POSTGLACIAL VEGETATION IN THE ERIE-OHIO AREA

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It is fitting that the Golden Anniversary program of this Academy should devote some time to the problems of Ohio vegetation. The diversity of natural vegetation in Ohio has interested observers from the days of the first explorations down to the present. Before the founding of the Academy, surveyors, geologists, and botanists all contributed to the record. A notable instance was Dr. John L. Riddell (1) who saw in the prairies of Ohio a remarkable phenomenon.

In more recent years the Academy itself has generously encouraged studies of Ohio vegetation. Needless to say the pattern of this vegetation has had profound influence on the agricultural and industrial life of the state. During the past twenty years, beside the important work of Dr. Braun at Cincinnati (2), there have been numerous studies by Dr. Transeau and his associates at Columbus. These studies have had valuable results in their application to pest control (3). They have illuminated the work of a generation of young biologists who are now applying their knowledge to problems of land use and management throughout this and other states. I am glad to record such a debt to the Academy and the many colleagues who have labored in its ranks.

Some notion of the diversity of Ohio vegetation may be obtained from Figure 1, showing various types and their irregular pattern of distribution. It may be said at once that no simple factor can be adduced as an explanation. No map of climatic configuration that I have ever seen can be superposed on this map of original vegetation. One can, it is true, see evidence for some large physiographic influences, notably glaciation and lake retreat (4). Yet detailed profiles through various types of plant community certainly show that here again there is no simple relationship between topography and vegetation.

One needs no better evidence of the multiplicity of factors operative in the Ohio landscape than to see how comfortably—until the axe and plow destroyed them—species and communities of differing geographical and climatic affinities got on in close proximity.

Transeau's paper on the Prairie Peninsula (5) in addition to its clear formulation of numerous problems, has served to emphasize the relative and complex character of Ohio climate. As time goes on we shall learn much more about this matter from the studies now under way in the Muskingum watershed (6).

Author's Note: Since preparing the accompanying article, the writer has made an extended study of the literature dealing with the question of xerothermic postglacial climate. In view of recent evidences from Europe, the references in this paper to a xerothermic period ought not to be regarded as excluding the possibility of significant aridity earlier than the pine period here referred to. However, it should be stated that no American bogs thus far examined give any indication of such conditions.

At the other edge of the prairie, Weaver and Albertson (7) have shown how definite may be the effect on community composition of a few years of protracted drouth. And I may add that my own casual examination of tree rings in the Osage region indicates that recurring drouths, lasting from two to ten years, have characterized at least the past two hundred years.

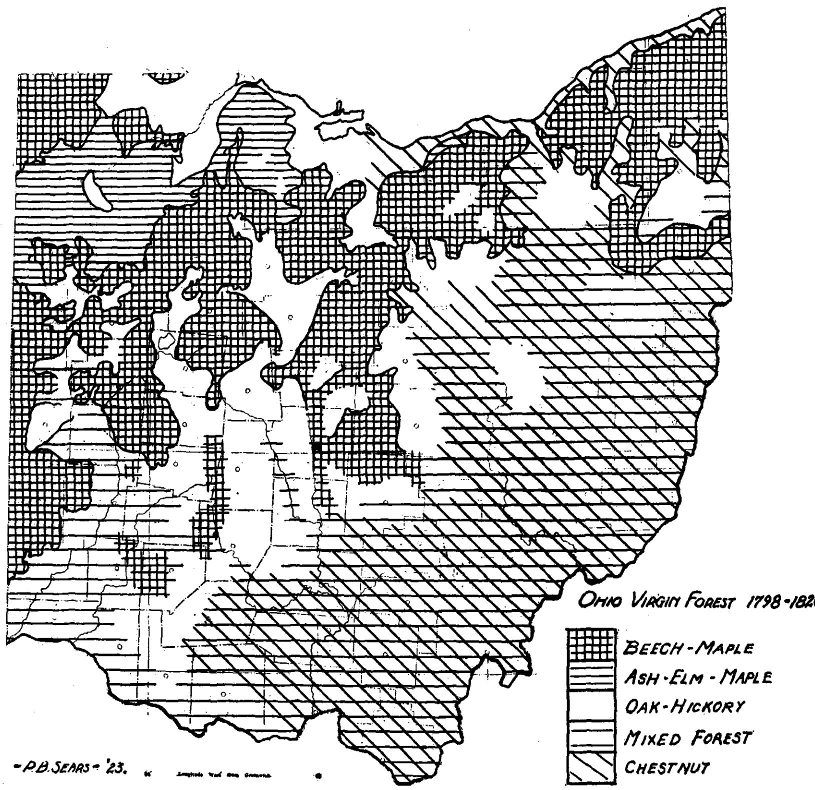


Fig. 1. A map of the original vegetation of Ohio based upon records of early surveys.

Because of the inadequacy of explanation based on existing conditions, students of vegetation have followed the steps of Asa Gray and other taxonomists in searching for historical data. In the case of Ohio, two important types of community—bog and grassland—present in a deciduous forest region have for many years emphasized the need for and importance of historical study.

Beginning in 1925 and for ten years thereafter, I employed the technique of pollen analysis in trying to trace the general course of vegetation changes throughout the Middle West. Several years were required for getting acquainted with the American pollen (8), a circumstance which materially slowed the procedure.

Taxonomists and others had already accumulated a good deal of evidence, not only of migration in the wake of the retreating glacier but of postglacial changes which involved east-and-west shifts of vegetation (9), presumably due to changing humidity of climate. The former presence of coniferous forests in Ohio and elsewhere in the deciduous forest region was readily established by pollen analysis. Its demonstration is now a routine experience which can be used as a laboratory exercise. Wherever there is a peat deposit whose sedimentation began in late glacial time, the presence of abundant coniferous pollen can be shown by microscopic examination of the deep layers of peat or marl.

It happens that the first bog I studied was likewise the oldest, situated on the crestline of the state, east of Bucyrus (10) (Fig. 2). The record here begins with an abundance of fir, gradually shifting to spruce,

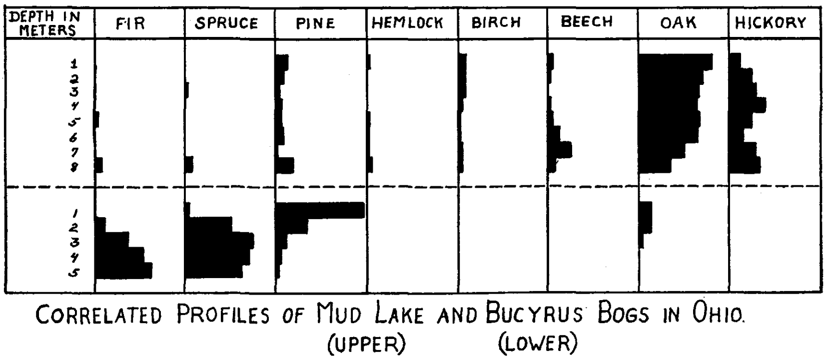


Fig. 2. Combined pollen profile of Bucyrus (lower) and Mud Lake (upper) bogs.

and then to pine. The pine in turn is replaced by increasing amounts of hardwood pollen, but the record is not complete because the top of the deposit has been destroyed.

This pine maximum toward the end of coniferous time is widespread, and was interpreted, correctly, I still believe, to indicate a period of increasing aridity.

Subsequent analyses of bogs in deep kettle-holes, where peat formation has gone on more or less continuously up to the present, indicated that the deciduous period has been much more prolonged than we were to suspect from the truncated record of the Bucyrus bog. One of the best examples of this is the Mud Lake Bog in Ashland County (11). Among our unpublished records of some 25 bogs, however, we have found ample confirmation. This is also generally true of profiles that have been published by the growing number of other workers throughout Eastern North America.

Taking the Mud Lake Bog as an example (Fig. 2), we find a strong showing of beech and hemlock at the beginning of deciduous time, then once again in recent layers, a behaviour paralleled by the record of birch.

Hickory, however, shows a reciprocal curve, being strongest about two-thirds up from the bottom, when beech and hemlock were greatly reduced.

Here again we reasoned that the beech and hemlock, replacing pine, indicated warming and increased moisture. Above that point the hickory maximum we interpreted as a second dry—but now warm—interval whose waning was marked by the return of beech and hemlock. If our reasoning was correct, we had established the existence and position of the elusive xerothermic period postulated by Gleason (9) and others as an explanation of the prairie relicts east of the present prairie.

Let me acknowledge that this was dangerous reasoning, based on a minimum of evidence. In justification let me say that the profiles, instead of being erratic, showed long consistent drifts in the course of change, and that the genera we were using are excellent climatic indicators. It is of interest that Professor Fuller at Chicago, on first seeing it, pronounced the sequence obtained from the two bogs—Bucyrus and Mud Lake—an excellent confirmation of the Blytt-Sernander hypothesis of postglacial climate that had been developed in Europe (12).

Two problems immediately presented themselves. One was that of confirming or disproving the general sequence. The second was that of chronology. The first problem required the widescale study of peat profiles and their comparison. This had to be done as rapidly as good work would permit, and to that end a considerable number of other workers were given assistance in learning the proper technique.

It is of course clear that no analysis is complete without supplementary study of the basin from which the peat comes. But the basins will keep, and the peat frequently in these days of rapid exploitation will keep, and the peat in these days of rapid exploitation frequently will not. For that reason, our first objective was to secure just as many pollen profiles as possible.

The results of these studies showed clearly enough that there are definite regional types of peat profile, with their characteristic pollen trends. Furthermore, the presence of an early dry—cool—pine period seemed to be pretty general in the older, longer profiles. Above that, corresponding to the Mud Lake hickory maximum, presumably warm-dry, many at least of the profiles showed a maximum of oak as compared with more mesophytic species. The most important exception seemed to be the findings of Voss in Lake County, Illinois, to which further reference will be made.

As to the problem of dating, we did as others have had to do: used what means we could, pending the time when an accurate varve chronology would be afforded to us. So we obtained by three independent means some notion of the normal rate of peat accumulation. Knowing full well that this sort of measure has to be used with the utmost caution, we at least obtained estimates which indicated that we were dealing with magnitudes of the same general order as the precisely dated European records (13).

Meanwhile criticism arose from several sources. Doubt was expressed concerning the dependability of our counts, based on 100 to 200 grains per sample. As a result, Barkley (14), working in Oklahoma, made a study of the statistical principles involved and showed clearly that no practical gain may be expected by counting more than 150 grains per sample.

The second criticism was based on the studies of Voss (15) in Illinois, already referred to. It has been urged by Fuller (16) so that some attention should be given to it here. The Lake County profiles of Voss showed a replacement of conifers by deciduous forests, mainly oak, at the end of the first third of the record. Thereafter the deciduous forms exhibited what seemed to be an irregular fluctuation, giving no clear evidence of any climatic or vegetational change.

It should be noted, however, that Voss' own profiles from farther north showed a concave conifer curve, increasing at the top, complementary to a convex deciduous curve. This would appear to agree in general with either (a) the upper portion of our Ohio curves, or (b) with our whole curve if we assumed that the humid beech-hemlock interval was merely a local phenomenon.

To allow for this possibility, and to afford a scheme that could be definitely tested, I then proposed an hypothesis that postglacial time had been marked by a long period of warming and perhaps drying, up to a maximum from which it has since receded (17).

This of course does not take care of the Lake County bogs. But in explanation it must be said that there is no means of distinguishing the species of oak in these profiles from Illinois. And anyone who knows the oak-hickory region is well aware that red oak is more mesophytic than certain members of the white oak group. A fluctuation from red oak to white oak or vice versa in this region would be very significant if we could demonstrate it. But with all species of oak necessarily lumped, any such phenomenon would remain masked.

Furthermore, these profiles contain no mention of grass pollen, although it usually is pretty well preserved and should be of the greatest importance in indicating fluctuations at the margin of the grasslands. So far as climatic evidence is concerned, then, my own judgment with regard to the Illinois bogs is to recognize that they fail to support the xerothermic idea. What they might reveal if the species of oak could be determined and if grass pollen could be found in them would be of great interest and value.

Meanwhile, serious considerations were brought forward by the thorough studies of Wilson in Northwestern Wisconsin (18), where pollen profiles had been studied with reference to the recessional stages of Lake Superior and the present-day plant successions. In general the profiles fitted into the series obtained by workers from Minnesota eastward through Quebec. Predominantly coniferous at the base, they exhibited a slight shift toward oak at higher levels, followed by a recent increase in spruce, i. e., a return of conifers. Yet when compared with current successional changes these profiles in Wisconsin seemed explicable in terms of local plant succession under a climate like the present.

Without some basic climatic change, however, one would scarcely expect to find such a remarkable parallel trend in local succession on a front extending from the northern Great Lakes to the Atlantic. Moreover, both in Europe and America the sequence, conifer-hardwood-conifer, has been established as characteristic of interglacial periods, one of which the present may well represent.

It is of the greatest interest, therefore, to know that a recent study[1] of Ohio peat deposits has enabled Wilson to correlate them with the Wisconsin profiles and confirm the fact of recent climatic change, including a xerothermic period corresponding to the oak maximum noted by him.

Meanwhile it is in order to present the results of further study at Oklahoma, Oberlin, and Yale. Miss Eleanor Galloway who had been trained with Dr. Wilson was given access to much of my unpublished material and found a definite relation between profile type and bog

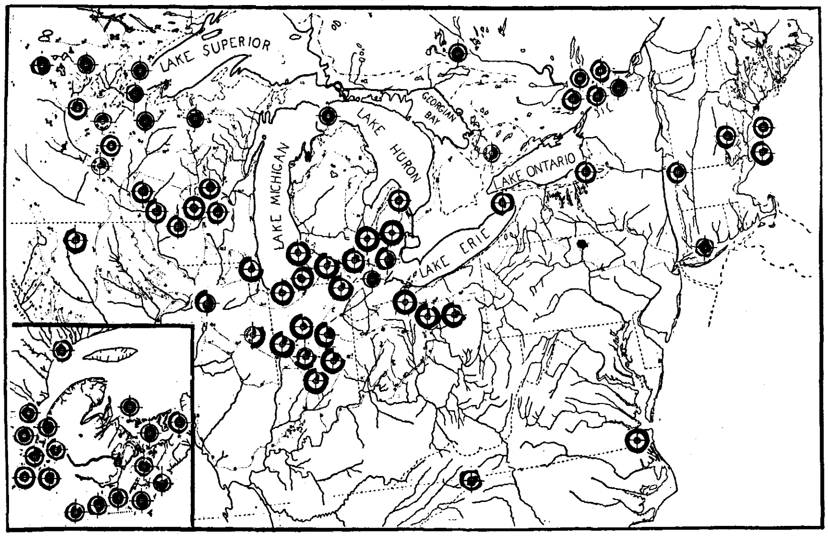


Fig. 3. Clock diagrams showing postglacial changes in frequency of conifers (inner circle) and deciduous (outer circle) trees. (From Preston Smith.)

location. Her manuscript is not now at hand, but as I recall it, a line approximating the Fourth Wisconsin Substage limit is roughly a boundary south of which are bogs whose profiles are mainly deciduous, while those to the north are largely coniferous. Mixed types are intermediate in position.

Last year this problem of correlation was resumed by Mr. Preston Smith at Oberlin, our immediate aim being to trace the course of postglacial migration of certain trees. First compiling a critical map of glacial boundaries, data from nearly 70 bogs were assembled and plotted in the form of clock diagrams. Proceeding clockwise, these circles show the changing frequency from bottom to top of the bog.

The first of these shows the relative position and abundance in each

[1]Unpublished. Not seen until after this paper was read before the Academy.

profile of conifers (inner) and deciduous (outer) species (Fig. 3). The second gives the same information for hemlock (inner) and beech (outer) (Fig. 4). No correction is made for differences in time represented by a given profile, except as this is indicated by the position of each bog.

Yet the map shows very clearly the location of Miss Galloway's deciduous, mixed, and coniferous profile types with reference to glacial retreat. Likewise the southwesterly movement of *Tsuga* and the northerly movement of *Fagus* are evident.

Further light on postglacial migration is available by taking five representative genera, *Tsuga*, *Quercus*, *Fagus*, *Carya*, and *Tilia*, and noting the order of their appearance in as many profiles as possible.

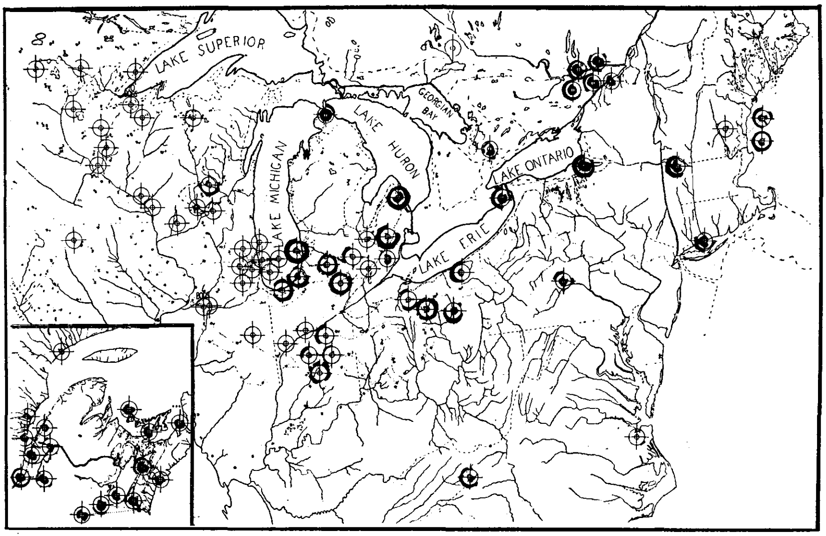
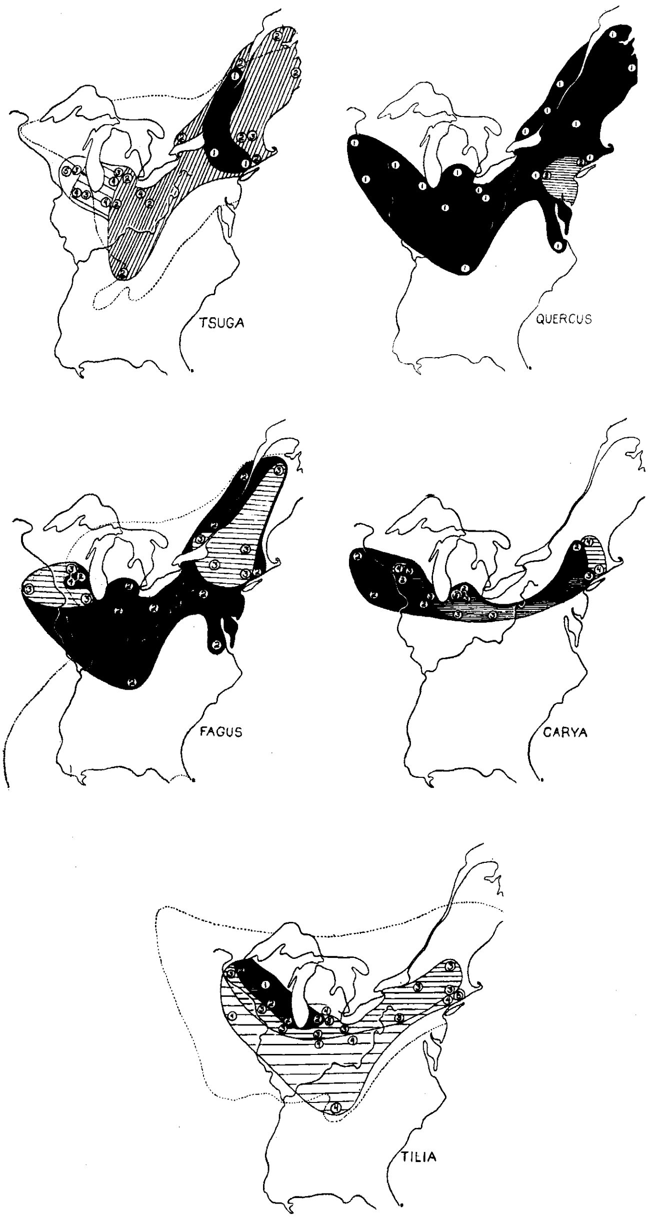


Fig. 4. Clock diagrams showing postglacial changes in frequency of hemlock (inner circle) and beech (outer circle). (From Preston Smith.)

Plotting this data for each genus separately, a series of contours is obtained indicating the direction of its postglacial advance. For graphic purposes, the area in which it was earliest has been indicated in black. This is assumed to represent, in general, the "center" of its postglacial distribution. Except for *Quercus* and *Carya*, the present range limits of each are indicated by a dotted line.

The dispersion of *Tsuga* westward and northeastward from the New England area is apparent from Figure 5. Further pollen analyses, such as the unpublished work of Cain in the South Carolina Piedmont, will shed light on the late glacial movements of this genus north into New England. Undoubtedly former land areas now submerged were involved in this late glacial migration, preceding the postglacial movement shown on the map. For *Tsuga* is well established in the Southern Appalachians and certainly must have been there throughout the Wisconsin glaciation.



Figs. 5–9. Order of postglacial appearance of five important genera. Numbers indicate relative order of each in the series of five.

It is noteworthy that *Quercus* (Fig. 6) was first of the five everywhere except in the region where *Tsuga* had that position, centering about Long Island. The general northward advance of *Quercus* in postglacial times is evident, and in keeping with the size and complexity of that genus.

The diagram for *Fagus* (Fig. 7) clearly suggests a general northerly advance. The presence of *Fagus* in the Arkansas-Oklahoma boundary, and of sugar maple relicts 200 miles further west indicates that the Southwest, as well as the Appalachians, may have been an important place of retreat during glaciation.

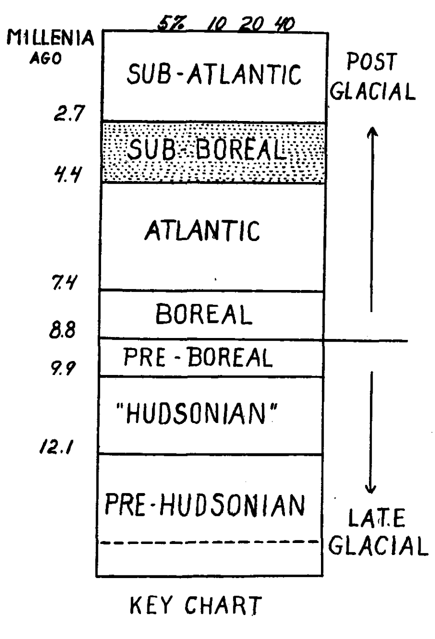


Fig. 10. Correlation of American and European chronologies with sample profiles for *Tsuga* and *Fagus* from New England and Ohio. Note minima for both genera during Sub-Boreal (xerothermic period). (From Preston Smith.)

Moreover a westerly center for *Carya* (Fig. 8) is suggested strongly, but as in the case of *Fagus*, we need more data from places like southern Illinois.

The diagram of postglacial migration for *Tilia* (Fig. 9) shows a definite movement toward the East and South. This also raises questions regarding a westerly glacial refuge. Certainly *Tilia* is today a dominant in the transition forests at the margin of the grasslands in Eastern Nebraska.

Finally I have permission to draw upon the data accumulated by Mr. Preston Smith (18). Using the varve counts of Antevs, north from New England, he has connected bog sedimentation with a definite postglacial chronology. He has also correlated bog reports over a wide area, having developed a method of plotting a particular kind of pollen in terms of its own frequency.

His scale is shown in Figure 10. For our purpose its most significant use is in confirming the existence of a warm-dry (xerothermic) period, the Sub-Boreal, as well as the general migration facts for beech and hemlock already indicated in this paper. The Sub-Boreal, it will be noted from the figure, is marked by a definite reduction in beech and hemlock, as compared to more xeric forest trees.

SUMMARY

This paper discusses the evidence from pollen analysis which establishes the existence of a postglacial warm dry period in eastern North America. This period has been an important factor in the pattern of present day native vegetation. The migrations within the glacial area of *Quercus, Tsuga, Fagus, Carya,* and *Tilia* are also traced. In general terms, the advance of *Quercus* and *Fagus* was northerly. *Tsuga* was dispersed from the northeast; *Carya* and *Tilia* from the west.

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