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FACTORS FAVORING THE PERSISTENCE OF A RELIC ASSOCIATION OF EASTERN HEMLOCK IN INDIANA¹

By REXFORD F. DAUBENMIRE

Scattered through the deciduous forests of Indiana there are relic colonies of eastern hemlock, Tsuga canadensis. These colonies, with quite an appreciable group of other species, including herbs and shrubs (1), are generally considered as remnants of a previous southern extension of their natural species ranges. After these species had been forced southward by the conditions accompanying the advancing ice caps, their postglacial movements, in keeping pace with the retreating ice masses back to their original climax ranges, were very irregular. Thus, in the course of postglacial reorganization of the vegetation, hemlock as a species resumed its more northerly range found in the Lake Forest which covers the area immediately north of the Great Lakes. However, the irregularity of the northward migration resulted in the isolation of numerous colonies in territory which ecologically belonged to another type of association, and which territory eventually would be claimed by the latter species as they too resumed their more northerly range in the postglacial period. When such relic communities become surrounded by the natural climatic climax of the region, there is the inevitable struggle for the possession of the land surface. During the shifting of the associations through such a period of intense competition for space, the relic species usually come to occupy that part of the topography which is less favorable to the natural climatic species, i. e., where competition is less keen. And so it is that relic colonies or associations are usually to be found where the adverseness of ecological factors allow the relic to compete successfully with the more indigenous species, whether they eventually dwindle to the extinction of the outposts, or whether they become established as minor edaphic climaxes.

A series of ecological investigations was made by the writer in order to get a comparative measurement of the factors as they exist in the typical broadleaf Beech-Maple forest and in a relic coniferous association of hemlock. The following accounts of soil moisture, soil acidity and evaporation studies will be found in more detailed form in another

³This paper was delivered in part before the Colorado-Wyoming Academy of Science at Boulder, Colorado, November, 1930. paper by the writer (3). All these investigations were carried out in the northern part of Parke county, Indiana, where one of the most extensive and most successfully competing areas of such relic hemlock colonies is found.

The soil of this region is underlain immediately by a soft sandstone which has been eroded down into a dendritic pattern of sandstone canyons or steep bluffs which may be composed of soft shale. In this area hemlock forms dense and almost pure stands along the upper limits of the bluffs and canvons and a narrow strip of gradually sloping land immediately next to the precipice rim. The Beech-Maple climax of the region is an upland forest climax which usually comes down to the immediate edge of the hemlock association. Since bluffs which are not inhabited by hemlock do not develop into the Beech-Maple climax, it was concluded that some set of conditions peculiar to the precipice areas were so unfavorable to Beech-Maple development that here the hemlock could successfully compete. The study includes investigations into air and soil temperatures, evaporation, soil moisture and soil acidity, in both hemlock and Beech-Maple associations, during the part of the growing season from the middle of June to the first of September of 1929 and 1930.

A duplicate series of soil samples from the 1, 3, 6, 12 and 18-inch layers of soil was taken in both associations each week for soil-moisture studies. When the moisture contents of the two soils were compared with their respective wilting coefficients, derived arithmetically from the moisture equivalents (2), some very significant facts were brought to light. In the upper layers of hemlock soil, the moisture content went below the wilting coefficient, i. e., no growth water was available. from the middle of July throughout the summer, except for a period immediately following a rain. The lower layers of soil under hemlock are almost constantly lacking in growth water during this period, due to a small percentage of penetration. This latter condition is undoubtedly the result of the root habit of hemlock, which has a most intricate and matlike formation of rootlets about one inch thick just beneath the duff and completely covering the soil in the denser stands. This system of rootlets increases the absorptive surface and presents it in a manner which is conducive to nearly complete absorption of the precipitation before any water can percolate below the root layer. Beech-Maple soils were found to contain growth water at all depths throughout the summer. A constant supply of growth water is of great importance to mesic plants, and its lack under the hemlock may alone be responsible for the

inhibition of beech and maple seedlings from such places as the hemlock occupies. This deficiency in soil moisture under hemlock may be attributed largely to the tree itself; however, in view of the fact that Beech-Maple trees do not get established on such ridges which are unoccupied by the hemlock, it would seem to indicate that the location alone is an initial factor in drought because of the perfect drainage incurred by the proximity to a steep incline.

The acid ranges of both surface and subsoils (6-inch depth) in both associations were determined by twenty sets of soil samples (one surface and one subsoil sample) taken under five different stands of the hemlock, and fifteen sets from four different localities in the Beech-Maple. When compared, the acid ranges of the surface soils varied widely between the two forest types and there was an appreciable gap of sixtenths of a pH between the two ranges when plotted on the same scale (3). Hemlock surface soil had an acidity of pH 3.6 to 4.7, and the Beech-Maple ranged from pH 5.3 to 7.0. The subsoils occupied an intermediate portion of this part of the scale and their ranges overlapped so much as to indicate no great difference in acidity between the relic and broadleaf soils at this layer. Such a marked acidity of the hemlock surface soils is probably a cause for the exclusion of other species once the association is started, rather than an edaphic condition which is originally conducive to the establishment of the community. In fact, the hemlock seems to inhibit other species so completely as to keep out practically all of the numerous herbs which grow typically under Beech-Maple.

The temperatures of the soils were taken with glass-rod chemical thermometers thrust horizontally out into the soil at 1, 3 and 6-inch levels below the surface, from a wood-lined trench. Surface soil temperatures were found to be essentially alike in both associations, which was to be expected, since evaporation (3) and air temperature at 6 inches above the forest floors, vital factors in the control of soil temperature, were found to be equal also in the two forests. The average temperatures of the 3 and 6-inch layers under hemlock were 1 and .5 degrees C. lower, respectively, than these layers under the Beech-Maple (3). While this difference is slight, it gives the physiological advantage again to the Beech-Maple association.

Average daily fluctuation ranges are negligible in both the air temperature studies, being only .7°C greater in the hemlock, and in the soil temperature study, where they are almost identical.

The following table shows a summary of data derived from temper-

ature readings (Centigrade) taken at 6:00 a. m., 12:00 m. and 6:00 p. m., on one day of each week:

| | Average Daily Fluctuation | Average Temperature |
|--------------|------------------------------|------------------------|
| AmHemlock | . 8.6 | 22.9 |
| Beech-Maple | . 7.9 | 23.1 |
| Soil Hemlock | 2.3 | 19.9 |
| 3' | 1.5 | 18.1 |
| 6' | 0.8 | 17.9 |
| Bcech-Maple1 | 2.2 | 19.8 |
| 3' | ′ 1.4 | 19.1 |
| 6' | 0.8 | 18.4 |

TEMPERATURE READINGS

SUMMARY

A comparison of several vital ecological factors in a relic colony of hemlock and in its surrounding and more indigenous climax of Beech-Maple, indicate that whenever these factors differ (in soil moisture, soil temperature and soil acidity), the most favorable extreme is found in the hemlock environment. Air temperature and evaporation studies indicate no appreciable difference between the environments of the widespread climax and the relic edaphic climax.

In view of the factors considered, a particular site, which by means of its topography is conducive to extreme drainage and consequently presents a dry soil for plant occupation, is the only adverse condition which the hemlock may make use of in getting established. Once established, a secondary group of conditions arises, through the presence of the hemlock itself, which tend to inhibit the seedlings of competing plants and thus secure the permanency of this relic association.

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