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THE GENETIC DEVELOPMENT OF THE FORESTS OF NORTHERN MICHIGAN; A STUDY IN PHYSIOGRAPHIC ECOLOGY.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. XXVII.

HARRY NICHOLS WHITFORD.

(WITH EIGHTEEN FIGURES)

PORTIONS of the summers of 1898, 1899, and 1900 were spent by the writer in studying physiographic ecology at several points in northern Michigan. The work of the first two summers was under the personal direction of Dr. H. C. Cowles, to whom the writer is indebted for many valuable suggestions. Indeed, the work set forth in the present paper is little more than the testing and working out in detail the ideas on physiographic ecology developed by Dr. Cowles in his lectures at The University of Chicago and in his published papers. Credit is due Mr. W. B. McCallum for the photographs used to illustrate this article, with the exception of *figs. 1* and *4*, which were obtained by Mr. E. N. Transeau.

It should be clearly understood that the conclusions reached are based mainly on observations and are presented tentatively. They are published in the hope that they may be thoroughly tested by other observers, and if necessary modified or discarded altogether. It is the writer's belief that only along lines similar to those advocated here can the problems of forest distribution be successfully solved.

I. FACTORS.

The factors to be taken into account in attempting to explain the relations that exist in different plant associations are so complex that it will be well to consider them in detail. Since the object of this paper is to answer some of the questions involved in the development of forests, special emphasis will be laid upon those factors which appear to be related to tree growth. In order to understand the distribution of trees the subject must be approached from both the negative and affirmative standpoints. In other words, the question is, why are there forests on certain physiographic formations and none on those which lie close by? Also within the forest itself there predominates now one and now another tree type. In some places the coniferous forest is prominent, in others the maple-beech-hemlock type is the chief feature. Indeed, if enough regions are studied an indefinite number of combinations may be observed. Thus not only must the presence or absence of trees be explained, but also where trees are present a reason must be given for the dominance of any particular kind of forest. If these questions can be answered satisfactorily, some light will be thrown on the origin and development of forests. In the answer three sets of factors are involved, climatic, ecological, and historical.

A. **Climatic factors.** The greater part of the eastern half of the United States is a potential forest. Here the two great climatic factors, *temperature* and *moisture*, are favorable to the development of forest trees. When a climate makes possible the development of any predominant type of vegetation that type is called a *climatic formation*.[1] To be specific, the eastern half of the United States has a *forest formation*. But if a bird's-eye view of any portion of this formation be obtained, there will be found within it groups of other plant types. These are designated by Warming[2] *plant societies*. Within this vast forest

[1] SCHIMPER, A. F. W.: Pflanzengeographie auf physiologischer Grundlage. 1898.

[2] WARMING, E.: Plantesamfund. 1895. German edition, translated by Knoblauch. 1896.

formation there are prairie, beach, dune, heath, swamp, and other plant societies; also the forest itself may be divided into a number of different forest societies. This leads naturally to the consideration of those factors that make up the plant society conditions.

B. **Ecological factors.** For convenience this set of factors may be divided into edaphic, atmospheric, hydrodynamic, and biotic.

EDAPHIC FACTORS. Schimper[3] has regarded the soil and its properties so important that he has given the name *edaphic formations* to those *societies* which owe their existence to the peculiarities of the soil. More than any other form of vegetation trees need a firm anchorage medium, and hence a deep soil. Since the roots are the absorbing as well as the holdfast organs, the water content of the soil is important. Warming's classification of plant societies[4] into xerophytic, hydrophytic, and mesophytic is based upon the amount of water in the soil. More plant societies doubtless owe their characteristic physiognomies to the amount and condition of the water in the soil than to any other one factor. Since trees present a greater transpiration surface than other forms of plants they must occupy those positions where there is sufficient water to maintain the transpiration current. This excludes them from those regions where the water content of the soil approaches the minimum; a stagnant condition of soil water is likewise injurious to trees. Probably here the exclusion of air and the presence of humic acids prevent the healthy growth and activity of the root system. In order that the forest condition may be obtained, therefore, the soil must be well drained, as well as watered.

The physical properties of the soil play an important rôle, for upon them depends the capacity of the soil to hold water. The water-holding properties of the different kinds of soil are too well known to need treatment here. The heat-absorbing and heat-retaining qualities of soils must be taken into account, for they often determine the presence or absence of certain plants.

[3] *Op. cit.* [4] *Op. cit.*

Again, the soil furnishes the plant certain organic and inorganic compounds, and hence its chemical properties should be considered. As a rule, inorganic salts are present in sufficient quantities in the soil; indeed in salt marshes the presence of too great a quantity of salt in the water excludes trees, except in a few instances. Soils are more often deficient in organic compounds. Organic decay, since it furnishes most of the available nitrates, is of great importance. The amount of *humus* is so essential that it often determines the character of a forest, not only in furnishing the nitrogen to the plants, but also in ameliorating the physical properties of the soil. Nitrifying bacteria are necessary for the conversion of organic matter into nitrates, and if these are excluded the processes of organic decay discontinue, and consequently a condition like that present in sphagnum swamps is developed. Here, generally speaking, trees are excluded, except a few characteristic species.

We must look to the soil factors for an explanation of our most characteristic plant societies. There must be a soil. The water in the soil must be sufficient. The soil must be aerated. The amount of organic and inorganic compounds must not be too great or too little, and usually the soil must contain bacteria or other fungi for organic decay. If all these conditions are present in the right proportions, the soil is capable of supporting a luxuriant tree growth.

ATMOSPHERIC FACTORS. By atmospheric factors are meant those which influence the aerial parts of plants. They include radiant energy in the form of *heat* and *light*, and also the influence of *wind*. Of these light is the most important. The tree by virtue of its many planes of plagiotropic branches gives a greater surface on which the light may fall than is found in any other plant form. Principally because it has worked out this successful light relation, it is ecologically the culminating type of plant body. Once a dense forest is established, all forms of low vegetation, except those species that have special shade adaptations, are driven out. Attention has already been called to the necessity of heat as a climatic factor. Heat may also be an ecological factor. In exposed situations the water and humus contents of the soil may be dried out. For example, a forest may be cleared and thus exposed to the sun's rays to such an extent that the soil factors will be changed considerably. It is obvious that it is difficult to separate the light and heat factors. While it is a benefit for a plant to get as much light as possible up to a certain point, along with the light the plant may absorb too much heat.

The carbon dioxid content of the air is so constant that it plays little or no part as an ecological factor. Those plants nearest the ground are slightly favored by the greater amount of carbon dioxid in the lowest layers of the atmosphere. The effect of winds on trees, however, is often pronounced in exposed situations. Besides destroying trees the wind may injure them to such an extent that in the struggle with disease and with other trees they will be the first to succumb. The wind is of great importance also in that it causes excessive transpiration. The effect of wind on seed distribution is so pronounced that, other things being equal, those plants whose seeds are most easily distributed will stand the best chance in a given area. In conclusion, therefore, the atmospheric factors of light, heat, and wind must be taken into account in trying to explain the presence or absence of certain plant societies.

HYDRODYNAMIC FACTORS. The term hydrodynamic is used here to designate the action of tides and waves upon strand vegetation, and the action of stream and ocean currents in distributing seeds. These factors may play an important part in determining the peculiarities of plant societies, hence the necessity of keeping them in mind.

BIOTIC FACTORS. Two plants cannot occupy the same soil at the same time. The struggle for a foothold in the soil may take place between species of the same kind or of different kinds. Again, the struggle may be between plant societies, as the forest and heath, or forest and prairie. The line along which two societies meet has been called the tension line. Here it is that the struggle is most pronounced. If the other ecological factors remain constant, the tension line does not change. In that case, for instance, the forest does not advance on the heath nor the heath on the forest. But, as will be shown in the discussion of the historical factors, the conditions as a rule are changing constantly. Not only may the struggle be between the forest on the one hand and some other type of plant society on the other, but it may be between different kinds of forests.

The struggle between plants and animals may have an important bearing on the explanation of any given floral region. In civilized communities man has changed the whole nature of the vegetation. His influence is seen where forests are cleared for timber and fuel, or for purposes of cultivation; also indirectly where forest and prairie fires are active. Again in regions where stock is raised trees are damaged or kept from spreading by the ravages of domestic animals. Insect life may also be an important factor in explaining the floral character of a given region.

In concluding this discussion of the ecological factors, it is well to note again that the three great physical media—soil, air, and water—are all influential in bringing about certain plant physiognomies. These, together with the biotic factors, make that variety in the landscape of any region which is shown in the plant societies that are present.

C. **Historical factors**. The third great set of factors that play a part in the understanding of plant associations has been designated historical, for it involves the element of time. It means simply that the geological and physiographic forces have changed and are changing the factors so far considered as to make absolutely necessary a readjustment of plant formations and plant societies to meet the new conditions. Diastrophic movements may submerge large areas of land and thus destroy all terrestrial vegetation or force it to migrate to unsubmerged parts. On the other hand, when there is an addition to the land area a condition is obtained where there can be noted the successive stages in the reclamation of such an area by vegetation. Again, in the last glacial epoch the ice sheet in its advance destroyed vegetation and modified the climate beyond the limits of its advance, so as to bring about an arctic vegetation where there formerly existed a temperate floral formation.

Erosive forces also come into play. The advance and retreat of the ice sheet changed the physiographic features. Drainage lines were dammed up and lakes were formed. It is the belief of glaciologists that the great lakes, at least in part, were formed in this way. Oscillations in the change of the front of the ice sheet changed the levels of lakes and left old beaches, other sand formations, and cliffs, thus bringing into existence new topographic forms and new soil conditions. With the final retreat of the ice sheet the normal processes of water erosion began again. Drainage lines became reestablished, and with the aid of decaying vegetation the lakes began to be filled up. The longer an area of land has been free from the ice sheet, the more nearly have its drainage lines become firmly established. It is evident then that the edaphic conditions in a region recently vacated by the ice will be decidedly different from those that have been exposed to the erosive force of water. The more nearly a region reaches base level the more stable will be the edaphic conditions. The recent work of Cowles[5] on the Chicago region shows clearly the successive stages in the advance toward the climax condition. He was also the first[6] to bring out clearly the dynamic conditions due to physiographic changes. It is evident that the existing plant societies must not be looked upon as fixed, but rather as changing from year to year; sometimes slowly, as in the case of swamps; or sometimes with rapidity, as in the case of dune societies.

II. THE SAND SOCIETIES.

The islands of North Manitou and Beaver at the northern end of Lake Michigan, the adjoining mainland on the Michigan

[5] COWLES, H. C.: The physiographic ecology of Chicago and vicinity; a study of the origin, development, and classification of plant societies. BOT. GAZ. 31: 73–108, 145–182. 1901.

[6] COWLES, H. C.: The ecological relations of the vegetation of the sand dunes of Lake Michigan. BOT. GAZ. 27: 95–117, 167–202, 281–308, 361–391. 1899. *Idem;* The physiographic ecology of Northern Michigan. Science 12: 708, 709. 1900.