

TOPOGRAPHIC RELIEF AS A FACTOR IN PLANT
SUCCESSION

GEO. D. FULLER, UNIVERSITY OF CHICAGO

It is now generally accepted that there is a tendency for one plant community to pass to another in a somewhat definite series, from the pioneer vegetation of a region through successive phases to a community that is very decidedly richer and more mesophytic than any of the earlier vegetation. This series of changes has been designated plant succession, and has been extensively discussed by Cowles (1), Clements (2), and others. The final phase in the succession differs from the pioneer and intermediate ones, not only in its greater mesophytism, but also in its permanence and is termed the climax phase. Throughout the northeastern United States the climax plant community is a mesophytic forest in which deciduous trees predominate, and it has been assumed by many that all parts of the region will eventually be dominated by this, the richest type of vegetation that the climate is able to support. Progress towards this climax will vary much in the character of the different stages and in the rapidity with which they succeed one another, the differences being determined largely by the character of the soil, the development of its drainage, and the composition of adjacent vegetation. Man's activities in cutting and burning may cause temporary or even permanent halting or retrogression, but otherwise the progress will be steadily towards the climax even although the movement be imperceptibly slow.

While many ecologists have regarded the climax vegetation as limited by the climate only, others have seen in soil a limiting factor and recognized the establishment of permanent plant communities of distinct character due to the conditions of the soil. These communities would be called "edaphic climax communities," and they would be less mesophytic than the climatic climax of the region. Such communities have also been termed "temporary climax communities" by those who believe that they will eventually pass to the climatic climax, al-

though the steps in the succession may be almost infinitely slow.

Among the most striking examples of edaphic or temporary climax communities are the pine barrens of New Jersey so well described by Taylor (3) and by Harshberger (4), and the similar forests of scrub pine in Michigan spoken of as "the plains" by Spalding (5) and others.

In New Jersey the area is within a region capable of supporting a highly mesophytic forest in which chestnut, beech, maple and certain oaks are conspicuous. Further, the sandy plains have been continuously out of water for long ages, and are occupied by a plant community that gives evidence of being an "old climax condition infinitely more ancient than anything in the surrounding area"; nevertheless this vegetation is far below the climax of the region in mesophytism and in comparison with it is to be classed as a primitive community.

The vegetation of the sand plains of Michigan is similar to that of New Jersey. The principal tree of the former, *Pinus Banksiana*, closely resembles in habit and ecological relations the *P. rigida* which dominates the latter, while the associated forms in each instance are decidedly xerophytic, and very similar both floristically and ecologically as may be seen by comparing the descriptions of Taylor (3) and Gates (6). The Michigan "pine barrens" are in a region where the climax forest is characterized by the dominance of beech, maple and hemlock.

Many different causes have been given for the permanency of this primitive type of forest over the Michigan sand plains, but such attempted explanations have usually emphasized the character of the soil, its lack of fertility, its poor water supply, and its deficiency in humus or in essential mineral constituents. Harper (7) asserts with some plausibility that the difficulty is that the sandy soils leach freely and hence prevent the accumulation of any considerable amount of plant food material. Whatever may be the cause, the fact of the

apparent permanency of a primitive type of forest within a region of a mesophytic climax seems established beyond question, and also the further fact that this scrub pine forest is in both Michigan and New Jersey associated with a soil of almost pure sand and a topography of low relief.

In Michigan there exist other areas of sandy soil exhibiting quite different conditions of forest development. These are to be found more particularly along the western shore of the lower peninsula in the form of sand-dune areas of varied extent. The soil does not seem to be essentially different than that of the sand plains some miles farther inland, in fact, if there is a difference it seems to lie in the direction of the dunes having more nearly absolutely pure sand, free from any other soil whatever, than the sandy plains. The latter have frequently some small admixture of loam or similar fine material. But while the soil is similar the same cannot be said of the vegetation for while primitive stages closely resembling those of the sand plains are evident in portions of the forest cover of the dunes more particularly in newly formed areas, much of the older portions are covered by the climax forest of the region. Such a forest has been described by Waterman (8) in the Frankfort region, and it has also been seen by the writer at many different points, extending from Sawyer, at the south end of Lake Michigan to Bay View, Fox and Beaver Islands well to the north. This climax forest, although developed upon pure sand, differs very slightly from that upon other soils in the region the dominating trees being beech, maple and hemlock.

It is true that some dune areas such as those covering a portion of the Big Sable Point area, near Ludington, seem to have remained for a very long time with a very primitive vegetation cover, but adjacent portions of the same area are in climax forest.

What has caused this great difference in the rate of succession in these sand areas? In the opinion of the writer the differences in the topography relief have played an important part. It is a fact established by

frequent observation that in sand areas where dune building has been extensive and dunes of considerable height have developed there occur sheltered depressions where mesophytic vegetation soon becomes established on account of the lower evaporating power of the air and the consequent increased accumulation of humus. Such islands or centers of mesophytism are too well known and their occurrence will be too readily admitted to require further demonstration, but their importance as centers from which mesophytism spreads to surrounding territory has not been sufficiently recognized. From such centers go the seeds or other organs of dissemination to the fringe within shelter of the central forest association, and so completely is the spreading of the members of the climax forest accomplished that soon the very tops of the higher dunes are covered with beech and maple while adjacent plains remain in xerophytic scrub pine.

The successional stages may include as in southern Michigan, a pioneer pine forest with an evergreen undergrowth of *Juniperus*, *Arctostaphylos*, *Pyrola*, *Linnaea* and associated forms, a succeeding xero-mesophytic oak forest dominated by *Quercus velutina* and becoming gradually more mesophytic as indicated by the invasion of *Q. alba* and *Q. rubra*, and this in turn gradually giving way before the encroachment of *Tsuga canadensis*, *Acer saccharum*, and *Fagus grandifolia*. Farther to the north the oaks disappear but the maple and hemlock remain with equally mesophytic undergrowth, and such tree associates as the white spruce, *Picea canadensis*, and the yellow birch, *Betula lutea*. Whatever may be the modifications in the rate and phases of the succession the ultimate and comparatively speedy arrival at a rich mesophytic climax forest association leads to the conclusion that the high relief of sand dunes affords an excellent demonstration of the importance of mesophytic centers, developed in protected local areas, in inducing and hastening the development of the more advanced stages in plant succession.

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