We are accustomed to think of history in terms of what man has done, or perhaps, in terms of the great events of the building of the world—earth history. Probably few, however, connect history with plants. Yet we can trace the vegetational history of our state through long periods of geological time. To do this we must gather evidence from fields outside the realm of botany, going in turn to geology, soil science, meteorology, and at times to physics and chemistry.

As with records of human activity, the earliest vegetational history is extremely hazy. In fact we cannot even surmise what may have been the nature of the plant cover of the first land of the state to emerge from the Paleozoic seas—except that we know it must have been extremely primitive. Later, in the shales of Devonian and Carboniferous times, definite records are preserved for us of a flora of increasing complexity but still profoundly unlike that of today. But it is not of these ancient floras that I wish to speak. We shall pass over these early records and see what happened next. Through a long interval of time, records are absent. We build our skeleton of events from the known happenings on other land areas of North America. The forerunners of our modern vegetation have arisen; gradually they increase in number and variety and in area occupied, until in Tertiary time, forests of present day aspect and with many of the species of today covered the land.

To this point our history is built for the most part on fossil evidence. Later history must be reconstructed largely from the pattern of existing vegetation, though certain types of fossil evidence will still be utilized, and soil types will give us clues.

Toward the close of Tertiary time let us picture Ohio—or the land that is now called by that name: Clothed with deciduous forest whose species were many of them plants ranging over vast territory—even over Europe and Asia, encircling the globe in temperate latitudes. Far to the north
were belts of unlike vegetation, much as there are today—belts of evergreen forest, of stunted and dwarfed trees and shrubs, and tundra and arctic wastes.

Then a great cataclysm occurred, upsetting the established equilibrium of ages, creating tensions so great that whole masses of vegetation were set on the march. Far up in the north, in the Hudson Bay region, snow and ice were accumulating, forming the nucleus of a great glacial advance which was to overwhelm the northern half of the country. As the ice sheet grew and slowly advanced southward, temperature and moisture conditions were greatly modified along the ice edge. Slowly the vegetation retreated southward under the pressure of climatic change. Many constituents of the retreating vegetation were overtaken and annihilated: how many we can never know. But a goodly number escaped, many of which are here today.

At the time of maximum extent of the continental ice sheets of North America, much of Ohio was buried under hundreds of feet of ice. In the western part of the state where the southward advance was greatest, the ice margin was at one time south of the position of Cincinnati. Not once, but several times, did such ice advances take place and between each glacial advance were long warm interglacial periods when the ice retreated far to the north or disappeared entirely from continental North America. Each of the several advances which came in this direction left mantles of glacial drift whose margins are clearly discernible and which tell us just how far the ice retreated. A survey of a glacial map will show us that the land surfaces of Ohio are not all of the same age. The southeastern quarter of the state is unglaciated, and hence very old; the remainder, or glaciated part of the state is much younger. In this glaciated part we may recognize three sections: First is a strip in the east-central part of the state, expanding southwestward, which is covered by glacial deposits left by one of the older ice advances, the Illinoian. Second, the great central band which stretches from the northeast counties westward and southwestward is of Wisconsin age and records the last glacial advance. In the region of the Miami and upper Little Miami valleys, are deposits of slightly earlier age, the Early Wisconsin. Third are the lake plains in the northwestern part of the state, formed by the forerunner of Lake Erie, the glacial Lake Maumee of the close of the
Pleistocene. The pattern on the map may be thought of as produced by a series of superimposed deposits, the lower and older projecting somewhat beyond the upper and younger, arranged much as are the shingles on a roof. For each of these regions the vegetational history is distinctly different, and in none is the vegetation static; changes are still in progress.

In the unglaciated section, the vegetation covering has been continuous from Tertiary time throughout the Pleistocene or glacial epoch to the present. In the glaciated section all vegetation was wiped out by the ice, and the vegetation of this, the greater part of Ohio, has entered since the melting of the ice in a series of migratory waves of unlike kind. Its vegetation is comparatively young.

Returning now to the unglaciated southeastern section of Ohio, let us pick up the threads of our history in the forests of Tertiary time, deciduous forests of the sort we know today. Though no part of unglaciated Ohio is more than 60 or 70 miles beyond the glacial boundary, we may say on the basis of botanical evidence that its vegetation was not profoundly affected by the ice sheets. Doubtless, narrow strips of arctic tundra and boreal forest bordered the ice margin; then beyond was undisturbed deciduous forest. Could this be possible in the proximity of continental glaciers? We believe so. The phenomenon of glaciation may be brought about without extreme refrigeration, even at the center of ice accumulation. A lowering of average temperatures 5 to 7 degrees Fahrenheit, together with certain precipitation changes might be enough to bring on another glacial advance. At the limit of ice advance, melting exceeds onward movement, that is, the position of the ice margin is determined by the warmth of the climate, not by its coldness. If we look at the narrow coastal strip of Greenland, extending only about 40 miles out from under an ice cap thousands of feet thick, we find a vascular flora made up of approximately 400 species in 50 families—and this at latitudes between 60 and 80 degrees, and bathed by cold polar seas.\(^1\) Ohio has 2300 species (including several hundred recent introductions) which is less than six times the number of Greenland's flora. To be sure, the flora of Greenland is Arctic, but no more so than at the same latitudes of continental North America far removed from ice caps. In Alaska, forests

are growing in the accumulated detritus on top of glaciers. In Alberta, some of the muskegs are permanently frozen at depths of two feet, yet there is abundant vegetation including spruce-fir forests. So even where conditions are much more extreme than there is any reason to believe they were at any time in southeastern Ohio during the Pleistocene, there are forests.

I have digressed from the recounting of the sequence of events in Ohio for so often the belief is voiced that the refrigeration of climate must have extended for hundreds of miles beyond the ice front. Yet existing evidence strongly contradicts this belief. Also, the acceptance of the premise that temperature effects were not pronounced beyond the ice margin is necessary for the continuance of our historical framework.

The southeastern part of the state supports, or did before the white man entered, forests closely comparable to those of Kentucky and West Virginia to the south; forests of mixed composition containing a fair proportion of distinctly southern species, a number of which find the limits of their range in this area or do not extend far beyond it. In the thousands of years since glaciation they have advanced but little.

At some time early in the Pleistocene—earlier than the date of the first advance of ice of which we have record in Ohio—the humid climate which had prevailed for so long changed and drier conditions ensued, especially in the north-central states. This was a climate more suitable to grassland development, and the grasslands of the West moved eastward and southeastward into southern Ohio, into what is now Adams county. Remnants of this vegetation still persist in Adams County. The position of these remnants on or near pre-Illinoian divides, and the composition of communities tell us much about these oldest Ohio prairies, and give us a clue to their age. This xerothermic period was terminated by the advance of the Illinoian ice sheet, the oldest and most extensive ice sheet of which we have record in Ohio. With the advancing ice which overwhelmed most of this great prairie lobe, northern vegetation moved southward, crowded into a narrow strip on and near the ice margin. The arbor

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vitae, hemlock, white pine and yew, and many other plants, established themselves in favorable situations. A few of them still remain, scattered groups of individual species or relic boreal colonies.\textsuperscript{4} They tell us of the period of invasion by this type of vegetation. Their geographic distribution, clearly shown by maps giving county records of occurrence, shows that they are almost limited to the marginal band of the un-glaciated section\textsuperscript{5}. Since the close of glaciation southeastern Ohio has been enriched by the addition of southern plants which are still spreading northward.

Let us turn now to the great glaciated area of Ohio. Instead of a vegetational cover of great antiquity, here is one which started anew on the great wastes of ground up rock material—drift—left by the glaciers. Instead of soils prepared through the ages for occupancy by plants, here was raw material, not soil, unweathered, unfertilized by humus, unsuitable to any but pioneers which could endure the poor soil, the exposure, the excess of water left in depressions or the barrenness of cliffs or polished rock surfaces.

Not once, but many times, the glaciers advanced. So we have not to trace a single sequence but a complex series of advances and retreats, of north and south waves of migration, modified or even interrupted by lateral movements. The oldest glaciated area in Ohio, the southern portion which is covered by drift of Illinoian age, was first populated about four-hundred thousand years ago. The moderating climate was quite humid and plants requiring a large amount of soil water found a favorable environment. The events which followed are obscure. We may surmise that they were similar with certain exceptions to those which we know occurred on the youngest drift area. The history of the last few thousand years is clearly outlined by certain vegetational developments observable today. These I shall consider as a part of the recent history of Ohio's vegetation. But before we are ready for this, let us examine the youngest glacial areas of the state.

Here has been an uninterrupted development since the final retreat of the ice. Each step is outlined by the nature of relic communities and the inter-relations of communities. And

even more positively, perhaps, is the story told in the fossil pollen preserved in the bogs of northern Ohio.

Let us picture the gradual retreat of the ice, which everywhere leaves behind it an irregular mantle of drift. Depressions are filled with water from the melting ice, hummocks are dry or moist depending on their size and the frequency of rains. Plants of many kinds are growing in the detritus on the ice margin and on the older land adjacent to that being uncovered. From these plant seeds are carried by wind and other agencies into the barren land. The arctic tundra of the ice margin retreats northward following closely the melting ice. Bog plants such as Sphagnum, cotton grass and sedges of the Arctic established themselves in and around the pools, and we can picture scenes much like those to be found in comparable areas today. The ice retreated farther and farther; the plants of boreal or northern coniferous forest crowded into the tundra. Spruce and fir trees, at first dwarf and subarctic in appearance, later forming true Canadian forests, appeared. These probably at one time occupied much of the central and northern part of the state, enclosing the ponds and bogs, which by now were surrounded by belts of bog shrubs and larch and arbor vitae. In the western part of the state, perhaps even elsewhere, the occupancy by spruce and fir may never have been complete.

Almost concurrently with the warming of climate, rainfall decreased. Prairie began to advance from the west, and many a prairie plant found suitable environment in the still unforested glacial plain, or along the open bog borders wherever these were dried by the lowering water table. Where spruce-fir forest had been established, it began to thin out and other trees more suitable to the drier climate entered. For a time, then, pine forests held sway in certain sections. But the dominancy of evergreen forests could not continue long under the pressure of advancing southern deciduous trees. Oaks and hickories began to mix with the pines. An increase in the humidity of climate made it possible for the deciduous forest to invade some of the prairie areas, as well as to replace the pine forests. Deciduous forests of mixed aspect were established—forests essentially like those of today.

Changes have taken place since in the composition of the forest, paralleling climatic shifts from dry to moist and back again. Records indicate two dry and two moist periods in post-glacial time.
Some among you may be wondering what is the basis for this fabrication, how authentic it is, or whether it is just a story constructed on probability.

For evidence let us look at any one of the bogs of Ohio. In Champaign County, for instance, is one in which may be found a number of northern plants—a relic colony far removed from other vegetation of its kind and reminiscent of conditions long since passed. How did the plants get there? Not by a jump of hundreds of miles from present day northern bogs, but during the methodical northward retreat of these plants along the retreating ice front. Why do they stay? Because the more southern deciduous forest vegetation is not suited to these habitat conditions, and hence the stress of competition does not kill out the survivors of an earlier vegetation. While the typical zonation in the bog displays open sedge areas, shrub border, arbor vitae or white cedar forest and lastly, deciduous forest, there are departures from this sequence. This same bog area gives abundant evidence of the eastward spread of grassland species. Many of these are found in the drier open parts, where the sequence passes from bog to prairie and then to deciduous trees. Wherever the conifer forest border had not become established prior to the dry climate period, prairie vegetation entered. There were many such spots and some of them from which all vestige of natural vegetation is gone may still be identified by the soil. Anyone following one of the main highways southwestward from Columbus cannot fail to see these black soil areas.

Instead of floristic evidence, some may prefer to rely on fossil evidence. We have it, too, in some of our bogs. The work of Dr. Sears on pollen analysis of bogs demonstrates the early occupancy of a spruce-fir forest, its gradual supplanting by a pine forest or by pine and oak forests, and the final replacement of these by wholly deciduous forests.

In all probability the progression of events was greatly slowed down in the northern part of the state, and the period of occupancy by spruce-fir forest greatly lengthened. This was due in part to the more northerly latitude and in part to

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the proximity of the large glacial lake occupying the Lake Erie basin. This lake was fed by melting ice, hence it was constantly at a low temperature. This, together with the more northern latitude conspired to hold off deciduous invasion until relatively recent time.

When the ice nearly receded from the last of the Great Lakes, Lake Ontario, and the St. Lawrence valley was still ice-covered, a Mohawk-Hudson outlet to the sea was established. Later, toward the close of glaciation and many thousand years after the ice had left Ohio, an encroachment of the sea extended up the St. Lawrence valley into Lake Ontario and Lake Champlain. The Champlain-Hudson River valley became a salt water strait. The Great Lakes everywhere were receding, reaching nearly the outlines of today. Long stretches of sandy lake shore and the lake plains of northwestern Ohio were exposed. Into this new land invaders came, invaders from the adjacent forest to the south, from the extended prairies to the west, and from the Atlantic region to the east. The invasions from both east and west are clearly shown by the plants growing in the lake region today. Many western xerophytes, some of which are not found in the central prairie counties, occur. And such Atlantic coast species as the sea rocket and seaside spurge are at home along Lake Erie.

The glaciers have gone from the continent of North America. As far as can be ascertained from weather records, climate is not changing. Yet our vegetation is not static, but constantly changing. The thirty thousand years, more or less, which have elapsed since the ice finally disappeared from our state has not been long enough to permit a complete adjustment of vegetation. Development is still in progress. Almost anywhere where natural primary vegetation remains we may see the evidence of change, of the replacement of one community by another, or what ecologists call succession.

Every plant succession is directed by both internal and external factors, and wherever conditions are similar, all pass through the same stages. The entire post-glacial sequence of vegetation has been directed by climatic change, and hence may be considered a climatic plant succession. The relatively recent vegetational history of Ohio is written in the stages of successions which are in progress now, successions directed by

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changing topography or the reactions of the vegetation itself. For each different region the lines of development are different, so to trace accurately the history of any section, its successions must be worked out with care and detail. One general trend seems evident everywhere—development is toward the establishment of mixed deciduous forests of the type which have so long held dominance in the southeastern part of the state and have become well established in many places in glaciated southern Ohio.

Vegetational development has fairly well kept pace with physiographic development. Where a mature topography is reached, plant succession has progressed farther. Wherever topography is youthful, successional development lags. This is shown by maps offered by Sears for parts of the north-central counties. My own work in the drift plains of the southwestern counties shows the same relations. This relation of vegetational development to maturity in the erosion cycle is also readily demonstrated by a comparison of the vegetation of glaciated and unglaciated regions.

It is only in areas of youthful topography that we can trace vegetational development uninterrupted by the regressive changes initiated by erosion. Vegetational development is in progress everywhere; it is less complicated where caused mainly by the reactions of vegetation itself.

Let me trace one such developmental series as an example of the changes now in progress in virgin forest areas of Ohio's vegetation. We shall look at the flat and undissected Illinoian drift plain in southwestern Ohio. The area is a plain in which there are very shallow almost unnoticeable depressions from one to five feet in depth. The soil is fine-grained, compact, impervious. The water table is high, and the larger, and deeper depressions are covered with shallow water for part of the year. Through thousands of years these depressions supported swamp vegetation; many of the plants now growing in them are decidedly northern in distribution, plants persisting here from early post Illinoian time. Trees adapted to the swamp habitat were lacking; sedges and shrubs remained in control. Gradually the water table was lowered, relatively, and pin oak began to invade. An open pin oak forest with sedge ground cover came to occupy the depression. Pin oak

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is exceedingly intolerant of shade. It cannot succeed in the shade of other trees. Such open pin oak forests are the first forests to occupy these depressions. In the open spaces between the large pin oak trees, the light conditions are still suitable for pin oak, and more enter. This invasion is possible only if the water is not too deep; any pronounced invasion is correlated with temporary lowering of the water table. In recent years, this has in places been brought about by ditching, and dense stands of pin oaks have entered in the open spaces in the virgin pin oak forest.

The shade produced by even a partially closed stand of pin oak makes conditions suitable for other tree species. White oak, shell-bark hickory and sometimes black oak invade. Gradually these trees grow up; the old pin oaks die out and a white oak-hickory or white oak forest is established. Shade is increasing, a layer of humus is forming, root competition is increasing. Beech, one of our trees which is most tolerant of shade, enters in the understory. A white oak forest with beech as an understory is the result. In such a forest, the white oak trees are several hundred years old. The young beech trees are thriving in the shade of the white oaks, and are ready, when old age takes a tree, to replace white oak by beech. Not in a single step, but very gradually this change takes place; finally a beech forest is established. If we figure the time necessary to allow for this forest development, we find that 2000 years would not be long enough if each forest type could follow directly on another without transition phases, without the long periods of change which we see going on everywhere. Many times that amount—a hundred thousand years perhaps—has been required for the establishment of the beech forest, the ultimate or climax stage in this succession on the wet flats of Illinoian drift.

This beech forest is the most advanced stage which is possible on the youthful topography persisting here. Only as a more mature topography develops with the dissection of the area by streams can vegetational development go further. Then the mixed forests of southern expression which are climatically possible here may enter.

Through such developmental changes, Ohio's vegetation finally became established. A complex mosaic of forests types, interrupted here and there by swamps or prairie openings, by cliffs and sandy beaches, became established. Into this
primeval Ohio, the white man entered, and with him the greatest destruction of natural vegetation of all post-glacial time.

Let me close with a quotation—a description of Ohio's forest in 1834, just one hundred years ago:

"The scenery now, even for the forest, was becoming unusually grand. It repeatedly broke away from you, so as to accumulate the objects in the picture, and to furnish all the beauties of light, shade and perspective. The trees, too, were mostly oak, and of finest growth. Their noble stems ran up some hundred feet above you and were beautifully feathered with verdant foliage. There they ran off in the distance, park-like, but grander far, in admirable grouping, forming avenues, galleries and recesses, redolent with solemn loveliness; and here, they stood before you like the thousand pillars of one vast imperishable temple for the worship of the Great Invisible. Well might our stout forefathers choose the primitive forests for their sanctuaries. All that art has done in our finest Gothic structures is but a poor, poor imitation!"

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