A BOTANICAL SURVEY OF THE HURON RIVER VALLEY

VIII. EDAPHIC CONDITIONS IN PEAT BOGS OF SOUTHERN MICHIGAN

GEORGE PLUMER BURNS

(WITH EIGHT FIGURES)

In a paper read before the Society for Plant Morphology and Physiology at the Philadelphia meeting (1904), the author called attention to the fact that the plants in peat-forming lakes near Ann Arbor, Michigan, are by no means all xerophytic. With xerophytes are found many plants whose structure is either mesophytic or hydrophytic, and the conclusion was drawn that in the vicinity under consideration one should no longer refer to a peat bog, as such, as a xerophytic habitat (2).

TRANSEAU (17), in a very interesting paper dealing with the distribution of bog and swamp plants, stated that the two were found growing together in the bogs of southern Michigan, and accounted for the present mixture of the two kinds chiefly on historical and climatic grounds.

PENNINGTON (13) concludes that the bogs in southern Michigan are heterogeneous habitats and demand detailed study.

LIVINGSTON (12), DACHNOWSKI (7, 8), and TRANSEAU (18) in experimenting with bog water have found that it is not the same in all zones. The samples of water taken for experimental purposes were generally from under *Larix*, *Drosera*, *Sarracenia*, *Andromeda*, *Cassandra*, *Vaccinium*, *Eriophorum*, etc., that is, from zones with marked xerophytic plants.

The distribution and position of zones of plants in the bogs of southern Michigan have been given by DAVIS (9), TRANSEAU (18), the author (3, 4), and others. On the side of greatest depth the following zones are found:

I. *Zone of submerged plants*.—Plants in this zone usually do not go to great depths. In many lakes no vegetation is found at a depth of 12 feet (3.66 m.). The chief plants are *Chara*, *Cera-*

tophyllum demersum, *Naias flexilis*, *Potamogeton lucens*, *P. natans*, *P. zosteræfolius*.

II. *Zone of water lilies*.—This zone is confined to shallow water seldom over 5 feet (1.5 m.) in depth. The characteristic plants are *Castalia odorata*, *Nymphaea advena*, *Brasenia Schreberi*.

III. *Zone of floating sedges*.—The mat formed by these sedges is very firm and usually about 18 inches (45.8 cm.) in thickness. The chief mat-forming plants are *Carex filiformis* and *C. oligosperma*. Associated with these, some playing an important part in mat-formation, are *Menyanthes trifoliata*, *Dulichium arundinaceum*, *Eriophorum viridi-carinatum*, *Drosera rotundifolia*, *Aspidium Thelypteris*, *Onoclea sensibilis*, *Equisetum limosum*, *Eupatorium purpureum*, *E. perfoliatum*, *Mentha arvensis* var. *glabrata*, *Scutellaria galericulata*, *Utricularia* sp., *Calopogon pulchellus*, *Campanula aparinoides*, *Arethusa bulbosa*, *Galium trifidum*, *Aster junceus*, *Potentilla palustris*, *Solidago serotina* var. *gigantea*, *Lysimachia terrestris*, etc.

IV. *Zone of bog shrubs*.—The characteristic plants of this zone are *Chamaedaphne calyculata*, *Andromeda polifolia*, *Betula pumila*, *Nemopanthes mucronata*, *Sarracenia purpurea*, *Vaccinium Oxycoccus*, *V. macrocarpon*.

V. *Zone of tamaracks*.—The principal plants are *Larix laricina*, *Cornus stolonifera*, *Osmunda regalis*, *O. cinnamomea*, *Rhus Vernix*, *Aster junceus*. In areas where the tamarack is thick there is no undergrowth.

VI. *Zone of poplars and maples*.—This zone is often of great width for reasons pointed out in a previous paper (4), and has the greatest variety of species of any zone. Some of the plants found are *Acer rubrum*, *A. saccharinum*, *Populus tremuloides*, *P. grandidentata*, *Prunus serotina*, *Quercus rubra*, *Q. bicolor*, *Sambucus canadensis*, *S. racemosa*, *Salix discolor*, *S. rostrata*, *Spiraea salicifolia*, *Cornus stolonifera*, *Ilex verticillata*, *Cephalanthus occidentalis*, *Rosa carolina*, *Epilobium adenocaulon*, *Verbena hastata*, *Solanum Dulcamara*, *Polygonum sagittatum*, *P. hydropiperoides*, *Geum rivale*, *Rumex britannica*, *Impatiens biflora*, *Viola blanda*, *Solidago canadensis*, *S. graminifolia*, etc.

VII. *Zone of marginal willows*.—*Salix nigra*, *S. lucida*, *S. dis-*

color, *Cornus stolonifera*, *Ilex verticillata*, *Rubus idaeus* var. *aculeatissimus*, *R. hispidus*, *R. villosus*, *Rosa carolina*, *Vitis vulpina*, *Alisma* *Plantago-aquatica*, *Acalypha virginica*, *Agrostis alba*, *Bidens cernua*, *Cicuta bulbifera*, *Carex vulpinoidea*, *C. scoparia*, *Eleocharis tenuis*, *Eupatorium perfoliatum*, *Geum strictum*, *Glyceria nervata*, *Juncus effusus*, *Lycopus americanus*, *L. virginicus*, *Lactuca canadensis*, *Ludwigia palustris*, *Pilea pumila*, *Polygonum Hydropiper*,

FIG. 1.—First Sister Lake near Ann Arbor, Mich.; the photograph shows the zonal arrangement of plants at the southwest corner; five zones can be distinguished as follows: water lily, bog sedge, bog shrub, tamarack, maple-poplar; the adjacent uplands are covered with oak-hickory woods; photograph by STEELE.

P. sagittatum, *Penthorum sedoides*, *Ranunculus pennsylvanicus*, *R. scleratus*, *R. delphinifolius*, etc. (fig. 1).

A study of the partial lists given above shows that they are not all xerophytes. There are at most only three zones which have bog flora as the characteristic plants. These are the floating sedge, the bog shrub, and the tamarack zones. In the first of these only those plants rooting deep in the mat can be called bog xerophytes; those rooting in the surface layers are hydrophytes. The other zones are occupied by hydrophytes or mesophytes.

The flora of the postglacial lakes studied in southern Michigan may be classified thus:

Vegetation in postglacial lakes	{	Hydrophytes	{ Submerged plants Water lilies
		Xerophytes	{ Floating sedges Bog shrubs Tamaracks
		Hydrophytes or mesophytes	{ Poplar-maples
		Hydrophytes	Marginal willows

An investigation has been carried on for several years by the author and some of his advanced students to determine as far as possible the edaphic conditions in the different areas outlined above. A short report has been given (5) and a more detailed account of some of the results is given in this paper.¹

Temperature

The aerial parts of the bog plants are subjected to great extremes in temperature. Situated, as they are in the area under discussion, in low basins with often very steep sides, the air from the adjacent uplands drains into them, producing a temperature several degrees lower than that on the surrounding uplands during the night and early morning. During the day, however, very high temperatures have been recorded. Such temperatures have also been recorded by GANONG (10, 11) in New Brunswick.

Unless otherwise stated in the text, all temperature readings given in this paper, both for soil and air, were taken with Richard Frères, Paris, thermographs belonging to the University of Michigan. These instruments are shown in fig. 2 in the shelter in which they were kept in the field. The one on the left records the air, the other the soil temperatures. It was found, unfortunately, that the soil thermometer was unreliable when the tempera-

¹ Bog conditions in southern Michigan, which lies toward the southern limit of their distribution in this country, seem to be quite different from bog conditions farther north described by GANONG (11). This point was emphasized also by TRANSEAU (17, 18). See also BASTIN and DAVIS (1).

ture of the air fell near the freezing point, and hence the early spring and late fall data were untrustworthy. In any temperature of the air ranging above 7° C., the records were found to be reliable.

The temperature of the air at First Sister Lake, in the floating sedge zone, compared with that on high ground in Ann Arbor at 7 A.M. is given below.

FIG. 2.—Thermographs in the bog shrub zone at First Sister Lake; the one on the left is recording air, the other soil temperature; photograph by STEELE.

TABLE I

DIFFERENCES IN TEMPERATURE IN BOG AND UPLAND; BOTH RECORDS WERE MADE WITH THERMOGRAPHS

WEEK	HIGHEST		LOWEST	
	Bog	Upland	Bog	Upland
April 26-May 3.....	5° C.	$14^{\circ} 7$ C.	-1° C.	$2^{\circ} 4$ C.
May 3-May 10.....	7	10.1	4	0
May 10-May 17.....	11	18	-1	0
May 17-May 24.....	10	14.2	-2	3.6

Table I shows that in the morning the temperature of the air in the bog is several degrees lower than that of the upland. The only exception in a much larger collection of data than published

here was seen in the lowest point reached during the second week when the upland went to 0, while the bog remained 4° warmer.

The records of the thermographs show wide variations in air temperatures. In 1907, during the week April 26–May 3, it ran from 21.5° C. to -4.5° C.; in 12 hours it rose from -4.5° C. to 16° C.; May 11, from 6 A.M. to 8 A.M., the air was -4° C.; May 13 at 1 P.M. it reached 28° C.; May 16 at 3 A.M. it was only 1.5° C. Low temperatures were recorded during the summer. On June 28 the air got as low as 4° C. July (1907) was the hottest month, judged from the lowest temperatures reached, the lowest for the month being 7° C. at 6:15 A.M. the 27th. In August the low records were: the 1st, 9° C.; 3d, 6° C.; 4th, 6° C.; 13th, 7° C.; 22d, 3.5° C.; 25th, 5° C. August 6, 1904, a maximum-minimum thermometer was hung in the top of an 8-foot tamarack in the sedge zone at Dead Lake. It showed a maximum of 37.8° C. and a minimum of 5.5° C.

These figures show that the temperature of the air is comparatively low during the entire summer during the night. The coldest time came at 1 A.M. or about 7 A.M. On the other hand, day temperatures may run very high. The hottest time of the day was about 1 P.M.; it seldom came as late as 2 P.M. Fig. 3 reproduces the air record for the week July 2–9, 1906, taken in the floating sedge zone at First Sister Lake.

The temperature of the soil, on the other hand, shows very slow variations during the season. There is great difference in soil temperatures at different depths, and they warm up very slowly, except for the shallow surface layer; they never get very cold. When making contour maps of the bottom of these lakes (3, 4) in winter, it was soon learned that although the ice might be 10 inches (25.3 cm.) thick over open areas, a good thrust of the drill would usually send it through the thin ice near and beneath the tamaracks. Even in most severe weather it was necessary to wear rubber boots, as the thin ice continually broke under one's weight. What ice is formed, however, lasts long into the spring.

In taking soil temperatures, a square piece was sawed out of the peat and carefully removed. The long bulb of the thermo-

graph was then inserted in the side of the opening parallel to the surface for about 18 inches (45.8 cm.), and the piece of peat was replaced. The surface arrangement was left as nearly normal as possible. Some of the records were made at Dead Lake, but most of them were made at First Sister Lake.

FIG. 3.—Temperature record of the air for the week July 2-9, 1906, taken in the sedge zone at First Sister Lake; the highest was $31^{\circ}\text{C}.$, the lowest $3.5^{\circ}\text{C}.$; this occurred about 5 A.M., July 6.

Fig. 4 shows a partial record of the results which were obtained at the latter lake at different depths in the tamarack zone. *A* is taken from the figures of TRANSEAU (18, p. 421) and gives the readings at a depth of 1 inch (25 mm.). At this depth the rise in temperature is quite rapid and resembles that of the adjacent uplands. At the time the leaves began to appear, May 27, it had reached $17^{\circ}\text{C}.$ Line *B* gives the record for a depth of 4 inches

FIG. 4.—Diagram showing variation in temperature at different depths and at different seasons in the tamarack zone; *A*, 25 mm.; *B*, 10.2 cm.; *C*, 20.4 cm.; *D*, 45.8 cm. below the surface.

(10.2 cm.) to June 1. The temperature at this point does not rise so rapidly as that just given, and on May 25 had reached $9^{\circ}\text{C}.$ The dotted line *C* gives the temperature at 8 inches (20.4 cm.). This record shows that during the spring, when leaves are unfolding, the soil temperature at this depth remains comparatively low; not until July 22 did it reach $14^{\circ}\text{C}.$ This was held for about a month (July 22-August 24), when it gradually began

to lower. The readings given in line *D* were taken 18 inches (45.8 cm.) below the surface, and were continued for only a short time; the temperature was surprisingly low.

The next figure (fig. 5) was furnished by Mr. HAROLD STEELE, and gives the results of short readings in several zones. These readings were made in 1904 at the same lake. The soil readings

FIG. 5.—Temperature reading taken in different zones at First Sister Lake by STEELE, in summer of 1904; explanation in text.

are taken 18 inches (45.8 cm.) below the surface. This shows that the soil under the tamaracks is the coldest. The same is reported by TRANSEAU (18). As the writer had only one set of thermographs at his command, the readings could not be made simultaneously, but the data gathered seem to show that this made little difference in this case, as the temperatures were stationary. The soil temperatures were: tamarack, 6° C.; bog shrub, 7°5 C.; poplar, 7°5 C.; and bog shrub, 10° C. These

temperatures for the last two were lower than the author obtained for these zones. As has been pointed out, there is great variation in the poplar zone, and one should have a better knowledge of the exact location before attempting to explain this difference. The temperature under the bog sedge also varies with the width of the floating bog and the proximity to the zone of bog shrubs. That is, the temperature remains more constant when one gets away from the open water.

Average records made by a class with ordinary thermometers for six weeks in the summer of 1906, 3 inches (7.6 cm.) below the surface, were as follows: open water, 18° C.; bog sedge, 17° C.; tamarack, 15° C.; maple-poplar, 17° C.; marginal willows, 18° C.; outer edge of marginal zone with no shade at 1:15 P.M., 22° C.

These readings show a wide divergence of soil temperatures in the zones under consideration, and also at different depths in the same zone. This calls for a study of the depth of the root systems. For example, the high temperature of the soil at 25 mm. represents the condition for germination of the many seeds of "drained swamp" plants which yearly lodge in the bog. This taken with the weak light and humid air, which will be considered later, makes an excellent place for germination of these seeds. On the other hand, the study of the root system shows that temperatures found at a depth of 45.8 cm. in the bog sedge and tamarack zones, especially, could not have a direct influence on the plants growing above, as they did not root in that layer but only in the surface layers. This is true even of the largest trees. Added to this fact is the additional consideration that peat is a very poor conductor of heat. The soil readings in these zones which are of the greatest importance are those taken near the surface in a study of reproduction, and those at moderate depths in the study of the present flora.

These data become ecologically important in the light of the work of TRANSEAU (18, p. 22), who has shown by experiment that a temperature of 10°8 C. causes a diminution in the development of both roots and leaves. Although the trees began to open their buds the last of May, it was not until July that the temperature about the roots of the tamaracks reached a higher temperature.

This was after the most active vegetative period. Conditions in the bog shrub zone closely resemble those just described. In bog sedge the records show less regularity and resemble more closely swamp conditions, especially, as has been said before, in bogs where this zone is narrow.

In the two outer zones, the temperatures recorded resemble more closely the upland and drained swamp conditions. Here they ranged about 18° C., in July reaching this mark early in the summer. They would have a less detrimental effect upon the root systems of the plants in these zones.

FIG. 6.—Record of soil and air temperatures made at First Sister Lake, Ann Arbor, Mich., August 23–30, 1907; the instruments were in the bog sedge zone; the bulb of the soil thermograph was 20.4 cm. below the surface; the upper line shows record of the air, the lower the soil thermograph.

Fig. 5 also shows the range of air temperatures for the periods given above. The results are similar to those already given by the author.

The record of the soil and air thermographs for one week, August 23 to August 30, is reproduced in fig. 6. This is only one of numerous records which were taken, and shows the very slight variations in the temperature of the soil and the great variations in the temperature of the air. The greatest variation in soil was about 1° C.; that of the air was 17° C. In fig. 3, the variation in air temperature was 25.5° C.

Water table

The variations in the position of the water table from year to year and from month to month play a very important part in the succession of plant societies in these bogs. In 1908 the level of the water in all bogs of southern Michigan was high. In 1901-1904, when the maps of Dead Lake were made (3), there was an island near the center, and it was customary to row out there and leave the supplies when working at the lake. That island in 1908 was submerged, and one could row over it in 18 inches (45.8 cm.) of water. The flora of upland forms had disappeared with the exception of some stunted willows, and in its place were a few potamogetons, chiefly *P. heterophyllus*. At Whitmore Lake, north of Ann Arbor, the same rise in water has occurred, and what was a peninsula in 1904 is now an island. The same fact is recorded by DAVIS (9, p. 162).

During a series of wet years the change in water level affects the vegetation in all zones except perhaps on the lakeward side of the floating sedge, which rises and falls with every change of level. Along shallow shores the factor is sufficient to control the character of the vegetation, as has been pointed out in the case of the island at Dead Lake. Its influence is also profound in those zones where the peat is solid. It may rise above the surface to a depth of several inches. With this rise there is also found an increase in the humidity of the air. During such periods *Sphagnum* sp. spreads rapidly toward the shore and may assume quite an important position in all zones except perhaps the marginal. An interesting example of the behavior of this moss during wet and dry periods is found at Mud Lake. Here a section was made which showed alternating layers of *Sphagnum* and *Polytrichum* corresponding to the wet and dry periods of previous years. As many as four layers were easily distinguished at Mud Lake.

In one case measured the shrubs stood in water which was 18 inches (45.8 cm.) deep one summer, and in water of various depths less than that for a period of at least three years. These plants then must be able to endure submergence for a long period, as has been pointed out by DAVIS.

During wet periods bog plants show a tendency to move shoreward. This is due to local conditions rather than to historic factors. Such movement is only temporary.

In the summer of 1909 the island in the center of Dead Lake had begun to reappear. During the late summer the ground appeared in the higher parts, showing that the water level was getting lower. In less than ten years the island disappeared and in part reappeared, which indicates that these wet and dry periods may be of short duration. This is contrary to the belief, often expressed, that in southern Michigan they last about thirty years each.

The effect of the dry periods upon vegetation is also very marked. The relation of such periods to plant succession has been emphasized by DAVIS, who believes that they offer an explanation of the xerophytic structures of bog plants (9, p. 160). During such periods the surface layers of the peat become exceedingly dry; this may extend to a depth of several feet. Fires which reduce the surface several feet are of common occurrence. The effect of fires upon plant succession has been given by PENNINGTON (13).

During this time there is very little water available in these surface layers for plants, and, as it will be shown later that the movement of water in peat is slow, it can easily be seen that the habitat is very dry, even omitting the usual factors of humus acid, low temperature, bog toxins, etc. The following table is given by DAVIS taken from WARRINGTON (19).

TABLE II
PARTS OF WATER PER 100 PARTS OF DRY SOIL

Type of soil	When plants wilted	Absorbed from moist air
Coarse sandy	1.5	1.15
Sandy garden.....	4.6	3.00
Fine humus sand.....	6.2	3.98
Sandy loam.....	7.8	5.74
Calcareous.....	9.8	5.20
Peat.....	49.7	42.30

DAVIS says: "If these results are correctly reported, it appears that peat may appear very wet and yet contain no water for plants growing in it, so that

those plants which habitually grow at levels of peat bogs, where the surface strata can dry out, must have xerophytic adaptations if the climate is such that drying out of these levels may occur."

In addition to the variation in water level due to wet and dry periods, there is the variation from month to month during each year. This difference is shown in fig. 7, which gives the results obtained April 20–August 3, 1905, in the zones at First Sister Lake. The data were gathered for the most part by STEELE. Holes were

FIG. 7.—The results of measurements taken to determine the variations in water table in the different zones at First Sister Lake; variations are given in cm.

dug in the peat of the different zones to a considerable depth, and a stick placed in a horizontal position at the top. From this stick measurements were taken daily to the top of the water standing in the holes. These were plotted and the result shows in the figure just given.

The bog sedge zone shows practically no variation, although there would have been some, especially on the landward side, had the measurements been started very early in the spring. This however would be too early to affect the vegetation. The open water shows some variation in the summer, but the bog

sedge rises and falls with it, and there is little variation during the growing season.

The other zones show a gradual lowering of the water table, beginning quite rapidly June 8 and continuing until July 3. At this time a heavy rain fell, raising the water level sharply in all zones. After this there was a rapid lowering of its position in all zones until the close of measurements, except in the bog shrub; this showed a slight rise.

The greatest variation, as has been said, was in the marginal zone. On April 20 the water was 7.2 inches (18 cm.) above the surface of the peat. This gradually lowered until the water table was 38.4 inches (96 cm.) below the surface. A variation of 45.6 inches (113 cm.) was recorded.² In the maple-poplar zone the variation was 18.4 inches (46 cm.); in the tamarack zone, 12.4 inches (31 cm.); in the bog shrub zone, 6.8 inches (17 cm.). These figures show that the loose peat acts as a dam, holding the open water in the lake from flowing back to the outer zones. The same fact was reported by a former student (14) at the small bog near Carpenter's Corner. Here a central area was found with the characteristic bog flora of this region, while the greater part of the original lake was occupied by a mixed flora, with red maple and poplar as the dominant trees. This seemed to be an example of the "lagging behind of a xerophytic group of plants in a hydrophytic habitat," but borings showed that the water table was only 1.4 inches (6 cm.) from the surface. The temperature of the soil and character of the peat were the same as generally found under such plants. A few rods to the east, under the maples, the water table was several feet below the surface.

An excellent example of the holding back by peat of the water in a lake was related to me by a former student, after he had examined the above chart. A farmer living near his home had a peat bog with a very wide marginal zone and a low shore of considerable width. During dry years he was able to cultivate this ground with good returns, but during wet years he always lost his crop. Accordingly, in order to secure continuous use of his

² In the report in *Science* N.S. 29:269, the height of the water above the surface should have been added, making a total of 113 cm.

land, he dug a ditch from the margin to the open water during the dry season of 1903. As soon as his ditch was opened, the water flowed from the open lake to the margin and he lost the use of the land entirely.

These examples show that there is very little movement of water in peat. The water may be several feet higher in one zone than in an adjacent one; the difference in height depends upon the nature of the peat. This fact is well known to persons traveling on northern bog areas.

The variations here shown to occur in the position of the water table in different zones during the summer and in the same zone during the season, bring very strong additional proof to the statements of DAVIS regarding the xerophytic structures of bog plants, which were quoted above in the discussion of bogs during a dry period of years. During the season the plants growing in these bogs are subjected to high water level in the spring, when the water table in all zones is approximately level with the open water of the lake. During the hottest and driest months of the summer the water supply is greatly reduced by a lowering of the water table, and when water is removed by the surface layers, it is very slowly replaced by that of the deeper parts. It is only in these surface layers that these plants root. In any bog where a clearing of any extent has been made, one finds areas where the tamaracks have been blown over during storms; these show that even the largest trees root in the surface layers only.

It has been shown in fig. 7 that the water table in the various parts of the bog stood at different heights during the summer. This is the controlling factor which makes the bogs in this region heterogeneous habitats, supporting xerophytes in three zones and hydrophytes or mesophytes in other zones.

The first effect of lowering the water table, as has been pointed out, is to make the habitat xerophytic, and one would expect that those areas where the water table is lowest would be most xerophytic. A glance at the plants shows that this is not the case; the outer zone in this lake is occupied by hydrophytes. This is due to secondary changes. Immediately after the water lowers, a number of other changes set in which produce the opposite

effect. With the decrease in the position of the water table, there is an increase in the oxygen supply, the number of soil organisms, and a rise in temperature. These produce a change in the composition of the peat, making water more and more available for plants and making the habitat less and less xerophytic. In older parts where this process has been going on for years, there is a decrease in the volume of the peat and a lowering of the surface. In the areas studied around Ann Arbor, this seems to be the explana-

FIG. 8.—Station under the tamaracks, showing *Chamaedaphne* almost entirely dead; the light value here was 0.033; photograph by STEELE.

tion of the marginal ditch characteristic of bogs there. In other areas different reasons have been given, but they do not seem to explain the condition found in this region (16). During wet periods the width of this ditch is often greatly increased, as has been pointed out previously. In such an area only those plants can grow which can stand high water during a term of wet years and high water during the spring of every year. The vegetation which is found here is much the same as that found under these conditions along the borders of our streams. The peat found

below the lowest level to which the water table gets in the driest times is red, while that above varies from red to brown and black. As has been pointed out, plants do not root in the red peat.

Humidity

Only a few readings were taken with some evaporimeters belonging to the Carnegie Institution and loaned by LIVINGSTON. The total evaporation for seven weeks was as follows: under tamaracks in sphagnum, 275 cc.; on floating sedge, 321.7 cc.; in an adjacent oak-hickory grove, 860 cc.; in an open field bordering the lake, 1056 cc. The last figure is short two days because the instrument was broken. These data, however, give conditions only near the surface, and are of value only in a study of germination in the different zones. It has been pointed out recently (21) that great variations are found in short distances above the surface in the amount of water lost by evaporimeters. A lack of instruments made it impossible to study this phase of the subject.

Light

Light readings were made with the usual form of photometer. It was found that the light falling upon the tallest plants in all zones was approximately the same. Great differences were found between these values and those light values found at the surface in the different zones. With light value in the open as 1, the following values were found: under *Chamaedaphne*, 0.0026; under tamaracks, 0.033; under brambles found in a clearing society where maple and cherry seedlings were found in large numbers and some few individuals of each had reached a height equal to the brambles, the light was only 0.00022; among the leaves of the brambles it was 0.166. The value 0.033 seems to be the minimum light requirement for *Chamaedaphne* in the region about Ann Arbor. Fig. 8 shows dead *Chamaedaphne* at First Sister Lake where the light value was 0.033.

The data recorded above show that the bogs of southern Michigan are for the most part not xerophytic habitats, but by far the largest areas are either hydrophytic or mesophytic. Only two or perhaps three of the zones can be considered as xerophytic habitats;

the two are bog shrub and tamarack. To these might be added, depending upon its width chiefly, the bog sedge. This conclusion is justified both by a study of the vegetation and the physical conditions. It is believed that the data furnished at least point strongly toward the supposition that these zones are today xerophytic habitats, even though they also prove that these same areas cannot long remain so. Numerous attempts have been made to explain the xerophytic structures in the plants found in these zones, but only slight reference need be made to them in this paper.

Some have regarded the peat bog as a hydrophytic habitat. Thus WHITFORD, after adding to other factors that of "insufficient aeration of the soil which prevents a healthy growth of the root system of land plants and also bars the presence of nitrifying bacteria," says that "these probably bring about xerophytic structures of plants so commonly seen in hydrophytic habitats." He quite correctly regarded the bog chiefly as a hydrophytic habitat. In the area in which he worked also the true bog plants were not as limited in their distribution as in southern Michigan. It is quite probable that other conditions would enter into a detailed study of bogs in the northern part of the state (20).

CLEMENTS (6) feels "that the current explanation of xerophytic bog plants, etc., is probably wrong, and that the discrepancy between the nature of the habitat and the structure of the plant is to be explained by the persistence of a fixed ancestral type."

SCHIMPER (15) attributes the xerophytic structures to the presence of humus acids in peat which impede absorption. LIVINGSTON (12) has shown that any effect produced by humus acids must be chemical, as "bog waters do not have an appreciable higher concentration of dissolved substances than do the streams and lakes of the same region." NILSSON attributes differences in structure between swamp and bog plants to a difference in food supply, but this will not hold in this area.

TRANSEAU believes from his observations and experiments that "in so far as southern Michigan is concerned (18, p. 36), the substratum temperatures prevailing in bog areas do not seem to be adequate to account for the presence or absence of bog plants

or their xerophilous structures. Experiments suggest, however, that farther north this factor is of prime importance"; again, on page 37, "an examination of all physical and chemical data now available fails to account for the differences in the flora of the bog and swamp areas of this region. The most important factor is believed to be the physiographic history. Where the habitat dates back to Pleistocene times and has remained undisturbed, we find today the bog flora. Where the habitat is of recent origin or has been recently disturbed, we find the swamp flora, or a mixture of bog and swamp species."

DACHNOWSKI (7, 8) believes from his experimental work that the condition which gives rise to xerophily and to zonation in bog plants "lies rather in the toxicity of the soil substratum, that is, in the production of unfavorable soil conditions brought about by the plants themselves." This author further says that "if water transpired is replaced by bog water," which would be the case to a limited extent during the summer when the water table was low and conditions for transpiration excellent, "the soils become more toxic." That is, the first effect of lowering the water table would tend to make the habitat more xerophytic. Further, "decrease in toxicity always follows aeration of the soil and drainage"; that is, an increased lowering of the water table admits oxygen, decreasing the toxicity of the soil and making the habitat less xerophytic. With this is also associated an addition of humus which increases the capacity of the soil "for the adsorption and retention of the toxins." If the results obtained by DACHNOWSKI are correctly explained by him as due to bog toxins, they do not conflict with the data recorded in this paper. It is to be hoped, however, that his studies will be pushed farther.

DAVIS, as has been pointed out earlier in this paper, believes that the bog is a xerophytic habitat, due to the drying of surface layers and the ability of peat to hold large amounts of water which are not available for the plants. The data given in this paper are in accordance with this view, and it appears to the author to more nearly cover conditions than any of the other theories advanced. It is not contradictory to the experimental work of the authors cited; this has been shown in the case of the work of DACHNOWSKI.

TRANSEAU suggested that in the regions farther north the temperature of the soil may be of prime importance. Temperature readings in deeper layers in the bogs of southern Michigan than those which he discusses, and yet not too deep for the root systems, resemble those of northern areas, and it is probable, in the light of his experiments, that they may be a controlling factor, even in those of southern Michigan.

YAPP (21), in his excellent paper dealing with the relation of marsh flora to evaporation, has shown that great variation exists in the amount of water that is evaporated by instruments placed at different heights above the surface. Hence two plants may grow side by side and yet not be under identical conditions. He produces a large amount of data, especially concerning factors affecting the aerial parts of plants. He concludes that "any argument drawn from mere proximity of position, without reference to the varying physiological problems of the different species, is entirely insufficient," and that "the arguments of authors, who insist that the so-called xerophytic structures of marsh plants can have no reference to present-day conditions, because both xerophytic and non-xerophytic species often grow side by side in nature, are entirely inconclusive."

Summary

1. The bogs around Ann Arbor are not xerophytic habitats, as such, but contain xerophytic, hydrophytic, and even mesophytic areas.

2. A study of the conditions in those areas which now are xerophytic indicates clearly that xerophytic conditions in bogs of southern Michigan will shortly disappear.

3. The presence of definite groups of plants in each zone is due chiefly to soil conditions found in that zone; also to position of the water table and secondary changes dependent thereon, as aeration, temperature, composition of the peat, etc.

4. The absence of certain plants from certain zones is due to decrease in the amount of light. *Chamaedaphne* apparently is not able to grow in this area in a light of 0.033.

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