geoabstracts Ltd.

Pennington, W. (Mrs T. G. Tutin), 1986. Lags in adjustment of vegetation to climate caused by the pace of soil development. Evidence from Britain. Vegetatio 67: 105–118.

Peters, A. & Webb III, T., 1979. A radiocarbon-dated pollen diagram from west-central Wisconsin. Bull. Ecol. Soc. Amer. 60, p. 102.

Ridley, H. N., 1930. The dispersal of plants throughout the world. Reeve, Ashford.

Ritchie, J. C., 1986. Climate change and vegetation response. Vegetatio 67: 65−74.

Schwartz, M. W., 1985. A critical investigation of regression Techniques and data collection methods to improve estimates of the pollen/tree relationship. M.S. Thesis, University of Minnesota, Minneapolis.

Swain, A. M., 1978. Environmental changes during the last 2000 years in north-central Wisconsin: Analysis of pollen, charcoal and seeds from varied lake sediments. Quat. Res. 10: 55−68.

Ward, R. T., 1956. The beech forests of Wisconsin − changes in forest composition and the nature of the beech border. Ecology 37: 407−419.

Ward, R. T., 1958. The beech forests of Wisconsin − their phytosociology and relationships to forests in the state without beech. Ecology 39: 444−457.

Ward, R. T., 1961. Some aspects of the regeneration habits of American beech. Ecology 42: 828−832.

Webb, S. L., 1983. The Holocene extension of the range of American beech (*Fagus grandifolia*) into Wisconsin: paleoecological evidence for long-distance seed dispersal. M.S. thesis, University of Minnesota, Minneapolis.

Webb, S. L., 1986. Potential role of passenger pigeons and other vertebrates in the rapid Holocene migrations of nut trees. Quat. Res., in press.

Webb III, T., 1974. A vegetation history from northern Wisconsin: Evidence from modern and fossil pollen. Amer. Midland Nat. 92: 12−34.

Webb III, T., 1982. Temporal resolution in Holecene pollen data. In Proceedings Third North American Paleontological convention, Vol. 2, p. 569−572.

Webb III, T., 1986. Is vegetation in equilibrium with climate? How to interpret late-Quaternary pollen data. Vegetatio 67: 75−91.

Webb III, T., Howe, S. E., Bradshaw, R. H. W. & Heide, K. M., 1981. Estimating plant abundances from pollen percentages: The use of regression analysis. Rev. Paleobot. Palyn. 34: 269−300.

Webb III, T., Cushing, E. J. & Wright, H. E., Jr. 1983. Holocene changes in the vegetation of the midwest. In H. E. Wright, Jr. (ed.) 'Late-Quaternary Environments of the United States, Vol. 2, The Holocene,' p. 142−165. Univ. of Minnesota Press, Minneapolis.

West, R. G., 1961. Late and post-glacial vegetational history in Wisconsin, particularly changes associated with the Valders readvance. Amer. J. Sci. 259: 766−783.

Woods, K. D. & Davis, M. B., 1982. Sensitivity of Michigan pollen diagrams to Little Ice Age climatic changes. AMQUA Abstr. (1982) p. 181.